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#### Content of volume **96** 2022

Dhirendra Kumar Pandey, Franz T. Fürsich, Matthias Alberti, Ranajit Das, Federico Olóriz Sáez	
First population-level study of the ammonite genus <i>Hildoglochiceras</i> Spath, and the Lower Tithonian record of the Hildoglochiceras Horizon in the Kachchh Basin, India	1
Werner Schwarzhans, Helmut Keupp	
Early teleost otolith morphogenesis observed in the	
Jurassic of Franconia, Bavaria, southern Germany	51
Volker Dietze, Andreas Hofbauer, Hans Rieber, Norbert Wannenmacher, Günter Schweigert	
Ammonites and stratigraphy of the Achdorf Formation	
(Braunjura Group; Aalenian) at the Wochenberg hill near	
Schömberg-Schörzingen (W Swabian Alb, SW Germany)	69

#### Werner Schwarzhans, Fumio Ohe, Yuki Tsuchiya, Atsushi Ujihara

Lanternfish otoliths (Myctophidae, Teleostei) from the Miocene of Japan ......103

#### Franz-Josef Scharfenberg, Helmut Keupp, Johann Schobert

#### **Michael Krings**

An unusual specimen of the enigmatic fungal reproductive unit *Windipila spinifera* from the Lower Devonian Rhynie cherts of Scotland .......145

#### Franz T. Fürsich, Matthias Alberti, Dhirendra K. Pandey, Wagih S. Ayoub-Hannaa

Jurassic bivalves from the Spiti area of the Himalayas, northern India ......153

#### Joachim Gründel, Helmut Keupp, Fritz Lang, Alexander Nützel





### First population-level study of the ammonite genus *Hildoglochiceras* Spath, and the Lower Tithonian record of the Hildoglochiceras Horizon in the Kachchh Basin, India

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#### Abstract

A Hildoglochiceras-rich horizon is reported from a thin carbonate intercalation within the siliciclastic Upper Jurassic Jhuran Formation of the Jara Dome, western Kachchh Mainland. The Hildoglochiceras specimens have been used for the first population-level study of the genus based on a multivariate analysis. High phenotype instability in the large sample confirms the occurrence of transient forms between morphospecies. Key morphological traits for interpreting Hildoglochiceras are stated, and the morphospecies Hildoglochiceras kobelli (Oppel) and H. kobelliforme (Bonarelli) are interpreted as a dimorphic pair. The ammonite-rich level is interpreted as a Hildoglochiceras Horizon, which is related to a transgressive pulse and maximum flooding zone interrupting largely restrictive conditions for ammonites. The endemic character of Hildoglochiceras is confirmed and related to its environmental restriction to shelf areas on the palaeomargins of the Trans-Erythraean Trough. A comprehensive review of biostratigraphic interpretations of Hildoglochiceras shows the influence of natural and experimental forcing factors. The uppermost Kimmeridgian to lowermost Upper Tithonian interval is the widest biostratigraphic range assumable for Hildoglochiceras based on existing reports, but most probably it was restricted to, or at least better represented in, Lower Tithonian horizons. The Hildoglochiceras Horizon described here is correlated with a lower part of the Albertinum/Darwini Zone in the Secondary Standard Scale for ammonite-based bio-chronostratigraphy in European and West-Tethyan areas. According to the current state of knowledge, a local rather than wide regional significance is favoured for Hildoglochiceras records before its significance for precise correlation across the Trans-Erythraean Trough.

#### Keywords

Jurassic, ammonites, Hildoglochiceras, biostratigraphy, morphospecies

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#### Introduction

Tithonian sediments extend across the Kachchh Basin (Fig. 1) from marginal eastern to open marine western areas, the latter showing high concentrations of ammonites. Pandey et al. (2016) recorded three Tithonian ammonite zones within the Kachchh Basin. These were correlated with two upper Lower and two Upper Tithonian Tethyan ammonite zones (Pandey et al. 2016: fig. 13). These authors reported a Hildoglochiceras Horizon based on the record of a single specimen 1.5 km ESE of the Katesar Temple, in the western part of the Kachchh Mainland (Fig. 1), which they correlated with the Lower Tithonian (two-fold division) Tethyan Semiforme Zone.

In contrast to previous reports, the present contribution focuses on the analysis of the *Hildoglochiceras* assemblage retrieved from a condensed unit in the Jara Dome near Lakhapar (Fig. 1), consisting of 85 moderately preserved fragmentary and nearly complete ammonite specimens. Out of these, 72 specimens have been taxonomically assigned to the *Hildoglochiceras kobelliforme* (Bonarelli) – *H. kobelli* (Oppel) group; nine represent different taxa of *Haploceras*; two have been assigned to *Taramelliceras* sp. gr. compsum (Oppel) – kachhense Spath, or *Parastreblites* sp. gr. *hoelderi* Donze and Énay; one has been assigned to *Aulacosphinctoides* sp. ind. and an incomplete form of Virgatosphinctinae has been tentatively interpreted as *Virgatosphinctes* s.l. sp. ind.

The favourable sample size obtained of *Hildoglochiceras* allows the first population-level study of this ammonite genus, which opens up new perspectives for interpreting *Hildoglochiceras* in palaeobiological terms. Multivariate analysis has been performed for the first time, revealing the most typical morphological features for identification of *Hildoglochiceras* at the species level i.e., shell diameter, coiling degree in terms of the amplitude of the umbilicus, whorl thickness, whorl-section design, and width of a lateral grove.

The present collection of *Hildoglochiceras* specimens retrieved from a ca. 1.9-m-thick, burrowed mixed siliciclastic-carbonate intercalation within the siliciclastic Middle member of the Jhuran Formation at the Lakhapar section of the Jara Dome, represents a single bio-horizon interpreted as a maximum flooding zone (MFZ; Fürsich et al. 2021). The meaning of this Hildoglochiceras Horizon must be evaluated with future research to clarify its relationship with the previously proposed *Kobelliforme* Zone in western Rajasthan, India (Jain and Garg 2015;



Figure 1. Geological map showing localities of Hildoglochiceras in the Jara Dome and Katesar section, Kachchh Mainland.

but see below). Hence, given the common instability in the assumed range of *Hildoglochiceras* species according to previous interpretations (e.g., Krishna 1982–2017; Krishna et al. 1982; Krishna and Pathak 1994; Garg et al. 2003; Rai and Garg 2010; Pandey et al. 2013; Jain and Garg 2015; Pandey et al. 2016), a careful revision of past biostratigraphic interpretationsis is made. In such a context the most common hypothesis pointing to the Tethyan Semiforme/Verruciferum Zone in the secondary standard scale for the Tethyan realm across Europe (Geyssant 1997) is evaluated. The revision tries to clarify the degree of reliability of previous biostratigraphic interpretations and stresses the local significance of interpretations related to data reliability.

# Location, geological section, and environmental conditions

The *Hildoglochiceras* assemblage discussed in the present study has been collected from a 1.9-m-thick horizon in the western Jara Dome northeast of Lakhapar (23°43'42.5"N, 68°57'54.7"E; Fig. 1). Lithostratigraphically, the so-called Hildoglochiceras Horizon belongs to the Jhuran Formation (Fig. 2; also see Fürsich et al. 2020), which follows on top of the Jumara Formation after a

stratigraphic gap including parts of the Upper Oxfordian and Lower Kimmeridgian. In the study area, the Jhuran Formation reaches a thickness of 715 m and can be subdivided into four members, informally called Shivparas siltstone, Tapkeshwari Sandstone, Umia Ammonite and Trigonia Sandstone members (Fig. 3a, b). After relative sea-level highstands with fully marine conditions and diverse ecosystems in the Bathonian to Oxfordian time interval, the siliciclastics of the Jhuran Formation document the filling of the Kachchh Basin towards the Early Cretaceous (compare Alberti et al. 2013, 2019). In this general situation, the study area was located in a more distal, basinal setting and still exhibited marine conditions during the entire Late Jurassic, but water depths and faunal diversities decreased. Fossils are generally rare except for a few horizons, with the Tithonian Green Ammonite Beds (=Umia Ammonite Beds) ca. 266 m above the Hildoglochiceras Horizon being the most conspicuous and prominent containing abundant ammonites, belemnites, and a diverse bivalve fauna (Pandey et al. 2016; Fürsich et al. 2021). These levels represent a maximum flooding zone and in lithostratigraphic terms can be interpreted as the upper part of the Shivparas siltstone member of the Jhuran Formation. In contrast, the Hildoglochiceras Horizon is less prominent and older, being found approximately 357 m above the base of the formation (Fig. 3a). It also represents a maximum flooding zone and contains



\*Hildoglochiceras, Aulacosphinctoides, Virgatosphinctes s.l.
<sup>1</sup>Krishna et al. 2011; Pandey et al. 2012, 2014, 2016
<sup>2</sup>Cariou & Hantzpergue 1997; Wierzbowski 2008





Figure 3. a, b. Lithology of the stratigraphic succession of the upper part of the Jhuran Formation in the western part of the Jara Dome (compare Fürsich et al. 2021).



Figure 3. Continued.

a rich fauna consisting of ammonites, bivalves, gastropods, brachiopods, belemnites, echinoids, and nautiloids. Changing water depths are evident by cross-bedded sandstones underneath the Hildoglochiceras Horizon and the dark-grey silty clay overlying the unit. A second bed with *Hildoglochiceras* has been described from the Jhuran Formation of the Katesar section northwest of the Jara Dome (Pandey et al. 2016). This second bed is much higher in the succession (only about 30 m below the Green Ammonite Beds; Pandey et al. 2016: fig. 3) and is therefore believed to be younger in age.

The Hildoglochiceras Horizon forms the top of an 11-m-thick, rubbly, coarse-grained sandstone with remains of large-scale trough cross-stratification. At the locality (1), where the ammonites are most abundant (23°43'35"N, 68°57'55.1"E), the top of the underlying calcareous sandstone is highly irregular, covered with an iron crust, and appears to represent an emersion horizon (Fürsich et al. 2021). The lowermost level of the Hildoglochiceras Horizon contains abundant juvenile Hildoglochiceras and haploceratids (Fig. 8M). Several 100 m further north, a more complete section shows the horizon to be 150 cm thick, underlain by 200 cm of decalcified rubbly medium-grained sandstone, which overlies a coarse-grained calcareous sandstone. The Hildoglochiceras Horizon is a subangular, poorly sorted coarse-grained sandstone with a calcareous (micritic) matrix. Locally, the carbonate content is so high that the quartz grains float in the matrix. The top 100 cm are softer, poorly indurated, more marly and appear to be more fossiliferous. The change to the overlying argillaceous silt is poorly exposed but appears to be gradual. There are no primary sedimentary structures but abundant signs of bioturbation, including large Thalassinoides and Gyrolithes. The density of biogenic hardparts is moderate, but stands out in the stratigraphic succession, which is largely unfossiliferous. Apart from ammonites, the fauna is composed of rare belemnites, nautiloids, bivalves (close to 50 taxa), gastropods, serpulids, echinoids, crinoids, brachiopods, decapods, and sponges. Altogether, the benthic macrofauna consists of more than sixty taxa, although apart from the bivalves the various groups are represented only by a few taxa each. Wood fragments are common and most of them are bored by bivalves. Vertebrate remains include rib fragments and vertebrae, as well as an articulate flipper of a marine reptile (?ichthyosaur; compare Fürsich et al. 2021).

The preservation of the fauna is quite variable. The benthic macroinvertebrates are commonly fragmented, but their ornamentation is well preserved. Originally calcitic shells are preserved and originally aragonitic shells (e.g., ammonites, gastropods) have been transformed into calcite. The fact that nearly all loose ammonites are internal moulds is a recent artifact: When weathering out from the rock, the shell remained in the rock. This explains the poor preservation of the ornamentation, which is not a feature produced, for example, by abrasion during Jurassic times.

The Hildoglochiceras Horizon clearly represents a time interval of low rates of net sedimentation. The influx of

coarse-grained siliciclastics, connected to brief high-energy episodes, gradually ceased or at least became highly episodic during formation of the horizon. Instead carbonate mud accumulated during extended low-energy periods. Intense bioturbation led to mixing of both types of sediment to result in an extremely poorly sorted mixed carbonate-siliciclastic unit. Keeping in view the high diversity and moderate density of the fossils, a certain degree of condensation is highly likely. Whether there is in addition a gap in the sedimentation at the base of the unit can not be determined and remains speculative, especially as there is no clear-cut erosion surface at the base due to bioturbation.

Remarks on selected biostratigraphic interpretations of taramelliceratins and *Hildoglochiceras*, and their palaeoenvironmental and stratigraphic context in epicontinental shelves surrounding the Trans-Erythraean Trough, and the adjacent SE-Neotethyan palaeomargin

Because the analysed *Hildoglochiceras* assemblage includes a single taramelliceratin ammonite, an updated revision of biostratigraphic interpretations based on taramelliceratin and *Hildoglochiceras* records is assumed to be a useful base for the current study. This revision follows transects of selected areas in the Trans-Erythraean Trough (Fig. 4) in chronologic order, including punctual references to related information from areas elsewhere, while complementary comments focus on data and correlations using microfossils and paying special attention to cases, in which the reported information was directly retrieved from specimens of *Hildoglochiceras*. Finally, a stratigraphic context is considered for interpreting the *Hildoglochiceras* biostratigraphy.

#### Taramelliceratins

The biostratigraphic interpretation is based on the revision of selected reports of post-Early Kimmeridgian taramelliceratins across the Trans-Erythraean Trough. It shows the occurrence of a source-species with wide palaeogeographic range and relatively high morphological variability (i.e., reports of *Taramelliceras compsum* (Oppel 1863a)) and related forms, from eastern Africa and the Indian subcontinent, hence from both sides of the Trans-Erythraean Gulf-to-incipient-proto-Seaway.

# SE-Neotethyan palaeomargin (Himalayas: Spiti, Nepal)

The taramelliceratin species Ammonites nivalis was erected by Stoliczka (1866) and revisited by Uhlig (1903:



Figure 4. Palaeogeographic map showing the location and boundaries of the Trans-Erythraean Seaway (modified after Énay and Cariou 1997, 1999; Alberti et al. 2015).

p. 70-72, pl. 7, fig. 8) as Oppelia (Neumayria) nivalis, Stoliczka sp. (sic). The latter author re-described and re-illustrated the incomplete type-specimen, a phragmocone collected from an unknown stratigraphic horizon of the Spiti Shales at Kibber in the Spiti Valley of the Indian Himalayas and reinterpreted its relationship with the group of Ammonites compsus Oppel. The interpretation of Oppelia (Neumayria = Taramelliceras) nivalis (Stoliczka) reported from the Himalayas and Madagascar is inconclusive, as recently stated by Énay (2009) based on the ammonite assemblages he analysed from Nepal. Pathak and Krishna (1993) reported Taramelliceras sp. together with Aspidoceras iphiceroides (Waagen) from their early Late Kimmeridgian Torquatisphinctes assemblage in sections of Spiti Valley, Himachal Pradesh, India. They correlated this assemblage with the Intermedius Zone in Kachchh and the

Acanthicum Zone in Europe, while they stated a co-occurrence of the Kimmeridgian taxa Torquatisphinctes, Pachysphinctes, Aspidoceras, Streblites, and ?Taramelliceras from the Indian Himalayas. Pathak (1997) reported ammonite assemblages from the Spiti area, Himachal Pradesh, India, including Taramelliceras sp., which he considered relevant for interpreting the Upper Kimmeridgian and the Kimmeridgian-Tithonian boundary. Unfortunately, his Kimmeridgian-Lower Tithonian reference beds in the Chichim section were each several tens of meters thick, which places biostratigraphic uncertainty on particular ammonite taxa within his Pachysphinctes assemblage. Pandey et al. (2013) investigated ammonite assemblages from the Spiti Shale Formation of the Spiti Valley and reported Taramelliceras sp. from their top Kimmeridgian horizons in their Pachysphinctes assemblage (ca. 13 m thick), together with Kossmatia, Paraboliceras, and Glochiceras. These authors used first (FAD) and last (LAD) appearance data as well as relative abundances to define ammonite assemblages throughout stratigraphic intervals several to tens of meters thick, mentioning precise levels of ammonites, but without indicating the particular thickness of ammonitiferous levels or describing the ammonites. Pandey et al. (2013) used their records of Taramelliceras and Glochiceras as typical references for a Kimmeridgian age in the Tethys Himalaya and used their overlying Aulacosphinctoides assemblage to identify the base of the Tithonian. In their Aulacosphinctoides assemblage, the co-occurrence of Aulacosphinctoides and Hybonoticeras hybonotum in the western Indian Himalayas was based on Pathak (1993, 1997) and Pathak and Krishna (1993), as well as on citations in Krishna et al. (1982, 1996, 2011), Fatmi and Zeiss (1999) and Énay (2009) to correlate it with the Hybonotum Zone of the Tethyan Standard. However, data in these citations do not support such an interpretation, especially since the reinterpretation of Hybonoticeras records in Kachchh by Krishna et al. (1996). In contrast, a correlation with the Hybonotum Zone without records of Hybonoticeras was assumed, for example, by Krishna et al. (1982), as well as correlation of H. ornatum with Tithonian instead of Kimmeridgian horizons (e.g., Krishna and Pathak 1993). Moreover, Fatmi and Zeiss (1999) placed their Pottingeri Zone at the base of the Tithonian, based on a single phragmocone (56 mm in diameter) of Hybonoticeras difficult to interpret from the illustration. They did not include Hybonoticeras as a marker in their lowermost Tithonian correlated with the Hybonotum Zone, and rightly placed H. ornatum in the Beckeri Zone in Kachchh. These authors placed Aulacosphinctoides in the Spiti area above Hybonoticeras hybonotum and correlated it with the Darwini Zone and with the Semiforme Zone in northern Pakistan. Finally, Énay (2009) did not report Hybonoticeras from the Tithonian nor included a reference to this genus in his correlations with areas from the Trans-Erythraean Trough.

#### Selected data of the Indo-Malagasy margins

In Pakistan, Fatmi (1984) and Fatmi and Zeiss (1994, 1999) reported taramelliceratins as relevant ammonites for characterizing the Upper Kimmeridgian (three-fold division) from the Axial Belt of Baluchistan. These authors identified Taramelliceras aff. compsum (Oppel) and Taramelliceras cf. kachhense (Waagen) together with Indian and local species of Hybonoticeras, as well as Taramelliceras aff. oculatiforme (De Zigno), Taramelliceras cf. subkobyi Spath, and Taramelliceras (?Oxyoppelia) cf. pseudopolitum (Berckhemer) co-occurring with Hybonoticeras beckeri (Neumayr). It is worth mentioning the comparative paucity of local taramelliceratins compared with their occurrence in India and Europe, the latter being slightly more common towards the north, in the youngest Kimmeridgian deposits. Illustrations of taramelliceratins from the Middle Member of the Sembar Formation of Fatmi and Zeiss (1999) demonstrate a dominance of incomplete specimens and/or fragments belonging to the group of *Taramelliceras compsum* Oppel and allies, associated with scarce, new local forms. These authors identified *Taramelliceras* cf. *kachhense* Spath and assumed its common appearance in the Middle and probably Upper Kimmeridgian of Kachchh. They concluded that *Taramelliceras kachhense* Spath occurs in the lower part of the Beckeri Zone or just below, as it is associated with their *Hybonoticeras alternicostatum* sp. nov. in the first horizon/bed they described from southern Baluchistan.

Southwards along the Indian palaeomargin, Waagen (1875, pl. 10, fig. 5) illustrated Oppelia kachhensis n. sp. from the Katrol Group (=Jhuran Formation) of the Katrol Range in Kachchh. The shape and ornamentation of this species is certainly close to the phenotype range of Taramelliceras compsum (Oppel) either to be included in the latter species or to be interpreted as a local variant, as later considered by Spath (1928). Spath probably studied the largest collection of post-Early Kimmeridgian taramelliceratins from India, indicating that 11 of 13 species showed a morphological relationship or transition to the Taramelliceras compsum-kachhense morpho-group. Three of these species are presently regarded as synonyms of T. compsum Oppel, and only one of Spath's new species has no morphological affinity with the T. compsum-kachhense morpho-group. Spath (1928) regarded Taramelliceras kachhense Waagen age-equivalent to the Eudoxus and Beckeri? zones and his species transitorium and cf. succedens Oppel in Zittel (1870) of exclusive Beckeri age. Spath (1928) interpreted a major part of his Middle Kimmeridgian Taramelliceras to be related to the Taramelliceras compsum group, which is age-equivalent to the Eudoxus-lowermost Tithonian stratigraphic interval in west-Tethyan and Mediterranean areas, while he interpreted kachchense Waagen to be the most variable species in Kachchh. Spath (1928) identified Taramelliceras kachchense specimens as being very close to T. compsum (Oppel), with forms transient to other Indian "species". These innumerable morphologic transitions are represented by his specimens labelled as T. aff. kachchense, cf. compsum, aff. franciscanum, transitorium, pseudoflexuosum, aff. holbeini, and the gibbosum-akher group. The assignation by Spath (1928) of his two specimens of Taramelliceras planifrons n. sp. to the Eudoxus or Beckeri? zones could be of great interest since he recognised a morphologic similarity with "Oppelia" nivalis Stoliczka (and Uhlig 1903). This could be the sole "precise" approach to the age interpretation of Stoliczka's species, but the locality of these two specimens of Spath is not known. Spath (1933) highlighted that new species of ammonites such as Taramelliceras and Waagenia (= Hybonoticeras) from Kachchh have equivalent types in Europe. This author reiterated the common occurrence of Taramelliceras belonging to the compsum-holbeini group in his Lower Katrol Group, throughout deposits of assumed Beckeri to Steraspis age in his Middle Kimmeridgian (= Upper Kimmeridgian to lowermost Tithonian). The latter of these

two species being included in *Taramelliceras compsum* (Oppel) in the pioneer "modern" revision by Hölder (1955).

Krishna (1983) reported Taramelliceras sp. from the Torquatisphinctes-Pachysphinctes-Lithacoceras assemblage in Jaisalmer, interpreting a Kimmeridgian? - Early Tithonian age. Krishna and Pathak (1993: fig. 2) demonstrated the co-occurrence of Taramelliceras and Hybonoticeras (H. pressulum Neumayr and H. kachhensis Spath) in the upper range of Taramelliceras kachhense Waagen and T. transitorium Spath, throughout their mid-Bathyplocus to upper Katrolensis zones of their Upper Kimmeridgian strata in Kachchh. Krishna et al. (2000) characterized common, thin ammonitiferous horizons containing Taramelliceras, Aspidoceras, and Hybonoticeras in the lower part of the Beckeri Zone across Kachchh. Krishna (2017: fig. 2.36) reported the co-occurrence of Taramelliceras and Hybonoticeras in the Lower Katrol Member, from the Linguiferus Subzone (B-IV horizon) to the Pressulum Subzone (K-IV horizon), which he correlated with the upper Eudoxus Zone and the lower part of the Beckeri Zone in Europe. Moreover, Krishna established the first occurrence of macroconchiate Taramelliceras kachhensis (Waagen) in the A-II horizon of the Kachhensis Subzone of the Alterneplicatus Zone (Krishna and Pathak 1991). In contrast, he interpreted the first occurrence of Taramelliceras transitorius Spath in the younger B-IV horizon of the Bathyplocus Zone (Krishna et al. 1995; Krishna 2017).

Working in Madagascar, Collignon (1959) included in his "Zone à Hybonoticeras hybonotum et Aspidoceras acanthicum" several species of Taramelliceras previously known from Kachchh. Among these, he recognised morphologic affinities with Taramelliceras kachhense (Waagen), whose illustrated specimens from Kachchh show a tuberculation that varies highly in strength, and with other "species" described from Kachchh by Spath with accentuated inflection of ribs at the middle flank, at least in the inner whorls. Other close "species" are Taramelliceras transitorium Spath, undoubtedly related to the Taramelliceras compsum group (T. kachchense Spath included), and the inner whorls of the T. kachchense Spath var. belamboensis Collignon. The recent evaluation of Collignon's stratigraphy points to the lack of lowermost Tithonian horizons characterized by hybonoticeratins in Madagascar (Enay 2009), which could be compatible with unfavourable conditions for Tethyan ammonites and/or with the presence of stratigraphic gaps.

#### Selected data of the East African margin

Authors working in eastern Africa also reported *Taramelliceras* from the Indo-Malagasy margin. In southern Yemen, Howarth (1998) reported ammonite assemblages ("faunas") averaged from "horizons" commonly several metres in thickness in several sections. Selected ammonite records indicate that "Fauna 7" containing *Hybonoticeras ornatum* (Spath) must be latest Kimmeridgian in age, as in southern Spain, while no reliable evidence of Lower

Tithonian horizons was registered from southern Yemen, and the stratigraphical gap indicated by Howarth (1998) might embrace the entire Lower Tithonian. Howarth and Morris (1998) reported the poorly known Late Kimmeridgian Taramelliceras (Metahaploceras) subsidens (Fontannes), a late-to-latest Kimmeridgian member of the Taramelliceras compsum group (Hölder 1955), from a faunal assemblage containing Hybonoticeras ornatum (Spath) above the older assemblage containing Taramelliceras (T.) compsum (Oppel) and Lithacoceras (Subplanites) mombassanum (Dacqué). Again, no Lower Tithonian strata containing taramelliceratins can be documented from southern Yemen, while the occurrence of both Taramelliceras compsum and its descendants is clear, with assumed local, palaeoenvironmental imprints on their phenotypes interpreted as new species.

Dacqué (1910) interpreted Upper Jurassic ammonites from more southern regions in eastern Africa, and his discussion of *Oppelia (Neumayria) trachynota* Oppel, later revisited by Hölder (1955), reveals the occurrence of analogous Kimmeridgian forms in the upper part of the Jhuran Formation in India, which point to the group of *Taramelliceras compsum*. Dacqué (1910) concluded that Tithonian ammonites are absent from eastern Africa.

From Somalia, early descriptions reported Tethyan, Indian, and Himalayan-Tibetan ammonites of Middle-Late Kimmeridgian and Middle Tithonian ages (e.g., perisphinctins in Crick 1897), but no clear Early Tithonian ones (three-fold divisions for these stages). Spath (1925b) discussed the different ammonite distribution in Somalia and western Kachchh. Highlighting the relevance of his Taramelliceras kachchense Fauna from the latter area, he envisaged that it potentially colonised eastern Africa. Spath regarded the group of "Neumayriceras" compsa-holbeini as distinct, in which he included Neumayria kachhense (Waagen) from Blake's Kachchh collection as a close relative of Neumayriceras compsum (= Ammonites flexuosusgigas Quenstedt = Taramelliceras compsum (Oppel)) of Late Kimmeridgian age (Eudoxus and Beckeri zones). Spath (1933) mentioned the occurrence of small specimens of Ammonites steraspis Oppel, which would indicate the existence of latest Kimmeridgian to earliest Tithonian horizons in Somalia, while Spath (1935) reported a single specimen plus another doubtful specimen of Taramelliceras from there.

Valduga (1954) described ammonite assemblages from eastern Ethiopia (Ogaden) and reported *Taramelliceras* sp. cf. *pseudoflexuosum* (Favre), which is Middle Kimmeridgian in age (three-fold division), showing a phragmocone difficult to distinguish from *Taramelliceras compsum*. Later authors either included the species erected by Favre in the latter species or excluded it from *Taramelliceras compsum*. Zeiss (1971) proposed a preliminary biostratigraphic framework for eastern Ethiopia with regional taxa co-occurring with European ones. Among the latter, European *Taramelliceras* were relevant in southern Ogaden. The occurrence of *Taramelliceras prolithographicum* and *T*. cf. *gaetanoi* was interpreted as lowermost Tithonian, while T. greenackeri, T. intersistens, and T. klettgovianum were placed in the upper Middle Kimmeridgian (three-fold division). Curiously, no taramelliceratins were reported from the Upper Kimmeridgian, where regional species or local variants of Hybonoticeras were correlated with the Beckeri Zone in Europe. Based on Berckhemer and Hölder (1959), Hölder and Ziegler (1959), Donze and Énay (1961), and Schweigert and Zeiss (1999), all these taramelliceratins could indicate uppermost Middle-Upper Kimmeridgian horizons, although horizons belonging to the Kimmeridgian-Tithonian boundary cannot be excluded. Zeiss (1984) reported taramelliceratins from "horizons" in several sections of Ethiopia: Taramelliceras cf. gaetanoi (Fontannes) (=Parastreblites) at Lalin; assumed combined records of Taramelliceras pseudoflexuosum (Favre), T. aff. greenackeri (Moesch), and T. cf. transitorium Spath from a single "horizon" at Geldoh; T. aff. intersistent Hölder, and T. aff. greenackeri (Moesch) together with T. klettgovianum modeli and cf. pseudoflexuosum (Favre), and T. prolithographicum (Fontannes) together with Neochetoceras sp. n. aff. steraspis (Oppel), from three respective "horizons" at Aggare. The biostratigraphic reinterpretation of Zeiss (1971) confirms the occurrence of dominant European and secondary Indian species of taramelliceratins in the upper Middle to uppermost Kimmeridgian, without excluding Kimmeridgian-Tithonian boundary horizons across eastern Ethiopia.

Beyrich (1878) was probably the first to use taramelliceratins (Oppelia trachynota Oppel), together with some perisphinctins, from Kenya to interpret the occurrence of Alpine Kimmeridgian forms in the Mombassa area. Together with his previous identification of Hybonoticeras hildebrandti n. sp. (Beyrich 1877), it allows us to interpret these records as representing Upper Kimmeridgian horizons. Futterer (1894) confirmed the occurrence of Oppelia trachynota (Oppel) together with a long list of perisphinctins, which he placed in the Acanthicum Zone (as reported by Dacqué 1910), but these perisphinctins rather indicate late Middle to Late Kimmeridgian ages. Therefore, the taramelliceratin is possibly better interpreted as belonging to the T. compsum group. However, Dacqué (1910) denied the occurrence of Kimmeridgian and Tithonian deposits with ammonites in the Mombasa area and across East Africa, with probable local exceptions in the case of the Kimmeridgian in Somalia and Ethiopia. In fact, the Mexican specimen illustrated by Burckhardt (1906), and regarded by Dacqué (1910) as conspecific with Oppelia trachynota (Oppel), came from the upper-Middle to Upper? Kimmeridgian (see also Hölder 1955 for a re-evaluation of Dacqué's interpretation of the species Ammmonites trachinotus Oppel). According to Dacqué's (1910) revision of ammonite collections from East Africa, as well as the revision made by Spath (1933), taramelliceratin ammonites would be uncommon there. Arkell (1956) only cited Taramelliceras cf. kachhense (Waagen) from the Beckeri Zone (his Middle Kimmeridgian) at the eastern slopes of Coroa, Mombasa, and from his Lower Kimmeridgian strata north of Mombasa referring to Spath (1930) and D'Arcy

Exploration Co., respectively. The more recent contribution by Verma and Westermann (1984) provided the first precise horizon-based biostratigraphy from East Africa (the Freretown area near Mombasa), with descriptions of T. (Taramelliceras) trachynotum (Oppel)? in horizons of the Beckeri Zone and T. (Taramelliceras) cf. kachhense (Waagen) mainly in horizons of their Hybonotum Zone. The subsequent revision by Schweigert et al. (2012) restricted Lower Tithonian horizons to the uppermost part of the section, based on a loose specimen of Hybonoticeras ex. gr. hybonotum (Oppel) and placed the Hybonoticeras illustrated by Verma and Westermann (1984) in the Late Kimmeridgian. Schweigert et al. (2012) confirmed the occurrence of Taramelliceras kachhense (Waagen), did not mention T. (Taramelliceras) trachynotum (Oppel)?, and added T. transitorium Spath without comments i.e., all being Taramelliceras species that belong, at least, to the group of Taramelliceras compsum Oppel.

From Tanganyka, present Tanzania, Dietrich (1925) identified large Taramelliceras cf. compsum and Taramelliceras sp. from the "Tendaguruschichten" and related them with the T. trachinotus and T. compsum groups. Dietrich envisaged his Taramelliceras sp. to be similar to the Mexican Oppelia (Neumayria) sp. from San Pedro del Gallo, which Burckhardt (1912) interpreted as close to Taramelliceras holbeini Neumayr and, therefore, at least related to, if not conspecific with, the group of Taramelliceras compsum (Oppel). Dietrich (1925) also mentioned that the size of the shells was larger than that commonly found in European forms. Spath (1933) assumed that Taramelliceras species from Tanganyka were commonly equivalent to those from the Lower Katrol Beds (= Jhuran Formation) in Kachchh. Arkell (1956) reinterpreted older collections from Tanzania, including the Dietrich collection, and reported Taramelliceras cf. compsum (Oppel) and Taramelliceras cf. harpoceroides Burckhardt from the Middle Kimmeridgian (three-fold division; Mutabilis-Pseudomutabilis zones) of the Mahokondo region. The latter species name probably resulted from Arkell (1956) renaming Oppelia (Neumayria) sp. ind. described and illustrated by Burckhardt (1912), who stated its resemblance with Oppelia holbeini Oppel in Neumayr (1873). All these European species are usually interpreted as being synonyms of Taramelliceras compsum (Oppel).

All the comments above reveal the common occurrence of *Taramelliceras* belonging to the *T. compsum* group and related local variants across shelf areas of the Trans-Erythraean Trough, as well as the scarcity of ammonites typically related to horizons close to the Kimmeridgian-Tithonian boundary, *Hybonoticeras* included. Co-occurrence of *Taramelliceras* with latest Kimmeridgian *Hybonoticeras* has been proven on opposite shelves of this region, but it is more commonly reported from Indo-Malagasy areas. In contrast, their co-occurrence in lowermost Tithonian horizons is rarely noticed. Hence, and according to the information available, unfavourable conditions for Tethyan ammonites during high sea-levels close to Kimmeridgian-Tithonian boundary times, and/or stratigraphical gaps, should be considered widespread or at least common across shelf areas of the Trans-Erythraean Trough.

#### Hildoglochiceras

## SE-Neotethyan palaeomargin (Himalayas: Spiti, Nepal)

The first record of a Hildoglochiceras fauna was from the Tibetan Himalayas (Ammonites kobelli Oppel, 1863b), based on two specimens collected some years earlier (1854-1857) by the Schlagintweit brothers without precise stratigraphic control. Stoliczka (1866) recognized limitations in the stratigraphic reliability of the previous contributions he revised, and interpreted Spiti Shales and Kachchh deposits to represent Middle but not Upper Jurassic strata, without mentioning species now interpreted as Hildoglochiceras. Stoliczka recognized a general morphological variability in ammonites when the material was abundant enough. Revisions by Uhlig (1903, 1910) highlighted the biostratigraphic meaning and biogeographic separation of the groups of Hecticoceras latistrigatum in Spiti and H. kobelli in Kachchh, both of which interpreted as Hildoglochiceras by later authors, while assuming a Kimmeridgian age possibly extending to Early Tithonian, an age-uncertainty applied to all the oppeliids he revised. Krishna (1982) provided a first modern re-evaluation of ammonite biostratigraphy of the Spiti Shales facies across Himalayan to New Guinea areas based on field data. Krishna et al. (1982) and Krishna (1983) analysed a Hildoglochiceras-Virgatosphinctes assemblage in the central-western Himalayas, including Hildoglochiceras kobelli (Oppel), Virgatosphinctes densiplicatus [recte denseplicatus] (Waagen), Kossmatia, and Paraboliceratoides, and attributed them to the Middle Tithonian following the preliminary interpretation made by Zeiss (1968; but see below). This ammonite assemblage possibly reveals differences in ammonite ranges, or in ammonite taxonomy, with respect to later interpretations for Nepalese areas by Énay (2009). Krishna (1987) reported the occurrence of the Hildoglochiceras-Virgatosphinctes assemblage from India and Himalayan areas and correlated it with the Middle Tithonian. Pathak and Krishna (1993) and Krishna and Pathak (1994) identified Hildoglochiceras in their Rajnathi and Virgatosphinctes zones from Spiti and Niti and correlated it with the Tethyan upper Darwini to Ponti zonal interval. However, the ammonite assemblage reported from Gete and Chichim in the Spiti Valley could indicate, or partially include, latest Kimmeridgian horizons, if the later biostratigraphic proposal made by Énay (2009) for Nepalese areas is accepted. In addition, Pathak (1997) reported ammonite assemblages including Hildoglociceras kobelli from his Lower Tithonian bed 9 with Spiticeras from the same area. As his bed 9 is 40-50 m thick in the Chichimand Gate (= Gaitey) sections, the precise biostratigraphic range of these records within the corresponding

ammonite assemblage is unknown. Pathak (1997) correlated his Hildoglochiceras-Virgatosphinctes assemblage with a rather imprecise stratigraphic interval embracing parts of the Fallauxi and the Ponti zones in west-Tethyan areas. Énay and Cariou (1997, 1999) assumed a Late Tithonian age for Hildoglochiceras associated with V. denseplicatus (= Malagasites of Early Tithonian age in Énay 2009), both of which members of the upper horizon with oppeliid-rich beds in their Virgatosphinctes fauna from Nepalese areas. More recently, Énay (2009) expressed a similar uncertainty to that shown by Uhlig (1903, 1910) about the precise age of Nepalese streblitins, with occasional reference to particular ammonite assemblages of Kimmeridgian to latest Middle Tithonian ages. Reinterpreting previous contributions about ammonite assemblages from Himalayan areas, Énay (2009) synthesized correlations of Nepalese ammonites and expressed uncertainty about the age interpretation of the genus Hildoglochiceras. In addition, Énay (2009) used the single known record of his ?«Semiformiceras» aenigmaticum n. sp. for supporting a correlation with the Semiforme-Verruciferum Zone in Europe. However, this is not a reliable hypothesis since without ventral groove and with a tricarinate venter, his dubious «Semiformiceras» aenigmaticum seems closer to a local, bizarre Neochetoceras, which better agrees with his interpretation as Neochetoceras-trans-Semiformiceras of the darwini Neumayr group (Énay 1983, 2009). All this speaks against a precise age interpretation, but the allusion to darwini Neumayr suggests Lower but not lowermost Tithonian horizons stratigraphically below the general correlation of Hildoglochiceras horizons with the Mediterranean middle Lower Tithonian Semiforme-Verruciferum Zone (two-fold division). Enay (2009) also reported Hildoglochiceras from his Upper Kimmeridgian Paraboliceras Beds (preliminary correlation with Europe), but he raised doubts about the stratigraphic provenance of these specimens. Additionally, it is worth noting that Neochetoceras ranges from the latest Kimmeridgian to late but not latest Middle Tithonian in the Tethyan area of Europe. Pandey et al. (2013) investigated ammonite assemblages from the Spiti Shale Formation of the Spiti Valley and included Hildoglochiceras in the Virgatosphinctes assemblage (ca. 27 m), with Virgatosphinctes as the dominant taxon of an assemblage relatively impoverished when compared with those from close-by areas such as Gete and Chichim in the Spiti Valley. Uhligites and Kossmatia from this Virgatosphinctes assemblage were approximately correlated with the Darwini Zone according to their association with Hildoglochiceras, Aulacosphinctoides, Spiticeras, Gymnodiscoceras, Paraboliceratoides, and Holcophylloceras reported from the Gete-Chichim area by Pathak (1997). However, this correlation contradicts Pathak (1997) who correlated his Virgatosphinctoides Zone based on ammonites collected from a tens-of-metres-thick succession and with a major part of the Fallauxi and lower Ponti zones. The statement of Pandey et al. (2013) recognizing the difference in ammonite ranges from nearby areas in the western Himalayas is of interest but, unfortunately, these authors did not provide any information on the particular thickness of ammonitiferous levels nor any description of ammonites.

#### Selected data of the Indo-Malagasy margins

Throughout transitional regions between the SE-Neotethyan Margin just discussed and the northernmost segment of Indo-Malagasy margins, Spath (1939, p. 123) reported his fossil assemblage "p", dominated by limonitic berriasellins (Blanfordiceras, Neocosmoceras, Protacanthodiscus), holcostephanins (Proniceras, Spiticeras) and rare himalayitins (Himalayites) from "glauconitic shales and sandstones (Belemnite Beds) overlying top of Jurassic" (sic), which is locally marked by a conglomeratic limestone. He assumed his fossil assemblage "p" to be placed at the bottom of the Belemnite Beds, of Early Cretaceous age. As well as identified in other localities mentioned by Spath (1939), some fragments of Aulacosphinctoides preserved in "a compact marl of peculiar yellowish, gray" (sic) were also recognized in the fossil assemblage "p", as well as rare Hildoglochiceras cf. propinguum (Waagen), while he illustrated a poorly preserved Hildoglochiceras sp. ind. group of propinquum Waagen, sp. (ibid., pl. XVIII, fig. 8a, b). This author interpreted these ammonites in the lowermost part of the Belemnite Beds to be inherited from older Tithonian horizons. Fatmi (1972) highlighted the condensed nature of Jurassic deposits in NW Pakistan, including the Lower Tithonian and the association of Aulacosphinctoides, Virgatosphinctes, and Hildoglochiceras in northern Pakistan, Trans Indus Ranges, while interpreting the former to mark his lowermost Tithonian, and indicating as "not zoned" his Lower Tithonian below Hildoglochiceras (ibid., Fig. 6). Fatmi (1972) described Hildoglochiceras sp. indet. collected 6.09 m above the base of the Chichali Formation and attached to the flank of Aulacosphinctoides gr. uhligi Spath. Slightly southwestwards from the areas worked by Spath (1939) and Fatmi (1972), Fatmi (1973) described Hildoglochiceras latistrigatum (Uhlig) and Hildoglochiceras cheemaensis sp. nov. from ~70 cm above his Kimmeridgian Hybonoticeras sp. ind., in sandy calcophosphatic concretions included in soft, greenish-glauconitic silty sandstone with common small torquatisphinctins he interpreted as Aulacosphinctoides from the upper part of the lower member of the Chichali Formation at the Khauri Nala section in the Shaikh Budin Hills (Marwat Range) of northern Pakistan. Fatmi (1973) suggested that "the incoming of Aulacosphinctoides and other associated genera in Shaikh Budin Hills helps in defining the Kimmeridgian/Tithonian boundary".

Southwards, based on data from Kachchh and the literature, Waagen (1875) first recognized the high correlation potential of *Harpoceras kobelli* across Indian areas and suggested an age corresponding to "about the middle of the Kimmeridgian group". Spath (1924) erected *Hildoglochiceras* for *Hecticoceras kobelli* (Oppel), designating *Hecticoceras latistrigatum* Uhlig as type species,

and raised doubts about records of kobelli in the Katrol Group. Spath (1925a) supported the high correlation potential of Hildoglochiceras kobelli (Oppel) across Spiti as well as throughout eastern and western Trans-Erythraean shelves. Spath (1928) interpreted Hildoglochiceras spp. from the Middle Katrol Group (= upper Kimmeridgian in Spath 1933), while acknowledging the record of H. kobelli from the Trigonia smeei Beds of Tanganyka (present Tanzania) and raised doubts about species level separation of Haploceras (Hecticoceras) spira Zwierzycki from H. kobelliforme Bonarelli. Spath (1933) placed the Hildoglochiceras Beds stratigraphically below those with Virgatosphinctes in Kachchh, asserted the wide geographic range of the taxon across India and East Africa, and concluded a late Early to Middle Portlandian age, above barren Katrol sandstones and below the Umia Ammonite Beds with himalayitins close to his Portlandian-Tithonian boundary. Krishna (1983) proposed a Middle Tithonian age for his Hildoglochiceras-Virgatosphinctes assemblage across Kachchh and the Salt Range-Attock-Hazara areas, as well as of the Himalayan Spiti-Malla and Johar areas, while referring it to the Early Tithonian in his Torquatisphinctes-Katroliceras-Subdichotomoceras assemblage in Kachchh. Krishna (1984) reported a Kobelli Zone containing Hildoglochiceras and Aulacosphinctoides to characterize his Middle Tithonian in some areas of Kachchh, including the stratigraphic interval ranging from the Early Tithonian Albertinum/Darwini Zone to the top of the Ponti/Burckhardticeras Zone in Europe, while restricting his Early Tithonian time interval to the Katrolense Zone, correlated with the Hybonotum Zone. Krishna (1987) correlated discontinuous records of his Hildoglochiceras-Virgatosphinctes assemblage across Tethyan-Himalayan areas, as well as in the western and north-western Indian subcontinent, to the Middle Tithonian below the first occurrence of himalayitins indicating the Late Tithonian. Of special interest for comparison and correlation are Himalayan records provided by Pathak and Krishna (1993). In addition to Taramelliceras and Hybonoticeras from their Upper Kimmeridgian (see above), these authors reported Hildoglochiceras from two ammonite-rich stratigraphic intervals, 40 and 50 cm thick, from two sections in Himachal Pradesh, India, and provided a range chart showing the co-occurrence of Hildoglochiceras, Indodichotomoceras, Uhligites, Gymnodiscoceras, Kossmatia, and Paraboliceras from the base of Tithonian. Without mentioning potential condensation, the assemblage reported by these authors could be close to that of the Paraboliceras Beds characterized by Énay (2009) at Chohkor, Nepal, thus pointing to a Late Kimmeridgian-earliest Tithonian age. In addition, Pathak and Krishna (1993) mentioned Hildoglochiceras spp., together with Indodichotomoceras and Katroliceras, characterizing the Kobelli Zone (Krishna 1984) at Gajinsar, as well as the assemblage of Hildoglochiceras with Aulacosphinctoides, Indodichotomoceras and Katroliceras (Rajnathi Zone to Virgatosphinctoides Zone of Krishna and Pathak 1993) at Ler-Katrol in Kachchh. Both these assemblages were correlated with the Middle Tithonian and the uppermost

Lower Tithonian (upper Darwini Zone) in Europe. Pathak and Krishna (1993) stated that Hildoglochiceras and Virgatosphinctes belong to two successive assemblages registered in Indo-Himalayan areas, in contrast to previous hypotheses (e.g., Énay 1973). All this information could indicate that Hildoglochiceras occurs in horizons older than usually interpreted at the time. This is supported by Krishna et al. (1996), who stated the extreme rarity of Hildoglochiceras SE of Ler, whereas the single record reported from the Lakhapar section was preliminarily assigned to the lower part of the Virgatosphinctoides Zone, Rajnathi Subzone of their Lower Tithonian, and was correlated with the upper Darwini Zone of Europe. Pandey and Krishna (2002) characterized ammonite biohorizons from the siliciclastic succession in Jaisalmer, added the Natricoides Zone containing Hildoglochiceras together with Aulacosphinctoides spp. and Virgatosphinctes spp., and correlated it with the Tethyan Semiforme/Verruciferum Zone based on the occurrence of rare Tethyan Haploceras, a genus which has a long biostratigraphic range exceeding that of the Tithonian. Hildoglochiceras also co-occurs with the oldest Virgatosphinctes in the lowermost part of the overlying Communis Zone, which they correlated with the Tethyan Fallauxi Zone. Bardhan et al. (2007) interpreted Hildoglochiceras to be Late Tithonian in age and restricted to Indo-Malagasy areas. Pandey et al. (2010) interpreted evolutionary trends in Indian Virgatosphinctinae, and their correlation with 3<sup>rd</sup> order transgressive-regressive cycles. The combination with data provided by Spath (1933) from Gudjinsir (i.e., the co-occurrence of Hildoglochiceras spp., Indodichotomoceras spp. and a single species of Aulacosphinctoides?) opens the possibility for a potential biostratigraphic range of Hildoglochiceras from the uppermost Kimmeridgian Katrolensis Zone, Infundibulum Subzone, to the Lower Tithonian Virgatosphintoides Zone, a biostratigraphic range which contrasts with the previous interpretation of Pandey and Krishna (2002). Krishna et al. (2011) analysed the relationship between the diversity of ammonite assemblages and relative sea-level fluctuations, i.e., "inferior order cycles" (sic) than those proposed by Pandey et al. (2010). These authors related stratigraphic intervals characterized by a strong dominance to near exclusivity of virgatosphinctins with shallowing to early regressive trends, and the occurrence of himalayitins with transgressive ones. No explanation, however, was given for the absence of Lower Tithonian hybonoticeratins during an interval of global high sea-level or the occurrence of Hildoglochiceras horizons with an assumed high correlation potential within reinforced regressive trends in the Ler-Katrol areas of Kachchh.

Pandey et al. (2016) reported a single specimen of *Hildoglochiceras latistrigatum* from a 10 cm thick conglomerate with fine sandy siltstone or laminated fine-grained sandstone pebbles in a ferruginous silty fine-grained sandstone matrix approximately 30 m below a maximum flooding zone (MFZ) composed of bioturbated, strongly ferruginous, glauconitic, fine-sandy siltstone beds containing scattered coarse quartz grains from the Katesar section

northwest of the Jara Dome. These authors correlated their Hildoglochiceras horizon from western Kachchh Mainland with the Tethyan Semiforme/Verruciferum Zone following Énay (2009). Finally, Krishna (2017) reinterpreted previous proposals of Tithonian biostratigraphy, as well as 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> order T-R cycles in Kachchh. He interpreted a major 1<sup>st</sup> order regressive trend during Kimmeridgian and Tithonian times, with 2<sup>nd</sup> and 3<sup>rd</sup> transgressive trends for the Pottingeri (= Hybonotum Zone) and Natricoides (= Semiforme+Fallauxi zones in illustrations, but only to the Semiforme Zone in the text) zones. Krishna (2017: 124) interpreted the Natricoides Zone to be the most fossiliferous interval, containing Hildoglochiceras spp. (H. latistrigatum Oppel through the lower three subzones, and H. kobelli Oppel in a single subzone above). In addition, he stated MFS (Krishna 2017: 245) conditions near the top of the Natricoides Zone, the latter being a stratigraphic interval which has a variable record across Kachchh Mainland. According to Krishna, Tithonian deposits overlie Late Kimmeridgian ones in the eastern Mainland, whereas in the western mainland a variable situation exists.

Further south, from Madagascar, Lemoine (1910– 1911) assumed a Sequanian-Kimmeridgian age for the upper horizons containing *Aspidoceras* (*acanthicum* group) and *Hecticoceras kobelli* (Oppel) in the Maromandia region (NW Madagascar). He promoted the recognition of an Indo-Malagasy faunal province based on the occurrence of the latter ammonite taxon, for which he recognised within-species rather than species-level variability. Besairie (1930) citing ammonite lists from previous studies reported *Hecticoceras kobelli* (Oppel) and *Perisphinctes denseplicatus* (Waagen) among Bathonian to Kimmeridgian ammonites from the Calcaires glauconieux d'Antsalova studied by Barrabé (1929) and himself (Lemoine 1910). Besaire (1930) also mentioned that Barrabé (1929) reported

Hecticoceras kobelli (Oppel) and Perisphinctes natricoides Uhlig from the Marnes et Calcaires du Kimmeridgien of the Bemaraha region. Besairie (1930) regarded the occurrence of ammonitiferous deposits of Tithonian age as doubtful. Besairie (1946) characterized his green-glauconitic-sandy Portlandian strata in Madagascar by Virgatosphinctes associated with Hildoglochiceras, Haploceras and Aulacospinctes at Antsalova and Ampranosamonta, and highlighted the resemblance between the Upper Jurassic strata of Madagascar and Kachchh. This author mentioned a wide stratigraphic gap affecting Middle and Upper Jurassic deposits, except across the region of Maintirano in west-central Madagascar where Middle Kimmeridgian deposits with Waagenia (=Hybonoticeras) underlie the Upper Kimmeridgian Streblites Beds. Arkell (1956) correlated Hildoglochiceras horizons from Tendaguru and Madagascar with his Upper Kimmeridgian and Tithonian strata above Middle Kimmeridgian deposits with Hybonoticeras Beds throughout East Africa and Madagascar. Collignon (1957) identified Hildoglochiceras spp. from his sandy Lower Portlandian (= Lower Tithonian), together with Virgatosphinctes, Haploceras, and locally Taramelliceras nivale (Stoliczka in Uhlig), above a 30-80 m thick barren, argillaceous interval overlying horizons with common Katroliceras, Hybonoticeras, Taramelliceras and Streblites, which characterised his Kimmeridgian interval with Torquatisphinctes north of Analavelona, south-western Madagascar. In the investigated region, Upper Portlandian (= Upper Tithonian) limestones with Aulacosphinctes and belemnite-rich clays, overlie horizons containing Hildoglochiceras spp. In the most fossiliferous outcrop located in the Mandarano River valley, Collignon (1957) recorded Hildoglochiceras spp., with local variants of kobelli, in an ammonite assemblage containing Taramelliceras sikyliense n. sp., Hybonoticeras mandaranum n. sp., Physodoceras avellanum (Zittel), Virgatosphinctes spp., Aulacosphinctoides spp., and Subdichotomoceras spp., among others. These taxa were collected from a 20-m-thick succession of undescribed lithology. In addition, this author reported a 10-15-m-thick interval with Hildoglochiceras, interpreted as Early Portlandian (= Early Tithonian) in age, underlying an intermediate 1-m-thick interval with Aulacosphinctes and scarce Hildoglochiceras, below 15 m containing Blanfordiceras interpreted of Late Portlandian (Late Tithonian) age. Collignon (1960) added new species and varieties of Hildoglochiceras. Collignon (1961) confirmed a two-fold division of his Tithonian strata of Madagascar, with the Hildoglochiceras kobelli Zone below and the Aulacosphinctes hollandi Zone above and recognized a trend of decreasing similarity between ammonites from Madagascar, Kachchh, Spiti, Asian, African, and European Tethyan margins of Asia, Africa, and Europe, and even Andine areas. According to him, Hildoglochiceras kobelli (Oppel) occurs in Kachchh, Spiti, and East Africa, thus documenting its correlation potential. Collignon (1964) reported a stratigraphic gap across the Ankihitra region, NW Madagascar. There, the Lower Tithonian Hildoglochiceras kobelli Zone with Hildoglochiceras spp. overlies his Lower Oxfordian Trimarginites villersensis and Properisphinctes bernensis Zone. Collignon also mentioned occasional records of black ammonites of Kimmeridgian age (Torquatisphinctes and aspidoceratids) in the Betsiboka area (west-central Madagascar), as well as Hybonoticeras hildebrandti (Beysere) indicating his Lower Kimmeridgian in the Antsalova region further south. He mentioned Hybonoticeras mundulum (Oppel), Physodoceras avellanum (Zittel), and Taramelliceras nivale (Stoliczka) among the ammonites belonging to his Hildoglochiceras kobelli Zone in argillaceous-marly deposits without giving further lithostratigraphic details. Collignon and Razafimbelo (1964) reported common Hybonoticeras (his Middle Kimmeridgian) from Maroandravina, NW Madagascar, and horizons with Hybonoticeras from their Middle Kimmeridgian clays and marls with concretions from Befotaka. According to them, the youngest Hybonoticeras is overlain by barren clays potentially of Late Kimmeridgian age, which are followed by horizons with Late Tithonian Aulacosphinctes. Alternatively, these authors envisaged the occurrence of a widespread stratigraphic gap in Madagascar corresponding to their Late Kimmeridgian.

#### Selected data of the East African margin

On the opposite side of the Trans-Erythraean Trough (East Africa), Zwierzycki (1914) first reported epicontinental deposits with assumed Tithonian ammonites from the Trigonia smeei Beds at Tendaguru in Tanzania. Among the ammonites there occur Haploceras (=Hildoglochiceras) kobelli and other related species, together with latest Kimmeridgian to Tithonian haploceratids and perisphinctids indicating a probably mixed fauna, including species reported from Kachchh and Spiti. In fact, these Trigonia beds correspond to the Indotrigonia africana Beds of Bussert et al. (2009), which range from the Upper Kimmeridgian to Lower Tithonian in their figure 2, show signs of frequent reworking, and probably correspond to a complete T-R cycle in shallow-water environments. Hildoglochiceras kobelli and related species were also reported by Dietrich (1925, 1933). Arkell (1956) correlated Hildoglochiceras horizons from Tendaguru and Madagascar with beds containing Anavirgatites in Somalia, and Virgatosphinctes in Harrar (Ethiopia) to represent his Upper Kimmeridgian and Tithonian (up to the Lower/Upper Tithonian boundary, two-fold division, at present). Verma and Westermann (1984) assumed the occurrence of Hildoglochiceras in the Himalayas, Madagascar, Tanzania, Cuba, and Mexico, without commenting on the new genus Salinites erected by Cantú-Chapa (1968) for Mexican-Caribbean Hildoglochiceras. These authors correlated the Lower Tithonian Hildoglochiceras kobelli Zone of Madagascar (Collignon 1964) with the Lower Tithonian (two-fold division) above the Albertinum/Darwini Zone and the correlative Triplicatus and Vimineus zones in Europe, including the Upper Kimmeridgian of Collignon in Madagascar.

#### Reports from different areas in the Americas

The available information includes data from Mexico, Cuba, and Argentina. Imlay (1939) reported Hildoglochiceras from his Portlandian and Upper Tithonian in Mexico, and Imlay (1952) gave a synthetic list of ammonite species from the Pimienta Formation of eastern Mexico. This list cannot be interpreted as revealing the actual co-occurrence of Mexican Hildoglochiceras, Pseudolissoceras, and Durangites, among others, since there is no precise reference to ammonite horizons as is commonly the case in this author's figured stratigraphic columns. In fact, these Mexican Hildoglochiceras were later reinterpreted as a new genus (Salinites Cantú-Chapa, 1968), which exhibit tighter coiling and a ventral keel on the inner whorls. This genus has been proven to be Late Tithonian to Early Berriasian in age as noted by Trejo (1975), who recorded Hildoglochiceras aff. grossicostatum Imlay (= Salinites) in his Upper Tithonian Crassicollaria Zone, Crassicollaria massutiniana-Crassicollaria parvula Subzone, in Mexico (see Villaseñor et al. 2012 for an updated correlation). Hence, Imlay's Hildoglochiceras should be reinterpreted as Salinites.

From Cuba, Imlay (1942: p. 1444–1445, pl. 2, figs 1–7) described *Hildoglochiceras* cf. *H. grossicostatum* Imlay and *Hildoglochiceras* cf. *H. alamense* Imlay, two Mexican species he had previously erected (Imlay 1939). This information was adopted by Judoley and Furrazola (1968: p. 19, 24, 25, 29), who cited Imlay (1942) and reported these "*Hildoglochiceras*" species from Lower and Middle Tithonian black limestones and the Viñales Limestone, while assuming a biostratigraphic range of *Hildoglochiceras* from the Late Kimmeridgian? (doubtful) to the Portlandian (common) and Tithonian (rare). As commented earlier, these Mexican-Cuban forms were rightly re-interpreted later on as *Salinites* Cantú-Chapa (e.g., Cantú-Chapa 1968; Myczynski 1989).

In Argentina, Leanza (1980) described and illustrated a single, small specimen as Hildoglochiceras wiedmanni n. sp. (size of shell: 22 mm) from his Pseudolissoceras zitteli Zone at Cerro Lotena, Neuquen, based on material housed in the collections of Tübingen University, Germany. Vennari (2013), based on the material housed at the FCEN-UBA (Facultad de Ciencias Exactas y Naturales -Universidad de Buenos Aires) collection, merely reported Hildoglochiceras sp. ? from a 1.80-m-thick interval in a single section (Las Loicas) in southern Mendoza, above Pseudolissoceras zitteli and below Aulacosphinctes proximus, and hence correlated it with Middle Tithonian horizons. Based on the scarcity of available material and the single illustration provided by Leanza (1980), these two records are difficult to evaluate, but Leanza's specimen seems to be a rare, local? glochiceratin-like form instead of Hildoglochiceras due to the unusual position of the lateral groove above the ribbing inflexion, as well as the design of the dorsal edge of this groove, the whorl section with a wide-rounded venter, and inner flanks without marked umbilical edge. These Argentinian records, reported from stratigraphic horizons dated with ammonites known from other, distant areas, might represent a limited immigration of a late Hildoglochiceras (?) or, more probably, local glochiceratin-like ammonites (see Barthel 1962 for Lower Tithonian Glochiceras from Neuburg, southern Germany, with external displacement of a subtle lateral groove).

#### Ammonite-based correlations including *Hildoglochiceras*: Attempts of a global synthesis

The information, on which this chapter is based, includes that of Arkell (1956), Énay (1964, 1972, 1973, 1980, 2009), Zeiss (1968), and Fatmi and Zeiss (1999), whereby the interpretations made by Arkell (1956) and Zeiss (1968) strongly influenced subsequent interpretations. Arkell (1956) assumed that *Hildoglochiceras* and *Pseudolissoceras* co-occurred in Mexico but, in fact, Arkell (1956: p. 651) misinterpreted Imlay (1939). The latter did not report the co-occurrence of the two genera but reported *Pseudolissoceras* from beds containing *Mazapilites* in the neighbourhood of the Cañón del Buey across the Cuesta

de los Colorines, with clear indication of Pseudolissoceras characterizing his Kimmeridgian-Portlandian boundary. Imlay (1939) interpreted Hildoglochiceras as belonging to his upper Portlandian and Tithonian deposits; e.g., Hildoglochiceras in beds with Kossmatia and Durangites (H. grossicostatum and H. carinatum in Sierra de Parras; Imlay 1939: table 8), and Hildoglochiceras from beds with Substeueroceras and Proniceras (H. inflatum and H. alamense in S<sup>a</sup> Jimulco, as well as in his species description; Imlay 1939: table 9). Arkell (1956: p. 651) was also wrong when citing Hildoglochiceras in the inclusive list of ammonites from the Pimienta Formation given by Imlay (1952: p. 971). That list cannot be interpreted as a precise biostratigraphic reference (which is usually provided by the latter author in the stratigraphic sections in his papers). All these citations of Mexican Hildoglochiceras preceded their correct re-interpretation as Salinites by Cantú-Chapa (1968).

Zeiss (1968) clearly recognized a major problem when correlating, based on ammonites, the Lower Tithonian strata of the Frankenalb (southern Germany) with those of the Indo-Malagasy province. However, following Arkell (1956), Zeiss (1968: p. 137, table 6) accepted the co-occurrence of *Hildoglochiceras* and *Pseudolissoceras* in Mexico. He therefore assumed a Middle Tithonian age (Semiforme Zone) and not a Late Tithonian age, which is indicated by carefully reading Imlay (1939). This interpretation of Zeiss (1968) was widely accepted in later interpretations, even though this author stated that the precise biostratigraphic range of *Hildoglochiceras* was unknown at the time, as it is at present.

Énay (1964, 1972, 1973, 1980, 2009) often focused on Tithonian ammonites and their palaeobiogeographic distribution. Enay (1964) interpreted Hildoglochiceras as an accessory member of an inclusive assemblage characterizing the Lower Tithonian (two-fold division) in his Himalayan Indo-Malgache Province, where a zonal division was schematically shown, while Hildoglochiceras was only included for Madagascar. In addition to the known distribution of Hildoglochiceras across India and East Africa, Énay (1972, 1973) assumed the occurrence of Hildoglochiceras in Mexico and Cuba, without commenting on the new genus Salinites (Cantú-Chapa, 1968), and placed Hildoglochiceras together with Virgatosphinctes in the lower part of his Upper Tithonian, which included calpionellid zone B horizons with Proniceras elsewhere (i.e., Berriasian horizons). Thus, this author reinterpreted the Hildoglochiceras kobellli Zone of Collignon in Madagascar in clear contrast to the proposed correlation with the European Semiforme Zone made by Zeiss (1968). Énay (1972) recognized a 30- to 90-m-thick intercalation of poorly fossiliferous sandy deposits between the re-interpreted Lower and the Upper Tithonian in Madagascar and Kachchh. In contrast, he quoted a small thickness for the Upper Kimmeridgian Pictus Zone of Collignon from southern Madagascar, which he re-interpreted as the upper part of the Lower Tithonian, including the Middle Tithonian of Zeiss (1968). Énay (1973: p. 297, table 1) envisaged condensation to explain the occurrence of Hildoglochiceras

in Virgatosphinctes beds from Madagascar, while placing this genus above Zitteli horizons and lateral barren equivalents in Madagascar and Kachchh in basal Upper Tithonian deposits below the first occurrence of calpionellids. Énay (1980) accepted the genus Salinites for Mexico-Caribbean Hildoglochiceras and maintained an Upper Tithonian position for true Hildoglochiceras in Indo-Malagasy areas, and Énay and Cariou (1997, 1999) did the same for Spiti, Thakkhola and Papua-New Guinea. Later on, Énay (2009) assumed a variable stratigraphic interval for Hildoglochiceras (Lower Tithonian Semiforme to Ponti zones in Nepal, the Semiforme Zone in Kachchh, and the Lower to lowermost Upper Tithonian? in Madagascar).

Prior to the interesting assumption made by Fatmi and Zeiss (1999), who recognized potential variability when correlating Hildoglochiceras horizons, it is worth mentioning the report by Fatmi (1973) of Hildoglochiceras as secondary component of an ammonite assemblage dominated by small and moderately preserved torquatisphinctins interpreted as Lower Tithonian above his upper Kimmeridgian Beckeri Zone with Hybonoticeras in northern Pakistan. Unfortunately, this author did not provide biozone-level correlation for his Lower Tithonian within and outside Pakistan, while recognized a difference with the ammonite assemblage containing Hildoglochiceras in Kachchh. It has to be highlighted that Fatmi (1972, 1973) did not mention a discontinuity between Beckeri Zone deposits and his Lower Tithonian with Hildoglociceras, which was identified less than one meter above. However, his assumed condensation, the shallow-water conditions with signs of current activity, and post-morten drift of ammonite carcasses, could be in accordance with hiatuses in the reported sandy deposits containing calcophosphatic concretions overlying thin calcareous-glauconitic-ferruginous horizons with broken ammonites and belemnites above Hybonoticeras; in addition, the perisphinctins he illustrated need revision. Later, Fatmi and Zeiss (1999) attempted a worldwide correlation of ammonite assemblages from the Sembar Formation in Balochistan, Pakistan. They did not record Hildoglochiceras but assumed a variable correlation of Hildoglochiceras horizons in southern Balochistan with stratigraphic intervals embracing the Tethyan Semiforme to lower Ponti zones. This interpretation contrasts with the original proposal of Zeiss (1968).

#### Abridged, updated interpretation of *Hildoglochiceras* biostratigraphy based on ammonite data

The revision of biostratigraphic interpretations of *Hildo-glochiceras* records elsewhere indicates a certain uncertainty concerning correlations based on ammonite data, but a relative stability concerning the Tethyan Semiforme or Semiforme/Verruciferum Zone (early Middle Tithonian, three-fold division, or middle Lower Tithonian, two-fold division). This is the general accepted correlation, especially since the middle of the 20<sup>th</sup> century due to uncritical acceptance of the proposed correlation of Zeiss (1968), who did not further investigate the doubts he had expressed and thus promoted the erroneous assumption of Arkell (1956) about data from Mexico. Also confirmed is the occurrence of *Hildoglochiceras* in ammonite assemblages of variable composition and a dominance of endemic forms across separate areas, leading to a variability in the assumed biostratigraphic ranges.

Given the occurrence of a single specimen of taramelliceratin ammonites in the *Hildoglochiceras*-rich sample, for which a precise stratigraphic control is available, the comments below focus on the lower range interpreted for *Hildoglochiceras*, especially to provide a comprehensive view based on ammonite biostratigraphy, with special attention paid to views that have been proposed since the middle of the past century.

Across Himalayan areas, the Hildoglochiceras-Virgatosphinctes assemblage, including Virgatosphinctes denseplicatus, Kossmatia, and Paraboliceratoides, has been usually interpreted as Middle Tithonian during the 1980s, but more recent information point to interpretations of mixed, time-averaged ammonite assemblages. In NW India Hildoglochiceras, together with Aulacosphinctoides spp. and Virgatosphinctes spp., was reported from the Natricoides Zone, correlated with the Semiforme/Verruciferum Zone -i.e., the usual correlation. Correlations with a wider range in the Tethyan biostratigraphic scheme have been commonly proposed since the 1990s, while the interpretation of Hildoglochiceras has been changed from an accessory member of a Lower Tithonian (two-fold division) inclusive assemblage of the Himalayan and Indo-Malagasy areas to be diagnostic of a particular stratigraphic interval, on its own or occurring as part of ammonite assemblages of variable composition.

Of special interest for the case study are interpretations pointing to older horizons, within the total range interpreted by authors, at least as unexplored possibilities. Thus, the correlation with upper Darwini to Ponti horizons includes associated taxa that could indicate a latest Kimmeridgian age according to Nepal biostratigraphy (Énay 2009). Co-occurrence with the doubtful ?«Semiformiceras» aenigmaticum n. sp. (= Neochetoceras-trans-Semiformiceras group of darwini Neumayr in Énay 2009) rather indicates an Early but not earliest Tithonian age in Nepal, below horizons correlated with the Semiforme Zone. This also agrees with the range of Neochetoceras from latest Kimmeridgian to late but not latest Middle Tithonian. Also reported from Nepal is the occurrence of Hildoglochiceras in the Paraboliceras Beds of latest Kimmeridgian age, but this is a case of clearly stated imprecise stratigraphy. In what has been interpreted as lowermost Tithonian beds in Himachal Pradesh, India, Hildoglochiceras has been reported from thin, ammonite-rich stratigraphic intervals, co-occurring with Indodichotomoceras, Uhligites, Gymnodiscoceras, Kossmatia desmidoptycha (= Stevensia in Énay 2009), and Paraboliceras, an assemblage that resembles that of the Paraboliceras Beds of Nepal, hence pointing to a Late Kimmeridgian-earliest Tithonian age.

Moreover, local rare records of *Hildoglochiceras* came from the lower part of the Virgatosphinctoides Zone, Rajnati Subzone, correlated with the upper Darwini Zone in Himachal Pradesh, as well as together with *Indodichotomoceras* spp. and rare *Aulacosphinctoides* (?), probably indicating the uppermost Kimmeridgian Katrolensis Zone, Infundibulum Subzone, to Lower Tithonian Virgatosphinctoides Zone. All these reports indicate at least local records of *Hildoglochiceras* clearly below *Virgatosphinctes* in Himachal Pradesh and Kachchh, but reworking cannot be not excluded.

Data from northern Pakistan indicating the occurrence of *Hildoglochiceras* together with dominant, local torquatisphinctins slightly above uppermost Kimmeridgian deposits with *Hybonoticeras* cannot be conclusively interpreted, since sandy glauconitic deposition opens the possibility for hiatuses and reworking. This also applies to records in uppermost Tithonian to Lower Cretaceous horizons (basal Belemnite Beds; cf. Spath, 1939). At present, no conclusive correlation of these Pakistani faunas is available at the Tethyan standard biochronozone level for ammonites.

Correlation with biochronozones younger than the Semiforme/Verrruciferum Zone also exist, based on the record of *Hildoglochiceras* together with the youngest *Virgatosphinctes* in the lowermost part of the overlying Communis Zone, which was correlated with the Fallauxi Zone and interpreted to represent the lower Upper Tithonian before the erection of the genus *Salinites*. Even correlation with imprecise Upper Tithonian has been proposed for *Hildoglochiceras* as endemic form from Indo-Malagasy areas, correlated with basal Upper Tithonian deposits below the first occurrence of calpionellids in Spiti, Thakkhola and Papua-New Guinea.

In Madagascar, in light of stratigraphic uncertainties a revision of ammonite taxonomy and biostratigraphy is needed. A two-fold division of the Tithonian was proposed, with the Hildoglochiceras kobelli Zone below the Aulacosphinctes Hollandi Zone. The Lower Tithonian Hildoglochiceras kobelli Zone has been correlated with the Lower Tithonian above the Albertinum/Darwini Zone and the correlative Triplicatus and Vimineus zones in Europe, with inclusion of the Upper Kimmeridgian of Collignon. The reference to a stratigraphical gap affecting upper Kimmeridgian horizons is of interest, and may be even wider as in NW Madagascar where the Hildoglochiceras kobelli Zone overlies Oxfordian deposits. Hildoglochiceras associated with Virgatosphinctes, Haploceras and Aulacosphinctes has been reported, and Hildoglochiceras has been mentioned associated with Perisphinctes natricoides in more calcareous deposits and below Upper Portlandian (Upper Tithonian) limestones with Aulacosphinctes, and belemnite-rich clays. Of special interest is the co-occurrence of Hildoglochiceras with Virgatosphinctes, Haploceras, and locally Taramelliceras in sandy Lower Portlandian (Lower Tithonian) beds, above a thick barren, argillaceous interval that overlies horizons with common Katroliceras, Hybonoticeras, Taramelliceras, and Streblites -i.e., the typical Kimmeridgian interval with Torquatisphinctes in Madagascar. Stratigraphically imprecise are reports of *Hildoglochiceras* from a 20-m-thick glauconitic interval together with *Taramelliceras*, *Hybonoticeras*, *Physodoceras*, *Virgatosphinctes* spp., *Aulacosphinctoides* spp., and *Subdichotomoceras* spp., as well as that of *Hybonoticeras*, *Physodoceras* and *Taramelliceras* from the *Hildoglochiceras* kobelli Zone in argillaceous-marly deposits. In addition, condensation has been envisaged to explain the occurrence of *Hildoglochiceras* in *Virgatosphinctes* beds from Madagascar, where *Hildoglochiceras* was placed above Zitteli horizons and lateral barren equivalents as in Kachchh. *Hildoglochiceras* has also been reported below *Blanfordiceras* interpreted as Late Portlandian (Late Tithonian) in age.

Reports from East Africa refer to *Hildoglochiceras* retrieved from the *Trigonia smeei* Beds, re-interpreted as the *Indotrigonia africana* Beds, which correspond to a probably complete T-R cycle of Late Kimmeridgian-Early Tithonian age affecting shallow-water environments with common signs of reworking.

American reports of *Hildoglochiceras* were dismissed from Mexico-Carribean areas after the erection of the Late Tithonian to earliest Berriasian genus *Salinites*. Scarce reports of *Hildoglochiceras* from Argentina came from the *Pseudolissoceras zitteli* Zone, as well as from overlying horizons below *Aulacosphinctes* and have been correlated with middle Tithonian horizons. However, the illustrated material raises doubts, and the ammonites might represent rare, local, glochiceratin-like taxa.

Finally, as commented above, recent proposals assume variable biostratigraphic ranges and correlations in separate areas of the Trans-Erythraean Through (Lower Tithonian Darwini Zone for western Himalaya, Semiforme to Ponti zones for central Nepal, Semiforme Zone for Kachchh, and lowermost to lower Upper Tithonian? for Madagascar). At present, an unsolved limitation of special relevance for ammonite-based correlations, including this case study, is the occurrence of barren or ammonite-poor siliciclastic deposits below Hildoglochiceras horizons in western India (Kachchh, Jaisalmer) and Madagascar, overlying the youngest Hybonoticeras locally, and in Tanzania, as well as potential hiatal condensation in Pakistan. Hence, in the absence of age-diagnostic Tethyan ammonites in Hildoglochiceras horizons, the present interpretation of Hildoglochiceras records must be made in terms of local stratigraphic meaning. Therefore, geographical fluctuation of interpreted biostratigraphic ranges is foreseeable and most probably due to different palaeoenvironmental conditions relatively restricted for ammonites across shelf areas in the Trans-Erythraean Through. In addition, the potential role of local erosion and reworking cannot be dismissed and should be carefully investigated in each case.

According to the revision of records of *Hildoglochiceras* and associated ammonites, it is relevant to recognize the common occurrence of underlying ammonitiferous horizons with *Taramelliceras* and Late Kimmeridgian *Hybonoticeras*, locally even together with lowermost Tithonian *Hybonoticeras*. Hence, in horizons without clear evidence of reworking nor with records of Tithonian *Hybonoticeras*, the oldest records of *Hildoglochiceras* suggest the Lower but not lowermost Tithonian (three-fold division), thus a correlation with horizons belonging to the Tethyan Albertinum/Darwini Zone is proposed (Fig. 2).

Future research carried out with precise biostratigraphic control, based on bed-by-bed sampling, is needed before inferring interpretations of the age of the youngest records of Hildoglochiceras within the Tithonian, but variation in biostratigraphic ranges must be expected from separate areas, each of which should be interpreted with clear statements. The usual correlation of Hildoglochiceras horizons with the Tethyan Semiforme/Verruciferum Zone, which has been favoured or promoted as conclusive in the past, is not supported by published ammonite biostratigraphy. The Hildoglochiceras bio-horizon described below agrees with this interpretation, while the co-occurrence of the single eroded taramelliceratin ammonite points to the lower part of the Albertinum/Darwini Zone. That specimen may have been reworked, suggesting that the emersion surface at the base of the Hildoglochiceras Horizon may represent a wide stratigraphical gap.

#### Correlations based on microfossils

Correlation of Indian ammonite faunas has also been attempted with microfossils, especially dinoflagellates and foraminifers. In addition, calcareous nannoplankton and acritarchs have been used. Unfortunately, Francis and Westermann (1993) rightly stated the inconclusive correlation of assumed Tithonian intervals in India with European ammonite standard bio-chronozones, and this situation seems to persist. Concerning Hildoglochiceras, recent contributions offer rather misleading information. Garg et al. (2003) reported dinocysts retrieved from particular ammonites, Hildoglochiceras included, collected from Himalayan areas. The assemblage of dinoflagellate cysts recovered from specimens of this genus was recognized as "extremely meagre" by these authors, and did not include Omatia montgomeryi nor Gonyaulacysta jurassica, the assumed markers for the late Early Tithonian, while other diagnostic forms such as Aldorfia aldorfensis and Broomea simplex are also known from horizons with Blanfordiceras and Paraboliceras, respectively. Based on these data, Garg et al. (2003) interpreted the biostratigraphic range of Hildoglochiceras as late Early Tithonian, correlated with the Semiforme to Pontizones in Europe without critical revision of the information available. Khowaja-Ateeguzzaman et al. (2006) synthesized dinocyst data in their catalogue of Indian records. These authors cited ranges of guide taxa previously reported from Hildoglochiceras remains from Himalayan areas. Khowaja-Ateequzzaman et al. (2006) interpreted range extensions into Upper Tithonian to Lower Valanginian horizons (e.g., Aldorfia aldorfensis), as well as range restriction to the upper Lower Tithonian (e.g., Broomea simplex) co-occurring with Kossmatia and Paraboliceras. This contrasts with age-interpretations made for these ammonites by Pathak

and Krishna (1993) in the Spiti Valley and by Énay (2009) in Nepal. However, the two dinocyst taxa mentioned were interpreted as age-diagnostic for Hildoglochiceras. In addition, these authors interpreted the range of the acritarch Nummus similis to extend into the Barremian, although it is commonly referred to the upper Lower Tithonian. Jain and Garg (2015) reported a stratigraphically precise but rare Hildoglochiceras assemblage containing several species of this genus co-occurring with Aulacosphinctoides from western Rajasthan. On this basis, they proposed a Hildoglochiceras kobelliforme Zone of mid Early Tithonian age (two-fold division), above Virgatosphinctes interpreted of Early Tithonian age, and below records of himalayitins of Late Tithonian age. However, Aulacosphinctoides has been usually interpreted as Lower to lowermost Middle Tithonian since the 1990s (e.g., citations in Énay 2009; but see Pathak and Krishna 1993; Pandey et al. 2010; Krishna 2017). As usual, Jain and Garg (2015) correlated their new biozone with the Tethyan Semiforme Zone without precise supporting statements, and assumed correlation across Indo-Madagascan areas and with Argentina. Moreover, they commented on previous records of the dinocysts Aldorfia aldorfensis and Bromea simplex (presumably those reported by Garg et al. 2003), among others, together with the achritarch Nummus similis, all of which were assumed to support their proposed correlation, although no microfossils from the European middle Lower Tithonian (two-fold division) were mentioned. Jain and Garg (2015) interpreted Broomea simplex as a precursor of the late Early Tithonian Omatia montgomeryi Zone, which is known from the Indo-Pacific Realm, the Himalayas, Madagascar, and Mexico, and interpreted it to indicate the ammonite zonal interval from Semiforme to Ponti zones of mid to late Early Tithonian age in Europe. They assumed their Hildoglochiceras assemblage to represent the Semiforme Zone in the Kachchh and Jaisalmer basins of western and northwestern India, which they envisaged as the probable center of origin from which Hildoglochiceras dispersed to the Himalayas and Argentina during phases of global high sea-level.

Concerning benthic foraminifera, Garg (2007) reported successive assemblages from the Rupsi Shale in Jaisalmer, northwestern India, and related diversity of agglutinated foraminifers to salinity fluctuations and variable connections to open sea-waters in the estuarine environments he investigated. The most diverse Trochammina-Reophax-Ammobaculites assemblage includes Trochammina quinqueloba, which was used to characterize Kimmeridgian to Early Tithonian ages. Interestingly, the Trochammina-Reophax-Ammobaculites assemblage co-occurs with the Pachysphinctes-Aulacosphinctoides assemblage and underlies the Aulacosphinctoides-Hildoglochiceras assemblage of assumed early Early Tithonian age. Based on the record of Indian Aulacosphinctoides by Pandey et al. (2010), Hildoglochiceras reported by Garg (2007) points to its occurrence in horizons older than usually assumed, even the possibility that it occurs in latest Kimmeridgian or Kimmeridgian-Tithonian boundary horizons. He related

this to improved open marine connections due to the highest eustatic sea-level during Jurassic times. Southwards, from Kachchh, Faisal (2008) reported benthic foraminifer assemblages from the Ler Dome and mentioned the occurrence of Virgatosphinctes, Hildoglochiceras, Aulacosphinctes, common Haploceras elimatum (Oppel), and Trigonia in sandstones of the Upper Katrol Shales, which were interpreted to be Portlandian in age. In fact, the occurrence of common Haploceras agrees with a Tithonian age, but the oldest records of this genus are from the uppermost to top Kimmeridgian horizons in southern Europe. Hence, in the absence of direct correlation of diagnostic ammonites from southern Europe and the Trans-Erythraean Through, no conclusive interpretation can be achieved about biostratigraphic ranges and correlation based on benthic foraminifers, but there are local Hildoglochiceras occurrences just above the Kimmeridgian based on the combined records of benthic foraminifers and ammonites.

Calcareous nannoplankton has been reported by Rai and Garg (2010) from the Rupsi Member at Jaisalmer, northwestern India, which had previously been dated as Kimmeridgian and then as Kimmeridgian to Early Tithonian age based on ammonites and benthic foraminifer assemblages (Das Gupta 1975; Rai and Garg 2010; Jain and Garg 2012; Pandey et al. 2014; Pandey and Pooniva 2015). This nannofossil assemblage is composed of Cretarhabdus conicus, Cyclagelosphaera margerelii, Diazmatolithus lehmanni, Discorhabdus sp., Ethmorhabdus gallicus, holococcolith spp., Heleneachiastia, Lotharingus hauffii, L. sigillatus, Lucianorhabdus sp., Watznaeuria barnesiae, W. britannica, W. fossacincta, Zeugrahbdotus embergeri, Z. erectus, and Z. sp. This diverse assemblage includes cosmopolitan forms and was retrieved from one specimen of Himalayites sp. from the upper Rupsi Shale containing Hildoglochiceras together with Aulacosphinctoides (see comments above). Based on late Early Tithonian nannofossil data, the upper part of the Rupsi Shale was reinterpreted to correspond to the late Early Tithonian NJ12b (T) Polycostella beckmanii Subzone (recte NJ-20B) of Bralower et al. (1989), but Himalayites is unknown from horizons older than the Upper Tithonian elsewhere, and therefore its co-occurrence with Himalayites should be restudied. On the other hand, record of late Early Tithonian nannofossils, Early Tithonian Hildoglochiceras and Aulacosphinctoides and Himalayites from a thin horizon suggests time-averaging by reworking.

According to data in Bown and Cooper (1998), wide-ranging species (e.g., between Lower to Middle Jurassic and Cretaceous horizons) dominate the nannoplankton assemblage reported by Rai and Garg (2010). Of special relevance are species included in the assemblage reported by Rai and Garg (2010) that have known LADs below Kimmeridgian or Tithonian horizons in Tethyan areas. They include *L. sigillatus* (LAD at the top of the Middle Oxfordian Tenuiserratum Zone in Bown and Cooper 1998 (= upper Plicatilis-lower Transversarium zones in Cariou et al. 1997), and within the Middle Oxfordian at the NJ-

T13a-NJT13b boundary in Casellato 2010) and L. hauffii (LAD in top-Bathonian horizons according to Bown and Cooper 1998, but within the Upper Oxfordian, middle part of NJT13b according to Casellato 2010). There are forms with FAD below the Tithonian and LAD within the Lower Cretaceous as it is the case with C. conicus, with FAD within the Kimmeridgian Eudoxus Zone (Bown and Cooper 1998), but according to Casellato (2010) within Lower Cretaceous horizons, corresponding to an uppermost Middle to lowermost Upper Berriasian range according to Tavera (1985). Also included are forms with Tithonian to Early Cretaceous ranges, such as Diazmatolithus lehmanni that Bown and Cooper (1998) assumed, with doubts, to have Tithonian and Albian records. However, later an Upper Tithonian-Lower Berriasian range throughout the Transitorius-Jacobi zonal interval was confirmed by Svobodová and Košťák (2016) in southern Spain, together with other species cited by Rai and Garg (2010), such as Cyclasgelosphaera margerelii, Watznaeuria barnesiae, W. britannica, W. fossacincta, Zeugrahbdotus embergeri, and Z. erectus.

At first, the occurrence of Watznaueria spp. in the assemblage reported by Rai and Garg (2010) agrees with the common record of this taxon in Kuwait, where its acme, associated with Cyclagerosphaera margerelii and rare Diazmatolithus lehmanni and Nannoconus sp., has been interpreted to indicate Kimmeridgian horizons below the FAD of Conusphaera mexicana minor (Kadar et al. 2015), an usual marker of lowermost horizons within the Tithonian. In the nannoplankton assemblage reported by Rai and Garg (2010), the absence of common records of Conusphaera and Nannoconus, of which the latter is not mentioned as member of the assemblage but only merely cited later in text, contrasts with the late Early Tithonian age interpreted by these authors. Their age-interpretation was based on Zeugrhabdotus embergeri, Nannoconus compressus, and Ethmorhabdus gallicus, supported with reference to the Polycostella beckmanii Subzone of Bralower et al. (1989). The latter authors placed the Polycostella beckmanii Subzone in their Upper Kimmeridgian, below the FAD of Conusphaera mexicana minor, which is a marker for lowermost Tithonian horizons (e.g., Casellato 2010) slightly above the Kimmeridgian-Tithonian boundary placed close to the base of M22An (Ogg et al. 2016). The age assignment made by Rai and Garg (2010) implicates a two-fold division of the Tithonian, despite of some reference to the Middle Tithonian, and their emphasis on the three diagnostic nannoplankton species mentioned deserves some attention.

According to the revision of calcareous nannofossil zonations and correlations from the Tethyan Realm made by Casellato (2010), the first appearance (FAD) of *Zeugrhabdotus embergeri* in Bralower et al. (1989) correlates with the Hybonotum-Darwini Zone boundary, although it was placed in uppermost Kimmeridgian horizons by Bralower et al. (1989), who interpreted their Embergeri Subzone NJ-19B to characterize uppermost Kimmeridgian horizons just below the FAD of *Conusphaera mexicana minor*. In fact, Casellato (2010) reported the FAD of Zeugrhabdotus embergeri close to the Kimmeridgian-Tithonian boundary in the Lombardian Basin, younger within the Tithonian in the Trento Plateau, and showing more variable Tithonian records in the DSDP Site 534 A where its FAD is placed slightly below the NJT14-NJT15 boundary (within CM22R), thus younger than interpreted by Bralower et al. (1989). Casellato (2010) placed the FAD of Zeugrhabdotus embergeri as a secondary bio-event within transitional horizons between Kimmeridgian and Tithonian (= lowermost Tithonian?) and clearly below the FAD of Conusphera mexicana minor, which she selected as the main bio-event for identification of mid-CM22n horizons in Tethyan areas, slightly above the base of the Tithonian promoted by Ogg et al. (2016). Lescano (2011) assumed a latest Kimmeridgian age for the FAD of Zeugrhabdotus embergeri, and an earliest Tithonian age for the NJ19-B Embergeri Zone, which he placed just below the FAD of Conusphaeramexicana minor.

Nannoconus compressus is not included among the selected bio-events in the western Tethys, it is not even recorded as a guide fossil, but has been recorded from several levels within the Tithonian. Its reported FADs are older (Bralower et al. 1989) and younger (Casellato 2010) in NJT15b from DSDP Site 534A, while its LAD has been placed near the top and bottom of NJT16b in the same site according to Bralower et al. (1989) and Casellato (2010), respectively. Bralower et al. (1989: fig. 14) assumed a Middle Tithonian range, but placed the LAD in their CM19 which indicates the Upper Tithonian Durangites Zone. The record from southern Spain (Bralower et al. 1989: fig. 6), in contrast, refers to the lower part of CM20n, which rather indicates the Upper Tithonian lowermost Transitorius Zone horizons (Svobodová and Košťák 2016). Casellato (2010) placed the range of Nannoconus compressus between the upper NJT15b and the NJT16a/ NJT16b boundary within CM20 at DSDP Site 534A, which in fact would include an upper part of CM21 embracing mid to upper Lower Tithonian to mid Upper Tithonian horizons (two-fold division) according to the zonal scheme of Casellato (2010) for Tethyan areas, i.e., the mid to upper Admirandum/Biruncinatum Zone to the Transitorius Zone. Ethmorhabdus gallicus is a long-ranging taxon (FAD in Toarcian and LAD in Upper Tithonian to Lower Cretaceous?) according to Bown and Cooper (1998). Its LAD could represent a 2<sup>nd</sup> event in the lower Upper Tithonian according to the correlation chart in Casellato (2010).

Another comment refers to the *Conusphera mexicana* Zone, which in Bralower et al. (1989) corresponds to their NJ-20 Zone, but not to NJT12 as mentioned in Rai and Garg (2010), and to NJT15 plus the majority of NJT16a in Casellato (2010). In Bralower et al. (1989), the *Conusphera mexicana* Zone embraces the major part of their Lower Tithonian, while it has been correlated with a stratigraphic interval between undetermined horizons close to the mid-Semiforme/Verruciferum Zone and the uppermost part of the Burckhardticeras/Ponti Zone according to Casellato (2010). Bown and Cooper (1998) correlated the FAD of *Conusphera mexicana* with horizons within the Scitulus Zone (= Albertinum/Darwini Zone in Geyssant 1997, and the upper Hybonotum to lower Darwini zonal interval in Zeiss 2003). Casellato (2010) placed the FAD of *Conusphera mexicana* in the lower Tithonian, slightly above of that of *Conusphera mexicana minor*, which she selected as marker for the identification of lower Tithonian horizons within the mid-CM22n in Tethyan areas, slightly above the base of the Tithonian proposed by Ogg et al. (2016).

As the previous review of ammonite biostratigraphy and correlations, the review of selected microfossil data reveals that most assumed correlations follow the most usual proposal based on ammonite biostratigraphy and thus are of little help with rare but interesting exceptions (e.g., benthic foraminifers in Garg 2007). Hence, in absence of direct correlation among diagnostic ammonites from southern Europe and the Trans-Erythraean Through, no conclusive interpretation seems to be achieved about biostratigraphic ranges and correlation based on microfossils.

In summary, dynocyst data retrieved from specimens of *Hildoglochiceras* in the *Hildoglochiceras kobelliforme* Zone containing *Aulacosphinctoides*, above *Virgatosphinctes* and below himalayitins, proposed for the mid-Early Tithonian and correlated with the Tethyan Semiforme Zone in Rajasthan, represent an assemblage, in which no index taxa for the Lower Tithonian are present. Microfossils from the European middle Lower Tithonian (two-fold division) have not been discussed, but the Omatia montgomeryi Zone has been correlated with the Semiforme to Ponti zonal interval of mid to late Early Tithonian age, and hence the *Hildoglochiceras* assemblage has been interpreted to represent the Semiforme Zone and is related to a global high sea-level.

The Rupsi Shale in Jaisalmer, northwestern India, has been also investigated for benthic foraminifera. Benthic foraminifera turned out useful for characterising palaeoenvironments in terms of salinity and variable open marine connections in the estuarine environments. The most diverse assemblage included Trochammina guingueloba of assumed Kimmeridgian to Early Tithonian age co-occurring with the Pachysphinctes-Aulacosphinctoides assemblage, which underlies the early Early Tithonian Aulacosphinctoides-Hildoglochiceras assemblage. As discussed above, previous interpretations of Indian Aulacosphinctoides suggest that it occurs in uppermost Kimmeridgian or Kimmeridgian-Tithonian boundary horizons, and hence these data obtained from benthic foraminifers have a high reliability, which seems to be a rare case. Southwards, at Ler Dome in Kachchh, the Portlandian age of benthic foraminifers from sandy intercalations of the Upper Jhuran Formation with Hildoglochiceras, Virgatosphinctes, Aulacosphinctes, common Haploceras elimatum (Oppel), and Trigonia could also correspond to uppermost Kimmeridgian horizons in southern Europe according to the oldest record of Haploceras in Tethyan areas. However, no conclusive interpretation is available since lower Upper Tithonian horizons cannot be dismissed, if Aulacosphinctes was correctly identified. Moreover, recent correlation of the "Trigoniaschichten" with *Hildoglochiceras* in Tanzania allows considering a biostratigraphic range including horizons of latest Kimmeridgian age.

Concerning calcareous nannoplankton, the biostratigraphic interpretation is also inconclusive, as is usual for nannofossil assemblages without data on taphonomy, diagenesis (degree of dissolution), and relative abundances, especially where mesotrophic conditions as those assumed for the relatively restricted Indian shelves might have acted against large and diverse assemblages of calcareous nannoplankton. Together with stratigraphic and/ or sampling incompleteness, this finally produces different biostratigraphic ranges of given taxa from separate areas. Based on the biostratigraphic discussion, the late Early Tithonian age tentatively interpreted by Rai and Garg (2010) is not conclusive, and a larger range from the latest Kimmeridgian to Middle to Late Tithonian based on updated biostratigraphic correlations must be explored with better and more numerous samples. The reference to the co-occurrence of Hildoglochiceras with Aulacosphinctoides could point to horizons older than those interpreted by these authors and raises serious doubts about the right identification as Himalayites of the specimen that provided the nannoplankton assemblage. The nannoplankton data reviewed does not support ages older than Late Tithonian for Himalavites, and the studied sample most likely suffered from some natural or analytical limitation.

# A stratigraphic context for interpreting the biostratigraphic range of *Hildoglochiceras*

All the comments above point to persistent doubts about the real extent of the entire range of Hildoglochiceras, especially about its oldest and youngest records. A major limitation to the correct knowledge is the recurrent association of Hildoglochiceras with endemic or regional ammonite faunas, which rarely include taxa providing reliable correlations with distant regions, as well as with the European Biostratigraphic Standard Scale (e.g., Geyssant 1997), and are subject to a variable taxonomy. Also limiting is the scarcity of precise reference to local stratigraphy - i.e., details of particular sections where Hildoglochiceras has been reported - and the rarity of samples reported at population level and reports of data retrieved bed-by-bed. Thus, based on isolated records from more or less separate areas, misinterpretations, and/or assumed biostratigraphic positions and correlations without support based on precise analyses, a rather fuzzy biostratigraphic range has been postulated for Hildoglochiceras in the past. Restricted to interpretations of the Lower Tithonian (two-fold division) since the early 1960s, interpretations of Hildoglochiceras biostratigraphy have been fluctuating depending on the division used for the Tithonian stage - i.e., two-fold (e.g., Énay 1964, 1972, 2009; Covacevich 1976; Krishna 1983, 1984, 1987, 2017; Verma and Westermann 1984; Pathak and Krish-

na 1993; Pandey and Krishna 2002; Pandey et al. 2010, 2016) or three-fold (e.g., Zeiss 1968; Covacevich 1976; Krishna 1987). Aside from the usual correlation with the Semiforme/Verruciferum Zone in Europe following Zeiss (1968; but see above, and Geyssant 1997), range extensions in the Indian-Himalayan areas have been proposed downward (Albertinum/Darwini zones in Europe: Krishna 1984; Pathak and Krishna 1993; Krishna et al. 1996; ?Énay 2009) and upwards to a variable extent (Fallauxi to Ponti-Burckhardticeras zones in Europe: Krishna 1983, 1984; Pathak and Krishna 1993; Pathak 1997; Pandey and Krishna 2002; Pandey et al. 2013). Only some proposals include uppermost Kimmeridgian horizons (e.g., Pandey et al. 2010) or Upper Tithonian horizons (e.g., Énay 1972; Bardhan et al. 2007). In addition, based on published data, the possibility for latest Kimmeridgian horizons has not received adequate attention.

Assuming a relationship between ammonite records and sea-level, whether eustatic or relative, sequence stratigraphic arguments must be taken into account. According to the revision made, the largest biostratigraphic range theorically assumable for Hildoglochiceras – uppermost Kimmeridgian to lower Upper Tithonian - represents a time-span too long for persistence of the transgressive character rightly interpreted for Hildoglochiceras horizons, especially when its endemic character is taken into account. Concerning the lower limit of the biostratigraphic range of Hildoglochiceras, special attention must be paid to the local to regional occurrence of underlying deposits poor in ammonites or barren. This is known from Madagascar (e.g., Collignon 1957, 1964; Collignon and Razafinbelo 1964; Énay 1972, 1973), India (e.g., Spath 1933; Énay 1972, 1973; Pandey et al. 2016; this paper), and Tanzania (e.g., Bussert el al. 2009). In addition, there are Hildoglochiceras horizons with evidence of reworking and taphonomic condensation in India above sandy, fossil-poor horizons (e.g., Pathak and Krishna 1993; Pandey et al. 2016; this paper), and cases of regional absence of ammonites (e.g., Spath 1933 for Kachchh; Krishna 1987 for NW India and Balouchistan). Allusions to condensation of Hildoglochiceras horizons from Madagascar must be confirmed.

Given that transgressive pulses are not necessarily related to eustasy, a scenario of tectono-eustatic pulses of local incidence and of inconclusively known timing must be considered. These pulses were most probably diachronous across given segments of palaeomargins of the Trans-Erythraean Trough, which would explain the variability of stratigraphic gaps, lithofacies, and age of ammonite-poor horizons underlying Hildoglochiceras records, regardless of whether the latter consist of isolated specimens or of rare population samples. Stratigraphic gaps of variable extent and sealed by Hildoglochiceras horizons or at least by Tithonian horizons are known (e.g., Howarth 1998 for Yemen; Krishna 2017 for western India; Collignon 1964 for Madagascar), which could reflect condensation, reworking, non-deposition, erosion, or a combination of these. Such a situation would mask the oldest records of

Hildoglochiceras in unstable shelf environments across the Trans-Erythraean Trough, which increasingly extended towards the south. All of this agrees with the palaeoenvironmental dynamics in these shallow-water environments where deposition of siliciclastics prevailed during latest Jurassic times of high sea levels - mainly latest Kimmeridgian to earliest Tithonian - and during the early Middle Tithonian. Assuming a warm-temperate, seasonal climate without evidence of major fluctuations, with higher aridity for East African (winter-wet biome) versus Indian-Madagascar palaeomargins (Scotese et al. 1999, 2014; Rees et al. 2004; Bussert et al. 2009), siliciclastics with a poor to lacking ammonite record would increasingly result from regressive pulses with variable progradation and/or increasing erosion due to tectono-eustatic interactions. Hence, unfavourable conditions for ammonites can be expected due to local forcing. Geographically restricted records of Hildoglochiceras overlying deposits clearly older than Tithonian ones, or potentially included in a stratigraphic gap (southern Yemen; Howarth 1998, and the Natricoides Zone in the western Kachchh Mainland; Krishna 2017) are evidence of the influence of block-tectonics.

In addition to differences in the structure of the palaeomargins between India and Madagascar and to the stratigraphic architecture and epicontinental paleoenvironments (e.g., Bosellini 1992; Geiger 2004; Bussert et al. 2009), information from East Africa is of value, because records of ammonites from this region have been also related to transgressive pulses (e.g., Kapilima 2003). As in Madagascar, Hildoglochiceras records from East Africa rather relate to a potential faunal mixing, analytical (?) and/or natural (reworking) (e.g., Zwierzycki 1914; Dietrich 1925, 1933; Bussert et al. 2009), being associated with bivalve-rich beds from inner-shelf environments, the Trigonia smeei Beds at Tendaguru (= Indotrigonia africana Beds of Bussert et al. 2009). The latter authors recognised a complete Upper Kimmeridgian-Lower Tithonian T-R cycle for their Indotrigonia africana Beds, which cannot be correlated with the HST+TST conditions assumed by Pandey et al. (2010) for the same stratigraphic interval in India, nor with the corresponding T-R cycles interpreted by Krishna et al. (2011) and Krishna (2017). In addition to contrasting interpretations of cycles of particular relevance for the interpretation of Hildoglochiceras (e.g., a regressive cycle for the Natricoides Zone in Krishna et al. 2011; but see Krishna 2017), presumable variations in the order of the stratigraphic sequences pose limitations for their precise correlation. Moreover, in the absence of sedimentologic observations, the precise interpretation of the stratigraphic level and meaning of condensed horizons is difficult, and variations could result from interaction of local forcing factors (e.g., compare transgressive horizons in Krishna et al. 2000 with those in the papers cited above). Thus, the presence of glauconite in mixed siliciclastic-carbonate horizons containing Hildoglochiceras cannot be conclusively interpreted in terms of sequence stratigraphy, as long as its detrital vs. authigenic character and relative abundance is not known. In such a context, isolated records of Hildoglochiceras cannot be conclusively interpreted in terms of sequence stratigraphy, nor can they be reliably correlated in absence of association with Tethyan ammonites of biostratigraphic value. In contrast, records of Hildoglochiceras populations will offer a more reliable information demonstrating favourable conditions for these ammonites: These could be related to particular sea-level conditions and are of value for stratigraphic and palaeobiologic interpretations. Based on the previous comments, the Hildoglochiceras horizon described from the Middle member of the Jhuran Formation at the Lakhapar section, Jara Dome, in western Kachchh Mainland (Fig. 1), can be related to transgressive conditions and maximum flooding due to local to regional tectono-eustatic forcing. Possibly Hildoglochiceras occurred during a larger time interval of high sea-level during latest Kimmeridgian to earliest Tithonian (Hybonoticeras horizons) or, alternatively, during the middle Lower Tithonian (two-fold division).

#### Taxonomy

#### Methodology

Ammonites were collected in the field with the highest possible stratigraphic resolution and subsequently cleaned and photographed in the laboratory. The specimens are stored in the permanent collections of the K.S.K.V. Kachchh University. The following abbreviations correspond to dimensions measured with a digital calliper in millimetres (Fig. 5):

- D diameter of shell;
- **H** height of whorl;
- **H/D** percentage of height of whorl with respect to diameter of shell;
- T thickness of whorl;
- T/D percentage of thickness of whorl with respect to diameter of shell;
- U width of umbilicus;
- **U/D** percentage of width of umbilicus with respect to diameter of shell;
- H/T height and thickness of whorl ratio;
- WSG width of spiral groove;
- **HSG** distance from umbilical suture to lower boundary of spiral groove.

In addition, each specimen was assigned to a group depending on the location of the maximum whorl thickness expressed by #:

- Maximum thickness at lower boundary of spiral groove;
- Maximum thickness at upper boundary of spiral groove;
- 2 Maximum thickness at lower and upper boundary of spiral groove.



**Figure 5.** Diagram of dimensions of ammonites, measured with a digital caliper.

#### Order Ammonoidea Zittel, 1884 Suborder Ammonitina Hyatt, 1889 Superfamily Haploceratoidea Zittel, 1884

#### Family Haploceratidae Zittel, 1884

**Remarks.** The taxa described under this family are *Haploceras* Zittel, 1870 and *Hildoglochiceras* Spath, 1924. The shell of *Haploceras* shows fine growth lines when epigenized shell is preserved, while inner casts are smooth, with a small but variable umbilicus that initially opens gradually until the last ontogenic stage when it slightly unfolds. Macroconchiate *Haploceras* show a slightly flexuous peristome, while assumed microconchs are variable in size, incorporate wide and short lappets rather than narrow and pedunculated ones, but can resemble glochiceratins in the absence of peristomal structures. Incomplete specimens of *Haploceras* make species-level interpretations difficult.

Reports of the genus Haploceras have been variably interpreted before the mid-twentieth century when this genus was commonly applied to Kimmeridgian and Lower Tithonian glochiceratins elsewhere in the world (e.g., Ziegler 1958), while the present knowledge about microconchiates is inconclusive. Across the Trans-Erythraean Trough, Haploceras has been more frequently reported from the northern and eastern margins than from western ones, although it is a rare genus across the Himalayas (from Uhlig 1903 to Énay 2009). Southwards across eastern margins, Haploceras has been reported from southern Pakistan to Madagascar throughout the twentieth century (e.g., Lemoine 1910; Collignon 1960; Fatmi and Zeiss 1994). In contrast, across western margins, Haploceras was only registered from southern Yemen (Howarth and Morris 1998) and Tanzania (from Zwierczyki 1914 to Bussert et al. 2009), being absent or very rare in between.

Haploceras elimatum (Oppel, 1965) and allies represent the morphological group more widespread and have been commonly reported throughout epicontinental areas in the Trans-Erythraean Trough. Haploceras elimatum (Oppel, 1965) and Haploceras staszycii (Zeuschner, 1846) have commonly been recognized as close species, difficult to separate, for instance by Rod (1937) and by (Hölder and Ziegler 1959), even as representing a single species (Rod 1946). They represent a dimorphic pair (Barthel 1962). The macroconch embraces all but one Tithonian haploceratin species with polymorphic microconchs (Énay and Cecca 1986). According to the information available, the latter is a rather speculative proposal. Zeiss (2001) highlighted the existing options for interpreting dimorphism in haploceratins, and treated the morphologically close species *elimatum* and *staszycii* as separate units only for convenience. Based on all the above mentioned, these two morphospecies are here interpreted as conspecific and referred to as *Haploceras staszycii* by priority, with reference to the closest nominal morphological species reported from the Trans-Erythraean Trough.

*Hildoglochiceras* is commonly more evolute, characterized by a median lateral groove and, consequently, with an acute-oval to oval whorl-section, venter of variable width and height, a lateral sulcus above the lower one-third of the flanks, a variable shell-size for the beginning of ribbing, and more or less ornamented outer whorls. In the present collection, we recognise two groups within *Hildoglochiceras*; one interpreted as microconch and other as the corresponding macroconch. These two morphs have been separated on the basis of shell size and the diameter of the umbilicus. The macroconch shows a subrectangular to oval whorl section. See previous chapters for a revision of reports of *Hildoglochiceras* across the Trans-Erythraean Trough.

Another comparable genus to inner whorls of Haploceras and Hildoglochiceras is Glochiceras Hyatt, 1900, the shell of which is smaller and shows a variable whorl section, sculpture and peristomal structure. The umbilicus of Glochiceras opens suddenly at the end of the growth. In addition, some species of Glochiceras are also characterised by a median lateral groove like in Hildoglochiceras. But small size, a rather discoid shell with narrow venter, the type of peristome, and the biostratigraphic range of typical Glochiceras, i.e. from Oxfordian to Kimmeridgian, with scarce records from the Lower Tithonian (e.g., Ziegler 1958; Collignon 1960; Barthel 1962; Grigore 2019), may be diagnostic. These morphological features persist in the scarce Glochiceras reported from the lowermost Tithonian of Europe. Separation of glochiceratins and microconchite haploceratins can be difficult with incomplete specimens lacking the peristome.

Among evolute haploceratins with a comparatively wide ventral region, *Lingulaticeras* Ziegler, 1958 and *Paralingulaticeras* Ziegler, 1958 are relatively close in shell-type to *Hildoglochiceras*. Supposed lowermost Tithonian forms of the former are more involute and show a sculptured venter of variable width, while those of the latter develop a latero-ventral tuberculation.

#### Genus Haploceras Zittel, 1870

**Type species.** *Ammonites elimatus* (Oppel in Zittel 1868; SD Spath 1923); Tithonian.

#### Haploceras staszycii (Zeuschner, 1846)

Fig. 6A-G, L-N

Ammonites staszycii sp. nov., 1846 – Zeuschner: pl. 4, fig. 3. Ammonites elimatus sp. nov., 1865 – Oppel: 549. Haploceras elimatum (Oppel), 1868 – Zittel: 79, pl. 13, figs 1–7. Haploceras deplanatum sp. nov., 1875 – Waagen: 44, pl. 11, fig. 9a, b. Haploceras elimatum (Oppel), 1960 – Collignon: pl. 142, figs 536, 537.

Glochiceras deplanatum (Waagen), 1960 – Collignon: pl. 142, figs 540–542.

**Material.** Seven specimens, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/61, 62, 63, 64, 66 (all figured), 68, 69 (figured).

**Description.** Shell incomplete, compressed, involute with oval whorl section, moderately distinct to distinct umbilical shoulder, short and slightly arched umbilical wall. Maximum thickness of the shell is either at mid-lateral height or slightly below it. Height and thickness ratios with respect to diameter show variation. Suture lines preserved, densely frilled with most pronounced second lateral saddle, appears getting crowded anteriorly.

Remarks. The specimens represent only parts of phragmocones and show erosional external surfaces. The ornamentation is not preserved in the present specimens. They appear smooth, as is typical for inner casts. However, parts of the siphuncle are well preserved. In two of the specimens (KSKV2019Jara/63 and 64) small portions of shell are preserved, also indicating a smooth external surface. The largest specimen (KSKV2019Jara/61) measured in the present collection has a diameter of ca. 53 mm and the crowding of the last septa indicates that it has attained the adult size. At a given diameter, the diameter of umbilicus may be larger but in general, the morphological features such as the shape of the shell, whorl section, suture lines and dimensional proportions match Haploceras elimatum (Oppel) (Collignon 1960: pl. 142, figs 536, 537) recorded from the Hildoglochiceras kobelli Zone of Madagascar (Early Tithonian) with a shell and ventral region clearly wider than in Oppel's (1868) type. West-Tethyan Haploceras elimatum (Oppel) show more convergent, less inflated flanks, hence their "clear" separation from

Haploceras staszycii (Zeuschner). Zeuschner (1846, pl. 4, fig. 3) did not give a scale with his figure. Zittel (1868: 81) mentioned a close morphologic similarity between H. elimatum of Oppel and H. staszycii of Zeuschner and stated that the specimen illustrated in Zeuschner (1846) is rather large (Zittel 1868: "ein ziemlich grosses Exemplar") showing a smaller umbilicus and a wider shell than H. elimatum. Zittel's (1870) description of H. staszycii (Zeuschner) was based on 300 specimens gathered from Rogoznik, Maruszina, central Apennines, and Bavaria. Zittel highlighted the shell-width and flattened flanks as distinguishing features to separate H. staszycii (Zeuschner) from H. elimatum (Oppel), although, he found difficulty in separating the young specimens of the two species. Zittel also made a rather uncommon observation about the occurrence of a keel-like elevation on the venter in the inner whorls up to 30 mm in shell size, but no further author mentioned this feature. If all the dimensional proportions of the specimens of H. staszycii (Zeuschner) and H. elimatum (Oppel), which are available (see Table 1) together with those of Zeuschner's collection (300 specimens), croweding of septa in the largest phragmocone in the present collection and the figures of both the species illustrated by earlier workers are reviewed, there is a good possibility that H. staszycii (Zeuschner) represents the microconch whereas H. elimatum (Oppel) represents the marcoconch of the same species.

Haploceras subelimatum Fontannes (Collignon 1960: fig. 538) differs from Haploceras elimatum (Oppel) (Collignon 1960: pl. 142, figs 536, 537) in having a finer ornamentation, while the type of subelimatum in Fontannes (1879: 12, pl. 2, figs 5–6) shows a more compressed shell, and a general glochiceratin-like aspect. However, dimensional proportions are within the range of variation as seen in the specimens of the present collection (Fig. 7, also see table of dimensions). In the Stramberger specimen described by Oppel (1865: 549), the body chamber including the peristome is preserved. It measures 125 mm in diameter. The shell is either smooth or covered with fine curved growth lines.

Haploceras deplanatum Waagen (1875: 44, pl. 11, fig. 9a, b; Collignon 1960: pl. 142, figs 540–542) shows a similar H/T ratio (1.33–1.75) and U/D ratio (17–22) to the present specimens, however, Waagen's specimen (1875) shows a more flattened shell, while the specimen of Madagascar

Table 1. Dimensions of Haploceras staszycii (Zeuschner) and comparable species (in mm).

Specimen no.	D	н	H/D	Т	T/D	U	U/D	H/T
KSKV2019Jara/64	27.1	13.01	48.0	9.01	33.2	6.14	22.6	1.44
KSKV2019Jara/63	28.85	14.90	51.64	11.09	38.44	7.11	24.64	1.34
KSKV2019Jara/66	32.11	16.7	52.0	12.5	38.9	8.82	27.4	1.33
KSKV2019Jara/62	33.68	16.7	49.5	12.49	37.0	5.48	16.2	1.33
KSKV2019Jara/69	-	26.7	-	19.1	-	-	-	1.39
KSKV2019Jara/61	53.05	25.65	48.3	17.73	33.4	11.88	22.3	1.44
KSKV2019Jara/68	-	32.4	-	21.6	-	-	-	1.50
Haploceras elimatum (Oppel) (Zittel 1868: 79, pl. 13, figs 1–7)	50-145	-	46	-	31	-	18-23	-
Haploceras elimatum (Oppel) (Collignon 1960: pl. 142, fig. 536)	94	48	51	34	36	17	18	1.4
Haploceras elimatum (Oppel) (Collignon 1960: pl. 142, fig. 537)	78	39	50	28	36	16	20	1.39
Haploceras subelimatum Fontannes (1879: 12, pl. 2, figs 5–6a, b)	34	14.9	44	8.8	26	8.8	26	1.69
Haploceras subelimatum Fontannes (Collignon 1960: pl. 142, fig. 538)	47	22	47	16	34	9	19	1.37
Haploceras staszycii (Zeuschner) (Collignon 1960: pl. 142, fig. 539)	28	14	50	12	43	4	14	1.16
Glochiceras deplanatum (Waagen) (Collignon 1960: pl. 142, fig. 540)	24	11	46	7	29	4	17	1.57
Glochiceras deplanatum (Waagen) (Collignon 1960: pl. 142, fig. 542)	26	12	46	9	35	5	19	1.33
Glochiceras deplanatum (Waagen) (Collignon 1960: pl. 142, fig. 541)	27	12	44	8	30	6	22	1.5
Haploceras deplanatum Waagen (1875: 44, pl. 11, fig. 9a, b)	27	14	51.8	8	30	6	22	1.75



Figure 6. A–G, L–N. *Haploceras staszycii* (Zeuschner, 1846). A. KSKV2019Jara/63, left side view of phragmocone, note well preserved suture lines; B, C. KSKV2019Jara/64; B. Left side view of phragmocone; C. Apertural view showing broken aperture along a septum; D. KSKV2019Jara/66, apertural view; E. KSKV2019Jara/69, apertural view showing broken surface along a septum; F, G. KSKV2019Jara/62; F. Left side view of phragmocone, note well preserved suture lines; G. Apertural view; L–N. KSKV2019Jara/61; L. Right side view of phragmocone; M. Apertural view; N. Outline of whorl-section; H–K, O. *Haploceras* sp.; H, O. KSKV2019Jara/65; H. Apertural view along a broken surface of phragmocone; O. Right side view showing phragmocone and a part of body chamber; I–K. KSKV2019Jara/67; I. Vental view; J. Apertural view; K. Left side view of body chamber; P–T. *Hildoglochiceras kobelliforme* (Bonarelli, 1894) (m); P–S. KSKV2019Jara/1, inner cast with epigenized shell preserved; P. Right side view of moderately evolute specimen (U ≈ H), with subtle uncoiled outer whorl (probable adult), body chamber 180° with peristomal vestige (dorsal branch on inner cast?); Q. Suture lines at the end of phragmocone, note increased density at the end of phragmocone; R. Apertural view, note epigenized shell clearly identifiable on the ventral region; S. Oval whorl section with narrow venter, wide lateral groove on the body chamber; T. KSKV2019Jara/2. inner cast, left-side view of nearly complete adult specimen with clear final uncoiling, partial preservation of epigenized shell, ca. 180° of preserved body chamber on inner cast of comparatively fine-to-medium sandstone.

(Collignon 1960, pl. 142, fig. 542) has a thicker whorl section at the corresponding diameters. If all the specimens described by Waagen and Collignon belong to the same species, then apparently there is a large range of variation in the H/T ratio (Fig. 7). In fact, later authors denied a conspecifity, and raised doubts about the interpretation of the Waagen type as *Haploceras* or *Glochiceras* given the absence of the peristome (e.g., Ziegler 1958). Waagen (1875) mentioned that the umbilical edge is not distinct. In contrast to his description which includes arched lateral surfaces and a steep slope of the umbilical wall. In the present specimens, the umbilical shoulder is moderately distinct, like in the specimens from Madagascar.

Furthermore, Collignon (1960: pl. 142, figs 540–542) assigned *H. deplanatum* to *Glochiceras*, because of their small size, but in the specimens figured by Collignon, there is no indication of a lateral groove and opening of the shell, which should have been visible at that diameter. In fact, his specimens are incomplete. Secondly, *Glochiceras* s. str. ranges from the Oxfordian to Kimmeridgian (Arkell et al. 1957: L274), but a single specimen was reported from the Lower Tithonian in Neuburg (Barthel 1962), and the records of *Glochiceras* reported by Collignon (1960) from the assumed Early Tithonian *Hildoglochiceras* kobelli Zone of Madagascar need confirmation.

Biostratigraphy. Haploceras staszycii (Zeuschner) is a long-ranging species from the Upper Kimmeridgian to Tithonian and Lower Berriasian horizons elsewhere. The available data across the northern and eastern margins of the Trans-Erythraean Trough, indicate that Haploceras s.str. is a rare genus from the Spiti Shales. Spath (1933) assumed that Uhlig (1903) reported only a single example of Haploceras s. str., which is correct in the case of Haploceras indicum Uhlig, 1903 (coll. Diener, middle division of the Spiti Shales in Chojan), a form morphologically close to the Tithonian type of Haploceras staszycii (Zeuschner), or a local variant of this taxon. Yin and Énay (2004) reported and illustrated Haploceras sp. from a Lower Tithonian Uhligites-Aulacosphinctoides Assemblage in the Tibetan Himalayas, and envisaged that it resembles H. caractheis Zeuschner, the nominal species of reference for Énay and Cecca (1986). However, this cannot be evaluated from the illustration provided by Yin and Énay, while the occurrence of Haploceras from the Tibetan Himalayas was not confirmed by Énay (2009).

In southern Pakistan, Fatmi and Zeiss (1994) reported (without illustration) *Haploceras* cf. *elimatum* (Oppel) and *Haploceras* sp. from Upper Tithonian strata from the Chakkary/Draber and Phai sections, together with himalayitins or even above, in their "third fossil horizon" that may include some reworked ammonites. From Jaisalmer, Pandey and Krishna (2002) reported upper Lower Tithonian *Haploceras* together with *Hildoglochiceras* from their Communis Zone, and Krishna (2017) used records of the long-ranging genus *Haploceras* from Jaisalmer and Pakistan to interpret a mid-Early Tithonian age for the Natricoides Zone.

Waagen (1875) reported some species of *Haploceras* from Kachchh, but used this genus in a broader sense than it is used today, and applying it to forms from horizons most probably older than those typical for this ge-

nus. His Haploceras deplanatum does not belong to this genus, and his Haploceras propinguum collected from the lowest beds of the Katrol Group (= Jhuran Formation) "immediately above the oolite with Asp. perarmatum", on the south side of Keera Hill near Charee, could refer to his Middle Kimmeridgian (i.e. to the Eudoxus-Steraspis stratigraphic interval according to Spath 1933) hence pointing to an extended lower range for Haploceras into the Kimmeridgian or, alternatively, to a large local stratigraphic gap if the taxonomic reinterpretation made by Spath (1933) applies. However, this latter interpretation at the genus level, recently assumed by Enay (2009), raises the need for a revision of the morphologic features typical of Haploceras. Spath (1924) recognized one example of Haploceras (= Glochiceras?) in the Blake collection, but no examples of Haploceras deplanatum Lemoine (non Waagen ?) sp. (= Glochiceras cf. Spath, 1928), which were commonly reported from Madagascar. Further Spath (1927: 6) identified abundant specimens of Haploceras elimatum (Oppel) included in an assemblage with belemnitids in the Andranosamonta Marls. He explained the scarcity of Haploceras in Kachchh due to the commonly occurring discontinuous sedimentary succession (Spath 1924, 1927). Nevertheless, there is a record of a Haploceras and Virgatosphinctes association within the Umia Group (= Jhuran Formation) (compare Spath 1927: 14). Spath (1928) reinterpreted the species Haploceras deplanatum Waagen with a lateral groove of variable depth as Glochiceras from the Middle Kimmeridgian (Beckeri Zone), and some of Waagen's (1875) species of Haploceras (H. deplanatum and H. propinguum) as forms transient from Middle Kimmeridgian Glochiceras of the G. fialar group to the genus Hildoglochiceras, respectively. Spath (1928) described a single Haploceras sp. close to a juvenile H. elimatum (Oppel) from the Upper Tithonian (Transitorius Zone?) of the Umia Group (= Jhuran Formation). He envisaged recurrent homeomorphism in long-ranging haploceratins, which he interpreted as inhabitants of warm waters, and highlighted that the smooth inner whorls of the common Taramelliceras of the T. kachense group from the Middle Kimmeridgian (Eudoxus and Beckeri? zones) with ventral reliefs resemble Haploceras charactheis Zeuschner. Spath (1931) mentioned earlier revisions of the single specimen of Haploceras propinquum Waagen, regarded it as a form probably transient to Hildoglochiceras (Spath, 1928), and later reinterpreted it as Hildoglochiceras (Spath, 1933). Spath (1933) reinterpreted Haploceras propinguum Waagen and Haploceras dieneri Waagen as Hildoglochiceras, and Haploceras cf. tomephorum Zittel to be a juvenile aspidoceratin. This author identified the Haploceras beds of Gudjinsir as the base of his Portlandian, with several species assigned to Hildoglochiceras, recognized Haploceras elimatum (Oppel) as the most common component in the Gudjinsir fauna of Kachchh, and among Kachchh species of Alpine-Mediterranean affinity, and described Haploceras sp. ind. juv. from his Tithonian Umia beds. Pandey et al. (2016) cited Haploceras cf. tomephorum Zittel among Upper Tithonian ammonites reported from the Kachchh Basin by earlier workers. Krishna (2017) reported Haploceras cf. *elimatum* (Oppel) from his Natricoides Zone–Communis Zone, Communis Subzone, which he interpreted as corresponding to a 3<sup>rd</sup>-order sequence with MFS in the Krafti Subzone, and correlated the Natricoides Zone with the Semiforme/Verruciferum Zone in Europe. Krishna identified the same stratigraphic interval and 3<sup>rd</sup>-order sequence in Jaisalmer.

In Madagascar, Lemoine (1910) refused to use the taxon-name Haploceras and reported abundant specimens of Lissoceras deplanatum (Waagen), which he clearly distinguished from elimatum (Oppel) and staszycii (Zeuschner) and interpreted to be younger (Tithonian). This author did not illustrate his Madagascan deplanatum, thus the equivalence with the type of Waagen cannot be evaluated. Spath (1925a) reinterpreted Lissoceras deplanatum (Lemoine non Waagen s.) as Haploceras elimatum (Oppel), illustrated from his Kimmeridgian horizons of Antsalova, which according to Lemoine shows some affinity with Haploceras indicum Uhlig (1903: 21, pl. 3, fig. 2a, b), a form that could be better interpreted as closer to Haploceras staszycii (Zeuschner). Spath (1925b) interpreted Haploceras elimatum (Oppel) as the most abundant ammonite in the undescribed collection from Madagascar, but had reservations concerning the high degree of similarity envisaged between ammonite faunas of Madagascar and Kachchh. Spath (1928) reconsidered the suture of his Haploceras elimatum (Oppel) from Madagascar (Spath 1925a) as being closer to that shown by Sicilian specimens of Haploceras staszycii Zeuschner. Spath (1933) mentioned Haploceras elimatum (Oppel) from the Besaire Collection, and recognized its low value for precise age-interpretations given its long stratigraphic range, as well as its common occurrence with Hildoglochiceras kobelli and latistrigatum at Antsalova. He also mentioned Haploceras staszycii (Zeuschner) from the same collection, recorded west of Mampikony, and highlighted the similarity among Madagascan ammonite assemblages and those known from Tendaguru (Tanzania), Kachchh, and Spiti. Collignon (1960) stressed the affinity of Tithonian faunas from Madagascar with those from Kachchh, Spiti, Kurdistan, SW Europe, and NW Africa, and described and illustrated diverse haploceratins from Lower Tithonian Kobelli Zone (Madagascar), including Haploceras gr. elimatum (Oppel) - subelimatum Fontannes, and Haploceras staszycii (Zeuschner). This author also reported Glochiceras deplanatum Waagen, which he interpreted as inconclusively known and comparable to smooth inner whorls of the more evolute Hildoglochiceras, and difficult to distinguish from inner whorls of Haploceras elimatum, except for the suture line.

Southwards along the western margin of the Trans-Erythraean Trough, Howarth and Morris (1998) reported *Haploceras stascyzii* (Zeuschner) from a 5 m interval with Upper Kimmeridgian perisphinctins and taramelliceratins at Wadi Arus, southern Yemen, and interpreted their Kilya Member to represent the Upper Kimmeridgian Beckeri Zone to Lower Tithonian Hybonotum Zone, while their new species *Haploceras umbilicatum* was recorded together with probable uppermost Tithonian to Lower Berriasian ammonites. No *Haploceras* were reported by Zeiss (1971, 1984) from Ethiopia, and no reports are available from Somalia. In Kenya, *Haploceras* seems to be absent (Beyrich 1877), or it was rare, because *Haploceras elimatum* (Oppel) early on recorded further south from the *Trigonia smeei* Beds at Tendaguru, Tanzania (Zwierczyki 1914), was interpreted as *Lissoceras* (Dietrich 1925, 1933; Spath 1925a, 1933; Bussert et al. 2009). Kapilima (2003) too did not report *Haploceras* from Tanzania.

Based on the preceding revision, the record of *Haploceras staszycii* (Zeuschner) – *elimatum* (Oppel) from the *Hildoglochiceras kobelli* Zone of Madagascar (Early Tithonian of Collignon 1960) cannot be used for a conclusive, regional age-interpretation in the Trans-Erythraean Trough, where its precise stratigraphy is unknown. However, the described specimens are interpreted to represent Lower Tithonian (three-fold division) horizons in accordance with the biostratigraphic interpretation of the here described *Hildoglochiceras*, a single specimen of *Aulacosphinctoides* and an incomplete virgatosphinctin.

#### Haploceras sp.

Fig. 6H-K, O

**Material.** Two specimens, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/65, 67 (both figured).

Table 2. Dimensions of Haploceras sp. (in mm).

Specimen no.	D	Н	H/D	Т	T/D	U	U/D	H/T
KSKV2019Jara/65	20.3	8.95	44.0	7.17	35.3	6.85	33.7	1.24
KSKV2019Jara/67	-	12.22	-	9.84	-	-	-	1.24

**Description.** Shell small, incomplete, compressed, involute subquadrangular whorl section with almost flat to slightly arched lateral surface, slightly arched ventral region, indistinct umbilical shoulder and short, steeply sloping umbilical wall.

**Remarks.** These are moderately preserved, small specimens that show abraded external surfaces. Specimen no. KSKV2019Jara/65 consists of the phragmocone and body chamber, whereas specimen no. KSKV2019Jara/67 is only a part of the body chamber. Except for the umbilical diameter, which is larger in the present specimen, other dimensional proportions are within the range of variation in *Haploceras staszycii* (Zeuschner) (Fig. 7), however, the subquadrangular whorl section and the umbilical diameter do not match any of the specimens of the present collection nor the species of *Haploceras* described by Waagen and Collignon, most probably due to their small size.

**Biostratigraphy.** The genus *Haploceras* shows a long biostratigraphic range from the latest Kimmeridgian to Early Berriasian. The interpreted age of the described specimen is Early Tithonian (three-fold division), in accordance with the biostratigraphic interpretation of described *Hildoglochiceras*, *Aulacosphinctoides* and an incomplete virgatosphinctin.



Figure 7. Scatter plot showing D:H/T ratios of some related species of Haploceras.

#### Genus Hildoglochiceras Spath, 1924

**Type species.** *Hecticoceras latistrigatum* Uhlig, 1903.

#### Hildoglochiceras kobelli (Oppel, 1863b) morphotype kobelliforme (Bonarelli, 1894) (m) Figs 6P-T, 8F, G, 9A-C, G, H

Harpoceras kobelli Oppel, 1875 – Waagen: 72, pl. 13, fig. 12a, b (non figs 11, 13 by Bonarelli 1894).

- Hecticoceras (Lunuloceras) kobelliforme sp. nov., 1894 Bonarelli: 95, 96.
- Hildoglochiceras kobelliforme (Bonarelli), 1928 Spath: 159, pl. 13, fig. 17.
- Hildoglochiceras kobelli Oppel, 1960 Collignon: pl. 143, figs 547–550.
- Hildoglochiceras sp. aff. kobelliforme (Bonarelli), 2009 Enay: 84, pl. 1, fig. 6a, b.

**Material.** 23 specimens, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/1–9, 21, 26, 32, 41, 45, 46, 48–51, 54, 55, 74, 75, KSKV2020Jara/15.

**Description.** Shell small consting of both phragmocone and body chamber with maximum shell diameter of ca. 50 mm (KSKV2020Jara/15), nearly complete, discoidal, compressed and evolute. Whorl section narrow subtrigonal to oval with narrow venter. Lateral sulcus at lower one-third of lateral height to mid-lateral height, wide, and terminates just above the base of the ventral branch of the peristome. Lateral surface flat, ornamented with faint sickle-shaped (falciform) ribs on the body chamber (e.g., KSKV2019Jara/1). A shallow spiral groove situated at one-third to one-half of the flank height of both phragmocone and body chamber. Spiral groove gradually changing in width with growth. Lower boundary of spiral groove higher than upper boundary (Fig. 6R, S), coinciding with maximum shell thickness. Inner, dorsal one-third of body chamber, i.e. area below the spiral groove, sloping towards umbilical seam with broadly arched umbilical shoulder region and steep umbilical wall. Peristome with lappets preserved. Suture lines well preserved, with denticulated lobes and saddles. Lobes slightly narrower than saddles (Fig. 6Q). First lateral lobe deep, moderately broad, with three short branches at the end. Second lateral lobe much shorter. At least two auxiliary lobes above the umbilical suture. First (external) saddle broad and short, with small secondary lobes. The last two suture lines are very close, almost touching.

#### Hildoglochiceras kobelli (Oppel, 1863b) morphotype kobelli Oppel (M)

Figs 8A-E, H-L, 9D-F, I

- Ammonites kobelli sp. nov., 1863b Oppel: 273, pl. 76, figs 1a–c, 2a, b.
- Hecticoceras (Lunuloceras) bonarelli sp. nov., 1894 Bonarelli: 95. Glochiceras deplanatum (Waagen), 1928 – Spath: 155, pl. 16, fig. 3, pl. 17, figs 9a, b.
- Hildoglochiceras kobelli Oppel, 1960 Collignon: pl. 143, figs 547–550.
- Hildoglochiceras nudum sp. nov., 1960 Collignon: pl. 145, fig. 567.

Material. 48 specimens, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/10-16, 19, 20,

G



**Figure 8.** A–E, H–L. *Hildoglochiceras kobelli* (Oppel, 1863b) (M); A, B. KSKV2019Jara/42. A. Left side view showing phragmocone and part of body chamber, note on both sides spiral grooves are developed even at a diameter less than 10 mm; C, D. KSKV2019Jara/39; C. Left side view; D. Right side view, bothshowing phragmocone and beginning of body chamber, presence of spiral groove even at diameter less than 10 mm and closely spaced crescentic ribs along the periphery towards the end of phragmocone, note beginning of crescentic ribs shown by triangles; E. KSKV2019Jara/40, right side view of a tiny (diameter ca 4 mm) specimen showing phragmocone and a part of body chamber. Note absence of spiral groove but presence of crescentic rib at dimeter less than 4 mm; H, I. KSKV2020Jara/12. H. Left side view; I. Right side view, showing a large part of body chamber perhaps up to peristome. Note on both sides spiral groove. This suggests present-day erosion. J–L. KSKV2020Jara/11; J. Apertural view; K. Ventral view; L. Right side view showing end of phragmocone and body chamber. Note on spiral groove on the body chamber and closely spaced crescentic ribs. F, G. *Hildoglochiceras kobelliforme* (Bonarelli, 1894) (m) KSKV2019Jara/32; F. Left side view; G. Right side vi

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M

22-25, 27-31, 33-40, 42-44, 47, 52, 53, 56-60, 70-73, 76-78, 81, KSKV2020Jara/11, 12, 14.

Description. Shell moderately large, consting of both phragmocone and body chamber with maximum shell diameter of ca. 95 mm (KSKV2020Jara/14), discoidal, compressed and evolute. Whorl section narrow subtrigonal to oval with narrow venter. Lateral sulcus at lower one-third of lateral height to mid-lateral height. Lateral surface flat, ornamented with sickle-shaped (falciform) or crescentic ribs, also seen on the juvenile specimens (Fig. 8A-E, H-L). The beginning of ribs variable, may start at a diameter less than 10 mm or even at diameter less than 4 mm. A shallow spiral groove situated at one-third to one-half of the flank height of both phragmocone and body chamber. Spiral groove gradually changing in width with growth. Spiral groove begins at a diameter less than 10 mm. Lower boundary of spiral groove higher than upper boundary, coinciding with maximum shell thickness. Inner, dorsal onethird of body chamber i.e., area below the spiral groove, flattened with obtusely rounded umbilical shoulder and steep to almost vertical umbilical wall (Fig. 10I). Suture lines moderately well preserved.

**Remarks.** The specimens are moderately preserved and abraded. In some cases, they consist of phragmocone and almost a complete or a part of body chamber, in few cases (e.g., KSKV2019Jara/1, 5) half a whorl of body chamber (180°) with preserved aperture . Several specimens are very small with their body chambers preserved. They are juveniles (e.g., KSKV2019Jara/39–44). The specimens represent internal moulds, i.e., without shell material and ventral keel, even in the smaller specimens. The ornamentation is mostly no longer preserved, similarly, the wide and moderately deep lateral groove in some cases is partially preserved on the body chamber, but unidentifiable in the phragmocone.

The morphological features described above match *Hildoglochiceras* Spath, 1924. The general absence of population size analyses of species described in the literature impedes their precise interpretation in terms of intra-species variability. Hence, the maintenance of species names is obligatory in the present analysis.

The dimensional proportions of different species of Hildoglochiceras Spath, 1924 described from the Indo-Malagasy faunal province by the earlier workers suggest comparable H/D, T/D and H/T ratios (H/D: 33-45%; T/D: 21-28%; H/T: 1.32 to 1.8). However, U/D ratio is increasing from 29 to 42% (Table 3), except for few specimens that should be rechecked for their measurements and/or identification. Interestingly, in the present collection, shell diameter and the diameter of the umbilicus distinctly show two groups; type 1: small shell diameter with large umbilicus (U/D: 40 to 25%) and type 2: large shell diameter with small umbilicus (U/D: 26 to 18%). H/T is smaller (1.3-1.8) in type 1, whereas it is greater (1.35-2.0) in type 2 (Table 4). In general, WSG and HSG show a trend of values increasing with shell size. Based on similarity in morphological features type 1 is considered here as microconch (small shell diameter and larger umbilical diameter) with lappets (only their bases are preserved just below the adapertural end of the lateral groove (Figs 6P, 8F), and type 2 as macroconch (large shell diameter and smaller umbilical diameter) without preserved peristome. However, both types are also represented by juvenile specimens (e.g., KSKV2019Jara/39-44).

Hildoglochiceras latistrigatum (Uhlig, 1903) matches present specimens in having a similar shape including whorl section and a maximum width along the lower lip of the lateral groove, but has a wider umbilical diameter (Uhlig 1903: 27, pl. 2, fig. 4; pl. 3, fig. 5; Pandey et al. 2016: 146, pl. 1, fig. 2a, b). Lacking data at the population level, no conclusion about the meaning of this difference can be drawn. The species has been reported ornamented with distant sickle-shaped ribs and growth striations, however, the ornamentation is variable and inner whorls are smooth.

Uhlig (1903: 28), while describing his new species *Hil-doglochiceras latistrigatum*, mentioned that the growth striations follow a similar pattern as in *H. kobelli*. Further he mentioned *H. latistrigatum* "approximates very closely to *H. kobelli*" Oppel but the differences between the two species make it impossible to merge them (Table 5). In fact, most of the characters mentioned are relative and thus are not tenable when several specimens are com-

Table 3. Dimensions of	different species of Hilde	oglochiceras Spath	from Indo-Malagasy f	aunal province (	in mm)
		•			

species	notation	D	н	H/D	Т	T/D	U	U/D	H/T
Hildoglochiceras latistrigatum (Uhlig) (1903: 27, pl. 2, fig. 4a-c)	A	64	20.8	33	13.2	21	27	42	1.58
Hildoglochiceras kobelliforme (Bonarelli) (Spath 1928: 159, pl. 13, fig. 17 suture line).	В	35	13	37	8.7	25	11.9	34	1.5
Hildoglochiceras sp. aff. kobelliforme (Bonarelli) (Enay 2009: 84, pl. 1, fig. 6a, b).	С	48	17	37	12	25	16	33	1.4
	D	34	13	38	9.3	27	11.4	33	1.4
	E	32.8	12	36	-		11	33	
	F	34	13	36	9.8	28	11.6	34	1.32
Ammonites kobelli Oppel (1863b: 273, pl.76, figs 1a-c, 2a, b)	G	65	24	36.9	15	23	25	38	1.6
Harpoceras kobelli Oppel (Waagen 1875: 72, pl. 13, figs 11)	Н	42	16	38	10	23.8	15	35.7	1.6
Harpoceras kobelli Oppel (Waagen 1875: 72, pl. 13, figs 13)	I	41	17	41.4	9.5	23.1	12	29.2	1.78
Harpoceras kobelli Oppel (=kobelliforme) (Waagen 1875: 72, pl. 13, figs 12)	J	36	13	36.1	8	22.2	12	33.3	1.62
Hildoglochiceras kobelli Oppel (Collignon 1960: pl. 143, fig. 547)	K	56	24	43	15	27	16	29	1.6
Hildoglochiceras kobelli Oppel (Collignon 1960: pl. 143, fig. 550)	L	56	22	39	14	25	18	32	1.57
Hildoglochiceras kobelli Oppel (Collignon 1960: pl. 143, fig. 548)	М	55	22	40	14	25	19	35	1.57
Hildoglochiceras kobelli Oppel (Collignon 1960: pl. 143, fig. 549)	Ν	42	17	40	11	26	12	29	1.54
Haploceras (Hecticoceras) spira Zwierzycki (1914: 49, pl. 5, figs I1-13; Spath 1928: 160).	0	33	13.2	40	8.91	27	10.56	32	1.48
<i>Oppelia plana</i> Waagen (1875: 56, pl. 11, fig. 3)	Р	26	10	38.4	6	23	8	30	1.6
Glochiceras deplanatum (Waagen) (Spath 1928: 155, pl. 16, fig. 3)	Q	67	29.5	44	16.7	25	16.1	24	1.7
Glochiceras deplanatum (Waagen) (Spath 1928: 155, pl. 17 figs 9a, b)	R	70	31.5	45	16.8	24	16.8	24	1.8
Hildoglochiceras nudum (Collignon) (1960: pl. 145, fig. 567)	S	43	19	44	12	28	10	23	1.58



Figure 9. A-C, G, H. Hildoglochiceras kobelliforme (Bonarelli, 1894) (m); A. KSKV2019Jara/3, inner cast, right side view of abraded, moderately evolute (U ≈ H) adult specimen with clear final uncoiling. Specimen without remains of epigenized shell and showing recrystallized phragmocone with last two suture lines slightly approached. Body-chamber 180° with sandy infilling including coarse to very coarse grains. Fading of lateral groove due to abrasion. B, C. KSKV2019Jara/8; B. Inner cast, left-side view of a part of body chamber showing moderately deep lateral groove; C. Oval whorl section with narrow venter and a wide, moderately deep lateral groove; G. KSKV2019Jara/9, internal cast with remains of epigenized shell, right-side view of comparatively evolute (U ≈ H), small specimen showing comparatively long body-chamber (>180°) with wide, moderately deep lateral groove unidentifiable on the phragmocone. Note remains of epigenized shell in the anterior body chamber, probable partial preservation of peristome with basal part of broken lappet, and sandy infilling. right side view; H. KSKV-2019Jara/4, internal cast, right side view of a part of body chamber (U ≈ H) showing shallow to moderately deep wide lateral groove; D-F, I. Hildoglochiceras kobelli (Oppel, 1863b) (M); D-E. KSKV2019Jara/11, internal cast; D. Apertural view; E. Anterior and left-side views of fragmented, comparatively involute specimen (U<<H) with high-oval outer whorl, showing abraded right-side with wide, shallow spiral groove on the preserved last septum of phragmocone and body chamber, better developed on the latter. Internal cast of outer whorls filled with calcareous fine-grained sandstone, inner whorls recrystallized. Note shell is completely eroded. F. KSKV2019Jara/10, internal cast with remains of epigenized shell, right-side view of comparatively involute specimen (U<<H) showing ca. one-third of body chamber with wide, shallow lateral groove that is imperceptible on the phragmocone of the outer whorl. Coarser, sandy infilling occupying the body chamber; I. KSKV2019Jara/81, whorl section of involute specimen of a large size with high-oval to acute outer whorl and extremely narrow venter.

**Table 4.** Dimensions of the specimens of the present collection assigned to *Hildoglochiceras kobelliforme* (Bonarelli) (m) and *kobelli* (Oppel) (M) (in mm). The specimens at the author's disposal were manually grouped into four types (Type 1 to Type 4). Type 1 – with large umbilicus (U/D: 40 to 25%), compressed whorl section (H/T: 1.3-1.8) and acute venter. They are microconch (m). Type 2 – with small umbilicus and (U/D: 26 to 18%), compressed whorl-section (H/T: 1.3-2.0) with acute venter. They are macroconch (M). Type 3 – small-sized specimens, juvenile of Type 1 & 2 (Fig. 10). The overlap of types 3 and 1 & 2 in the plot suggests that they belong to the same taxonomic group (see Fig. 14 below). Type 4 – are same as Type 2 but with preserved crescentic ribs on flanks (Fig. 10).

Specimen no.	D	н	H/D	т	T/D	U	U/D	H/T	WSG	HSG	#	Туре
KSK\/2019 Jara/1	45.6	16.2	35.5	10.3	22.5	157	34.5	1 57	2 30	6.24	0	1(m)
K3Kv20195818/1	45.0	10.2	33.5	10.5	22.5	13.7	54.5	1.57	2.39	0.24	0	i (iii)
KSKV2019Jara/1A	38.7	14.4	37.2	8.35	21.5	11.04	28.5	1.72	2.07	5.02	0	1(m)
KSK\/2010 Jara/2	31.6	12	37.0	7.8	25.3	10.6	33 5	15	1 0 2	117	Ο	1(m)
K3Kv20195818/2	51.0	12	57.9	7.0	20.0	10.0	55.5	1.5	1.95	4.17	0	I (III)
KSKV2019Jara/2A	-	9.2	-	5.6	-	-	-	1.64	0.6	3.6	0	1(m)
KSKV2019 Jara/3	37 7	147	38.9	81	21.4	11.8	31.2	18	5.60	2.62	0	1(m)
	07.7	14.7	00.5	6.14	21.4	11.0	01.2	1.0	0.00	2.02	0	1(11)
KSKV2019Jara/4	-	11.49	-	6.44	-	-	-	1.78	1.46	4.48	0	I (m)
KSKV2019.Jara/4A	-	12 22	-	6.8	-	-	-	1 79	1 99	4 77	0	1(m)
	~~~~	10	40.0	0.0		10.0	01.0		1.00	1.01	0	
KSKV2019Jara/5	32.2	13	40.3	8.9	26.6	10.0	31.0	1.46	1.92	4.91	-	1(m)
KSKV2019Jara/5A	27.7	12.3	44.4	7.1	25.6	8.3	29.9	1.73	1.9	4.64	0	1(m)
1(0)()(0010 )		10.1		0.00				1.61	0.01	5.04	-	1()
KSKV2019Jara/6	-	13.1	-	8.09	-	-	-	1.61	2.21	5.24	0	I (m)
KSKV2019Jara/6A	-	11.8	-	6.8	-	-	-	1.74	1.93	4.64	0	1(m)
KOK/(2010 Java /7		10.0		0.1				1 (7	1.05	4.0	0	1(
KSKV2019Jara//	-	13.0	-	8.1	-	-	-	1.07	1.35	4.8	U	I (m)
KSKV2019Jara/8	-	7.04	-	4.65	-	-	-	1.51	0.69	2.90	0	1(m)
KCK1/2010 Jara /84	20 F	07	10.4	E 0.2	04 E	E 0.2	20.4	1 70	0.60	2.05	0	1(m)
KSKVZU19Jala/oA	20.5	0.7	42.4	5.03	24.5	5.65	20.4	1.72	0.09	3.95	0	1(11)
KSKV2019Jara/9	41.8	16.1	38.5	10.0	23.9	13.7	32.7	1.6	2.39	5.0	0	1(m)
KCK1/2010 Jara /04	22.0	10 E	41 1	7 20	20 E	0.2	25.2	1 0 0	17	E 7E	0	1(m)
KSKVZUT9Jala/9A	32.0	13.5	41.1	7.30	22.5	0.3	25.5	1.02	1.7	5.75	0	1(11)
KSKV2019Jara/10	66.43	30.3	45.6	15.5	23.3	15.6	23.4	1.9	3.34	12.44	0	2(M)
KCK1/2010 Jara /104	E1 /1	25.2	40.0	10 70	247	10 12	107	1 00	2.6	10.2	0	2(14)
KSKVZU19Jala/10A	51.41	Z3.Z	49.0	12.72	24.7	10.15	19.7	1.90	2.0	10.5	0	Z(IVI)
KSKV2019Jara/11	83.0	38.6	46.1	18.7	22.5	21	25.3	1.8	4.02	17.59	0	2(M)
KSK1/2010 Jara/114		24.2		16.0				2.0	2 75	15 /	0	2(14)
KSKV2019Jala/11A	-	54.5	-	10.0	-	-	-	2.0	3.75	13.4	0	2(11)
KSKV2019Jara/12	-	29.5	-	15.04	-	-	-	1.96	3.1	12.09	0	2(M)
KSK1/2010 Jara/12	12.6	21	10.2	10 5	24.6	0.7	22.7	2	1 77	0 0	0	2(14)
KSKV2019Jala/13	42.0	21	49.Z	10.5	24.0	9.7	ZZ.1	Z	1.77	0.0	0	Z(IVI)
KSKV2019Jara/14	-	16	-	8.4	-	-	-	1.9	1.86	7.5	0	2(M)
KSK1/2010 Jora/144		112		7 2				1.05	15	6.0	0	2(M)
KSKVZU19Jala/14A	-	14.5	-	7.5	-	-	-	1.95	1.5	0.0	0	Z(IVI)
KSKV2019Jara/15	12.4	5.4	43.5	4	32.2	3	24.1	1.35	0.31	2.34	0	3(M)
KCK1/2010 Jara /16	15	6.0	41	4.1	07.0	2 5	22	1 5	0.41	2.46	0	2(14)
KSKVZU19Jara/16	15	0.2	41	4.1	27.3	3.5	23	1.5	0.41	2.40	U	3(IVI)
KSKV2019Jara/19	32.1	14.5	45	9.2	28.6	8.5	26.4	1.57	1.53	6.25	0	4(M)
KCK1/2010 Jara /10 A		17.0		10.1				1 71	1 50	7 40	0	4(1)
KSKVZUT9Jara/T9A	-	17.3	-	10.1	-	-	-	1./1	1.53	7.48	U	4(IVI)
KSKV2019Jara/20	-	20.2	-	12.37	-	-	-	1.63	3.34	7.22	0	4(M)
KCK1/2010 Jara /201		22.7		12.0				1 70	E EO	0 5 4	0	4(NA)
KSKVZU19Jala/ZUA	-	23.7	-	13.9	-	-	-	1.70	5.56	0.54	0	4(11)
KSKV2019Jara/21	18.4	8	43	5.4	29.3	5.5	29.8	1.4	0.6	2.64	0	1(m)
KSK1/2010 Jara /22	25.2	11 5	45.4	6.6	26	16	10	1 74	0.4	5.2	0	2(M)
KSKVZU19Jdid/ZZ	23.3	11.5	45.4	0.0	20	4.0	10	1.74	0.4	5.5	0	2(11)
KSKV2019Jara/22A	21.8	9.7	44.4	5.9	27.0	4.16	19.0	1.64	0.4	4.52	0	2(M)
KSK\/2010 Jara/23		1/1	_	73	-	_	_	1 0 2	1 / 8	10	Ο	2(M)
K3KV20195818/25		14.1	-	7.5	_	-	-	1.95	1.40	4.9	0	2(101)
KSKV2019Jara/24	-	10.5	-	5.53	-	-	-	1.89	0.75	4.06	0	2(M)
KSK\/2010 Jara/25	18.3	87	17 5	15	24.5	11	24	10	0.61	3.0	Ο	2(M)
K3KV20195818/25	10.5	0.7	47.5	4.5	24.5	4.4	24	1.9	0.01	5.0	0	2(101)
KSKV2019Jara/25A	-	6.3	-	3.4	-	-	-	1.8	0.34	2.53	0	2(M)
KSK\/2010 Jara/26	33.6	11.9	35.1	8.6	25.5	13 5	40	1 37	1 71	1 73	Ο	1(m)
K3KV20195818/20	55.0	11.0	55.1	0.0	20.0	13.5	40	1.57	1.71	4.75	0	1(11)
KSKV2019Jara/26A	24.02	10.18	42.3	7.0	29.1	7.76	32	1.4	1.16	4.67	0	1(m)
KSK1/2010 Jara/26P	174	7 2	41.0	<b>F</b> 4	21.0	51	20.2	1 0	0.5	2.0	2	1(m)
K3KV20195ala/20D	17.4	7.5	41.9	J.4	51.0	5.1	29.5	1.5	0.5	5.0	2	i (i ii)
KSKV2019Jara/27	-	13.55	-	7.29	-	-	-	1.85	0.96	5.65	0	2(M)
KSK\/2019 Jara/28	24 52	11 /0	46.4	6 56	26.7	6.01	24.5	1 73	0.96	41	Ο	2(M)
K3Kv20195818/20	24.52	11.40	40.4	0.50	20.7	0.01	24.5	1.75	0.90	4.1	0	2(101)
KSKV2019Jara/29	-	15	-	8.4	-	-	-	1.78	1.31	6.42	0	2(M)
KSK\/2019 Jara/30	-	14 57	-	8 51	-	-	-	1 71	2 18	5/19	Ο	2(M)
1010/20195010/50		14.57		0.51				1.71	2.10	0.40	0	2(101)
KSKV2019Jara/31	16.6	8.3	50.9	4.5	27.1	3.1	18.6	1.84	0.73	3.25	0	2(M)
KSKV2019 Jara/32	34.3	13.3	387	8 78	25.5	10 94	31.8	1 51	2 92	5 20	0	1(m)
	04.0	10.0	00.7	0.70	20.0	10.54	01.0	1.01	2.52	0.20	0	1(11)
KSKV2019Jara/32A	26.24	11.43	43.5	6.8	25.9	8.0	30.4	1.68	1.66	3.84	0	1(m)
KSKV2019Jara/33	19.27	8.3	43.0	4.4	22.8	4.19	21.7	1.8	0.45	2.9	0	2(M)
	12.27	0.0	1010		22.0		2,	1.07		10.6	0	2(11)
KSKV2019Jara/34	-	32.8	-	16.6	-	-	-	1.97	4.1	13.6	0	2(M)
KSKV2019.Jara/35	-	26.9	-	14 1	-	-	-	1 89	2 95	86	0	2(M)
KOK/(2010 Jana /26		07.0		10.0				0.0	0.0	11.0	0	0(14)
KSKV2019Jara/36	-	27.8	-	13.9	-	-	-	2.0	2.0	11.9	U	Z(IVI)
KSKV2019Jara/37	50.6	24.3	48.0	13.2	26.0	9.1	17.9	1.85	2.12	9.78	0	2(M)
KSK1/2010 Jara /274		15.0		77				1.00	17	6.00	0	2(14)
KSKVZU19Jala/3/A	-	15.5	-	1.1	-	-	-	1.90	1.7	0.22	0	Z(IVI)
KSKV2019Jara/38	21.7	9.7	44.7	5.24	24.1	5.23	24.1	1.85	1.18	3.6	0	2(M)
KSK1/2010 Jara/20	11 20	5 70	50.7	2 12	20	2 7 2	22.0	1 60	0.24	2.07	2	2(11)
K3KV2019Jala/39	11.30	J.70	50.7	3.42	30	2.75	23.9	1.09	0.54	2.97	2	3(11)
KSKV2019Jara/40	06.06	2.82	46.5	2.22	36.6	1.35	22.2	1.27	-	-	-	3(M)
KSK1/2010 Jara//0/	04.6	2.2	17.8	2.06	13.0	_	_	1 08	_	_	_	3(M)
K3KV2019Jala/40A	04.0	2.2	47.0	2.00	43.9			1.00				3(11)
KSKV2019Jara/41	14.9	6.5	43.6	4.9	32.8	4.7	31.5	1.32	0.45	2.59	0	1(m)
KSKV/2019 Jara / //2	12 0	57	47 5	3.46	28.8	2.64	22	1.64	0 1 8	2.26	Ω	3(M)
	12.0	0.7		5.40	20.0	2.04	~~~	1.04	0.10	2.20	-	0(11)
KSKV2019Jara/43	09.36	4.29	45.8	2.9	30.9	2.20	23.5	1.47	0.50	1.51	1	3(M)
KSKV2019, Jara/44	11.6	5.6	48 27	3 1 9	27 5	22	18 9	175	0.3	09	Ω	3(M)
	11.0	0.0	-0.27	5.19	27.0	<u> </u>	10.5	1.75	0.5	0.2	-	3(191)
KSKV2019Jara/45	19.22	8.30	43.1	5.97	31.0	6.52	33.9	1.39	1.5	3.2	0	1(m)
KSKV2019 Jara /46	-	916	-	1 90	-	-	-	1.83	1 1 /	3.6	Ω	1(m)
		5.10						1.00	1.14	0.0	-	1(11)
KSKV2019Jara/47	-	30.2	-	16.8	-	-	-	1.79	3.0	13.4	0	4(M)
KSKV2019Jara/48	-	11.0	-	5,99	-	-	-	1.83	0.85	4,49	Ο	1(m)
KOK/ (0010 L		10.05		7.0				1 44	4 -	4 77	~	4 (
KSKV2U19Jara/49	-	10.35	-	7.3	-	-	-	1.41	1.7	4.//	U	1(m)
KSKV2019Jara/50	-	8.87	-	5.20	-	-	-	1.70	0.35	3.35	Ο	1(m)
KCK/2010 Lana (51		0.07		5.20 E 40				1 70	0.00	0.4	0	1()
V9KAT01A78[9]2[3]2	-	9.27	-	5.43	-	-	-	1.70	0.98	3.4	U	i (m)
KSKV2019Jara/52	-	9.45	-	5.21	-	-	-	1.81	0.6	3.65	0	2(M)
KCK//2010 Lana /52		10.00		4.00				2.00	0.67	4.10	~	2(14)
V2V1A197919/22	-	10.28	-	4.99	-	-	-	2.00	0.07	4.13	U	∠(IVI)
Specimen no.	D	н	H/D	т	T/D	U	U/D	H/T	WSG	HSG	#	Туре
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KSKV2019Jara/54	18.21	8.92	48.9	4.73	25.9	4.12	22.6	1.88	0.38	3.69	0	3(M)
KSKV2019Jara/55	-	21.31	-	14.4	-	-	-	1.47	2.66	9.7	0	4(M)
KSKV2019Jara/56	-	19.9	-	10.5	-	-	-	1.89	2.26	8.1	0	2(M)
KSKV2019Jara/57	-	22.60	-	12.0	-	-	-	1.88	1.51	8.88	0	2(M)
KSKV2019Jara/58	-	28	-	15.7	-	-	-	1.78	2.0	12.6	0	2(M)
KSKV2019Jara/59	-	17.38	-	10.6	-	-	-	1.63	0.61	7.77	0	2(M)
KSKV2019Jara/60	-	14.8	-	8.12	-	-	-	1.82	1.52	6.07	0	2(M)
KSKV2019Jara/70	69.2	30.0	43.3	16.2	23.4	14.7	21.1	1.8	3.0	14.56	0	2(M)
KSKV2019Jara/70A	-	29.2	-	15.6	-	-	-	1.8	2.87	12.5	0	2(M)
KSKV2019Jara/71	-	21.9	-	11.4	-	-	-	1.9	1.96	8.56	0	2(M)
KSKV2019Jara/72	-	28.1	-	15.5	-	-	-	1.8	3.2	11.6	0	2(M)
KSKV2019Jara/73	-	22.8	-	12.1	-	-	-	1.8	2.3	10.7	0	2(M)
KSKV2019Jara/74	16.7	7.5	45.1	4.4	26.3	5.32	31.8	1.7	0.7	2.88	0	1(m)
KSKV2019Jara/75	-	8.87	-	5.4	-	-	-	1.64	0.76	3.51	0	1(m)
KSKV2019Jara/76	20.7	9.9	47.8	5.33	25.7	4.8	23.1	1.85	0.3	3.48	0	2(M)
KSKV2019Jara/77	-	12.8	-	6.4	-	-	-	2	1.64	4.38	0	2(M)
KSKV2019Jara/78	-	24.4	-	13.1	-	-	-	1.86	2.64	9.74	0	2(M)



**Figure 10.** Sketch diagrams of four types (Type 1 to 4) of specimens assigned to *Hildoglochiceras kobelliforme* (Bonarelli) (m) and *kobelli* (Oppel) (M). Type 1 – with large umbilicus, compressed whorl section and acute venter (m). Type 2 – with small umbilicus and compressed whorl-section with acute venter (M). Type 3 – small-sized specimens, juvenile of types 1 & 2. Type 4 – are same as Type 2 but with preserved crescentic ribs on flanks.

 Table 5. Comparison of morphological characters of *H. kobelli* (Oppel) and *H. latistrigatum* Uhlig (partially mentioned in Uhlig 1903: 28).

H. kobelli	H. latistrigatum
shell stout	shell not as stout as kobelli
width of whorl above spiral groove diminishing slowly	thickness of whorl above spiral groove diminishing rapidly
spiral groove narrower on the inner whorls wider in the outer whorls	spiral groove wider
lower margin of spiral groove not sharp and less high	lower margin of spiral groove much sharper and high
costae begin earlier (Fig. 8A–E)	costae begin later
spiral furrow starts later	spiral furrow starts earlier
costae dense (Fig. 8C, D, H, I, K, L)	costae wide apart
Umbilicus small	Umbilicus large

pared. Nevertheless, of several differences mentioned by Uhlig, the present specimens are closer to *Hildoglochiceras latistrigatum* in ornamentation. Unfortunately, Uhlig did not mention a larger diameter of the umbilicus in *H. latistrigatum* in comparison to *H. kobelli*, which is one of the distinctive characters.

The line of maximum inflation either along the upper or lower margin of the spiral furrow cannot be a distinguishing feature between *H. kobelli* and *H. latistrigatum*, because in one of the figures of *H. kobelli* from Madagascar (Lemoine 1910: 146, pl. 4, figs 1–4, and apertural view figured at https://science.mnhn.fr/institution/mnhn/ collection/f/item/r02008) it is clearly along the lower margin of spiral furrow. In juvenile forms (KSKV2019Jara/30, 40, 42), the elevation of the lower boundary of the spiral groove, whether higher or lower than upper boundary, may not be ascertained.

The morphological characters in the present specimens match Harpoceras kobelli Oppel (Waagen 1875: 72, pl. 13, fig. 12, non figs 11, 13), from the "Upper Katrol Group", south-west of Nurrha, in having similar proportional dimensions, but differ in having the maximum thickness of the whorl along the upper boundary of spiral groove, instead of along its lower boundary. Spath (1928: 159, pl. 13, fig. 17) mentioned the observation of Waagen (1875: 73, pl. 13, figs 11-13) and Lemoine (1910: 10 pl. 4, fig. 1-4) that H. kobelli Oppel is a very variable species with respect to the start of crescentic ribs (at a diameter of 25 mm or 30 mm or even later), number and sharpness/ thickness of ribs and width of lateral groove, which gradually widens with growth. The present specimens match well with such observation (Fig. 8C-E, H, I, K, L). According to Lemoine (1910: 10), H. kobelliforme (Bonarelli) and H. latistrigatum (Uhlig, 1903) are mere varieties of the same species. In fact, Lemoine (1910) was pioneer in highlighting the identification of the great variability within Hildoglochiceras. According to Lemoine, H. kobelliforme has an "abrupt margin of the shell", perhaps he meant an abrupt umbilical edge, H. latistrigatum shows a very wide furrow and H. kobelli has a less abrupt edge of the shell and a narrower furrow.

According to Spath (1928), *H. kobelli* Oppel and *H. kobelliforme* (Bonarelli) are morphologically similar. Further, Spath synonymised one of the specimens of Waagen (year) assigned to *Harpoceras kobelli* Oppel (Waagen 1875: 72, pl. 13, fig. 12) with *Hildoglochiceras kobelliforme* 

(Bonarelli). The suture line of this specimen (Spath 1928: 159, pl. 13, fig. 17) matches the suture lines of the present specimens. The other two specimens figured by Waagen as *Harpoceras kobelli* (Oppel) (Waagen 1875: 72, pl. 13, figs 11, 13) show either a lateral groove closer to umblical shoulder or a more transversely ovate whorl section.

Oppelia plana Waagen (1875: 56, pl. 11, fig. 3) from the "Katrol Group" (Kimmeridgian), south-west of Nurrha, is another comparable species with respect to its discoidal shape, proportional dimensions including umbilical diameter, smooth flanks with wide lateral groove and suture lines [see Hildoglochiceras? planum (Waagen) (Spath 1928: 160-161, pl. 19, fig. 5) at a diameter of 20 mm of Waagen's holotype (1875: 56, pl. 11, fig. 3) to Hildoglochiceras kobelliforme (Bonarelli)], but it has an oval whorl section with a rounded ventral region. Moreover, the present specimens are sculptured. The possibility of obliteration of ribs of the body chamber prior to final burial or general due to poor preservation due to weathering cannot be ruled out, especially as the matrix is a calcareous coarse-grained sandstone. Moreover, some doubts arise about the type described by Waagen (1875) since this author indicated "specimen with body chamber" in his figure caption, while Spath (1928, p. 160) stated that the "...fragmentary example described by Waagen is entirely septate and represents the inner whorls of a larger form, probably of the kobelli group entirely septate there...". The Madagascan specimens assigned to Hildoglochiceras planum (Waagen) (Collignon 1960: pl. 144, figs 558-560) are very close to Hildoglochiceras kobelliforme (Bonarelli), if the smooth shells are a result of abrasion or due to preservation like in most of the present specimens. Spath (1928: 160) raised doubts about species level separation of Haploceras (Hecticoceras) spira Zwierzycki from Tendaguru, Tanzania (1914: 49, pl. 5, figs | | -13) from H. kobelliforme Bonarelli. Based on morphological similarity and dimensional proportions (Table 3) including the umbilical diameter, the specimens assigned to Hildoglochiceras kobelli Oppel by Collignon (1960: pl. 143, figs 547-550) are identified as H. kobelliforme Bonarelli herein. Hildoglochiceras nudum Collignon (1960: pl. 145, fig. 567; D: 43, H: 19 (44), T: 12(28), U: 10 (23)) is similar in discoidal shape, presence of a feeble spiral groove and dimensional proportions including umbilical diameter to the present specimens assigned to H. kobelli Oppel, which is a macroconch. From the illustrations (Collignon 1960: pl. 143, fig. 567) ribs along the periphery can be clearly seen. In all probability Hildoglochiceras nudum Collignon is a junior synonym of H. kobelli Oppel. Similarly, Glochiceras deplanatum (Waagen) (Spath 1928: 155, pl. 16, fig. 3, pl. 17 figs 9a, b) shows a comparable discoidal shape, lateral spiral groove, peripheral ornamentation and proportional dimensions including a similar umbilical diameter (Spath 1928: pl. 17, fig. 9; D: 70, H/D: 45 T/D: 24, U/D: 24; pl. 16, fig. 3; D: 67, H/D: 44, T/D: 25, U/D: 24) to the present specimens assigned to H. kobelli Oppel (1863b).

Contextually, the Madagascan taxa H. planum (Waagen) (Collignon 1960) (m), Haploceras (Hecticoceras) spira Zwierzycki (1914) (m), *H. nudum* Collignon (1960) (M), and *Glochiceras deplanatum* (Waagen) (Spath1928) (M) may be individuals of the dimorphic pair of the species discussed here, based on the assumption of a wide intra-species variability affecting mainly, but not exclusively, the lateral and ventral sculpture. This is in accord with the interpretation made by Collignon (1960) of the species *Hildoglochiceras kobelli* Oppel, including his new var. *madagascariensis*, and contrasts with his generally typological approach resulting in species-rich ammonite assemblages.

*Hildoglochiceras* sp. aff. *kobelliforme* (Bonarelli) (Enay 2009: 84, pl. 1, fig. 6a, b) shows similar dimensional proportions, and occlusion of the lateral groove in the umbilicus, but the sculpture is well developed.

Data from Pakistan are difficult to evaluate due to their poor preservation (*Hildoglochiceras* sp. ind. group of *propinquum* Waagen sp.; Spath 1939, pl. 18, fig. 8a, b) and the lack of body chamber (*Hildoglochiceras cheemaensis* Fatmi, 1973, pl. 3, figs 10–12). The latter is a large, septate form that, at equivalent shell size, shows a similar whorl height, but a lower degree of coiling in comparatively flattish, narrower shells with smooth phragmocone, a wide lateral groove below the line of whorl overlapping showing an inner, crescentic edge, and decreasing depth adaperturally, and a low arched, wide venter without keel.

Concerning the species under study, scanning through descriptions and figures of the species mentioned above given by earlier workers (Oppel 1863b; Waagen 1875; Bonarelli 1894; Uhlig 1903; Lemoine 1910; Spath 1928; Collignon 1960; Énay 2009: pl. 1, fig. 6a, b), it is evident that H. kobelli (Oppel), H. kobelliforme (Bonarelli), and H. latistrigatum (Uhlig) are morphologically very close. In view of the larger umbilical diameter of H. latistrigatum (Uhlig), the present specimens have been assigned to the H. kobelli (Oppel) (M) and H. kobelliforme (Bonarelli) (m) group. It may be mentioned here that Enay (2009: 84, pl. 1, fig. 6a, b), in the description of Hildoglochiceras sp. aff. kobelliforme (Bonarelli), mentioned it as Hildoglochiceras cf. kobelliforme (Bonarelli) in the caption on page 248. The statistical analysis of Hildoglochiceras is given in chapter 5 (see below).

**Biostratigraphy.** Uhlig (1903, 1910) described the species of *Hildoglochiceras* from the Spiti Shales at Chidamu in the Himalayas of northern India. According to Spath (1933: p. 673), *Hildoglochiceras latistrigatum* (Uhlig 1903) from Spiti may be associated with the *Aulacosphinctoides* fauna (for the Natricoides Subzone see Pandey and Krishna 2002; Pandey et al. 2010), which had almost disappeared when *Virgatosphinctes* became dominant in the Early Tithonian.

Data from Spath (1939) and Fatmi (1972, 1973) indicate a generalized context of unconclusively known reworking in Pakistan. Limitations of the precise biostratigraphic interpretation of the *Hildoglochiceras*-rich horizon relates to the near-absence of precise information on *Hildoglochiceras* in particular sections and stratigraphic horizons elsewhere. In fact, despite usual correlations (since Uhlig 1903), the stratigraphic range of *Hildoglochiceras (H. kobelli* Oppel and related species) is inconclusively known, as rightly pointed out repeatedly by previous authors (e.g., Arkell 1956; Zeiss 1968; Énay 2009), or it is given as tentative in the most recent interpretation (Krishna 2017).

The biostratigraphic interpretation of the described Hildoglochiceras horizon is supported by the combination of local and region-wide observations (see above): (1) the absence of physical, stratigraphic features compatible with a wide stratigraphic gap in the section studied, but it could be inconclusive; (2) the local occurrence of transient forms between Neochetoceras and the Semiformiceras darwini Neumayr group in Nepal, the combined record of Hildoglochiceras and Paraboliceras in Himachal Pradesh (Spiti region, Himalaya), as well as by its rare record and tentative assignment to the lower part of the Virgatosphinctoides Zone at the Lakhapar section, Kachchh (Krishna et al. 1996); and (3) the common relationship between Hildoglochiceras horizons and transgressive pulses on epicontinental shelves across opposite palaeomargins of the Trans-Erythraean Through (India and Madagascar versus Tanzania). In this context, the present interpretation is compatible with the possibility of imprecisely known biostratigraphic differences between horizons of Hildoglochiceras from separate areas of the Tethyan embayment corresponding to the proto-Indian Ocean. An example of this can be the early report made by Waagen (1875) on his Haploceras propinguum Waagen later interpreted as Hildoglochiceras (from Spath 1933 to Énay 2009) – as coming from the lowest beds of the Katrol Group, just above "oolitic deposits with Asp. perarmatum at the Keera Hill near Charee". At first, this record would refer to the Kimmeridgian Group he correlated with Europe. This report would point to the Middle Kimmeridgian i.e., to the Eudoxus-Steraspis stratigraphic interval, according to Spath (1933), hence indicating records of the genus Hildoglochiceras older than usually interpreted, just above the stratigraphic gap envisaged by Spath (1933: table 1) for Kachchh. In addition, it may be noted that Paralingulaticeras-like forms resembling the groups of P. nodosum Berckhemer- P. parcevali Fontannes (subtly sculptured forms without and with lateral groove, respectively) and P. lithographicum Oppel (coarsely sculptured forms) are west Tethyan equivalents of comparatively stout shells of Paraglochiceras described and illustrated by Collignon (1960) from Kobelli Zone in Madagascar. These stouter forms are typical Madagascan "species", when compared to west Tethyan equivalents.

In accordance with the biostratigraphic interpretation of the taramelliceratin phragmocone described herein and the review of interpretations of *Hildoglochiceras* records by paying attention to palaeoenvironmental and stratigraphic contexts, two Lower Tithonian intervals related to transgressive pulses are considered. These correlate with the upper to uppermost Hybonotum–lowermost Albertinum/Darwini Zone, and with the lower Semiforme/Verruciferum Zone in the European Standard Scale, respectively. The former would agree with the record of forms intermediate between *Neochetoceras* and early *Semiformiceras*, and it would be compatible with the occurrence of *Parastreblites* during a regression before the subsequent lowstand characterizing deposits corresponding to the Albertinum/Darwini Zone interval. The second would point to an increasing sea level after Albertinum/Darwini times during the younger range of *Parastreblites*. Older (latest Kimmeridgian) and younger (post-Semiforme/Verruciferum Zone) time intervals are discounted due to the lack of evidence of a wide stratigraphical gap below the Hildoglochiceras horizon in the section studied.

### Family Oppeliidae Bonarelli, 1894 Subfamily Taramelliceratinae Spath, 1928

### Taramelliceratinae gen. and sp. ind.

Fig. 11A-F

(Taramelliceras sp. gr. compsum (Oppel)-kachhense Spath or Parastreblites sp. gr. hoelderi Donze and Énay)

Material. Two specimens, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/17 (figured), 79.

Table 6. Dimensions Taramelliceratinae gen. and sp. ind. (in mm).

Specimen no.	D	Н	Т	U	H/T	WSG	HSG
KSKV2019Jara/17	-	21.6	15.5	-	1.39	0.43	9.51

**Description.** Fragments of phragmocone of small size, moderately involute, compressed, with oval whorl section, indistinct ventro-lateral shoulders, and obtusely rounded ventral region. Ornamentation consisting of blunt, falcate, primary ribs with marked inflection slightly below the midflank. Swell at branching points at mid whorl height, along thin, faintly developed spiral groove. Secondary ribs crescentic, occasionally showing very subtle swellings that barely define the indistinct flank periphery and shoulders. Ventral region without identifiable ribs or tubercles. Suture lines relatively well preserved with smoothed peripheral frilling.

**Remarks.** The first specimen (KSKV2019Jara/17), a small fragment of a phragmocone, ca. 50 mm in size is an internal cast with accentuated variably preserved flanks. The left side has been abraded, except for the extreme outer flank that shows remnants of blunt secondaries, while the right side shows remains of a moderately coarse ornamentation across the flank, with a shallow and discontinuous lateral groove-like depression and selective collapse areas. The ventral region is unornamented, subtly raised on the mid-line, and flanked by the external ends of ribs, some of which show incipient oblique-radial swellings barely differentiated from the ribs, which do not contribute to the distinctness of shoulders. The state of preservation precludes any clear remains of tuberculation.

It seems that the right flank exhibits glochiceratin-taramelliceratin traits: (1) peripheral and widely spaced incipient swellings ("remains of tuberculation"?), occasionally located at points where two secondary ribs connect; and (2) a lateral groove-like depression slightly above the midflank. In contrast, the smoothed left flank preserves suture lines in such a way that attrition has been pervasive enough to distort ribbing severely and produced the peripheral frilling of septa; hence the suture-line smoothing corresponds to an erosion level being at least equivalent to rib thickness (compared with the sharper suture-line frilling preserved on the rightside). It is unclear whether differential preservation operated on a pathologic specimen (note symmetrical thickness of the internal cast with respect to the siphuncle) showing different lateral sculpture (Fig. 11A, B), or whether the present appearance merely is a taphonomic feature (comparatively smoothed left flank). The latter option would suggest weathering or reworking and abrasion. The latter would point to a distinct break in sedimentation and later bioturbation during renewed continuous deposition. Reworking is of special interest in the context of the biostratigraphic interpretation as commented in previous sections.

Comparative analysis. The taxonomic interpretation of incomplete oppeliids, as in the case of other Late Jurassic ammonites, is a very difficult task since diagnostic morphological features for identification at the genus and species levels only developed on middle and outer whorls, inner whorls being largely indistinct. This general pattern is taxon-dependent. This situation is accentuated when natural conditions (outcrop, deposition, preservation) and/or collecting limitations (sample size, sampling process) impede access to large samples from a given stratigraphic horizon, i.e., a particular bed representing continuous deposition during a relatively "short" time with no or only a low degree of within-habitat time-averaging. Overall, dominant depositional conditions in Kachchh during the Late Jurassic determined the rarity of records of large, "isochronous" ammonite samples enabling an analysis at the population level.

Based on the assumption that the lateral groove is real though defectively preserved, Paralingulaticeras may show a similar sculpture but it shows well-developed ventro-lateral tubercles, a much more slender, flatter shell with a lower degree of coiling, and the lateral groove is mainly developed on the body chamber. Among well-known European Paralingulaticeras species (cf. Ziegler 1958), P. nodosum Berckhemer with scarcely marked lateral groove and tuberculation, and the sparsely tuberculated P. parcevali Fontannes, are differently ribbed on the flanks, while the densely tuberculate and coarsely ribbed P. lithographicum Oppel clearly differs in shape and sculpture. These species of Paralingulaticeras occur in the latest Kimmeridgian Beckeri Zone and in the lowermost Tithonian, lower part of the Hybonotum Zone of Submediterranean (Ziegler 1958; Berckhemer and Hölder 1959) and Mediaterranean areas of the Western Tethys (Olóriz 1978; Caracuel and Olóriz 1999).

Among ornamented glochiceratins from eastern Gondwana, the Madagascan *Paraglochiceras* from the *Hildoglochiceras kobelli* Zone (interpreted as Early Tithonian in Madagascar) commonly have more globose shells with unsculptured inner flanks. *P. hirtzi* Collignon (1960: pl. 146, fig. 576) and *P.* aff. *propinquum* (Waagen) are relatively



**Figure 11. A–F.** Taramelliceratinae gen. and sp. ind. KSKV2019Jara/17. **A.** Internal cast, left side view of a fragment of phragmocone showing remnants of blunt secondaries along the periphery; **B.** Right side view showing moderately coarse ornamentation across the flank, with a shallow and discontinuous lateral groove-like depression and selective collapse areas; **C.** Suture line drawn from right lateral side, showing smoothed peripheral frilling; **D.** Line diagram showing oval whorl-section; **E.** Apertural view; **F.** Ventral view showing unornamented, subtly raised on the mid-line, and flanked by the external ends of ribs, some of which show incipient oblique-radial swellings; **G–I.** *Aulacosphinctoides* sp. ind. KSKV2020Jara/13; **G.** Ventral view showing broad ventral region, sedondary ribs crossing ventral region almost straight; **H.** Enlarged right side view of inner whorls (nucleus) showing moderately thick prosiradiate ribs and constrictions; **I.** Right side view of body chamber showing regularly bifurcating and occasionally, single primary rib, the nucleus part is represented by mould of the cast shown in fig. H; **J–L.** *Virgatosphinctes* s.l. sp. KSKV2019Jara/80; **J.** Line diagram showing suboval whorl section with obtusely rounded ventral region, distinct but obtusely rounded umbilical shoulder and steep umbilical wall; **K.** Right side view showing distant, thick, prosiradiate, primary ribs branching into thin, densely crowded five to six secondary ribs at mid-lateral height and displaying a slight forward concavity; **L.** Ventral view showing broadly rounded ventral region and secondary ribs crossing ventral region with slight forward-directed sinuosity.

close in shape but clearly differ in sculpture. *Hildoglochiceras* shows ventrolateral ribs that rarely bifurcate in the more finely ribbed species and does not have any dorsolateral ribs. *Hildoglochiceras colei* Spath (Collignon 1960: pl. 144, fig. 561) shows slightly more flattened and convergent flanks, and different external ribs. *H. parceumbilicatum parceumbilicatum* Collignon (1960: pl. 144, fig. 563) curiously resembles the smoothed left flank of specimen described herein. *Hildoglochiceras tenuicostulatum* Collignon (1960: pl. 145, fig. 568) shows a more crowded and delicate ribbing. Aside from the usual schemes of correlation, the precise biostratigraphic range of the genus *Hildoglochiceras* is not conclusively known, as has been discussed above.

If alternatively, the lateral groove is a secondary, preservational feature, there are two interpretations of the inner cast described:

(1) Parastreblites Donze and Énay 1961, which does not possess a lateral groove, shows a streblitoid whorl section in the outer whorls, but its inner whorls could be similar in sculpture to the Taramelliceras compsum group, since the mid-flank tuberculation of Streblites does not occur (Olóriz 1978). In fact, this tuberculation reveals Taramelliceras inheritance s. str., excluding the group of Taramelliceras trachinotum Oppel (Donze and Énay 1961) due to its clearly older age. Parastreblites has been recorded in the Lower Tithonian (three-fold division) Darwini Zone and in the upper Hybonotum-Albertinum (=Darwini) Zone in the western Tethys (southern Spain; Énay and Geyssant 1975 and Olóriz 1978, respectively), but potential records from latest Kimmeridgian to earliest Tithonian horizons cannot be excluded, if Oppelia gaetanoi Fontannes is considered. Inner whorls of some species of Parastreblites show morphologic affinity to the group of Taramelliceras compsum (Oppel) (e.g., Parastreblites hoelderi in Donze and Énay 1961). In fact, Parastreblites has been reported from distant areas outside Europe (Imlay 1942; Donze and Énay 1961; Leanza 1980; Parent et al. 2015), but there it is a rare, inconclusively known taxon showing a distinct morphology and wider biostratigraphic range with respect to European specimens. Even allusions to the Kimmeridgian genus Metahaploceras have been made for those Lower Tithonian ammonites.

(2) Taramelliceras is the alternative option for interpreting the incomplete inner cast described. First revised by Hölder (1955), Taramelliceras exhibits a notable intra-species variability and is represented by three main species groups in the Upper Jurassic, with the T. compsum group as the source for Mid-to-Late Kimmeridgian forms and their youngest offsprings. According to Hölder (1955), the T. compsum group was widely distributed, from Mexico to India, and Taramelliceras (Metahaploceras) occurred throughout East Africa. All these data reveal a Tethyan influence in the surrounding epicontinental areas on both sides of the Trans-Erythraean Gulf or incipient seaway, during rising sea-levels throughout late Middle to Late Kimmeridgian and Early Tithonian times (three-fold divisions). Berckhemer and Hölder (1959) revised Malm  $\epsilon$  to  $\zeta_3$  taramelliceratins from southern Germany and split the compsum group in subspecies, with diversified descendants during latest Kimmeridgian and earliest Tithonian times up to probably ζ<sub>2</sub> e.g., Taramelliceras

franciscanum Fontannes, which was preliminarily included by Hölder (1955) in Taramelliceras compsum. Olóriz (1978) confirmed the pronounced morphological variability in Tethyan specimens of Taramelliceras compsum (Oppel) from the Betic Cordillera in southern Spain and highlighted the relevance of this species and related forms during the Late Kimmeridgian (two-fold division) and the earliest Tithonian. Working on better preserved material from epicontinental deposits with a continuous sedimentary record, Baudouin et al. (2011) were able to demonstrate a high within-species variability in a large sample of Taramelliceras compsum, collected from two successive beds in fine-grained siliciclastic-carbonate rhythmites of the Mount Crussol type-section, southern France. From Hölder (1955) to Baudouin et al. (2011), Taramelliceras compsum has been interpreted to be very variable with respect to ribbing and tuberculation, including its inner whorls. Commonly, two lateral ribs connect to a single ventro-lateral tubercle at a relatively small shell size; other specimens with broader and slightly domed vs. raised ventral regions have a virtually smooth to clearly tuberculate midventer, respectively. Taramelliceras kachchense Spath has been interpreted to be a derived form from across Trans-Erythraean Through areas, where references to the group of Taramelliceras compsum (Oppel) have been common from Uhlig (1903) onwards.

The strongly ribbed left side of the analysed phragmocone excludes comparison with smooth forms such as *Taramelliceras nivale* (Stolizcka), an insufficiently known species reported from Himalayan and Madagascan areas.

Biostratigraphy. All this information supports the tentative interpretation of the incomplete phragmocone described as belonging to Taramelliceras sp. of the T. compsum (Oppel) – T. kachhense Spath groups. These two nominal species are most probably evidence of a Tethyan source and a local, derived taxon, respectively, the latter being a local phenotype expression related to colonization of shelves bordering the Trans-Erythraean Through. Thus, the biostratigraphic range of Taramelliceras could extend from Middle Kimmeridgian horizons to the lower part of the Lower Tithonian (three-fold-division), if the total range of the former species in west-Tethyan areas applies. Southwards, at the Indian-Malagasy palaeomargin, Collignon (1960) documented what he interpreted as Lower Tithonian Taramelliceras in Madagascar, but a more accurate biostratigraphy is needed before a definite conclusion can be reached, also with respect to its actual co-occurrence with Hildoglochiceras there, i.e., without reworking.

The stratigraphic range assumed for the Oppel species in west-Tethyan areas, with the youngest Taramelliceratinae occurring in the Albertinum/Darwini Zone, and the limited evidence of reworking in the stratigraphic interval sampled (a single specimen; see description above) points to the possibility that *Taramelliceras* occurs from levels with a minimum age of Early (earliest?) Tithonian (three-fold division). The assumed co-occurrence with *Hildoglochiceras* in Kachchh and Madagascar should be consistent with an age of the oldest *Hildoglochiceras* older than usually interpreted. The inconclusive evidence of lowermost Tithonian horizons in these areas could be the result of unfavourable conditions for ammonites and/or of stratigraphic gaps in connection with the change from coarse-grained siliciclastics to calcareous sediments. Apparently, regional tectonic forcing during earliest Tithonian times occurred close to the Jurassic eustatic maximum. Local variation in the time span involved in the stratigraphic gap cannot be dismissed in accordance with lateral facies changes of deposits containing *Hildoglochiceras* in the area (e.g., Pandey et al. 2016).

The alternative interpretation of the described phragmocone as *Parastreblites* sp. gr. *hoelderi* Donze and Énay (1961) is compatible with the biostratigraphic interpretation just proposed, based on the assumption that the biostratigraphic range of European *Parastreblites* (*Parastreblites*) s. str. is the reference for correlation, which might include the Ulmensis horizon (=uppermost Kimmeridgian or lowermost Tithonian according Donze and Énay (1961). However, even though being difficult to evaluate (e.g., Parent et al. 2011), the rare records of *Parastreblites* from the Zitteli Zone in Argentina (Leanza 1980; Parent et al. 2011, 2015; Vennari 2013) could be taken into account, but the illustration by Parent et al. (2015) of material collected from horizons above their Zitteli and Proximus zones rather excludes the assignment to *Parastreblites* s. str.

In the absence of age-diagnostic Tethyan and Indian ammonites in the reported ammonite assemblage, the Hildoglochiceras described here represent a local record but, being a sample of population size, it is the most relevant record of this genus that is available. The favoured biostratigraphic interpretation points to indeterminate upper Lower Tithonian horizons (three-fold division), correlated with a lower part of the Tethyan Albertinum/Darwini Zone, but slightly older horizons also might apply. This interpretation is based on: (1) underlying ammonite-poor, sandy deposits without evidence of relevant erosion at the top; (2) lacking records of Hybonoticeras, which are mainly interpreted to represent the uppermost Kimmeridgian across epicontinental deposits in the Trans-Erythraean Trough, and rarely lowermost Tithonian horizons; (3) the occurrence of transient forms between Neochetoceras and early Semiformiceras in neighbouring areas (Nepal), interpreted as probable evidence of morphological evolution towards early forms of Semiformiceras rather than a case of local, diachronous homeomorphism; (4) occurrence elsewhere in the Trans-Erythraean Trough of ammonites morphologically close to those belonging to Lower-to-lowermost Tithonian in West-Tethyan areas, and (5) the interpretation of the Hildoglochiceras horizon as recording a local maximum flooding zone. This interpretation agrees with the occurrence of ammonite remains morphologically close to virgatosphinctins, reported and illustrated with precise stratigraphic control ("Couches à Virgatosphinctes et Aulacosphinctoides" at Nupra, Thakkhola, central Nepal, by Énay (2009); and comments with precise citations in previous sections). The second alternative pointing to some horizons within the upper Albertinum/Darwini to lower Semiforme-Verruciferum zones is potentially correlatable with the early Middle Tithonian transgressive pulse in different areas worldwide but could involve a wider stratigraphic gap (Fig. 2).

### Superfamily Perisphinctoidea Steinmann, 1890 Family Perisphinctidae Steinmann, 1890 Subfamily Virgatosphinctinae Spath, 1923

### Genus Aulacosphinctoides Spath, 1923

Type species. Aulacosphinctes infundibulus Uhlig, 1910.

#### Aulacosphinctoides sp. ind.

Fig. 11G-I

**Material.** One specimen, *Hildoglochiceras* Bed of Jara Dome (Lower Tithonian); KSKV2020Jara/13.

**Description.** Shell moderately large (ca. 55 mm in diameter), evolute and depressed. Whorl section subcircular with uniformly arched flanks, umbilical shoulder regions and broad venter. Ornamentation consists of prorsiradiate, biplicate ribs, branching above mid-lateral height into finer secondary ribs, crossing ventral region almost straight. Primary ribs thick, moderately spaced, originating from umbilical suture slightly rursiradially. Occasionally, single primary rib. Constrictions seen on inner whorls. Umbilical wall steeply inclined.

Remarks. The outer whorl represents the body chamber, filled with micrite with dispersed coarse quartz grains. There is no sign of any suture lines. The specimen is slightly deformed showing an almost flat right lateral surface with maximum inflation at the ventro-lateral shoulder, whereas the left lateral surface is uniformly arched with the region of maximum inflation at mid-lateral height. The depressed whorl section, biplicate thick ornamentation and presence of constrictions in the inner whorls suggest the genus Aulacosphinctoides Spath. Due to the fragmented and deformed nature of the specimen a species identification is not possible. Nevertheless, the morphological characters are comparable with Aulacostephanoides infundibulus (Uhlig 1910: 371, pl. 66, fig. 3a-c, pl. 72, figs la-c (= lectotype), 2a-c, 3a, b, 4a-c; Yin and Énay 2004: pl. 3, fig. 7a, b; Énay 2009: 181, pl. 42, fig. la-c).

**Biostratigraphy.** The Aulacosphinctoides or Virgatosphinctes and Aulacosphinctoides assemblage suggests an earliest Tithonian age (see above) (Uhlig 1903, 1910; Spath 1933: 673; Pathak 1997, 2007; Pandey and Krishna 2002; Yin and Énay 2004; Énay 2009; Pandey et al. 2010, 2013).

### Virgatosphinctes s.l. sp.

Fig. 11J-L

- Perisphinctes (Virgatosphinctes) raja sp. nov., cf. 1910 Uhlig: 316, pl. 50, fig. 1a-d.
- Perisphinctes (Virgatosphinctes) minusculus sp. nov., cf. 1910 Uhlig: 317, pl. 56, fig. 2a-c.

**Material.** One specimen, Hildoglochiceras Bed of Jara Dome (Lower Tithonian); KSKV2019Jara/80.

**Description.** Shell large (the fragment is approximately 9 cm in diameter and judging by its curvature represents

around one-fourth of the phragmocone with a possible final diameter of 13 cm), evolute, slightly depressed (H: 35, T: 40.7, H/T: 0.85) or (H: 40, T: 41.6, H/T: 0.96) suboval whorl section with distinct but obtusely rounded umbilical shoulder, steep umbilical wall, lateral surface that converges smoothly in the obtusely rounded ventral region. Maximum whorl thickness slightly above umbilical shoulder. Ornamentation consisting of distant, thick, prorsiradiate, fascipartite/fasciculate ribs. Primary ribs originating from umbilical wall rursiradially, bending prorsiradially at umbilical shoulder, displaying a slight forward concavity on lateral surface, branching into thin, densely crowded five to six secondary ribs at mid-lateral height. Secondary ribs following the same course as primary ribs, one or two free secondary ribs inserted between adjacent primary ribs, maximum number of secondaries produced by a single primary rib may not exceed seven. Secondary ribs crossing ventral region with slight forward-directed sinuosity.

**Remarks.** The specimen represents a small fragment of the phragmocone with moderately preserved suture lines. Due to the fragmentary nature, ornamentation of inner whorls and of the body chamber is not known. The distant, thick, prorsiradiate, fascipartite/fasciculate ribs with forward-directed concavity on the lateral surface, branching into several fine secondary ribs, the suboval whorl section and H/T ratio are similar to *Perisphinctes (Virgatosphinctes) minusculus* Uhlig (1910: 317, pl. 56, fig. 2a–c; D: 108, H: 32, T: 36, H/T: 0.88, U: 47). However, the number of secondary ribs produced by one primary rib ranges from 9–10 instead of up to seven in the present specimen.

The ornamentation and whorl section of the outer whorl also match *Perisphinctes* (*Virgatosphinctes*) *raja* Uhlig (1910: 316, pl. 50, fig. 1a–d), but *P*. (*V*.) *raja* has a thicker shell (D: 143, H: 49, T: 57, H/T: 0.85, U: 58.3) and distant ribs in the inner whorls. The H/T ratio in the present specimen is intermediate between the two species discussed above (see also Uhlig 1910: 318).

No true virgatotomy s. str. is recognizable in the present specimen, and divisions seem to be rather fascipartite/fasciculate. Since 5–7 secondaries occur in particular divisions on the phragmocone, a greater number could be expected on the body chamber.

This fragment of phragmocone is too incomplete for a conclusive interpretation. The significant feature is the wide-oval whorl section, which rarely occurs in typical *Virgatosphinctes*, if Énay's (2009) classification is assumed (even with caution). *Virgatosphinctes* sp. C (Énay 2009: 168, pl. 32, fig. 4) is the only species showing a wide-oval whorl section, but its ribbing seems to be more crowded and with shorter primary ribs (Énay 2009: pl. 33, fig. 3). Also of interest is its early proliferation of secondary ribs, and the provenance from the "*Couches à Virgatosphinctes et Aulacosphinctoides*" at Nupra, in assumed Lower Tithonian below Nepalese *Hildoglochiceras* beds.

**Biostratigraphy.** Uhlig (1910) described the two species mentioned above without precise stratigraphy from Spiti and Chidamu areas, respectively. Based on the assemblage recorded here, the comparative analysis with species of known stratigraphy, and the proposed biostratigraphic interpretation for the *Hildoglochiceras* described, the specimen is assigned to indeterminate horizons within the Lower but not lowermost Tithonian (three-fold division), correlated with indeterminate horizons within the lower part of the Tethyan Albertinum/Darwini Zone, less probably with the upper Darwini to lower Semiforme-Verruciferum zones (Fig. 2).

# Statistical analysis of the specimens of *Hildoglochiceras*

Due to the fragmentary nature and obliteration of ornamentation, either due to bad preservation or abrasion, in most specimens described here as *Hildoglochiceras kobelliforme* (Bonarelli) (m) and *H. kobelli* (Oppel) (M) group, we found it difficult to ascertain the limits of variation within the morphological clades. Therefore, for better clarification and understanding the distinctness of the morphological clade various multivariate statistical analyses were performed.

### Data base

Out of 72 specimens of the present collection (i.e. excluding 18 specimens described by earlier workers; A-D, F-S in Table 3), only 41 samples were complete with all the information (such as diameter of shell, height of whorl, thickness of whorl, and diameter of umbilicus). For the remaining specimens, we imputed the missing data using 'MICE' (Multivariate Imputation by Chained Equations) software package implemented in R v3.5.1. Data imputation was performed using 'MICE' command employing the 'random forest' method, which generates the imputed value by taking the weighted average of the non-missing observations. The weightage is given on the proximity between the given sample with missing data and the specimen(s) with non-missing observations. Overall, two datasets were used for all downstream analysis: one containing information about the 41 complete specimens plus 18 previously published specimens with complete data (excluding 'E') (N = 59); the second dataset contains a total of 105 data including 87 data (of 72 specimens) from this study and those from 18 previously described specimens.

Subsequently, both datasets were normalized by factoring the height, thickness and umbilicus of the specimens as percentages of their respective diameters (H/D%, T/D%, U/D% respectively) and taking a ratio of the height and the thickness of the specimens (H/T).

### Results

### Hierarchical clustering analysis (HCA)

HCA was performed independently for the non-imputed (N = 59) and imputed (N = 105) datasets using the 'hclust' command in R v3.5.1. Euclidean distances among the specimens were calculated using the 'dist' command in

R. In both cases the normalized data (H/D%, T/D%, U/D% and H/T) were used for Euclidean distance calculation (Figs 12, 13). The Relevant point here is representation Type 1 of the present samples in the right major group in Fig. 12, clearly separated from the major grouping of Type 2 samples on the left. Moreover, Fig. 13 of imputed data shows a mixing of types. All of this reveals some degree of general cohesion of values, with the occurrence of transients.

Prior to PCA, all the specimens at the author's disposal were manually grouped into four types (Type 1 to Type 4) (see Table 4), based on their morphological similarities.

PCA was performed independently for the non-imputed (N = 59) and imputed (N = 105) datasets using 'prcomp' command in R employing the normalized data (Fig. 14a, b). The distribution of outliers is based on experimental data of individuals.

### Linear regression and likelihood ratio test (LRT)

We then aimed to assess the association between the four primary characters in the specimens: diameter of



### HCA with Non Imputed Data taking H/D%, T/D%, U/D%, H/T

Figure 12. Hierarchical Clustering Analysis (HCA) for the non-imputed (N = 59) dataset using 'hclust' command in R v3.5.1. Euclidean distances among the specimens were calculated using the 'dist' command in R. In both cases the normalized data (H/D%, T/D%, U/D% and H/T) were used for Euclidean distance calculation. Note the numbers are the last numbers of specimen number in the text (e.g., 1 for KSKV2019Jara/1), followed by Type 1, 2, 3, or 4 after a forward slash, which is followed by 'm' for microconch or 'M' for macroconch.



HCA with imputed data taking H/D%, T/D%, U/D%, H/T

Figure 13. Hierarchical Clustering Analysis (HCA) for the imputed (N = 105) dataset using 'hclust' command in R v3.5.1. Euclidean distances among the specimens were calculated using the 'dist' command in R. In both cases the normalized data (H/D%, T/D%, U/D% and H/T) were used for Euclidean distance calculation. Note the numbers are the last numbers of specimen number in the text (e.g., 1 for KSKV2019Jara/1), followed by Type 1, 2, 3, or 4 after a forward slash, which is followed by 'm' for microconch or 'M' for macroconch.



**Figure 14.** Principal Component Analysis (PCA). Based on their morphological similarities all specimens at the author's disposal were manually grouped into four types, Type 1 to Type 4; **a.** PCA for non-imputed dataset (N = 59) using '*prcomp*' command in R employing the normalized data; **b.** PCA for the imputed data set (N = 105). Note Type 1 (Circle) – with large umbilicus (U/D: 40 to 25%), compressed whorl section (H/T: 1.3–1.8) and acute ventral region. They are microconch (m); Type 2 (Triangle) – with small umbilicus and (U/D: 26 to 18%), compressed whorl-section (H/T: 1.35–2.0) and acute ventral region. They are macroconch (M); Type 3 (Diamond) – small-sized specimens, juvenile of types 1 & 2. The overlap of types 3 and 1 & 2 in the plot suggests that they belong to same taxonomic group. Type 4 (Square) – they are same as Type 2 but with preserved crescentic ribs on flanks.

shell, height of whorl, thickness of whorl, and diameter of umbilicus. Since ornamentation is poorly preserved (see above) we have not considered it in this analysis (this, in turn, supports the variability in ribbing, such as, diameter of appearance of ribs, crowding or number of ribs per unit area and relief or coarseness of ribs, identified by previous authors. We developed seven linear regression models considering the diameter of the umbilicus as the function of various combinations of diameter of shell, height of whorl and thickness of whorl. Models were developed using the 'glm' command in R. Regression coefficients (R<sup>2</sup>) were calculated using the 'lm' command; the association between the characters was statistically evaluated using a t-test considering a null hypothesis of no association among them.

Likelihood Ratio Test (LRT) among the seven models was performed using the '*Ir.test*' command present in the 'extRemes' software package implemented in R v3.5.1. LRT evaluated whether a given model is a better/worse fit to the data than the next higher model containing more parameters than the former in a chi square platform considering a significance level of 0.05.

The best model was selected on the basis of the lowest Akaike's Information Criterion (AIC) value obtained through the 'glm' function and the largest significant chisquare value obtained though LRT (Table 7).

# Discussion of statistical analyses

### Hierarchical clustering analysis (HCA)

On the one hand, the HCA performed with complete specimens was successful in representing the ontogenic history of the samples such that it grouped all Type 3 and Type 4 specimens together with Type 2 (left side of the Fig. 12). Nevertheless, it failed to cluster samples based on their diameters (Type 1 vs Type 2) with both larger and smaller types existing in two major clades. Palaeobiologically, the smaller specimens are juveniles of Type 2 and the ornamented specimens grouped under Type 4 again belong to Type 2 but their ornamentation escaped abrasion. Before, the statistical analysis for Type 3 it was not known whether it is a juvenile form of Type 2. At the first instance, it was not clear that ornamented specimens (Type 4) belong to same clade.

On the other hand, the tree generated by HCA with imputed data, potentially due to the inherent error associated with data imputation, largely failed to represent the true ontogenic history of the samples employed in our study (Fig. 13). Overall, the distance-based clustering, implemented in HCA, was largely unsuccessful in grouping the ammonite specimens under study.

Table 7. On the basis of linear regression analysis followed by post hoc likelihood ratio test, the diameter of umbilicus is mostly depen-
dent on the diameter of the shell and can be best modelled as the linear expression of diameter of the shell and the height of whorl. It
is least dependent on the thickness of the whorl, especially when modelled alongside the diameter of the shell.

Model No.	Model	AIC	R <sup>2</sup>	Adjusted R <sup>2</sup>	P-value				
Model 1	glm(a\$U ~a\$D)	277.6	0.8196	0.8164	2.20E-16				
Model 2	glm(a\$U ~a\$H)	319.2	0.6349	0.6285	4.41E-14				
Model 3	glm(a\$U ~a\$T)	292.6	0.7675	0.7635	2.2E-16				
Model 4	glm(a\$U ~a\$D+a\$H)	184	0.9643	0.9631	For D = 2.2E-16; For H = 2.2E-16, Overall = < 2.2E-16				
Model 5	glm(a\$U ~a\$D+a\$T)	276.6	0.8288	0.8227	For D = 3.79E-05; For T = 0.0886, Overall = < 2.2E-16				
Model 6	glm(a\$U ~a\$H+a\$T)	279.1	0.8211	0.8147	For FI = 0.000137; For T = 3.1E-10, Overall < 2.2E-16				
Model 7	glm(a\$U ~a\$H+a\$T+a\$D)	185.4	0.9647	0.9628	For D = 2.2E-16; For H = 2.2E-16, <b>For T = 0.462</b> , Overall = < 2.2E-16				
Likelihood Ratio Test									
	Chi square	P-value							
Model 1 vs. Model 4	95.661	1.37E-22							
Model 1 vs. Model 5	3.828	0.079							
Model 1 vs. Model 7	96.246	1.26E-21							
Model 2 vs. Model 4	137.250	1.06E-31	P value: Probability value		ability value				
Model 2 vs. Model 6	42.082	8.75E-11	AIC: Akaike information criterion						
Model 2 vs. Model 7	137.835	1.17E-30	R2: Regression coefficient						
Model 3 vs. Model 5	18.042	2.16E-05							
Model 3 vs. Model 6	15.451	8.64E-05							
Model 3 vs. Model 7	111.205	7.12E-25							

### Principal component analysis (PCA)

PCA of the data of variants, mentioned in Table 4, performed much better than HCA in grouping specimens together with both non-imputed and imputed data. PCA with complete specimens depicted two distinct clusters: largely consisting of Type 1 and Type 2 (analytically, Type 2 includes Type 3 and 4) specimens (Fig. 14a). We note here that there was a solitary Type 4 sample in our study that can be considered as 'complete' (the other specimens of Type 4 were broken and have limited dimensions). The typical result of two groupings of complete data is its character of exclusive, type-cohesive groups. Note the position of 'A' (*Hildoglochiceras latistrigatum* (Uhlig)) in the PCA of non-imputed values showing perhaps the farthest transient.

PCA with imputed data also generated two distinct clusters: one largely consisting of Type 1 specimens, together with many specimens labelled with "letters" (Table 3) and the second one largely containing Type 2 specimens (Fig. 14b). Interestingly, unlike PCA performed with complete specimens, the analysis with imputed data did not find any cluster for Type 3 or Type 4 specimens. The Type 3 specimens were largely grouped with Type 2 specimens, likely due to their ontogenic similarities. Type 4 is also the same as Type 2 but for the presence of ornamentation. Further, PCA depicted a clustering of ~18 samples belonging to all four types half-way between Type 1 and Type 2 clusters, indicating a characters overlap among specimens belonging to different 'Types', which are associated with their ontogenic history. In other words, these specimens belong to a palaeobiogical population.

# Linear regression and likelihood ratio test (LRT)

Linear regression analysis indicated that all three characters: the shell diameter, whorl height and whorl thickness are associated with the diameter of the umbilicus ( $R^2$  = 0.82, 0.63 and 0.77 respectively, P-value < 0.0001). The linear regression analysis with various combinations of the aforementioned characters indicate that the combined effect of the shell diameter and whorl height together best regulates the diameter of the umbilicus ( $R^2 = 0.96$ , P-value < 0.0001, AIC = 184). This is also supported by the LRT, which depicts that the addition of whorl height to a linear model containing the diameter of the shell, makes the model distinctly more superior to the model containing either of them alone. Interestingly, the linear combination of the shell diameter and the whorl thickness, and the linear combination of all three characters contributes little to the diameter of the umbilicus (P-value for thickness in the linear models = 0.09 and 0.46 respectively), indicating that the thickness of the whorl contributes the least towards the formation of the umbilicus (Table 7). This assertion points to the fact that some variation in shell thickness is irrelevant, which can be envisaged within the accepted variability at the population level. However, more interesting is the insignificant relationship that seems to result among shell size, whorl height, and whorl thickness, since the latter two are constructionally related, thus revealing inherent covariation, especially when no excessive shell size is reached within the platycone shell-type analyzed (also see Olóriz et al. 1997, 2002; Contreras et al. 2019)

The statistical analysis suggests that there are basically two groups: Type 1 – a microconch *Hildoglochiceras kobelliforme* (Bonarelli) and Type 2 – a macroconch *Hildoglochiceras kobelli* (Oppel). The two other groups Type 3 and Type 4) are also macroconchs; Type 3 is juvenile and Type 4 preserves ornamentation (Figs 10, 12–13).

### Conclusions

 The Hildoglochiceras-rich horizon reported from a thin carbonate intercalation within the siliciclastic Upper Jurassic Jhuran Formation of the Jara Dome, western Kachchh Mainland, interrupted largely restrictive conditions for ammonites in the area and is interpreted to reveal a transgressive pulse and maximum flooding zone.

- The Hildoglochiceras-rich horizon investigated provides the first population-level study of the genus based on a multivariate analysis, revealing occurrence of transient forms between morphospecies, a trait identified long time ago and supported by high phenotype instability in the large sample studied, which, in turn, raises doubts about the real meaning of Hildoglochiceras species reported in the literature.
- The morphospecies Hildoglochiceras kobelli (Oppel) and H. kobelliforme (Bonarelli) are interpreted as expression of the dimorphic pair of Hildoglochiceras kobelli Oppel and, therefore, are labelled as referent morphs for this palaeobiospecies.
- The endemic character of *Hildoglochiceras* is confirmed and has been related to its environmental restriction to shelf areas belonging to palaeomargins of the Trans-Erythraean Trough. Variability in local phenotype expression also affected the endemic fauna of virgatosphinctins, making agreements among interpretations of taxonomy, biostratigraphy, and correlation difficult.
- A comprehensive review of biostratigraphic interpretations of *Hildoglochiceras* points to the inconclusiveness of assumed biostratigraphic evidence and correlations, both resulting from reports mainly based on single to few specimens, the scarcity of Tethyan age-diagnostic taxa, and the reputed lateral and vertical discontinuity of ammonitiferous horizons of interest.
- Reports of *Hildoglochiceras* in the literature embrace uppermost Kimmeridgian to lowermost Upper Tithonian horizons as the widest biostratigraphic range assumable, but most probably, it was restricted to, or at least better represented in, Lower Tithonian horizons.
- Biostratigraphic misinterpretations inherited since the middle of the past century largely influenced the usual, oversimplified correlation with the Tethyan Semiforme/Verruciferum Zone. In contrast, the Hildoglochiceras Horizon described here is correlated with the lower part of the Albertinum/Darwini Zone in the Secondary Standard Scale for ammonite-based bio-chronostratigraphy in European and West-Tethyan areas.
- According to the current state of knowledge, a local rather than wide regional meaning is favoured for *Hildoglochiceras* records before its significance for precise correlation can be determined, either across the Trans-Erythraean Trough or, especially, with distinct ammonite assemblages reported from distant areas.

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# Early teleost otolith morphogenesis observed in the Jurassic of Franconia, Bavaria, southern Germany

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# Abstract

The otoliths described in this study are from the late Pliensbachian of the Buttenheim clay pit near Bamberg, Franconia, northern Bavaria, and represent one of the earliest teleost otolith assemblages known so far. A total of 351 otoliths have been recovered, many of which are well-preserved and of sizes that indicate they originated from adult specimens and can be considered morphologically mature. The assemblage contains seven species, four of them stem teleosts of the genus *Leptolepis* and three from the enigmatic otolith-based genus *Archaeotolithus*, which cannot be attributed to a firm systematic position. We describe three species as new: *Leptolepis buttenheimensis* **sp. nov.**, *Leptolepis steberae* **sp. nov.** and *Archaeotolithus doppelsteini* **sp. nov.** In addition, we review 49 otoliths from the original material of Schröder's (1956) publication that were uncovered at the University of Erlangen. This material stems from the late Toarcian/early Aalenian and early Callovian of Franconia. In this review, we accept only a few of the species described by Schröder as valid. The otolith associations from the Early and Middle Jurassic of Franconia, in combination with previously published material, allow for an assessment of the morphogenesis of early teleost otoliths. Early Jurassic teleost otoliths are represented by a few common and long-ranging species. A sudden burst in otolith diversity seems to have occurred during the Middle Jurassic and is first evident in the Bathonian.

# Keywords

Early Jurassic, Middle Jurassic, Leptolepididae, Leptolepis, Archaeotolithus, review

# 1. Introduction

Jurassic otoliths have rarely been studied. Frost (1924, 1926) and Stinton (in Stinton and Torrens 1968) described otoliths from southern England, Weiler (Neth and Weiler 1953; Martin and Weiler 1954 and 1965) described them from wells drilled in northern Germany, Hesse (2014) described them from a clay pit in northern Germany, and Schröder (1956) described them from Jurassic outcrops in Franconia. Delsate (1997) later described otoliths found *in situ* from *Leptolepis normandica*, which allowed for the first-time allocation of a large proportion of these

Jurassic otoliths in a systematic context. A further case of an otolith *in situ* was documented by Hesse (2014). Malling and Grønwall (1909) described a peculiar group of otoliths of unknown relationships from the early Jurassic of Bornholm, and Stolley (1912) described them from the middle Jurassic of Bad Harzburg, northern Germany. Stolley later established the otolith-based genus (which he called "typus") *Archaeotolithus* for this group.

The taxonomic identification of Jurassic otoliths meets certain problems besides a lack of comparability with otoliths of crown teleosts. One of the principal problems is their low level of morphological diversity. Other problems

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concern uncertainties in the level of inter- and intraspecific variations expected in the otoliths of these early bony fishes. Weiler (1954) noted that the interspecific diversity might have been rather low in such "primitive" otolith morphologies and established a plethora of otolith-based species based on vague, minute morphological differences. Schwarzhans et al. (2019) recent study of many otoliths, both in situ and in isolated otolith specimens from the late Jurassic Cavenderichthys talbragarensis, has indeed confirmed a low level of morphological diversity when compared with otoliths of the early Jurassic Leptolepis normandica; however, indications have also shown a "normal" level of intraspecific variability. In conclusion, these observations do not support the excessive number of species described by Weiler. In fact, Nolf (1985: p. 111) considers Weiler's works on Mesozoic otoliths as "constituting the most problematic part of the whole otolith literature." Revisions of Jurassic and early Cretaceous otoliths embedded in the handbooks of Nolf (1985 and 2013), and more specifically by Schwarzhans (2018), have recognized only a small fraction of Weiler's otolith-based taxa as valid but considered most of them synonymies of other taxa or of doubtful nature. Two studies of Jurassic otoliths-Neth and Weiler (1953) and Schröder (1956)-remain unreviewed because the type-material was not recovered.

Here we describe a large collection from the Early and Middle Jurassic of Franconia composed from two sources. The first is a collection of 351 otoliths of the latest Pliensbachian from the Buttenheim clay pit. The other contains 86 otoliths from the type-material of Schröder (1956) that stem from the late Toarcian/early Aalenian and from the early Callovian, both of which were located in the Geological Institute of the University of Erlangen. Schröder mentioned that he had 147 otoliths for study. Among the 86 recovered otoliths, 49 come from teleosts, and 37 are putative coleoid statoliths. The latter are not reviewed here. The collection of teleost otoliths contains 16 of the 18 nominal species described by Schröder, including 14 holotypes. The purpose of our study is to describe the early teleost otoliths stemming from probably the largest collection of early to middle Jurassic otoliths, thereby revising Schröder's work, which has rarely been cited because of the difficulties of interpreting his documentation and descriptions (see Nolf 2013 and Schwarzhans 2018).

### 2. Materials and methods

# 2.1. Localities and stratigraphic positions of the studied otoliths

The otoliths described in this study were collected in Upper Franconia, northern Bavaria, Germany, in a clay pit near Buttenheim, southeast of Bamberg. Specimens described by Schröder (1956) were collected from five locations near Bamberg and Nürnberg (Fig. 1). The otoliths from Buttenheim come from the clay pit of the Liapor Company at Altendorf, south of Buttenheim. Exposed in this



**Figure 1.** Location plate, Bavaria, southern Germany. The red star indicates the Buttenheim clay pit from which late Pliensbachian otoliths have been obtained. The yellow stars refer to locations sampled by Schröder (1956).

clay pit are the Lower Jurassic Amaltheenton Formation (upper Pliensbachian) and the Posidonia Shale (lower and middle Toarcian). All studied otoliths were obtained from the upper Pliensbachian Amaltheenton Formation, which consists of about 35 m thick homogenous grey claystone with intercalations of calcareous concretions.

The section is divided by four thin beds representing short phases of reworking by high water energy resulting from low-stand sea levels that caused winnowing of small grain sizes and enrichment of the reworked concretions (see Keupp and Schobert 2015; Keupp et al. 2016a, 2016b) (Fig. 2). The stratigraphic boundary between the top of the Margaritatus ammonite zone (Gibbosus subzone) and the basal Spinatum ammonite zone (Apyrenum subzone) is marked by the "pyrite-bed" that contains large ammonites of Amaltheus margaritatus up to 60 cm in size as well as the first Amaltheus salebrosus and Pleuroceras solare. This horizon is further characterized by an enrichment of small calcareous nodules of 1-4 cm in diameter that exhibit bioerosive scratch marks on the surface. The second reworking horizon, the "Quellhorizont" (spring horizon), marks the stratigraphic boundary between the Apyrenum subzone and the Hawskerense subzone, and bears the first Pleuroceras spinatum. The third reworking horizon, the so-called echinid-pectinid-bed (EPH), is characterized by a pebbly coquina and large reworked calcareous nodules that are extensively settled by a diverse association of hardground settlers (fungi, sessile foraminifers, serpulids, brachiopods, bryozoans, phoronids, cirripeds, rhabdopleurids, etc.; Keupp 2021a, c). The top of the Amaltheenton facies is marked by a fourth distinct reworking horizon, the "Bollernbank," which contains mass occurrences of belemnite rostra and reworked nodules



**Figure 2.** Stratigraphic scheme for the Buttenheim clay pit after Keupp (2021a). Otolith bearing sampled intervals are the 'echinid-pectinid-bed' (EPH), the 'source-bed' (Quellhorizont) and the *Apyrenum* subzone.

with endolithic borings of bivalves. Some of the nodules ("Hiatus-Konkretionen" sensu Voigt 1968) continued to aggregate during the onset of the bituminous shale formation of the Toarcian Oceanic Anoxic Event following a sedimentation gap of about 150 ky (Keupp 2021a).

The condensed sections between the first three reworking horizons are fossil rich and comprise mass occurrences of ammonites and other fossils. They represent sea level highstands with reduced sedimentation rates and some faunal immigration from the Tethyan Ocean in the south (see Keupp and Schweigert 2017). The section above the pyrite-bed of about 6 m thickness corresponds with the Apyrenum subzone and contains aragonitic shells of a diverse ammonite assemblages with Amaltheus laevigatus, A. margaritatus, A. salebrosus, Pleuroceras transiens, P. solare, P. apyrenum, and Amauroceras ferrugineum, which are often preserved with color patterns. Above the "Quellhorizont" the increasing fossil enrichment culminates in a mass occurrence of Pleuroceras spinatum. Most of the otoliths were obtained from the highest Pliensbachian level, where the EPH was about 2 m below the "Bollernbank" (333 out of 351 studied specimens); two are from the "Quellhorizont" and 14 were collected in the Apyrenum subzone. The otoliths are neomorphed in calcite from their presumed original composition in aragonite. The calcification has resulted in a more stable nature of the otoliths, even those with delicate and thin features, and has made them more resistant to mechanical recovery. Sometimes, healed fractures can be observed. On the downside, however, the calcite neoformation has sometimes resulted in incrustations on the surface of the otolith or creation of surface rugosity that partly obliterates morphological features.

Most of the material described by Schröder (1956) was collected from temporary outcrops in the vicinity of Scheßlitz, northeast of Bamberg. The transitional section of uppermost Toarcian and lowermost Aalenian was temporarily excavated along the riverbank of the small Leithenbach stream to the southeast of the village Kremmeldorf. Two additional localities of a similar stratigraphic position were mentioned without further details: Peulendorf near Scheßlitz (lower Aalenian) and Freiahorn, which is about 8 km north of Pottenstein (upper Toarcian). A landslide along the steep Middle Jurassic sandstone slopes of the Deisterbach valley, southeast of Pünzendorf and about 15 km east of Bamberg temporarily exposed lower Callovian clay containing pyritized ammonite molds (the so called "Goldschnecken") that are iridescent due to a thin limonitic skin. The stratigraphic position of the exposed strata was based on the occurrence of Macrocephalites and Hecticoceras (Schröder 1956). A single otolith (Otolithus kolbi) has been described from the Amaltheenton facies (Spinatum zone) from Teufelsgraben near Forth, east of Erlangen, at the banks of the small Schwabach river.

A good proportion of Schröder's type-material was recovered from the collection of the Geological Institute of the University of Erlangen, mostly from Kremmeldorf and Pünzendorf. The type specimens, including holotypes, were recovered from 14 out of 16 species described by Schröder and from otoliths he placed in Otolithus cf. ornatus Weiler, 1953. Not accounted for are the specimens pertaining to Otolithus liasicus and Otolithus kolbi. Most of Schröder's otoliths are rather small (< 1.5 to 1 mm in length) and, therefore, pose problems for reliable identification, as we discuss in the descriptive section. Other specimens are incomplete, have encrusted surfaces, or are otherwise damaged; thus, we found that only a relatively small fraction of otolith specimens was preserved well enough to serve as type specimens. The registration numbers on the recovered microslides do not match the numbers assigned in Schröder's publication. However, a comparison of the specimens with his drawings allowed for reliable correlation. In addition, Schröder apparently colored in red the labels of the specimens that are denoted in his work as holotypes. Thus, now only the Jurassic otoliths described by Weiler (1953) and two species described by Schröder (1956) remain unreviewed.

# 2.2. Characterization of early Jurassic otoliths and methodology

The otolith terminology follows Koken (1884), with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978). Three patterns of otolith morphologies have been observed in the early Jurassic: the *Leptolepis*-pattern, the *Xenoleptolepis*-pattern and the *Archaeotolithus*-pattern. Two of these patterns are observed in the Jurassic sediments of Franconia, namely the *Leptolepis*- and *Archaeotolithus*-patterns. The *Xenoleptolepis*-pattern has only been found in the early Jurassic of England. The two patterns identified in Franconia differ significantly, and each requires specific methods for their characterization.

The Leptolepis-pattern is characterized by a straight sulcus with a widened ostium, which is poorly defined against the cauda, and a vague, undifferentiated, and often poorly discernable colliculum. The rostrum is massive and long while the antirostrum is minute. The ostium opens to the anterior-dorsal rim along the entire stretch of the rostrum, but its colliculum is often separated from the predorsal rim of the otolith by a shallow ridge, which Schröder (1956) termed "crista anterior". Morphometric measurements are made for otolith length (OL), otolith height (OH), and otolith thickness (OT). The true length of the rostrum is measured from its tip to the tip of the antirostrum/termination of the upper margin of the ostium and is projected along the axis of the otolith. Due to their poorly defined ostium and cauda, their length cannot be measured, but their maximal height (OsH and CaH respectively) and the total length of the sulcus (SuL) is measurable.

The Archaeotolithus-pattern differs considerably and is characterized by a triangular otolith shape and an eccentrically positioned, dorsally shifted sulcus with vague margins and unclear distinction into ostium and cauda. The sulcus is often curved anteriorly and posteriorly in a manner that makes measuring difficult. Furthermore, the sulcus is open anteriorly and posteriorly it reaches very close to the posterior tip of the otolith; therefore, measurements of the length of the sulcus do not contain diagnostic value and are omitted. The length of the ostium and cauda (OsL and CaL) can be measured but is not very accurate, so the absolute values should be regarded with some caution. This leaves only OL, OH and OT as reliable measurements in these otoliths.

All otoliths were studied with a reflected-light microscope. Photographs were taken remotely controlled from a computer with a Canon EOS 1000 mounted on the phototube of a Wild M400 photomacroscope, and were captured at regular field-of-depth levels for each view. The individual photographs of each view were stacked using Helicon Soft's Helicon Focus software. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast, balance exposition, or retouch small inconsistencies, such as sand grains, incrustations, or pigmentation spots, insofar as doing so without altering the otolith morphology was possible.

### 2.3. Depository

Types, other photographed specimens, along with a selection of additional specimens, are deposited in the Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayrische Staatssammlung für Paläontologie und Geologie in München. Schröder's collection is cataloged under SNSB-BSPG 2022 III 1–62, and the Buttenheim collection is cataloged under SNSB-BSPG 2022 IV 1–18. Other specimens are kept in the private collection of B. Doppelstein, Berlin, B.Steber, Leibersdorf and in the collection of the senior author.

### 3. Results

### 3.1. Systematics

**Remarks.** The description of fossil otolith-based taxa principally represents a parataxonomy with taxa established by articulated skeletons. The risks of parataxonomy actually occurring varies greatly in the fossil record. For instance it is low for many young Cenozoic strata, for regions such as New Zealand where there is an abundance of otolith data but very few articulated skeletons, and for certain systematic groups such as the Ophidiiformes where fossil otolith data significantly prevail over skeletal material. In the case of Jurassic teleosts, however, there is a considerable wealth of skeletal data and relatively limited data of otoliths. The cause for this discrepancy may be the adverse effects of diagenesis over a long period of geological time for aragonitic fossils such as otoliths.

One aspect hampering the identifications of Jurassic otoliths is the fact that only a single case exists in which otoliths of fishes where were found *in situ*, namely in *Leptolepis normandica* (see Delsate 1997). This is the only otolith-based taxa from the early Jurassic that can be related to a skeletal record. Hesse (2014) figured another case of an otolith *in situ* in a fish identified as *Leptolepis* sp. from the lower Toarcian of the clay pit Klein Lehmhagen near Grimmen, western Pomerania. Unfortunately, this specimen is exposed only from the outside, but its outline suggests that it also represents *L. normandica*. The low level of morphological diversity of the early teleost otoliths also does not allow for a comparable level of phylogenetical evaluation such as skeletal material (see, e.g., Arratia 1996, 1997, 2004; López-Arbarello et al. 2008; Guinot and Cavin 2015).

The following section complements the review of Jurassic to early Cretaceous otoliths by Schwarzhans (2018). Species contained in that review are not described in detail and are only characterized by differential diagnoses. Only new species are described in full. Due to the relatively imprecise documentation in the publications of Weiler (1953) and Schröder (1956), we recommend not using names of not revised species. A specific consequence is the (temporary) suppression of *Leptolepis ornatus* (Weiler, 1953) as used in Schwarzhans (2018) and its replacement with *Leptolepis curvisulcatus* (Schröder, 1956) following our current review below.

Class Osteichthyes Huxley, 1880 Subclass Actinopterygii sensu Goodrich, 1930 Division Teleostei Müller, 1885 Order Leptolepidiformes s.l. Nicholson & Lydekker, 1889 Family Leptolepididae s.l. Nicholson & Lydekker, 1889 Genus *Leptolepis* Agassiz, 1832

### Leptolepis normandica Nybelin, 1962

Plate 1, figs 1-15

1956 Otolithus cf. ornatus Weiler, 1953 - Schröder: pl. 6, figs 1–3. 1956 Otolithus opalini - Schröder: pl. 6, fig. 9 (non figs 7–8).

- 1956 Otolithus cristatus Schröder: pl. 6, figs 13-14.
- 1956 Otolithus vastus Schröder: pl. 7, figs 36-38.
- 1956 Otolithus (Lycopteridarum?) brevis Weiler: pl. 3, figs 16-19.
- 1965 Otolithus (Lycoperidarum?) brevirostris Weiler: pl. 3, figs 20-23.
- ?1965 Otolithus (Lycopteridarum?) elegans Weiler: pl. 3, figs 24, 25, pl. 4, fig. 26.
- 1965 Otolithus (Lycopteridarum?) similis Weiler: pl. 2, figs 10– 13, pl. 3, figs 14–15.
- 1997 Leptolepis normandica Nybelin, 1962 Delsate: figs 1–5, pl. 1, fig. 4, pl. 2, figs 5–9 (otoliths *in situ*).
- 2013 Leptolepis normandica Nybelin, 1962 Nolf: pl. 6.
- 2014 Otolithus (Lycopteroidarum?) similis Weiler, 1965 Hesse: fig. 18A-G.
- 2014 Otolithus (Lycopteroidarum?) brevis Weiler, 1965 Hesse: fig. 19A-F.
- 2014 Otolithus (Lycopteroidarum?) ornatus Weiler, 1953 Hesse: fig. 20A-D.
- 2014 Otolithus (inc. sed.) sp. 1 Hesse: fig. 21A-C.
- ?2014 Otolithus (inc. sed.) sp. 2 Hesse: fig. 22A-B.
- 2014 Otolithus (inc.sed.) sp. 3 Hesse: fig. 23A.
- 2014 Otolithus (inc. sed.) sp. 5 Hesse: fig. 25A.
- ?2014 Leptolepis sp. Hesse: fig. 32 (otolith in situ).
- 2018 Leptolepis normandica Nybelin, 1962 Schwarzhans: fig. 1C-H.

2021b Leptolepis normandica Nybelin, 1962 - Keupp: fig. 9.3 B.

Material. 264 specimens: 251 specimens from the late Pliensbachian of Buttenheim: 8 specimens Apyrenum subzone (figured specimen SNSB-BSPG 2022 IV 1, Plate 1, fig. 10), 1 specimen "Quellhorizon" (figured specimen SNSB-BSPG 2022 IV 2, Plate 1, fig. 9), 242 specimens Hawkerense subzone (figured specimen SNSB-BSPG 2022 IV 3, Plate 1, figs 1-8, 11); 13 specimens from Schröder's collection from the late Toarcian to early Aalenian: paratype of Ot. cristatus from Kremmeldorf (SNSB-BSPG 2022 III 5, Plate 1, fig. 12), 4 specimens designated as Ot. cf. ornatus with 3 from Kremmeldorf and 1 from Peulendorf (SNSB-BSPG 2022 III 11-13), 3 paratypes of Ot. opalini from Kremmeldorf (SNSB-BSPG 2022 III 20-22, Plate 1, fig. 13), holotype of Ot. vastus from Peulendorf (SNSB-BSPG 2022 III 30, Plate 1, fig. 15), 4 paratypes of Ot. vastus from Kremmelsdorf (SNSB-BSPG 2022 III 31-34, Plate 1, fig. 14).

**Differential diagnosis.** Otoliths of *Leptolepis normandi*ca are more compressed than other coeval species of *Leptolepis* with an OL:OH ratio of 1.25-1.45 (vs. >.1.5), but less compressed than that of *L. steberae* sp. nov. (1.1-1.25). The rostrum is shorter than that of *L. buttenheimensis* sp. nov. ranging from about 30 to 36% of OL (vs. 37-45%), but longer that those of *L. steberae* sp. nov. (12-25%). The short postdorsal rim is higher than that of *L. curvisulcatus* and *L. kremmeldorfensis* and longer than that of *L. kremmeldorfensis*. The ostium tends to be wider in *L. normandica* than in coeval *Leptolepis* species except of *L. steberae* sp. nov. (OSH:CaH = 1.5-2.2 vs 1.25-1.6).

**Discussion.** Leptolepis normandica is the most common otolith-based species so far recognized in the Early Jurassic and the early Middle Jurassic (Pliensbachian to Aalenian). Its distinction from coeval species is not always easy to determine, particularly regarding L. curvisulcatus, and transitional forms exist. The type specimens of the synonymized species of Weiler (1965) and Schröder (1956) are mostly small and sometimes not very well-preserved; nevertheless, they bear the pertinent diagnostic characteristics. The specimens of this species exhibit a considerable variability, which may have led Weiler and Schröder to establish many species that can no longer be maintained after review. The variability encompasses primarily the shape of the postdorsal rim, width of the cauda and to a lesser degree its curvature, and ornamentation of the rims. Due to the large degree of variability, we have figured many specimens from Buttenheim in comparison to selected refigured specimens of Schröder. The largest specimen from Buttenheim is 2.85 mm in length; the largest specimen from Schröder's collection is 2.4 mm. Otoliths attributable to L. normandica have been found in Pliensbachian to Aalenian strata in Belgium (Nolf 2013), Luxemburg (Delsate 1997), England, and Germany.

### Leptolepis curvisulcatus (Schröder, 1956)

Plate 1, figs 15–19

1956 Otolithus curvisulcatus - Schröder: pl. 7, figs 25–27. 1956 Otolithus opalini - Schröder: pl. 6, figs 7–8 (non fig. 9). 1956 Otolithus schattenbergi - Schröder: pl. 6, figs 10–12. 2018 Leptolepis ornatus (Weiler, 1953) - Schwarzhans: fig. 1I–J, ?K.

**Material.** 15 specimens from Schröder's collection from the late Toarcian to early Aalenian: holotype of *Ot. curvisulcatus* from Kremmeldorf (SNSB-BSPG 2022 III 42, Plate 1, fig. 16) and 3 paratypes of *Ot. curvisulcatus*, thereof 2 from Kremmeldorf and 1 from Freiahorn (SNSB-BSPG 2022 III 43–45), holotype of *Ot. opalini* from Kremmeldorf (SNSB-BSPG 2022 III 16, Plate 1, fig. 19) and 3 paratypes of *Ot. opalini* from Kremmeldorf (SNSB-BSPG 2022 III 17–19, Plate 1, fig. 15), holotype of *Ot. schattenbergi* from Kremmelsdorf (SNSB-BSPG 2022 III 2, Plate 1, fig. 17), 6 paratypes of *Ot. schattenbergi* with 5 from Kremmelsdorf (SNSB-BSPG 2022 III 3–5, 47–48, Plate 1, fig. 18) and 1 from Peulendorf (SNSB-BSPG 2022 III 46).

**Differential diagnosis.** Leptolepis curvisulcatus is slightly more elongate than *L. normandica* with an OL:OH ratio of 1.4-1.6 (vs. 1.25-1.45), which is mainly caused by a relatively low postdorsal rim, which is also more rounded. Other proportions and characteristics are shared with *L. normandica*. Leptolepis curvisulcatus also differs from *L. normandica* in its longer ostium as compared to the length of its cauda, but because of the gradual transition from ostium to cauda, this feature cannot be measured unequivocally. The rounded and short postdorsal rim distinguishes *L. curvisulcatus* from the coeval *L. kremmeldorfensis*.

**Discussion.** The distinctions among the three nominal late Toarcian to Aalenian species *L. normandica*,



Plate 1. Otoliths of *Leptolepis normandica* and *L. curvisulcatus*. figs 1–15: *Leptolepis normandica* Nybelin, 1962; 1–11: From late Pliensbachian of Buttenheim, 1–8, 11: EPH horizon (SNSB-BSPG 2022 IV 3); 9: "Quellhorizon" (SNSB-BSPG 2022 IV 2); 10: *Apyrenum* subzone (SNSB-BSPG 2022 IV 1); 12: paratype of *Ot. cristatus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 5); 13: paratype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 20); 14: paratype of *Ot. vastus* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 34); 15: holotype of *Ot. vastus* from Peulendorf (SNSB-BSPG 2022 III 30). figs 15–19 *Leptolepis curvisulcatus* (Schröder, 1956); 15: paratype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 42); 16: holotype of *Ot. curvisulcatus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 42); 17: holotype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 2); 18: paratype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 47); 19: holotype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 42); 17: holotype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 2); 18: paratype of *Ot. schattenbergi* Schröder, 1956 from Kremmelsdorf (SNSB-BSPG 2022 III 47); 19: holotype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 47); 19: holotype of *Ot. opalini* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 16).

L. curvisulcatus, and L. kremmeldorfensis are all very subtle and it is possible that with more material becoming available from this time interval their nature and validity may have to be revised again. This is also because most specimens so far known from L. curvisulcatus and L. kremmeldorfensis are smaller than 1.5 mm in length and, therefore, cannot be considered morphologically mature. Schröder (1956) mentioned that the slightly curved shape of the sulcus (cauda) is a distinctive character of the species (hence the name curvisulcatus). However, this character does not seem to be reliable for its distinction from otoliths of L. normandica, and we therefore consider it to reflect a degree of variability.

The best-preserved and largest specimen that we attribute to *L. curvisulcatus* is a paratype of Schröder's *Otolithus opalini* of 2.55 mm in length (Plate 1, fig. 16), while the specimen selected as holotype represents a small and poorly preserved otolith of 1.25 mm in length (Plate 1, fig. 19). The holotype of *L. curvisulcatus* is the next best-preserved specimen of 2.25 mm in length, and we have thus chosen this name to represent this nominal species. Schwarzhans (2018) could not review Schröder's specimens and attributed similar specimens from the same stratigraphic interval to *L. ornatus* (Weiler, 1953). Unfortunately, Weiler's type-material has not been located and is not available for revision. His documentation is rather indistinct, so we therefore propose no longer using this name and instead refer to *L. curvisulcatus*.

#### Leptolepis buttenheimensis sp. nov.

http://zoobank.org/A335ABA4-315F-49F6-B9D7-11CD0F8CED66 Plate 2, figs 1-7

2021b Leptolepis ornatus (Weiler, 1953) - Keupp: fig. 9.3 A,C.

**Etymology.** Named after the type-locality Buttenheim near Bamberg, Franconia.

**Holotype.** SNSB-BSPG 2022 IV 4 (Plate 2, fig. 1), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 11 specimens: 10 specimens same data as holotype (SNSB-BSPG 2022 IV 5, Plate 2, figs 2–5, 7), 1 specimen same location, *Apyrenum* subzone (SNSB-BSPG 2022 IV 6, Plate 2, fig. 6).

**Additional material.** 48 specimens: same location as holotype, 45 specimens from the EPH horizon, 3 specimens from the *Apyrenum* subzone.

**Diagnosis.** OL:OH = 1.55-1.75; OH:OT = 4.0-5.0. Rostrum length 37-45% of OL. Ventral rim of ostium shallow and fading, and ostium relatively narrow; OsH:CaH = 1.25-1.6.

**Description.** Slender, thin otoliths up to 3.25 mm in length (holotype 2.65 mm). Ventral rim relatively shallow, regularly curved, deepest at or behind middle, and smooth to irregularly undulating. Rostrum very long, nearly half of otolith length. Dorsal rim behind ostial opening short, moderately elevated, broad and irregularly undulating. Posterior rim broadly rounded.

Inner face very slightly bent with distinctly supramedian sulcus. Ostium long, not expanding backward from rostrum and antirostral notch, about as long as cauda but separation poorly defined. Ventral margin of ostium indistinct, gradual, and shallow, resulting in relatively narrow ostium. Cauda very slightly flexed, terminating close to posterior tip of otolith. Dorsal depression very small, restricted to position above anterior part of cauda. No ventral furrow. Outer face flat to slightly concave with particularly thin and delicate rostrum, smooth dorsally and few indistinct furrows ventrally. Shallow umbo positioned near dorsal rim opposite to dorsal field of inner face.

**Discussion.** Leptolepis buttenheimensis is readily recognized by its elongated shape, extremely long rostrum, and very thin and delicate structure. However, a few morphologically transitional specimens exist with *L. normandica* in specimens smaller than about 2.2 mm in length, which are not considered to be fully morphologically developed. Another distinctive feature is the shallow and fading lower margin of the ostium as seen in figures 1a, 2, 3a, 4a, 5 and 7a on Plate 2. This development somewhat resembles otoliths of *Leptoelops rhenanus* (see below) where the lower margin of the ostium has become completely flattened and is level with the ventral margin of the cauda.

Leptolepis buttenheimensis is known only from the upper Pliensbachian of the type locality where it represents the second most common species.

### Leptolepis steberae sp. nov.

http://zoobank.org/35891115-EFFB-42C3-A196-CA22CEF8799D Plate 2, figs 8-12

**Etymology.** Named after Birgit Steber (Leibersdorf), who has intensely collected from the Buttenheim clay pit and provided specimens of this species which were instrumental for its recognition.

**Holotype.** SNSB-BSPG 2022 IV 13 (Plate 2, fig. 8), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 9 specimens same data as holotype (SNSB-BSPG 2022 IV 14, Plate 2, figs 9–12).

**Diagnosis.** OL:OH = 1.1-1.25. Rostrum short, its length 12-25% of OL. Ventral and dorsal rims regularly curving. Ventral rim of ostium shallow, often fading, no or very weak distinction of ostium and cauda.

**Description.** Nearly round, thin otoliths up to 2.5 mm in length (holotype 2.2 mm); OH:OT = 3.5–4.5. Ventral rim deeply and regularly curved, and smooth or intensely and finely crenulated. Rostrum short, blunt. Dorsal rim behind ostial relatively long, elevated, rounded, broad and irregularly undulating. Posterior rim broadly rounded.

Inner face distinctly bent with slightly supramedian sulcus. Ostium short, indistinctly separated from cauda, slightly expanding backward from rostrum and antirostral notch, about as long as cauda. Ventral margin of sulcus often indistinct, gradual, relatively straight with no or very feeble



Plate 2. Otoliths of *Leptolepis buttenheimensis* and *L. steberae.* figs 1–7 *Leptolepis buttenheimensis* sp. nov. from the late Pliensbachian of Buttenheim; 1: holotype SNSB-BSPG 2022 IV 4, EPH horizon; 2–7: paratypes SNSB-BSPG 2022 IV 5–6; 2–5, 7: EPH horizon;
6: *Apyrenum* subzone. figs 8–12: *Leptolepis steberae* sp. nov. from the Pliensbachian of Buttenheim, EPH horizon; 8: holotype SNSB-BSPG 2022 IV 13; 9–12: paratypes SNSB-BSPG 2022 IV 14.

indication of differentiation into ostium and cauda. Cauda straight, terminating close to posterior tip of otolith. Dorsal depression very small, restricted to position above anterior part of cauda. No ventral furrow. Outer face flat to slightly concave, with many short radial furrows particularly along ventral margin of otolith. No or very feeble postcentral umbo.

**Discussion.** *Leptolepis steberae* is a relatively rare and small species in the late Pliensbachian of Buttenheim. It

is recognized by its compressed, rounded outline with only a moderately projecting and rather blunt rostrum. Its OL:OH ratio is less than in contemporaneous congeners (1.1-1.25 vs. 1.25-175). The rostrum is shorter than in coeval *Leptolepis* species (12-25% of OL vs. 30-45%). Another typical characteristic is the nearly straight ventral margin of the sulcus, which is also often rather gradational.

### Leptolepis kremmeldorfensis (Schröder, 1956) Plate 3, figs 1–8

1956 Otolithus kremmeldorfensis - Schröder: pl. 7, figs 34–35.
1956 Otolithus amygdalinus - Schröder: pl. 6, figs 4–6.
?1956 Otolithus bambergensis - Schröder: pl. 6, fig. 19, pl. 7, fig. 20.
?1956 Otolithus franconicus - Schröder: pl. 7, figs 31–33.

**Material.** 11 specimens from Schröder's collection from the late Toarcian to early Aalenian: holotype of *Ot. kremmeldor-fensis* from Kremmeldorf (SNSB-BSPG 2022 III 35, Plate 3, fig. 1) and 1 paratype from Kremmeldorf (SNSB-BSPG 2022 III 36, Plate 3, fig. 2), holotype of *Ot. amygdalinus* from Kremmeldorf (SNSB-BSPG 2022 III 14, Plate 3, fig. 3) and 1 paratype from Kremmeldorf (SNSB-BSPG 2022 III 14, Plate 3, fig. 3) and 1 paratype for *Kremmeldorf* (SNSB-BSPG 2022 III 14, Plate 3, fig. 3) and 1 paratype for *Kremmeldorf* (SNSB-BSPG 2022 III 15), 1 paratype of *Ot. bambergensis* from Freiahorn (SNSB-BSPG 2022 III 10, Plate 3, fig. 4), holotype of *Ot. franconicus* from Kremmeldorf (SNSB-BSPG 2022 III 24, Plate 3, fig. 5) and 5 paratypes, with 4 from Kremmeldorf (SNSB-BSPG 2022 III 25, 27–29, Plate 3, fig. 6) and 1 from Freiahorn (SNSB-BSPG 2022 III 26).

**Tentatively assigned specimens.** 2 poorly preserved specimens from the late Pliensbachian of Buttenheim (SNSB-BSPG 2022 IV 15, Plate 3, figs 7–8).

**Differential diagnosis.** Leptolepis kremmeldorfensis shares its otolith and sulcus proportions with the coeval *L*. *curvisulcatus* and differs in its flat, low, and relatively long postdorsal rim. However, small specimens below 1 mm in length, which have been described as *Ot. bambergensis* and *Ot. franconcius*, mostly show a more rounded postdorsal rim similar to the status in *L. normandica*. Therefore, they are only tentatively attributed and could in fact represent juveniles of any other *Leptolepis* species.

**Discussion.** As with *L. curvisulcatus*, the validity of *L. kremmeldorfensis* should be regarded as provisional until larger otoliths have become available from the region and stratigraphic interval. Although a single larger otolith of nearly 3 mm in length, designated as *Ot. amygdalinus* by Schröder (1956), shares the characteristic shape of the postdorsal rim, it is otherwise too eroded to make a firm identification. Two poorly preserved specimens from the late Pliensbachian of Buttenheim are tentatively accounted for in *L. kremmeldorfensis* because of their relatively shallow and long postdorsal rim. If verified, it would extend the stratigraphic reach of the species significantly.

#### Leptolepis inaequalis (Weiler, 1954)

Plate 3, figs 9-11

1954 Otolithus (inc.sed.) inaequalis - Weiler: pl. 4, fig. 170.
1956 Otolithus calloviensis - Schröder: pl. 6, figs 17–18.
1956 Otolithus pünzendorfensis - Schröder: pl. 7, fig. 39.
2018 Leptolepis inaequalis (Weiler, 1954) - Schwarzhans: fig. 2E.

**Material.** 4 specimens: Weiler's holotype of *Ot. inaequalis* from the Callovian to Oxfordian of Kandern, Baden-Würtemberg (SMF P.3067, refigured in Plate 3, fig. 11); 3 specimens from Schröder's collection from the early Callovian:

**Differential diagnosis.** Leptolepis inaequalis is characterized by being very thin with nearly flat inner and outer faces. It shares these features only with *L. macrocephalus* (see below), from which it differs in its slightly slenderer shape (OL:OH = 1.5 vs. 1.35-1.4) and its shallow and rather long postdorsal rim (vs. rounded and expanded).

**Discussion.** Due to the fragile nature of these thin and delicate otoliths, only one complete specimen of *L. inaequalis* is known: the holotype from Weiler. All three specimens from Schröder, which we synonymized with *L. inaequalis*, are incomplete because they lack the rostrum, but they do show the typical flat inner face in combination with the shallow and long postdorsal rim. Schröder's drawing of the holotype of *Ot. calloviensis* indicates a complete specimen, but the one found in his collection is slightly damaged, which possibly happened after the drawing was made.

# Leptolepis macrocephalus (Schröder, 1956)

Plate 3, figs 12–13

1956 Otolithus macrocephali - Schröder: pl. 7, fig. 40. 1956 Otolithus guttaeformis - Schröder: pl. 6, figs 15–16.

**Material.** 3 specimens from Schröder's collection from the early Callovian of Pünzendorf: holotype of *Ot. macrocephalus* (emended spelling, SNSB-BSPG 2022 III 1, Plate 3, fig. 13), holotype of *Ot. guttaeformis* (SNSB-BSPG 2022 III 6, Plate 3, fig. 12) and 1 paratype (SNSB-BSPG 2022 III 7).

**Differential diagnosis.** Leptolepis macrocephalus differs from the coeval *L. inaequalis* in its more compressed shape, which is exhibited by a deeper ventral rim and a more expanded postdorsal rim and is expressed in the OL:OH ratio of 1.35–1.4 (vs. 1.5). It shares with *L. inaequalis* completely flat inner and outer faces, features that distinguish both species from all other known *Leptolepis* otoliths.

**Discussion.** Leptolepis macrocephalus and L. inaequalis form a small group of otoliths with a special trait of having flat inner and outer faces. They occur during the Callovian and possibly the early Oxfordian. Their attribution to the genus is therefore less certain than that of *Leptolepis* otoliths from the Early Jurassic (see above).

### Order Elopiformes Jordan, 1923 Family indet. Genus *Leptoelops* Schwarzhans, 2018

Leptoelops rhenanus (Weiler, 1954) Plate 3, figs 14–16

1954 Otolithus (Lycopteridarum?) rhenanus - Weiler: pl. 1, fig. 18. 1956 Otolithus rectisulcatus - Schröder: pl. 6, fig. 21. ?1956 Otolithus scissus - Schröder: pl. 7, figs 29–30. 2018 Leptoelops rhenanus (Weiler, 1954) - Schwarzhans: fig. 50.



Plate 3. Otoliths of *Leptolepis kremmeldorfensis*, *L. inaequalis*, *L. macrocephalus*, and *Leptoleps rhenanus*. figs 1–6: *Leptolepis kremmeldorfensis* (Schröder, 1956); 1: holotype of *Ot. kremmeldorfensis* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 36); 3: holotype of *Ot. amygdalinus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 36); 3: holotype of *Ot. amygdalinus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 14); 4: paratype of *Ot. bambergensis* Schröder, 1956 from Freiahorn (SNSB-BSPG 2022 III 10); 5: holotype of *Ot. franconicus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 24); 6: paratype of *Ot. franconicus* Schröder, 1956 from Kremmeldorf (SNSB-BSPG 2022 III 27). figs 7, 8: *Leptolepis* cf. *kremmeldorfensis* (Schröder, 1956), from the late Pliensbachian of Buttenheim, SNSB-BSPG 2022 IV 15. figs 9–11: *Leptolepis inaequalis* (Weiler, 1954); 9: holotype of *Ot. puenzendorfensis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 39); 10: holotype of *Ot. calloviensis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 39); 12: holotype of *Ot. guttaeformis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 39); 12: holotype of *Ot. guttaeformis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 39); 12: holotype of *Ot. guttaeformis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 3); 12: holotype of *Ot. macrocephalus* (Schröder, 1956); 12: holotype of *Ot. guttaeformis* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 6); 13: holotype of *Ot. macrocephalus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 1). figs 14–16: *Leptolepis rhenanus* (Weiler, 1954); 14: holotype of *Ot. rhenanus* Weiler, 1954 from the Callovian of well Bruchsal D 205 (core from 482 to 487 m) near Weingarten, Baden-Württemberg (SMF P.2953); 15: holotype of *Ot. rectisulcatus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 37); 16: holotype of *Ot. scissus* Schröder, 1956 from Pünzendorf (SNSB-BSPG 2022 III 40).

**Material.** 5 specimens: Weiler's holotype of *Ot. rhenanus* from the Callovian of well Bruchsal D 205 (core from 482 to 487 m) near Weingarten, Baden-Würtemberg (SMF P.2953, refigured in Plate 3, fig. 14); 4 specimens from Schröder's collection from the early Callovian of Pünzendorf: holotype of *Ot. rectisulcatus* (SNSB-BSPG 2022 III 37, Plate 3, fig. 15) and 1 paratype (SNSB-BSPG 2022 III 38), holotype of *Ot. scissus* (SNSB-BSPG 2022 III 40, Plate 3, fig. 16) and 1 paratype (SNSB-BSPG 2022 III 41).

**Diagnosis (from Schwarzhans 2018).** Thin, elongate otolith with an OL:OH ratio of 2.1. Rostrum about 40% of OL. Ostium dorsally open, its ventral margin level with the ventral margin of its cauda. Outer face with radial furrows near ventral rim.

**Discussion.** Leptoelops rhenanus is a very characteristic otolith that differs readily from Leptolepis otoliths in both its very slender shape and its absence of a ventrally widened ostium. Schröder's holotype of *Ot. rectisulcatus* lacks the rostrum, but otherwise it largely resembles Weiler's holotype of *L. rhenanus*. The specimens of *Ot. scissus* are also fragmentary, less well-preserved, and much smaller in size. They differ somewhat in the posteriorly elevated dorsal rim and a slight bend in the cauda. We consider these features aspects of an ontogenetical allometry, but we are aware that they could also indicate the presence of another species in the Callovian. We have therefore only tentatively attributed *Ot. scissus* to *L. rhenanus*, subject to finding additional and better-preserved specimens in the future.

### Actinopterygii indet. Family indet.

### Genus Archaeotolithus Stolley, 1912

**Type-species.** Designated here as *Archaeotolithus trigonalis* Stolley, 1912. Stolley (1912) established *Archaeotolithus* as an otolith-based genus, or, in his words, as a new "typus" (typ. nov.). He may have been considering *Archaeotolithus* to represent a collective group genus comparable to *Otolithus* as introduced by Koken (1884; see Schwarzhans 2012 in Addendum). However, we are of the opinion that the otoliths Stolley attributed to *Archaeotolithus* indeed represent a very specific and unique morphology, and, therefore, a formal otolith-based genus for this pattern is well-justified. This point also generates the need to select a type-species for the redefined otolith-based genus of Stolley (1912), which we represent here.

**Diagnosis.** Otoliths with a triangular shape that can reach about 7 mm in length. The three corners are the preventral, postventral and middorsal angles. Inner face convex; outer face flat, often with fine radial furrows starting from the middorsal angle. Otolith nucleus distinctly eccentric, visible on the outer face at the middorsal angle. Inner face with distinctly supramedian sulcus with often vague margins, particularly its ventral margin. Ostium and cauda intergrading and poorly distinguished. Ostium open anteriorly, its ventral margin deeply expanding downward. Cauda narrower, slightly downward-oriented toward **Species, distribution and stratigraphic ranges.** Three species are referred here to *Archaeotolithus: A. bornholmiensis* (Malling & Grønwall, 1909) from the Pliensbachian of the isle of Bornholm, Denmark, and Franconia; *A. doppelsteini* sp. nov. from the late Pliensbachian of Franconia; and *A. trigonalis* Stolley, 1912 from the late Pliensbachian of Franconia and the Bajocian of northern Germany. Malling and Grønwall (1909) also reported two additional, presumably *Archaeotolithus*, otoliths from the Pliensbachian of Bornholm in open nomenclature, which cannot be identified from their documentation.

**Relationships.** The relationships of *Archaeotolithus* are obscure. We are not entirely certain whether it represents a sagittal otolith, although this appears likely because of the presence of a sulcus on what is perceived as the inner face of the otoliths, or a lapillus. In any case its peculiar and highly characteristic morphology does not relate to that of any known teleost.

Three kinds of vaguely similar otoliths have also been reported from the Late Jurassic freshwater sediments of eastern Australia (Schwarzhans et al. 2019). This Lagerstätte is of interest because it bears four taxa of pholidophoriforms, one macrosemiiform and one chondrostean in addition to the most common fish, Cavenderichthys talbragarensis (Woodward, 1895), a "primitve" teleost. Otoliths in situ are only known from the latter, probably due to a function of its overwhelming abundance (Schwarzhans et al. 2019). It thus appears likely that the three Australian Archaeotolithus look-alike morphotypes belong to pholidophoriforms instead of chondrosteans (palaeonisciforms) as suggested by Schwarzhans (2018). Indeed, the Archaeotolithus morphotype best resembles the otoliths of extant lepisosteiforms (for figures, see Nolf 2013 and Schwarzhans et al. 2019). Therefore, the most likely candidates for relationships with Archaeotolithus may be expected in Ginglymodi or very basal Teleostei below the Leptolepidiformes level. We hope that otoliths will eventually be found in situ and this enigmatic otolith morphology can be reliably related to a systematic context.

# Archaeotolithus bornholmiensis (Malling & Grønwall, 1909)

Plate 4, fig. 1

- 1909 Otolithus bornholmiensis Malling & Grønwall: pl. 11, figs 14–16.
- 1912 Arcaeotolithus bornholmiensis (Malling & Grønwall, 1909) -Stolley: pl. 7, figs 4–5.

?2014 archaeotoliths group 1 - Hesse: fig. 28A-B.

**Material.** 1 specimen from the late Pliensbachian, *Hawkerense* subzone, of Buttenheim (SNSB-BSPG 2022 IV 7, Plate 4, fig. 1).

**Differential diagnosis.** Archaeotolithus bornholmiensis is the only species in the genus with almost no indication of a sulcus and further differs from its congeners in the



Plate 4. Otoliths of Archaeotolithus. fig. 1: Achaeotolithus bornholmiensis (Malling & Grønwall, 1909), from the late Pliensbachian of Buttenheim, holotype SNSB-BSPG 2022 IV 7, EPH horizon. figs 2–4: Archaeotolithus doppelsteini sp. nov., from the late Pliensbachian of Buttenheim, EPH horizon; 2: holotype SNSB-BSPG 2022 IV 8; 3–4: paratypes SNSB-BSPG 2022 IV 9. figs 5–7: Archaeotolithus trigonalis Stolley, 1912, from the late Pliensbachian of Buttenheim, EPH horizon, figured specimens SNSB-BSPG 2022 IV 12.

more strongly convex inner face. It is thus also the one most resembling the characteristics of a lapillus.

#### Archaeotolithus doppelsteini sp. nov.

http://zoobank.org/6CF0B3D2-345A-4225-BC1E-769F8444169F Plate 4, figs 2-4

2021b Lapillus unbekannter Zuordnung - Keupp: fig. 9.3 D.

**Etymology.** Named after Bernd Doppelstein (Berlin), who has intensely collected from the Buttenheim clay pit and provided the largest specimen of this species.

**Holotype.** SNSB-BSPG 2022 IV 8 (Plate 4, fig. 2), Clay pit near Buttenheim, upper Pliensbachian, *Hawkerense* subzone, EPH horizon.

**Paratypes.** 4 specimens same data as holotype (SNSB-BSPG 2022 IV 9, Plate 4, figs 3–4).

**Diagnosis.** OL:OH = 0.9-0.93; OH:OT = 2.8-3.6. Ventral rim deeply curved, middorsal angle with small process. Outer face with complex pattern of subvertical furrows.

**Description.** Very high-bodied otoliths up to 3.25 mm in length (holotype 2.2 mm) with rounded ventral rim and rounded postventral angle. Middorsal angle with small projection. Anterior and posterior rims smooth, ventral rim regularly and coarsely crenulated.

Inner face moderately convex with distinct supramedian positioned sulcus. Dorsal margin of sulcus relatively well-defined, ventral margin gradational and indistinct. Sulcus anteriorly open and ventrally widened, posteriorly curved slightly downward and terminating close to rounded postventral angle. Distinction in ostium and cauda indistinct or with broad shallow ventral bend at junction; OsL:CaL notably variable, ranging from 0.7 to 1.2. Outer face flat, with set of opposing subvertical furrows on preand postventral fields, diminishing in intensity with size.

**Discussion.** The relatively small holotype is well preserved whereas the large figured paratype (Plate 4, fig. 4) has severe incrustations across much of the sulcus that obliterate part of its morphology. *Archaeotolithus doppelsteini* is readily distinguished from its congeners by its deep ventral rim, rounded postventral angle, and process of the middorsal angle. It differs from *A. trigonalis* in its higher body shape, expressed in the lower OL:OH ratio (0.9–0.93 vs. 1.05–1.12) and the different proportions of the ratio OsL:CaL (0.7–1.2 vs. 0.3–0.4). Furthermore, the ornamentation of the outer face differs from that observed in its congeners.

### Archaeotolithus trigonalis Stolley, 1912

Plate 4, figs 5-7

1912 Archaeotolithus trigonalis - Stolley: pl. 7, figs 1–3.
2014 archaeotoliths group 2 - Hesse: fig. 29A–E.
2018 Archaeotolithus trigonalis Stolley, 1912 - Schwarzhans: fig. 8K.

**Material.** 25 specimens from the late Pliensbachian of Buttenheim: 2 specimens *Apyrenum* subzone (SNSB-BSPG 2022 IV 10), 1 specimen "Quellhorizon" (SNSB-BSPG 2022 IV 11), 22 specimens *Hawkerense* subzone (figured specimens SNSB-BSPG 2022 IV 12, Plate 4, figs 5–7).

**Differential diagnosis.** Otoliths with nearly equilateral triangular shape similar to *A. bornholmiensis* but distinctly less high-bodied than *A. doppelsteini. Archaeotolithus trigonalis* differs from *A. bornholmiensis* in being thinner, having a smooth outer face with exposed growth rings (vs with fine radial furrows starting from the middorsal angle), and showing a clear sulcus. It differs from *A. doppelsteini* not only in the otolith proportions and shape but also in the very short and strongly ventrally extended ostium and the rather straight, inclined cauda.

**Discussion.** Archaeotolithus trigonalis is the most common species of the genus in Buttenheim. It almost always shows some kind of incrustation on the inner face, which often obliterates the sulcus morphology. However, in some instances, such as the figured specimens, it can still be reliably identified. A similar incrustation is also seen on the large paratype of *A. doppelsteini*, which could have been caused by organic material that was attached to it during the early process of fossilization and mineralization.

### 3.2 Early teleost otolith morphogenesis

The earliest teleost otoliths are known from the late Sinemurian (Weiler 1965; Schwarzhans 2018), which is consistent with the first occurrence of leptolepidid skeletons in the fossil record (Arratia 1997). Only three otolith morphologies are known from the entire Liassic (early Jurassic): the Leptolepis-pattern, the Xenoleptolepis-pattern and the Archaeotolithus-pattern. Of these three, only the Leptolepis and the Archaeotolithus morphotypes have been found in Franconia. Liassic otoliths have so far only been found in England, Denmark, Belgium, Luxemburg, and Germany (Fig. 3). These occurrences reflect data from a rather restricted region and mostly comparable environments. Therefore, it is not surprising that the individual faunal assemblages are relatively similar, except for Xenoleptolepis that is absent in the southern German localities and Archaeotolithus that is absent in England.

The stratigraphic ranges and speciation levels vary considerably among the three morphotypes. Xenoleptolepis is known from two species: X. withersi from the Sinemurian and early Pliensbachian (Fig. 4) and a second species known from the single holotype, X. oncorhynchoides (Weiler, 1954), from the basal Cretaceous (Berriasian) of northern Germany. Archaeotolithus comprises three species ranging from the Pliensbachian to the Bajocian (Fig. 4), which all occur in parallel during the late Pliensbachian of Franconia. We don't know if similar morphologies found in freshwater otoliths from the Late Jurassic of Australia may represent a related group of fishes or not. Both the Xenoleptolepis and Archaeotolithus otolith morphologies have so far not been found in situ; therefore, their systematic position is unresolved. Xenoleptolepis most likely represents a stem teleost related to the Leptolepididae. The



**Figure 3.** Paleogeographic map of Europe at 175 Ma based on Blakey (2021). Stars indicate locations with otoliths from the Early to Middle Jurassic. The big violet star indicates the finding of otoliths *in situ* in skeletons of *Leptolepis normandica* from Delsate (1997). The red stars indicate localities from which otoliths have been studied for this article. Each star can represent more than one locality.

relationships of *Archaeotolithus* are completely obscure (see above). In any case, it is obvious that both morphotypes existed only across a restricted time period and do not exhibit any substantial degree of diversification.

The situation is somewhat different for the Leptolepis morphotype. Initially, it occurs more or less in parallel with the two other morphotypes. During the early Jurassic it also shows limited diversity (Fig. 4). The early Jurassic speciation level is low, with a maximum of five Leptolepis species occurring simultaneously (Nybelin 1974). Some of those nominal species are currently considered only tentatively valid, such as Leptolepis kremmeldorfensis or L. curvisulcatus. Another aspect is the relatively long stratigraphic range of the key species L. normandica, which is based on both skeletal and otolith material. Once otoliths have been found in situ, it is likely that one of the other Early Jurassic otolith-based Leptolepis species will represent the iconic skeleton-based L. coryphaenoides (Bronn, 1830). The situation changes drastically during the Middle Jurassic. Otolith finds in the Aalenian and Bajocian are relatively sparse, but in the Bathonian the number of species with a *Leptolepis*-type otolith morphology increase rapidly to 11 species that occur more or less simultaneously (Fig. 4). This increase brings with it some variations in the morphological pattern that Schwarzhans (2018) attributed to a set of different extinct otolith-based genera. However, the disparity in morphological diversity is still relatively low compared to the taxonomic diversity. Obviously, diversity spread faster than disparity.

Unfortunately, we do not know how the beginning disparity during the Bathonian matches with the early separation of clades seen in the skeletal record (Nybelin 1975; Arratia 1996, 1997; López-Arbarello et al. 2008; Guinot and Cavin 2015) because there is virtually no linkage with otoliths *in situ* during that time interval. The only exception is an otolith recovered "quasi" *in situ* in the phosphatized solution residue of a leptolepid head carved out from the stomach of a pholidophorid predator in a rock of Callovian age (Patterson 1975). Stinton (cited by Nolf 1985) considered this otolith to represent *L. coryphaenoides* and his rather schematic drawing was first published by Nolf (1985 and 2013). The otolith resembles the otolith-based



200 —

**Figure 4.** Stratigraphic chart depicting ranges of Early to Middle Jurassic otolith-based fish species. Red bars reflect ranges of localities from which otoliths have been studied for this article. The red asterisk indicates the stratigraphic position of the fishes with otoliths *in situ* described by Delsate (1997). Chronostratigraphy and ammonite zonation after Gradstein et al. (2020).

species *L. praeelops* (Stinton, 1968) from the Bathonian. It is unlikely to represent *L. coryphaenoides*, which does not extend so far up into the Middle Jurassic as Delsate (1997) noted. Schwarzhans (2018) has tentatively related some of the otolith morphologies found in the Bathonian to stem elopiforms (*Protoelops, Leptoelops*) and stem osteoglossiforms (*Archaeglossus*). Others, such as *Doggerichthys* and *Sphaeronchus* cannot be associated with any degree of likelihood.

Another question is whether the observed explosive burst of diversity associated with some degree of increase in disparity in the Bathonian otoliths represents a real evolutionary signal or is the result of a Lagerstätten effect. Guinot and Cavin (2015) analyzed a similar rapid increase in diversity observed in skeletal teleost remains of the Late Jurassic (based on Arratia 1997). They concluded that this apparent burst would in all likelihood represent a Lagerstätten effect. The rapid increase of otolith-based teleost species during the Bathonian relates to two specific localities in England described by Stinton (in Stinton and Torrens 1968). Stinton counted 368 otoliths, which have been reviewed and refigured by Schwarzhans (2018) and are of exceptionally good preservation. These finds are definitely apt to suspect a Lagerstätten effect. However, about as many otoliths (351) have been retrieved from the late Pliensbachian of Buttenheim that are predominantly also of good preservation quality and which only represent three *Leptolepis* and three *Archaeotolithus* species.

Therefore, when comparing the Bathonian assemblage described by Stinton and the Pliensbachian from Buttenheim described here, it becomes clear that the increase of teleost otolith-based species observed in the Bathonian must represent a real phylogenetic signal.

The question is when the evolutionary event took place. Otolith data from the Toarcian, Aalenian and Bajocian are sparse. The largest otolith assemblage studied in this interval is probably the one from the latest Toarcian to early Aalenian that was originally available to Schröder and amounted to 55 specimens. Most of the specimens are relatively small and poorly preserved; nevertheless, they seem to represent only three teleost species. Therefore, it seems that the burst of diversity happened between the early Aalenian and the late Bathonian, over a time interval of about 7 mya. This observation would also indicate that the Bathonian speciation level actually represents a window into early teleost evolution from an otolith perspective. Conversely, the teleost otolith associations of the Pliensbachian and Toarcian are characterized by few common and long ranging species as would typically be expected during an early evolutionary phase. Combined, the now known otolith record from the early and middle Jurassic represents a first view into the early teleost otolith morphogenesis.

# 4. Conclusions and outlook

The knowledge of Mesozoic otoliths has steadily increased in recent years and the data of older works have been reviewed (Nolf 2013; Schwarzhans 2018), although the data from the Early Jurassic were still sparse. The newly collected otoliths from the late Pliensbachian of Buttenheim and the review of Schröder's specimens from the late Toarcian/early Aalenian and early Callovian filled a gap in the stratigraphic sequence and helps to better understand the otolith morphogenesis of early teleosts and associates. The main results are as follows:

- Early Jurassic stem teleost otoliths are represented by few, common and long ranging species of the genus Leptolepis. The most common one pertains to L. normandica, which was calibrated by otoliths in situ (Delsate 1997; Nolf 2013).
- Other groups of uncertain relationships such as Xenoleptolepis, another putative stem teleost, and Archaeotolithus (a "pre-leptolepidid" fish) occur simultaneously but are much less common.
- Teleost otolith diversity has dramatically increased in the late Middle Jurassic (Bathonian) and may have gotten its initial boost in the relatively short time interval between the Aalenian and Bathonian.
- The disparity in morphological diversity of early teleost otoliths during the Early to Middle Jurassic trails their taxonomic diversity and is thus not comparable to the disparity observed in fish skeletons of the Late Jurassic.

The key to a better understanding of Jurassic otoliths is the calibration of their morphology through finds of otoliths *in situ*, particularly as more otolith assemblages emerge and a denser stratigraphic and wider morphological spectrum becomes available. Unfortunately, only otoliths of *Leptolepis* and *Cavenderichthys* have so far been found *in situ* of any Jurassic fishes. We would therefore hope that our colleagues will be mindful of prospects for finding otoliths *in situ* so that more of the enigmatic otolith morphologies can in the future be tied to the skeleton-based record.

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# Ammonites and stratigraphy of the Achdorf Formation (Braunjura Group; Aalenian) at the Wochenberg hill near Schömberg-Schörzingen (W Swabian Alb, SW Germany)

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# Abstract

In sections of the Achdorf Formation at the Wochenberg hill (western Swabian Alb, SW Germany), a succession of five ammonite biohorizons is distinguished (from bottom to top): the *crassicostatum* and *viallii* biohorizons of the Lower Aalenian (Bifidatum Subzone, Opalinum Zone) and the *latiumbilicus, discoidea*  $\alpha$  and *discoidea*  $\beta$  biohorizons of the Upper Aalenian (Murchisonae Subzone, Murchisonae Zone). The herein newly introduced *viallii* biohorizon is the youngest hitherto identified biohorizon of the Opalinum Zone (Bifidatum Subzone). A lectotype is designated for *Staufenia latiumbilicus* (Quenstedt, 1886), the index ammonite of the *latiumbilicus* biohorizon. The succession of biohorizons of the Murchisonae Subzone reflects the evolution of the graphoceratid late Aalenian ammonite genera *Staufenia* and *Ludwigia*.

# Keywords

Ammonite biohorizons, correlation, Germany, Graphoceratidae, Middle Jurassic, phylogeny

# 1. Introduction

The Upper Aalenian Achdorf Formation is an up to 60 metres thick series of claystones, arenaceous claystones and occasional limestone beds that crops out in the Wutach area as well as in the adjacent western and middle Swabian Alb (Franz and Nitsch 2009). Historically, this formation was lumped with a coeval succession of ferruginous sandstones of the Eisensandstein Formation in eastern Swabia and Franconia in the more biostratigraphically defined "Braunjura  $\beta$ ". The area of eastern Swabia had been well-known for its rich and diverse fossil content, namely ammonites, recovered from the long-abandoned iron mines in the vicinity of Aalen (Quenstedt 1856–1857; Oppel 1858) and was subsequently designated as name-bearing type area of the Aalenian Stage. In these

early days of stratigraphical investigations, only few Upper Aalenian ammonites from other areas in Swabia were reported. An exception is the area of the Wochenberg hill near Schömberg-Schörzingen. The Wochenberg is a hill located a few kilometres in front of the Upper Jurassic escarpment of the Swabian Alb. It is characterized by steep forested hillsides and an almost flat plateau formerly used for agriculture. Quenstedt (1886-1887) was the first to describe ammonites from there. Lörcher (1939) studied the litho- and biostratigraphy of several sections in the vicinity of Schörzingen and provided descriptions of the strata as well as their fossil content. The lithostratigraphic section and ammonites from this area were studied in greater detail by Rieber (1963) in his monograph on the ammonites of the "Braunjura  $\beta$ ". Apart from ammonites, only few other groups of fossils were studied from the area of

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the Wochenberg hill. Recently, Weis in Weis et al. (2021) described a new species of the belemnite genus *Acrocoelites* based on specimens from the Untere Wilflingen-Bank (formerly: Comptum-Bank) of the Wochenberg hill.

Since natural outcrops along the steep hillsides of the Wochenberg only expose short intervals of the lithological succession, the complete section could only be roughly estimated in former times and the succession of ammonite faunas was still incompletely known. Moreover, extensive ammonite material housed in institutional and private collections mostly lacked detailed information about the exact locality and bed from where it was collected. These deficiencies hampered the recognition of evolutionary trends in ammonite lineages, sexual dimorphism, and changes of faunal composition through time as well as faunal migrations. Thus, the only possibility to add these missing data are excavations, where the complete succession is sampled bed-by-bed. This precise sampling of sections allows deciphering the ammonite evolution and results in a high-resolution biostratigraphy, although intraspecific variation within large samples complicates determinations.

The aim of this study, which focusses on the ammonites, is to present the scientific results of our excavations, which were executed between 2014 and 2022.

# 2. Material and methods

Our scientific excavations (2014-2018) of the Staufensis-Bank took place at the southwestern edge of the Wochenberg hill, southeast of a model airfield. Several hundred ammonites of the genera Staufenia and Ludwigia/Brasilia and a sole Planammatoceras were collected precisely bed-by-bed. Subsequently (2021-2022), the rock interval between the Untere Wilflingen-Bank and the Staufensis-Knollenlage was excavated at another section c. 20 metres further to the west of the previous one, with special focus on the ammonite-bearing Obere Wilflingen-Bank. In addition, two smaller excavations (2017, 2021) at a distance of c. 50 m and c. 170 m further southeast (in the direction to road L 435 connecting the town Schömberg and the village of Deilingen) focussed on the Untere Wilflingen-Bank. Additional sections of the Untere Wilflingen-Bank were sampled at the headwaters of the Schörzinger Starzel River and 350 m in southeastern direction, as well as along the steep escarpment of the Wochenberg hill north of road L 435.

The herein studied ammonites have been prepared mechanically using pneumatic chisels and airbrasive iron powder. All illustrated specimens are stored in the



Figure 1. Location map. The outcrops of the Middle Jurassic are marked in gray.

collection of the Staatliches Museum- für Naturkunde in

Stuttgart (acronym: SMNS). The specimens are illustrated in natural size, if not otherwise stated.

# 3. Description of the section

Our lithostratigraphic description of the uppermost Opalinuston and Achdorf formations starts from the bottom of the section. It is a combination of our recent observations and measurements and those of Rieber (1963). We studied in detail the interval from the Untere Wilflingen-Bank up to the Staufensis-Bank (sensu Rieber 1963).

# 3.1. Opalinuston Formation

Above the 'Wasserfallschichten' [Waterfall Beds] (c. 8.8 m; Rieber 1963, text-fig. 2) follows the 'sandige Tonmergel' [Sandy Clay-Marls] (8.6 m) with the 'Zopfplatten' [*Gyrochorte* Beds] (4–4.5 m); the latter are positioned in the upper half of the 'sandige Tonmergel' (Fig. 2).

# 3.2. Achdorf Formation

Untere Wilflingen-Bank [Lower Wilflingen Bed] (= uWB; c. 1.6 m; = Comptum-Bank sensu Rieber 1963)

**Figure 2.** Section at the southern slope of the Wochenberg hill (modified after Rieber 1963, fig. 2 [Profil c]; the beds below the Wilflingen-Bank were not studied). The Obere Wilflingen-Bank is separately shown in Fig. 4. (W. F. = Wedelsandstein Formation, Sow.-Ool. = Sowerbyi-Oolith, Staufensis-B. und St.-B. = Staufensis-Bank, ?Sinon-B. = ?Sinon-Bank, Ob. Wilflingen-B. und oWB = Obere Wilflingen-Bank, Unt. Wilflingen B. und uWB = Untere Wilflingen-Bank, Subz. = Subzone, Murch. = Murchisonae, Co.= Concavum, St-B = Staufensis-Bank).



The Untere Wilflingen-Bank (formerly: Comptum-Bank, see Dietze et al. 2021a) consists of a chamosite-oolitic, gray-green to dark brown marly limestone, partly rich in fossils. In our excavation sites at the southern hillside of the Wochenberg, most ammonites occurred in the well-lithified beds uWB-4 and uWB-7. The thicknesses and lithologies of individual beds are almost identical in both sections. In other outcrops at the headwaters of the Schörzinger Starzel River, the Untere Wilflingen-Bank has an overall similar thickness, but at each section it shows some variation in respect of the thickness and lithology of individual beds. Like in our two excavation sites at the Wochenberg hill, the ammonites occur in two layers located in more or less the same position within the Untere Wilflingen-Bank. The frequency of ammonites in both fossiliferous horizons varies at the various localities.

- Bed uWB-1 (0.15 m): arenaceous clayey marls with weathered lithified limestone portions, yellow to beige.
- Bed uWB-2 (0.15 m): arenaceous marly limestone, occasionally with lithified portions of strongly weathered marly limestone, rusty.
- Bed uWB-3 (0.15 m): clayey marl, gray in its upper part; with a yellow-beige layer in its middle.
- Bed uWB-4 (0.4–0.5 m): lithified calcareous marl, partly chamosite-oolitic, partly arenaceous, with abundant ammonites and bivalves.

Bivalves: Isocardia cordata Buckman, Gresslya sp., Clavitrigonia brodiei (Lycett), Cl. sp. (small-sized), Pholadomya fidicula Sowerby, Entolium demissum (Phillips), Astarte elegans Sowerby, Inoperna sowerbyana (d'Orbigny), Parvamussium pumilus (Lamarck). Ammonites are concentrated slightly above the middle of the bed. Occasionally with a poorly lithified marly limestone layer (0.05 m) located slightly below the middle of the bed. In the latter case, the ammonites occur in the lower part of the bed.

Ammonites: Leioceras crassicostatum [M], L. goetzendorfense [M], L. paucicostatum [m], L. striatum [m]

- Bed uWB-5 (0.1–0.2 m): lithified calcareous marl, more marly developed at its base.
- Bed uWB-6 (0.08–0.1 m): unconsolidated, rusty calcareous marl.
- Bed uWB-7 (0.4–0.5 m): chamosite-oolitic or arenaceous, very hard bluish-gray calcareous marl, which splits into three separate beds when weathered. The bluish-gray calcareous marls exhibit a brown-beige weathering rim. Fossils are extremely rare. Above the basal layer (c. 0.1 m) follows a thin rusty layer. Usually, the only ammonites occur c. 0.15–0.2 m below the top of the bed within a 0.01 to 0.1 m thick layer of shell debris separating the two upper partial beds. Ammonites: *L. goetzendorfense* [M], *L. paucicostatum* [m], *L. striatum* [m]
- Bed uWB-8 (0.1 m): lithified calcareous marl.
- Bed uWB-9 (0.3 m) arenaceous clayey marl.

Ammonites: L. goetzendorfense [M]

- Bed uWB-10 (0.1 m): nodular calcareous marl.
- Tonmergel [Clay-Marl] (c. 3.2-4 m): this unit was not exposed and could not be studied. At the southern hillside of the Wochenberg we measured a vertical distance of c. 12-13 m between the top of the Untere Wilflingen-Bank (= Comptum-Bank sensu Rieber 1963) and the top of the Staufensis-Bank. This is in contrast to Rieber (1963, text-fig. 2, Profil c), who reported a much greater thickness of c. 24 m for this interval. After our new measurements, the vertical distance between the basis of the Obere Wilflingen-Bank [Upper Wilflingen Bed] and the top of the Untere Wilflingen-Bank [Lower Wilflingen Bed] is only 3.2-4 m (variable in different sites along the southern escarpment) and not 17.5 m as mentioned by Rieber (1963, text-fig. 2, Profil c Wochenberg). Rieber (1963) interpolated the distance between the "Comptum"-Bank up to the Staufensis-Bank across the Wochenberg hill from the northern to the southern hillside in several steps; this procedure may have resulted in significant measurement errors.



**Figure 3.** Section of the Obere Wilflingen-Bank at the southern slope of the Wochenberg hill (*viallii* biohorizon, Bifidatum Subzone, Opalinum Zone, Lower Aalenian).

# Obere Wilflingen-Bank [Upper Wilflingen Bed] (1.6-

1.7 m; Fig. 3)

In one of his sections, Rieber (1963, text-fig. 2, Profil c) showed a separate bed with a maximum thickness of 1 m that follows at a vertical distance of 14 m above the Untere Wilflingen-Bank. It seems that this obviously discontinuously developed bed may reach even greater thicknesses at some places of the Wochenberg hill. In the Katzensteige section near Gosheim, Rieber (1963 text-fig. 2, Profil b) termed a c. 1.45 m thick bed following 3.3 m above the "classical" ammonite-bearing "Comptum"-Bank ["Comptum"-Bed] (= Untere Wilflingen-Bank) as well as "Comptum"-Bank. This is why we refer to the higher bed as 'Obere Wilflingen-Bank'.

- Bed oWB-1 (0.3 m): the 0.2 m thick lower part of this bed (oWB-1a) consists of brown arenaceous calcareous marl with bluish-gray hard limestone lenses. The upper 0.1 m thick portion of the bed (oWB-1b) consists of a brown to brick-red marly limestone with abundant compressed ammonites. Ammonites (bed oWB-1b): Ancolioceras sp. [M], Leioceras sp. [M]
- Bed oWB-2 (0.25 m): same lithology as bed oWB-1a; from a calcareous lense within this bed, a single specimen of Ancolioceras subfalcatum was recovered. Ammonite: Ancolioceras subfalcatum [M]
- Bed oWB-3 (0.3 m): marly limestone, gray, brown in weathered state, with layers of compressed ammonites.

Ammonites: Ancolioceras sp. [M], Leioceras sp. [M]

- Bed oWB-4 (0.05 m): clayey marl, gray.
- Bed oWB-5 (0.05-0.1 m): lithified marly limestone, brown.

Ammonites: Leioceras sp. [?M]

Bed oWB-6 (0.2-0.25 m): marly limestone, weakly lithified, brown, with small limestone nodules (diameters 0.01-0.02 m). In its upper part layers with mostly compressed ammonites. Ammonites: Leioceras evertens [M], L. goetzendor-

fense [M], Ancolioceras subfalcatum [?m]

Bed oWB-7 (0.1-0.13 m): marly limestone, weakly lithified, with lenses of gray, hard limestone with a brownish weathering rim. Most of the limestone lenses did not contain fossils; a few of them contained shell fragments, and only a single one yielded a couple of ammonites.

Ammonites: Ancolioceras noszkyi [M], A. viallii [M]

Bed oWB-8 (0.1-0.15 m): clayey marl, gray in unweathered state; compressed ammonites occur frequently in layers.

Ammonites: Leioceras goetzendorfense [M], Ancolioceras sp. [M]

Bed oWb-9 (0.1-0.2 m): the lithology of this bed changes significantly within distances of a few metres. At the left side of our excavation at the southern hillside of the Wochenberg it is developed as a brown calcareous marl (0.1-0.13 m), partly rusty, containing hard, splintery gray limestone nodules almost lacking fossils, only occasionally with shell debris (up to 0.3 m in diameter), with a rusty-brown weathering rim. In the opposite side of our excavation, this bed is thicker (0.2 m) and there, the upper c. 0.05 m of the bed, which is developed as a densely packed bivalve shell bed, are commonly split off. The lower part of the bed (c. 0.15 m) is a gray-bluish limestone. Most ammonites occur in the marginal part of the nodules or of the limestone bed and reach at least partly the rusty oxidation zone; only few ammonites occurred in the centre of the limestone nodules or in the centre of the bed. Apart from a few marly layers with a relatively rich ammonite content, the majority of ammonites from the Obere Wilflingen-Bank originates from bed 9. In all other parts of the Obere Wilflingen-Bank ammonites are extremely rare. Only bed oWB-9 could be intensively sampled.

Ammonites: Ancolioceras aff. subacutum [M], A. citaae [M], A. viallii [M], A. cf. viallii [M], A. krymholzi [M], A. subfalcatum [M], A. aff. substriatum [m], Leioceras goetzendorfense [M], L. capillare [M], L. striatum [m].

Marly limestone (1.9 m): brown, c. 0.2-0.3 m above its basis with a layer of small gray limestone nodules (c. 0.05–0.1 m in diameter) surrounded by layered rusty weathering rims; numerous burrows. Ammonites: Ancolioceras sp.

- Limestone / marly limestone (c. 0.8 m; = ? Sinon-Bank sensu Rieber 1963, text-fig. 2, Profil c): At the very steep southern hillside of the Wochenberg which is thickly covered with soil and talus, this interval could only be localized at two small places. We did not find any ammonites there, but an intensive sampling of this bed was hampered by the steep slope. It is possible that a small sample of well-preserved ammonites from the Wochenberg hill in the G. and U. Bayer collection (SMNS) originates from this interval; however, the exact position of these ammonites (which are preserved in a shelly matrix) within the section, is unknown.
  - (0.05–0.1 m): hard, splintery, laterally thinning lenses of gray limestone with pyrite, no macrofossils recorded.
  - (0.0-0.2 m): weakly lithified marly limestone, brown.
  - (0.6 m): alternation of limestone, calcareous marl and marly limestone.
    - 0.1–0.2 m: limestone, mainly consisting of fine bivalve shell debris.
    - 0.02-0.04 m: weakly lithified marly limestone, brown, partly pinching out.
    - 0.1-0.12 m: splintery limestone, gray, no macrofossils recorded.
    - 0.25-0.3 m: several gray, irregularly thinning platy limestone benches with small lithoclasts, separated by lithified brown marly limestone. Between the limestone benches Zoophycos burrows occur. A massive bed in fresh state.

Clayey marl (c. 1.1-1.3 m): clayey to marly limestone, brown (not studied in detail).

Arenaceous limestone (0.9 m) [= Sehndensis-Knollenlage sensu Rieber 1963, text-fig. 2, Profil c): at our excavation site, this interval was developed as uniform bed. In fresh

state, the bluish to brown bed is splintery hard and apparently lacking macrofossils. In weathered state, it splits into several smaller beds. No ammonites were found.

Ammonites: *Staufenia "sehndensis"* [after Rieber 1963; SMNS, ex coll. G. and U. Bayer]

- **Clayey marl** (0.8–0.9 m): arenaceous, thin-bedded, brown-yellow, with rare reworked limestone pebbles, ichnofossils (*Zoophycos*) and occasional bivalves (*Pholadomya* sp.). The lowermost 0.1 m are lithified and amalgamated with the underlying calcareous marl.
- Staufensis-Bank (sensu Rieber 1963; 1.2-1.6 m): The thicknesses of individual beds within the Staufensis-Bank varies significantly over short distances. However, this variation does not hamper the recognition and correlation of these beds. Contrary to Rieber (1963), our new observations revealed that the uppermost layers are completely eroded at the Wochenberg hill. Since the lithostratigraphic term 'Staufensis-Bank' is defined in the wider area as the uppermost thicker set of limestones following below the Concava-Bank, we used the term Staufensis-Bank despite of this erosional lack of its uppermost part which otherwise yields the name giving index fossil Staufenia staufensis. The shell beds mainly contain small-sized ammonites, occasionally also larger-sized ones. Most specimens occur on the surfaces of several smaller beds into which the Staufensis-Bank can be split.
  - Bed St-B 1 (0.1–0.2 m): soft, marly limestone, brown-yellowish, rusty, lacking macrofossils.
  - Bed St-B 2 (0.05–0.1 m): soft, either an arenaceous marly limestone, or developed as a hard limestone with a bluish core; the only recorded macrofossil is the ichnofossil *Zoophycos*. Together, beds St-1 and St-2 have a constant thickness of 0.2 m.
  - Bed St-B 3 (0.05-0.1 m): marly limestone with poorly preserved, compressed *Staufenia* sp. Complete phragmocones are often locally accumulated, but nearly absent at other places.
  - Ammonites: Staufenia latiumbilicus [M] Bed St-B 4 (0.1–0.15 m): flaser-bedded calcareous
  - Bed St-B 4 (0.1-0.15 m): haser-bedded calcareous marl, arenaceous, in the centre more calcareous and of bluish colour, marginally brown; poorly fossiliferous, rare accumulations of nuclei of *Staufenia*, bivalves and shell debris.
  - Ammonites: St. latiumbilicus [M]
  - Bed St-B 5 (0.25–0.35 m): irregularly flaser-bedded arenite layers separated by platy shell beds with abundant bivalves (*Mytiloceramus* sp., *Meleagrinella elegans* (Munier-Chalmas)) and ammonites (almost exclusively *St. latiumbilicus*, only very rare fragments of *Ludwigia*), partly chamosite-oolitic.

Ammonites: *St. latiumbilicus* [M and m], *Ludwigia* aff. *crassa* [M], *L. armipotens* [M], *L. cf. subtuberculata* [m]

 Bed St-B 6 (0.05–0.15 m): arenaceous marly limestone, occasionally weathered with a rusty rim and a soft, ochre-coloured core. With lenses of bivalve shell debris containing small ammonites (almost exclusively *Staufenia*).

Ammonites: St. discoidea  $\alpha$  [M and m], Ludwigia tuberata [M], Brasilia howarthi [M]

- Bed St-B 7 (0.05–0.15 m): soft marly limestone with burrows, compressed *Pholadomya* sp., belemnites, very rare ammonites (three specimens).
   Ammonites: St. discoidea α [M], Ludwigia murchisonae [M], L. subtuberculata [m]
- Bed St-B 8 (0.4–0.6 m): compact, partly arenaceous marly limestone divisible into three subunits:
  - Bed St-B 8a (0.1 m): irregularly flaser-bedded arenaceous marly limestones; with platy or rusty layers at the very base. *Ludwigia* spp. locally very abundant, with large-sized specimens over 20 cm in diameter, accompanied by nuclei and phragmocones of *Staufenia*, rarely with complete bodychamber.

Ammonites: St. discoidea α [M and m], Ludwigia depilata [M], L. cf. depilata [M], L. tuberata [M], L. armipotens [M], L. reflua [M], L. murchisonae [M], L. subtuberculata [m], Brasilia theobaldi [M], B. elmii [M], B. falcatiformis [M]

 Bed St-B 8b (0.1-0.25 m): arenaceous marly limestone, intercalated with layers of shell debris; bivalves (*Mytiloceramus* sp., *Meleagrinella elegans* (Munier-Chalmas)) and ammonites are abundant. *Staufenia* is common, partly preserved with bodychamber; *Ludwigia* spp. are rarer than in bed St-B 8a.

Ammonites: St. discoidea α [M and m], Ludwigia depilata [M], L. tuberata [M], L. murchisonae [M], L. armipotens [M], L. reflua [M], L. subtuberculata [m], Brasilia baldii [M], B. theobaldi [M], B. falcatiformis [M], B. howarthi [M]

Bed St-B 8c (0.15-0.25 m): occasionally, the top of the Staufensis-Bank is formed by an up to c. 8 cm thick marly limestone; sometimes this bed is platy or arenaceous. In most other cases, it was formed by a 2-3 cm thick bed. Most ammonites were recovered from a discontinuous bivalve shell bed that occurred in the uppermost 10-15 cm of the Staufensis-Bank.

Ammonites: St. discoidea β [M and m], Ludwigia aff. murchisonae [M], L. fueloepi [M], L depilata [M], L. reflua [M], L. gradata [M], Brasilia bradfordensis [M], B. elmii [M], Planammatoceras aff. planinsigne [M]

Clayey marl (0.05-0.1 m).

**Clayey marl** (0.1 m): with scattered siderite concretions, often rusty weathered.

**Quaternary cover** (0.3–0.8 m): up to the surface c. 0.3–0.8 m talus, loam and soil.

The beds of the **Concava-Bank** and the **Sowerbyi-Oolith** (Rieber 1963) should be expected in a distance of c. 2 m above the top of the Staufensis-Bank; however, these beds were not present at our excavation sites. We were even unable to locate these beds anywhere else at the Wochenberg hill, except of its northern hillside, beyond the road L 435.

# 4. Description of the ammonite faunas

# 4.1. Preliminary remarks

Within Graphoceratidae, the Staufenia lineage is easily divisable into a succession of only moderately variable chronospecies. In contrast, the taxonomy of Leioceras/ Ancolioceras and Ludwigia/Brasilia is much more complex. There are no focussed evolutionary trends observable, and some morphologies can reappear independently multiple times. Moreover, ammonites of these groups vary considerably within a single biohorizon. Plenty of the recorded morphologies are not restricted to a single biohorizon, but range within several succeeding ones. Finally, from some well-sampled Aalenian beds such as the Scissum Bed of southern England (Buckman 1887–1907) or the Lower/Upper Aalenian transition of Bakonycsernye in Hungary (Géczy 1967) an extremely large number of potentially valid taxa were formally described. However, few or no nominal taxa of this time interval were reported from other regions. The distinction of these nominal taxa is difficult. Considering the great variation within this group of ammonites, both in coeval beds as well as in a succession of beds, it is disputable whether to assign a specimen to a taxon described from a stratigraphically older or younger bed. Adding new taxa would even complicate this taxonomic maze. Therefore, both in Leioceras/Ancolioceras and Ludwigia/Brasilia new species should be only introduced based on very strong arguments in favour. Fortunately, this was not necessary in the course of this study.

Despite the partly large samples recovered by bed-by-bed sampling it was often impossible to identify corresponding macroconchs (M) and microconchs (m) – females and males – with accuracy. Specimens of the Tethyan genera *Planammatoceras* and *Tmetoceras* are very rare.

# 4.2. The ammonite fauna of the Untere Wilflingen-Bank [= Comptum-Bank auct.]

The ammonite fauna of the Untere Wilflingen-Bank (formerly: "Comptum-Bank") in the western Swabian Alb was described by Rieber (1963) in great detail. He determined coarsely ribbed and broad macroconchiate specimens as *L. crassicostatum* Rieber; all other macroconchs were assigned to *L. comptum* (Reinecke). In the microconchs, the coarser ribbed forms were distinguished as *L. paucicostatum* Rieber (the holotype of the latter species originates from the Wochenberg hill), and the weakly sculptured ones as *L. striatum* (Buckman). Concerning the microconchs, we follow the classification and determinations by Rieber (1963). For the sake of completeness, we

here illustrate one example of L. striatum (Fig. 4.5) and one of L. paucicostatum (Fig. 4.9). It is remarkable that at the Wochenberg hill and in the headwaters of the Schörzinger Starzel River microconchs are significanthy more common than in the sections at Gosheim located only a few kilometres farther to the southwest. A possible reason for this variation might be that both living and preservational conditions for microconchs had been more favorable in the present day Wochenberg area due to a calmer environment (Rieber 1963). In Gosheim, macroconchiate specimens of Leioceras with a better rounded bodychamber are more common than at the Wochenberg hill. Thus, we cannot exclude a slight difference in age of the Untere Wilflingenbank at both places; however, this difference is below the biostratigraphical resolution. The former determination of the macroconchs as 'L. comptum' must be rejected since the rediscovered holotype of Reinecke's Nautilus comptus was found to be a latest Toarcian Pleydellia (Chandler and Callomon 2010). The Leioceras specimens illustrated in Fig. 4 provide an overview on the great variation within adult macroconchs from the Wilflingen-Bank at the Wochenberg hill. We assigned them to the two morphospecies L. crassicostatum Rieber (Fig. 4.1a, b) and – following Chandler and Callomon (2010) – L. goetzendorfense (Dorn) (Fig. 4.2a-4b, 8a, b, 10a, b). Extreme morphologies are very rare (Fig. 4.1a, b [broad section, extremely coarse-ribbed  $\rightarrow$  transitional to Ludwiga]; Fig. 4.10a, b [high section  $\rightarrow$  transitional to Ancolioceras]). In contrast to the illustrated material, most macroconchiate graphoceratids from the Wilflingen-Bank are juveniles. They still lack the typical rounded venter, which is only well developed on the bodychamber of adults. However, the bulk of our specimens is close to the morphology of the specimen illustrated in Fig. 4.4 (compare the specimens in Rieber 1963, pl. 1, figs 2-4, 8, 9, 12, 14).

Tmetoceras scissum (Figs 4.6a, b, 7a, b; Rieber 1963) is a rare Tethyan immigrant in the Jurassic of Swabia (Dietze and Schweigert 2020). Unfortunately, a perfectly preserved specimen of c. 45 mm diameter was lost during preparation.

# 4.3. The ammonite fauna of the Obere Wilflingen-Bank

The taxonomy and determination of the ammonites from the Obere Wilflingen-Bank is extremely complicated, since the stratigraphical position of this fauna is transitional between formally named taxa from older horizons of the Bifidatum Subzone (Opalinum Zone) and younger ones of the Haugi Subzone (Murchisonae Zone), similarly to the recently described case of the slightly younger *subfalcatum* biohorizon (Dietze et al. 2021b). Usually, the ammonites of the (Untere) Wilflingen-Bank both, in the eastern and western Swabian Alb, are classified in a few macroconchiate and microconchiate taxa (*L. "comptum"*, *L. evolutum*, *L. crassicostatum* and *L. striatum*, and *L. paucicostatum*, respectively) (Rieber 1963; Dietze et al. 2021a). By contrast,



Figure 4. (1a, b) Leioceras crassicostatum (Rieber) [M], SMNS 70640/1. (2a–4b, 8a, b, 10a, b) L. goetzendorfense (Dorn) [M]; (2) uWB-4, SMNS 70640/2; (3) uWB-7, SMNS 70640/3. (4) uWB-4, SMNS 70640/4; (8) uWB-8, SMNS 70640/5; (10) SMNS 70640/6. (5) L. striatum (Buckman) [m], SMNS 70640/7. (6a–7b) Tmetoceras scissum (Benecke); (6) SMNS 70640/8; (7) uWB-4, SMNS 70640/9. (9) L. paucicostatum Rieber [m], SMNS 70640/10. 2–4, 6, 8: southern slope of the Wochenberg hill. 1, 5, 7, 9, 10: headwaters of the Schörzinger Starzel river. 1–10: Achdorf Formation, Untere Wilflingen-Bank, Lower Aalenian, Opalinum Zone (Bifidatum Subzone), crassicostatum biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



Figure 5. (1, 11, 13) *Ancolioceras subfalcatum* (Buckman) [M and ?m]; (1) oWB-2, SMNS 70640/74; (11) oWB-9, SMNS 70640/90; (13) oWB-6, SMNS 70640/75. (2) *Leioceras* sp. [?M], oWB-5, SMNS 70640/76. (3) *A. viallii* (Géczy) [M], oWB-7, SMNS 70640/81. (4) *L. evertens* (Buckman) [M], oWB-6, SMNS 70640/77. (5) *A. noszkyi* (Géczy) [M], oWB-7, SMNS 70640/80. (6) *A. krymholzi* (Géczy) [M], oWB-9, SMNS 70640/84. (7) *A.* sp. [M], oWB-9, SMNS 70640/85. (8) *L. goetzendorfense* (Dorn) [M], oWB-6, SMNS 70640/78. (9, 16) *L. striatum* (Buckman) [M]; (9) oWB-7, SMNS 70640/82; (16) oWB-9, SMNS 70640/83. (10, 15) *L. capillare* (Buckman) [M]; (10) oWB-9, SMNS 70640/83. (12, 14) *A.* aff. *substriatum* (Buckman) [m]; (12) oWB-9, SMNS 70640/93. (14) oWB-9, SMNS 70640/91. 1–16: Obere Wilflingen-Bank, southern slope of the Wochenberg hill; Opalinum Zone (Bifidatum Subzone), *viallii* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



Figure 6. (1) Ancolioceras citaae (Géczy) [M], oWB-9, SMNS 70640/87. (2) A. cf. viallii (Géczy) [M], oWB-9, SMNS 70640/97. (3) A. aff. subacutum (Buckman) [M], oWB-9, SMNS 70640/92. (4, 5) A. viallii [M]; (4) oWB-9, SMNS 70640/88; (5) oWB-9, SMNS 70640/89. (6): Leioceras goetzendorfense (Dorn) [M], oWB-8, SMNS 70640/79. 1–6: Obere Wilflingen-Bank, southern slope of the Wochenberg hill; Opalinum Zone (Bifidatum Subzone), viallii biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

in Ancolioceras from the Haugi Subzone of the Wutach area and the eastern Swabian Alb plenty of nominal species and varieties are distinguished (Horn 1909; Dietze et al. 2021b). There is a gradual transition between the (morpho-)genera Leioceras and Ancolioceras (see Dietze et al. 2021b). The ammonites from the Obere Wilflingen-Bank exhibit numerous combinations of characters of nominal species, which hampers the determination of individual specimens. We classified all graphoceratid ammonites from the Obere Wilflingen-Bank either as Leioceras Hyatt, 1867 or Ancolioceras Buckman, 1899 [in Buckman 1887-1907] and considered further taxa mostly introduced by Buckman (1887–1907) (e.g., Cypholioceras, Cylicoceras, Geyerina, Hyattina, Mansellia, etc.) as subjective younger synonyms. Their continuous usage would make ammonite taxonomy from the Lower/Upper Aalenian transitional beds extremely complicated.

A relatively small ammonite with a ventrally rounded bodychamber bearing a prominent ribbing (Fig. 5.4) is determined as *Leioceras evertens* (Buckman, 1899 [in Buckman 1887–1907]). Several ammonites with a rounded bodychamber are assigned to *Leioceras goetzendorfense* (Dorn, 1935) (Figs 5.8, 6.6); they are morphologically indistinguishable from ammonites of the Untere Wilflingen-Bank of the western Swabian Alb. Two relatively involute *L. capillare* (Buckman, 1928 [in Buckman 1909–1930]) are poorly sculptured and exhibit only a weakly developed ventral shoulder (Figs 5.10, 5.15). Similarly, two microconchiate *L. striatum* (Buckman, 1899 [in Buckman 1887– 1907]; Figs 5.9, 5.16) are mophologically almost identical with specimens of the Untere Wilflingen-Bank.

Due to the gradation from the genus Leioceras into the genus Ancolioceras, some specimens cannot be assigned with confidence to the one or the other genus. Specimens closely resembling L. goetzendorfense (compare Rieber 1963, pl. 1, fig. 12), but with a more regular ribbing than developed in most graphoceratids from the Untere Wilflingen-Bank and showing a fastigate venter until the aperture (Figs 5.3; 6.4, 6.5), are included in Ancolioceras viallii (Géczy, 1967). One specimen exhibits the typical ribbing style of A. viallii, but has a very broad section with a rounded venter on the bodychamber (Fig. 6.2); it is clearly intermediate between the genera Leioceras and Ancolioceras and here determined as A. cf. viallii (Géczy). A. noszkyi (Géczy, 1967) (Fig. 5.5) has a very fine ribbing. Specimens determined as A. krymholzi (Géczy, 1967) (Fig. 5.6) and A. subfalcatum (Buckman, 1899 [in Buckman 1887–1907]) (Figs 5.1, 5.11; 5.13) are close to the majority of ammonites of the subfalcatum biohorizon (Dietze et al. 2021b). A. citaae (Géczy, 1967; Fig. 6.1) is recorded from the subfalcatum biohorizon as well. There is a striking resemblance of the latter with the holotype of Cylicoceras undatum Buckman, 1899 [in Buckman 1887-1907]; however, the latter originates from much older beds (opaliniformis hemera) at Haresfield Hill in South England. A. citaae differs from L. crassicostatum Rieber, 1963 by its more slender whorl section, a more involute umbilicus and a slightly higher whorl section. These three species (C. undatum, A. citaae and L. crassicostatum) represent morphological extremes within

the intraspecific variation of the respective chronospecies (Dietze et al. 2021a). In lateral view, Ludwigia praecursor Rieber, 1963 looks very close to A. citaae, however, it is distinguished by its ventrally forwardly bended ribs. A very involute, high-sectioned and large-sized specimen (Fig. 6.3) with a sharp venter and a uniform ribbing style is close to A. subacutum (Buckman, 1899 [in Buckman 1887-1907]). Our specimen differs from the latter by a higher number of intercalatory ribs; hence, we prefer a determination in open nomenclature as A. aff. subacutum. A. costatum (Buckman, 1888 [in Buckman 1887–1907]) is another similar form which exhibits characteristic shovel-like thickenings of the ribs on the bodychamber. Two microconchiate specimens (Figs 5.12, 5.14) are assigned to A. aff. substriatum (see Dietze et al. 2021b, pl. 5, fig. a1, 2), since A. subfalcatum is based on a macroconch.

# 4.4. The ammonite faunas of the Staufensis-Bank

### 4.4.1. latiumbilicus biohorizon

#### Genus Staufenia Pompeckj, 1906

Graphoceratids of the genus Staufenia from beds St-B 3-5 (latiumbilicus biohorizon) are generally assigned to Staufenia latiumbilicus (Quenstedt, 1886). Quenstedt (1886, pl. 57, Figs 8, 14) figured two specimens from the Wochenberg hill as Ammonites discus latiumbilicus that are illustrated herein (Figs 10.1a, b and Fig. 9.6a, b). Quenstedt (1886, p. 462, 464) mentioned that the species name refers to the relatively wide umbilicus of this ammonite. Since Quenstedt's third names are considered as subspecies (ICZN 2005) and the taxon latiumbilicus is neither preoccupied (Hölder 1958) nor a nomen oblitum (see e.g. Hoffmann 1913: 113; Rieber 1963: 42; Contini 1969: 32), the specific name St. latiumbilicus must be considered as valid (ICZN 1999, Art. 46). For the taxonomic stability, we here designate one of Quenstedt's syntypes (1886, pl. 57, fig. 8) as the lectotype (Fig. 10.1a, b).

For an exhaustive description of St. latiumbilicus we refer to Rieber's (1963) description of St. sehndensis, since he described St. latiumbilicus under that name. The previous identification of specimens from the latiumbilicus biohorizon as St. sehndensis (Hoffmann) should be abandoned after the formal validation of Quenstedt's third names. The taxon St. sehndensis, originally described from North Germany, is either a younger subjective synonym of St. latiumbilicus or a morphologically very close predecessor of St. latiumbilicus. Since the latiumbilicus biohorizon at the Wochenberg hill is the type horizon and locality of St. latiumbilicus, the herein documented specimens are topotypes. Hoffmann (1913: 114), when introducing St. sehndensis, mentioned that only the fact that Quenstedt (1886, pl. 58, fig. 5) misidentified one of his specimens as Ammonites discoideus prevented him to use "Ludwigia" latiumbilica (Qu.) instead of introducing a new species, "Ludwigia" sehndensis. At his time, designation of a lectotype, which would have avoided any confusion, was not common practice. Hoffmann (1913: 116) clearly mentioned a medium-sized specimen (pl. 6, fig. 4, text-fig. 1) (Fig. 9.4a, b) being the type of his new species *"Ludwigia" sehndensis*, what we must take as a holotype designation. Consequently, the longstanding opinion (Rieber 1963; Schlegelmilch 1985) that the loosely collected specimen of Hoffmann (1913, pl. 4, fig. 3) was the lectotype is erroneous. Both, Hoffmann (1913: 3) and Rieber (1963) interpreted *Staufenia sehndensis* as a chronospecies with which we concur.

The maximum size of Staufenia latiumbilicus is represented by a specimen of nearly 30 cm diameter (Fig. 8.5a, b). The unusually large size and the rounded umbilical edge of this specimen not developed in any other representatives of this species points to a pathology. Specimens with preserved bodychamber (Fig. 7.1a, b) are very rare; most specimens are phragmocones with a rather uniform diameter of c. 16-17 cm (Fig. 10.2a, b). Inner whorls can be smooth (Fig. 7.5), weakly ribbed (Fig. 7.4) or coarser ribbed (Fig. 9.1, 3). The ammonite illustrated in Fig. 9.3 and the holotype of St. sehndensis (Fig. 9.4a, b) are almost identical. The specimen of Staufenia Fig. 9.7 is strikingly similar to the paralectotype of St. latiumbilicus (Fig. 9.6a, b), except for the slightly earlier beginning of the egression of the bodychamber as indicated by the preserved spur line. The specimen of Fig. 9.5 is still reminiscent to Ancolioceras.

Microconchiate *St. latiumbilicus* vary in a wide range from almost smooth (Fig. 8.4), weakly ribbed (Fig. 7.3) to coarsely ribbed specimens (Fig. 7.2; Fig. 8.3a, b).

#### Genus Ludwigia Bayle, 1878

In the latiumbilicus biohorizon of the Wochenberg hill, ammonites of the genus Ludwigia are extremely rare. Besides c. 65 specimens of Staufenia only three fragmentary Ludwigia were recorded from bed St-B 5. These are morphologically intermediate between Ludwigia specimens from the opalinoides biohorizon below and those from the discoidea a biohorizon above; the ribbing is not falcate but only falcoid, like in most early representatives of the opalinoides biohorizon of the western Swabian Alb. In contrast to these early representatives, the younger forms of the latiumbilicus biohorizon lack the ventral bending of the ribs towards the aperture (Horn 1909, pl. 12, figs 1-7, pl. 13, figs 1-2; Rieber 1963, pl. 4, figs 3-9). Instead, the keel is laterally bordered by an unsculptured band, like in the younger "Artengruppe der L. murchisonae" (Rieber 1963, pl. 5, figs 7, 8, 14-17; Ureta Gil 1983, pl. 9, fig. 7). In our determinations, we focussed on the falcoid ribbing style of the stratigraphically older Ludwigia taxa and assigned the specimens from the latiumbilicus biohorizon to L. aff. crassa (Horn, 1909) (Fig. 8.1a, b) and L. armipotens (Buckman, 1904 [in Buckman 1887–1907]) (Fig. 8.2a, b), respectively.

### Genus Planammatoceras Buckman, 1922 [in Buckman 1909–1930]

Rieber (1963, pl. 8, fig. 10) illustrated an excellently preserved *Planammatoceras planiforme* (Buckman, 1922 [in Buckman 1909–1930]) from the *latiumbilicus* biohorizon of the Wochenberg hill.

#### Volker Dietze et al.: Achdorf Formation at the Wochenberg hill

# 4.4.2. *discoidea* α biohorizon

#### Genus Staufenia Pompeckj, 1906

The ammonites of the genus Staufenia from the interval St-B 6 to St-B 8b represent Staufenia discoidea (Quenstedt, 1886). Hoffmann (1913) designated the specimen from Schörzingen (= W or S hillside of the Wochenberg) illustrated by Quenstedt (1886, pl. 58, fig. 3) (Fig. 11.6a, b) as lectotype of St. discoidea. Accoring to its morphology, it originates from the discoidea a biohorizon. For an exhaustive description of St. discoidea we refer to Rieber (1963: 44). At the Wochenberg hill, the succession of an older St. discoidea a and a younger St. discoidea  $\beta$  form can be recognized (Fig. 21). In St. discoidea a, the umbilicus in juvenile and median stages is wider and the spur line of the outer whorl egregates less rapidly than in St. discoidea  $\beta$  (e.g., St. discoidea  $\alpha$  in Figs 11.1a, b, 5 and St. discoidea β in Figs 18.1, 18.4, Fig. 21, respectively). In complete adults (Fig. 13.1), the egregation of the bodychamber exceeds the mid-flank of the previous whorl. The maximum adult size of St. discoidea a reaches 25 cm, but most specimens are much smaller. The conchs become smooth at diameters of at least 50-60 mm so that larger specimens are remarkably similar to one another, except for the presence and strength of primary ribs in the umbilicus (Figs 11.1a, b, 11.5, 13.1, 14.3a, b). The sculpture of inner whorls can be almost smooth as in the lectotype of St. discoidea (cf. Figs 11.6a, b, 12.1, 13.3), weakly ribbed (Fig. 12.2; Fig. 13.4) or even coarse-ribbed (Fig. 12.3a, b). Some of the smooth-shelled inner whorls are still reminescent to the ancestral genus Ancolioceras. Microconchs, here termed as St. discoidea a [m], are either involute and weakly ribbed (Figs 11.2a, b, 13.2, 5), slightly stronger ribbed (Fig. 11.3a, b) or coarse-ribbed and evolute (Figs 11.4a, b, 13.6). Among macroconchs, specimens with weakly sculptured inner whorls predominate, whereas among the microconchs the coarse-ribbed evolute forms are more common. The sculpture continues up to the aperture in the microconchs; sometimes it weakens a little. When preserved, the microconchs show a spatulate apophysis (Fig. 13.5).

St. latiumbilicus is more evolute than St. discoidea  $\alpha$  and exhibits a more gradational egregation of the outer whorl as indicated by the preserved spur line (Fig. 21).

### Genera Ludwigia Bayle, 1878 and Brasilia Buckman, 1899 [in Buckman 1887–1907]

Concerning macroconchs, in the *discoidea* a biohorizon *Ludwigia* spp. with a subquadratic whorl section predominate; however, in several specimens, the ventral shoulder is rounded. In contrast, ammonites of the morphogenus *Brasilia* are comparatively rare. Most specimens of *Ludwigia* spp. correspond to the "Artengruppe der *L. murchisonae* (Sowerby)" ("species-group of *L. murchisonae* (Sowerby)") of Rieber (1963: 53) which he defined as follows: The primary ribs divide into two or sometimes three secondaries in the area between the umbilical edge and mid-flank. The primaries are prorsiradiate, whereas the secondaries are strongly rursiradiate just from the diverging point onwards or immediately distal from this position. Towards the ventromarginal shoulder, the ribs become slightly elevated.



**Figure 7. (1a–5)** *Staufenia latiumbilicus* (Quenstedt) [M and m]. Southern slope of the Wochenberg hill; Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. **1:** SMNS 70640/11 ([M], bed 3; **2:** SMNS 70640/12 [m], bed 3; **3:** SMNS 70640/13 [m], bed 4; **4:** SMNS 70640/14 [M], bed 4; **5:** SMNS 70640/15 [M], bed 5. Asterisk marks beginning of bodychamber. Scale bars: Figs 1.1a, b: 5 cm; Figs 2–5: 3 cm.



Figure 8. (1a, b) Ludwigia aff. crassa Horn [M], St-B 5, SMNS 70640/16. (2a, b) L. armipotens (Buckman) [M], St-B 5, SMNS 70640/17. (3a-4b) Staufenia latiumbilicus (Quenstedt) [m], St-B 5; 3: coarsely ribbed, evolute variety, SMNS 70640/18; 4: SMNS 70640/19. (5a, b): S. latiumbilicus (Quenstedt) [M], giant-sized specimen, ?pathological, SMNS 70640/20. 1a-5b: southern slope of the Wochenberg hill; Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), latiumbilicus biohorizon. Asterisk marks beginning of bodychamber. Scale bars: Figs 1a-4b: 3 cm; Figs 5a, b: 10 cm.



**Figure 9.** (1–3, 5–7) *Staufenia latiumbilicus* (Quenstedt) [M], (1) SMNS 70640/21; (2) SMNS 70640/22; (3) SMNS 70640/23; (5) SMNS 70640/24; (7) SMNS 70640/25. (6) Paralectotype, original of *Ammonites discus latiumbilicus* Quenstedt, 1886, pl. 57, fig. 14, Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut der Universität Tübingen), GPIT-PV-61327, Schörzingen [= Wochenberg]. (4) *St. sehndensis* (Hoffmann) [M], holotype, original of *Ludwigia sehndensis* (Hoffmann, 1913, pl. 6, fig. 4) from Sehnde, Sehndensis Subzone, Geowissenschaftliches Museum der Universität Göttingen no. 73226 (459-78). 1–3, 5, 7: southern slope of the Wochenberg hill. 1–3. 5–7 Achdorf Formation, St-B 5; Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 10. (1a–2b)** *Staufenia latiumbilicus* (Quenstedt) [M]. **(1a,b)** Lectotype, original of *Ammonites discus latiumbilicus* Quenstedt (1886, pl. 57, fig. 8), St-B 3–5, Wochenberg, Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut Tübingen), GPIT-PV-6132. **(2a, b)** St-B 5, SMNS 70640/26. **1–2:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *latiumbilicus* biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 11. (1a–6b)** *Staufenia discoidea* (Quenstedt) α. **(1)** [M], SMNS 70640/27, **(2)** [m], SMNS 70640/28, **(3)** [m], SMNS 70640/29, **(4)** [m], SMNS 70640/30, **(5)** [M], SMNS 70640/31. **(6)** Lectotype of *Ammonites discoideus* Quenstedt, 1886, pl. 58, fig. 3, SMNS 70640/32 [plaster cast; original in the Paläontologische Sammlung der Universität Tübingen (formerly: Geologisch-Paläontologisches Institut der Universität Tübingen), GPIT-PV-61330], Schörzingen [= Wochenberg]. **1a–5:** St-B 6, southern slope of the Wochenberg hill. **6:** St-B 6–8b. **1a–6b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 12. (1–3b)** Staufenia discoidea (Quenstedt) a [M], St-B 6. **(1)** SMNS 70640/32, **(2)** SMNS 70640/33, **(3)** SMNS 70640/34. **(4a, b)** Brasilia howarthi (Géczy) [M], St-B 6, SMNS 70640/35. **(5)** Ludwigia subtuberculata Rieber [m], St-B 7, SMNS 70640/36. **(6a, b)** L. murchisonae (Sowerby) [M], St-B 7, SMNS 70640/36. **(7a, b)**: L. tuberata (Buckman) [M], St-B 6, SMNS 70640/37. **1–7b**: southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea a biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 13.** (1–6) *Staufenia discoidea* α (Quenstedt). (1) [M], almost complete adult specimen, St-B 8b, SMNS 70640/38. (2) [m], almost complete specimen, with proximal part of apophysis, St-B 8a, SMNS 70640/39. (3) [M], smooth nucleus, St-B 8a, SMNS 70640/40. (4) [M], ribbed nucleus, St-B 8b, SMNS 70640/41. (5) [m], complete with apophysis, St-B 8a, SMNS 70640/42. (6) [m], coarsely ribbed variety, St-B 8b, SMNS 70640/43. **1a–6:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 14. (1a, b)** *Ludwigia armipotens* (Buckman) [M], St-B 8a, SMNS 70640/44. **(2a, b)** *L. tuberata* Buckman [M], St-B 8a or 8b, SMNS 70640/45. **(3a, b)** *Staufenia discoidea* α (Quenstedt) [M], St-B 8a, SMNS 70640/99. **1a–3b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 15.** (1a, b) Ludwigia depilata (Buckman) [M], St-B 8a, SMNS 70640/46. (2a–4b) L. subtuberculata Rieber [m], St-B 8a. (2) SMNS 70640/47, (3) SMNS 70640/48. (4) SMNS 70640/49. (5a, b) Brasilia elmii (Géczy) [M], St-B 8a, SMNS 70640/50. 1a–5b: Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea a biohorizon. Asterisk marks beginning of bodychamber. Scale bars: Fig. 1: 5 cm; Figs 2–5: 3 cm.



Figure 16. (1a, b) Ludwigia armipotens (Buckman) [M], St-B 8a, SMNS 70640/51. (2) L. reflua (Buckman) [M], St-B 8b, SMNS 70640/52. (3a, b) Brasilia howarthi (Géczy) [M], St-B 8b, SMNS 70640/53. (4a, b) B. falcatiformis (Géczy) [M], St-B 8a, SMNS 70640/54. (5a, b): L. murchisonae (Sowerby) [M], St-B 8b, SMNS 70640/55. 1a–5b: Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 17. (1)** *Ludwigia reflua* (Buckman) [M], SMNS 70640/71. **(2)** *L. murchisonae* (Sowerby), SMNS 70640/72. **(3)** *Brasilia baldii* (Géczy) [M], SMNS 70640/94. **(1–3)** Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8b, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea α biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

After forming a very gentle forwardly bended curve, the coarse ribs end abruptly near the ventromarginal edge, so that a relatively broad, smooth band is developed in the area between the ventromarginal edge and the keel.

Ludwigia tuberata Buckman, 1904 [in Buckman 1887-1907] (Figs 12.7a, b; 13.2a, b) has the broadest whorl section and the coarsest ribbing of all Ludwigia specimens of the discoidea  $\alpha$  biohorizon. In the inner whorls, the diverging points of the ribs bear shovel-like thickenings. The bulk of the Ludwigia specimens of this biohorizon represent L. armipotens (Buckman, 1904 [in Buckman 1887–1907]) and L. reflua (Buckman, 1899 [in Buckman 1887-1907]). Both taxa share a prominent, falcate ribbing on the inner and median whorls and a smooth band along the blunt keel. L. armipotens (Figs 14.1a, b, 16.1a, b) shows an almost quadratic whorl section, whereas in L. reflua (Figs 16.2, 17.1a, b) the ventral margin is well-rounded. L. murchisonae perrotae Géczy, 1967 is indistinguishable from L. reflua. Specimens with a more slender, high-ovale to subquadratic whorl section and a weak ribbing are assigned to L. murchisonae (Sowerby) (Figs 12.6, 17.2). One of the nuclei (Fig. 16.5a, b) corresponds exactly to the inner whorls of the holotype of L. murchisonae (Sowerby, 1827) (plaster cast SMNS 70640/73). Several large specimens (Figs 15.1a, b) correspond better to L. depilata (Buckman, 1925 [in Buckman 1909–1930]). All microconchiate specimens of Ludwigia spp. are assigned here to L. subtuberculata Rieber, 1963 (Figs 12.5, 15.2a-4b). Morphologically, they are quite uniform and only differ from one another by their quadratic or subquadratic whorl section. The sculpture of the phragmocone varies between strongly and weakly ribbed.

Specimens showing a high and slender whorl section are assigned to *Brasilia*. They vary in the shape of the venter (rounded to quadratic/subquadratic), the strength of the ribbing and in their involution. A relatively coarsely ribbed *Brasilia* (Fig. 17.3a, b) with a rounded venter is assigned to *B. baldii* (Géczy, 1967). *B. theobaldi* (Géczy, 1967) (SMNS 70640/95) differs from *B. baldii* by a slightly weaker ribbing. Specimens showing weakly convex flanks with a subquadratic whorl section and a wide umbilicus are here assigned to *B. falcatiformis* (Géczy, 1967) (Fig. 16.4a, b). Two of our specimens are assigned to *B. elmii* (Géczy, 1967) (Fig. 15.5a, b). *B. howarthi* (Géczy, 1967) (Figs 12.4a, b, 16.3a, b) is extremely lanceolate and involute.

## 4.4.3. discoidea β biohorizon

#### Genus Staufenia Pompeckj, 1906

All Staufenia specimens from this biohorizon represent *St. discoidea*  $\beta$ . In contrast, Rieber (1963: 14) assigned involute specimens from the uppermost layer of the Staufensis-Bank (St-B 8c) to *St. staufensis* (Oppel). This is seems plausible if only juveniles are considered (Fig. 18.2, 5, 6, 8). In the adults, however, the very narrow umbilicus of the inner whorls becomes rapidly wider on the median whorls (Fig. 18.1, 3–4), so that *St. discoidea*  $\beta$  represents a morphologically and chronologically intermediate form linking *St. discoidea*  $\alpha$  and *Staufenia staufensis* (Fig. 21). Most macro-

conchs are only weakly sculptured in the juvenile stage (Fig. 18.1–4, 6), and coarse-ribbed nuclei (Figs 18.7–18.8) are much rarer than in the *discoidea* a biohorizon below. The narrowing of the umbilicus seen in the evolutionary lineage from *Staufenia latiumbilicus* to *Staufenia staufensis* is associated with a gradual simplification of the suture line. This trend culminates in the very simplified suture of *Staufenia staufensis* (compare Rieber 1963, text-figs 17g, 17i, 19, 21).

From the *discoidea*  $\beta$  biohorizon, we recovered only a single, weakly sculptured microconchiate specimen of *St. discoidea*  $\beta$  (Fig. 18.5).

### Genera Ludwigia Bayle, 1878 and Brasilia Buckman, 1899 [in Buckman 1887–1907]

Specimens of *Ludwigia* spp. from the *discoidea*  $\beta$  biohorizon generally exhibit a more slender whorl section than those from the *discoidea*  $\alpha$  biohorizon. Specimens assignable to the genus *Brasilia* are still rare.

*L. reflua* (Buckman, 1899 [in Buckman 1887–1907]) (Fig. 20.4a, b) ranges up to the *discoidea* β biohorizon. The specimens determined in open nomenclature as *L.* aff. *murchisonae* (Sowerby) (Figs 19.1a, b, 19.4a, b) differ from typical *L. murchisonae* in their slightly stronger ribbing (see *L. murchisonae* in Buckman 1887 [in Buckman 1887–1907], pl. 3, figs 1, 2). *L. gradata* Buckman, 1904 [in Buckman 1887–1907] (Figs 19.3a, b, 20.3a, b) is weakly ribbed and exhibits an even more slender whorl section than *L.* aff. *murchisonae*. *L. gradata* might be alternatively assigned to *Brasilia*; the differentiation between both genera is somewhat subjective. An evolute specimen with a rounded venter and a consistently coarse ribbing with shovel-like appearance in the bifurction points, is assigned to *L. fueloepi* Géczy, 1967 (Fig. 19.2a, b).

Ammonites of the genus *Brasilia* from the *discoidea* β biohorizon are represented by *B. bradfordensis* (Buckman, 1887) [in Buckman 1887–1907] (Fig. 20.2a, b) and *B. elmii* (Géczy, 1967) (SMNS 70640/96).

### Genus Planammatoceras Buckman, 1922 [in Buckman 1909–1930]

A single, strongly weathered specimen (Fig. 20.1) is determined as *Planammatoceras* aff. *planinsigne* (Vacek, 1886). It differs from the lectotype of *P. planinsigne* by having weakly spinose diverging points of the ribs positioned higher on the flanks. In consequence, these nodes are arranged directly along the umbilical seam.

# 5. Revision of Quenstedt's (1886) ammonites from the Achdorf Formation of the Wochenberg hill or from Schörzingen

Quenstedt (1886) not only mentioned the Wochenberg hill itself but also the nearby village Schörzingen as finding localities of some ammonites listed below. Since the Achdorf Formation is not present within the village of Schörzingen, the specimens labeled with "Schörzingen" must either originate from the western or from the southern hillside of the



Figure 18. (1a–8) Staufenia discoidea (Quenstedt) β [M], St-B 8c, Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* β biohorizon. (1) SMNS 70640/56, (2) SMNS 70640/57, (3) SMNS 70640/58, (4) SMNS 70640/100, (5) SMNS 70640/59. (6) SMNS 70640/60. (7) SMNS 70640/61, coarsely ribbed variety.
(8) SMNS 70640/62, weakly ribbed variety. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 19. (1a, b, 4a, b)** *Ludwigia* aff. *murchisonae* (Sowerby) [M], **(1)** SMNS 70640/63, **(4)** SMNS 70640/64. **(2a, b)** *L. fueloepi* (Géczy) [M], SMNS 70640/65. **(3a, b)**. *L. gradata* Buckman [M], SMNS 70640/66. **1a–4b:** southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8c, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), *discoidea* β biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.



**Figure 20. (1)** *Planammatoceras* aff. *planinsigne* (Vacek) [M], SMNS 70640/67. **(2a, b)** *Brasilia bradfordensis* (Buckman) [M], SMNS 70640/68. **(3a, b)** *Ludwigia gradata* Buckman [M], SMNS 70640/69. **(4a, b)**: *L. reflua* (Buckman) [M], SMNS 70640/70. **1a–4b**: Southern slope of the Wochenberg hill, Achdorf Formation, Staufensis-Bank, St-B 8c, Upper Aalenian, Murchisonae Zone (Murchisonae Subzone), discoidea β biohorizon. Asterisk marks beginning of bodychamber. Scale bar: 3 cm.

Wochenberg. All specimens originate from the Murchisonae Subzone of the Murchisonae Zone (Upper Aalenian).

 
 Table 1. Revision of Quenstedt's (1886) ammonites from the Achdorf Formation of the Wochenberg hill or from Schörzingen.

Original name in	Locality	Revised name and	Biohorizon
Quenstedt (1886)		nomenclatorial status	
A. discus	Wochenberg	St. latiumbilicus	latiumbilicus
latiumbilicus, p. 462,		(Quenstedt), lectotype	
pl. 57, fig. 8		(designated herein)	
A. discus	Schörzingen	St. latiumbilicus	latiumbilicus
latiumbilicus, p. 464,		(Quenstedt),	
pl. 57, fig. 14		paralectotype	
A. discoideus, p. 466,	Schörzingen	St. latiumbilicus	latiumbilicus
pl. 58, fig. 5		(Quenstedt)	
A. discoideus, p. 465,	Schörzingen	St. discoidea	discoidea α
pl. 58, fig. 3		(Quenstedt), lectotype,	
		selected by Hoffmann	
		(1913)	
A. discus Zieten, p.	Wochenberg	Staufenia discoidea	discoidea α
462, pl. 57, fig. 7		(Quenstedt)	
Ammonites discus	Wochenberg	Staufenia discoidea	discoidea α
Zieten, p. 461, pl. 57,		(Quenstedt)	
fig. 6			

# 6. Bio-/chronostratigraphy and correlation

# 6.1. Bio-/chronostratigraphy

In our stratigraphical analyses, we focus on the beds of the Achdorf Formation and the directly overlying Sowerbyi-Oolith of the Wedelsandstein Formation.

# Bifidatum Subzone (Opalinum Zone, Lower Aalenian)

### crassicostatum biohorizon

The Untere Wilflingen-Bank contains the *crassicostatum* biohorizon. Typical ammonites of this horizon are the coarseribbed *L. crassicostatum* along with *L. goetzendorfense* [formerly misidentified as *L. "comptum"*] and numerous morphological varieties. For a distinction from the older *uncinatum* biohorizon we refer to Dietze et al. (2021a). In the *evolutum* biohorizon, the graphoceratids are markedly smaller and mostly weaker ribbed than those of the *crassicostatum* biohorizon (Dietze et al. 2021b).

### viallii biohorizon

The herein newly introduced viallii biohorizon of the Wochenberg hill was detected in the c. 1.7 m thick Obere Wilflingen-Bank. Its ammonite fauna is transitional between the ammonite fauna of the crassicostatum biohorizon (Rieber 1963) and that of the subfalcatum biohorizon (Dietze et al. 2021b). It yields ammonites of the genera Leioceras and Ancolioceras as well as transitional forms linking both morphogenera. L. goetzendorfense and L. striatum which first appeared in the crassicostatum biohorizon are now accompanied by L. evertens and L. capillare. The name-bearing species of the viallii biohorizon, A. viallii, is closer to Ancolioceras and hence assigned to this morphogenus. The morphospecies A. citaae, A. aff. subacutum,

A. krymholzi and A. noszkyi are already present in the viallii biohorizon, but become predominant in the younger sub-falcatum biohorizon of the Haugi Subzone.

The ammonite fauna of the crassicostatum biohorizon is more uniform than that of the viallii biohorizon. It is dominated by L. goetzendorfense (= L. comptum sensu Rieber 1963) with several extreme morphological varieties (see above and Rieber 1963). In comparison, the ammonite fauna of the viallii biohorizon looks much less uniform; approximately half of the ammonite fauna is represented by Ancolioceras, the other half by Leioceras (Figs 4, 5). The Tethyan genus Tmetoceras is only recorded from the crassicostatum biohorizon, but not yet from the viallii biohorizon. In the evolutum biohorizon described from the middle Swabian Alb relatively small-sized specimens of L. evolutum with some intraspecific variation predominate. L. evolutum itself is not present in the viallii biohorizon, but A. citaae exhibits some resemblance to L. evolutum var. comptocostosum (Dietze et al. 2021a, pl. 24, fig. 1). Apart from its coarser ribbing, L. evertens resembles L. evolutum var. costate (Dietze et al. 2021a, pl. 24, fig. 4). Dietze et al. (2021a) suspected that the evolutum biohorizon was younger than the crassicostatum biohorizon (Fig. 20). However, this can neither be verified nor falsified in the Wochenberg section, since no ammonites were recorded from the 3.6 m thick interval between the crassicostatum and the viallii biohorizon. In the viallii biohorizon, Leioceras spp. is still abundant; such morphologies become extremely rare in the subfalcatum biohorizon, where they are mostly replaced by Ancolioceras krymholzi, A. subfalcatum and A. subacutum. Additionally, in the subfalcatum biohorizon the first representatives of Ludwigia and questionable Staufenia spp. appear (Dietze et al. 2021b).

# Haugi Subzone (Murchisonae Zone, Upper Aalenian)

The Haugi Subzone was not recorded at the Wochenberg hill. However, it is quite possible that sediments of this age locally occur, such as the calcareous marls below the "Sehndensis-Knollenlage" ("Sehndensis nodular layer") which were not studied in detail by us or a 0.8 m thick alternation of limestones and marly limestones which correspond to the questionable Sinon-Bank sensu Rieber. Rieber (1963) reported "Staufenia" sinon from this bed at the Wochenberg hill.

# Murchisonae Subzone (Murchisonae Zone, Upper Aalenian)

### latiumbilicus biohorizon

This biohorizon (beds St-B 4–5) is exclusively characterized by its index ammonite *Staufenia latiumbilicus*. Ammonites of the genus *Ludwigia* are extremely rare and do not contribute to the recognition of this biohorizon. A differentiation towards the next older described *opalinoides* biohorizon is rather simple, since in the latter the genus *Ancolioceras* predominates (see Horn 1909; Rieber 1963),

Concavum	Formosum	yet to be worked out	?Geisingen, Ringsheim, Wutach
	Concavum	cavatum	Zollernalb (Wannenmacher et al. 2021), ?Kappishäusern, ?Metzingen [Rieber 1963]
Bradfordensis		decipiformis	Geisingen (Dietze et al. 2014)
	Gigantea	geisingensis	Geisingen, Öfingen (Dietze et al. 2014)
		gigantea sensu Contini	Geisingen (Dietze et al. 2014), Wutach (condensed)
	Bradfordensis	yet to be worked out	Aalen [Quenstedt 1886, Rieber 1963], Kuchen, Geislingen, Wutach (condensed)
		staufensis	Swabian Alb, Wutach [Quenstedt 1886, Horn 1909, Rieber 1963], Geisingen , Ringsheim
N Murchisonae H	Murchisonae	discoidea β	Wochenberg, Plettenberg [Quenstedt 1886, Rieber 1963]
		discoidea α	Wochenberg, Gosheim
		latiumbilicus	Wochenberg [Quenstedt 1886, Rieber 1963], ?Gosheim
		yet to be worked out	Gosheim
	Haugi	yet to be worked out	Gosheim, Geisingen, Aalen
		opalinoides	Geisingen, Wutach [Horn 1909, Rieber 1963], Wochenberg [Rieber 1963]
		subfalcatum	Aichelberg [Dietze et al. 2021b]
Bifidatum [ex Comptu Opalinum Opalinum		viallii	Wochenberg [here], ?Gosheim
	Bifidatum [ex Comptum]	evolutum	Aichelberg area [Dietze et al. 2021a]
		crassicostatum	Swabian Alb, Wutach [Rieber 1963], N Franconian Alb [Dorn 1935]
		uncinatum	Aichelberg area [Dietze et al. 2021a]
		bifidatum/rieberi	Aichelberg area [Dietze et al. 2021a]
	Opelinum	hansrieberi	Swabian Alb [Ohmert 1993 Dietze et al. 2018, 2021a]
		opaliniforme	Swabian Alb [Ohmert 1993, Dietze et al. 2021a]
	Opannulli	dilucidum <sup>1</sup>	Swabian Alb [Dietze et al. 2021a], Franconian Alb [Schulbert 2001]
		opalinum <sup>1</sup>	Swabian Alb [Dietze et al. 2021a], Wittnau [Ohmert 1993]

#### Table 2. Biohorizons in the Aalenian of SW Germany. Those which are recorded at the Wochenberg hill are shaded in dark gray.

Remark<sup>1</sup>: the opalinum and dilucidum biohorizons are recorded in the nearby claypit at Weilen unter den Rinnen.

whereas large-sized specimens of the lanceolate *Staufenia latiumbilicus* dominate in the *latiumbilicus* biohorizon. However, we want to point out that at least one or two further still undescribed biohorizons are developed between the *opalinoides* and the *latiumbilicus* biohorizon in the Aalenian of SW Germany (Aalen, Gosheim, Geisingen) (Table 2).

#### discoidea α biohorizon

The discoidea a biohorizon (beds St-B 6–8b) is characterized by its name giving species *Staufenia discoidea* a together with ammonites of the genus *Ludwigia*, which Rieber (1963) classified as "Artengruppe der *Ludwigia* (*L.*) *murchisonae*" ("species group of *Ludwigia* (*L.*) *murchisonae*"). The discoidea a biohorizon is distinguishable from the next older *latiumbilicus* biohorizon by yielding markedly more involute specimens of *Staufenia* accompanied by various *Ludwigia* spp. of the "Artengruppe der *L. murchisonae*" sensu Rieber (1963) and earliest representatives of *Brasilia*; the latter two ammonite groups are still absent in the *latiumbilicus* biohorizon of SW Germany.

### discoidea β biohorizon

The discoidea  $\beta$  biohorizon (Schicht St-8b) is characterized by the index species *Staufenia discoidea*  $\beta$  and an accompanying fauna containing *Ludwigia* spp., which Rieber (1963) summarized as the "Artengruppe der *Ludwigia* (*L.*) murchisonae". The discoidea  $\beta$  biohorizon mainly differs from the next older discoidea  $\alpha$  biohorizon by the evolutionary state of the genus *Staufenia*; *St. discoidea*  $\beta$  is morphologically transitional between *St. discoidea*  $\alpha$  and the younger, extremely involute *St. staufensis. Ludwigia* specimens of the *discoidea*  $\beta$  biohorizon have more slender whorl sections and a better rounded venter; a trend which continues up to *Brasilia* spp. of the Bradfordensis Zone. In the next younger *staufensis* biohorizon (Rieber 1963; Dietze et al. 2017), the ammonites of the genus *Staufenia* with its index *St. staufensis* are still more involute than those of the *discoidea*  $\beta$  biohorizon. The "Artengruppe der *L. murchisonae* sensu Rieber" is later replaced by the "Artengruppe der *L. bradfordensis*" sensu Rieber (1963); however, numerous transitional forms exist.

### Bradfordensis Zone (Upper Aalenian)

Beds of the *staufensis* biohorizon (Dietze et al. 2017) have not been recorded at the Wochenberg hill. Rieber (1963) interpreted nuclei of *Staufenia* from the *discoidea*  $\beta$  biohorizon as belonging to *St. staufensis*. This erroneously implied the presence of the Bradfordensis Zone and is corrected here. No beds of the Bradfordensis Zone have been recorded from the Wochenberg hill.

### Concavum Zone (Upper Aalenian)

Rieber (1963) reported the "Concava-Bank" near the Wochenberg hill, although he could not find any ammonites in this bed. The "Concava-Bank" most likely represents the Concavum Zone, as it is the case in other parts of the western Swabian Alb (Rieber 1963; Wannenmacher et al. 2021).

### Discites Zone (Lower Bajocian)

From a bed following immediately below the "Sowerbyi-Oolith-Knollenlage" ["Sowerbyi-oolith nodular layer"], Rieber (1963) recorded the ammonite genus *Hyperlioceras*. A fragmentary Sonninia sp. labelled as originating from the Sowerbyi-Oolith of the Wochenberg hill is stored in the palaeontological collection of Tübingen University. These two finds clearly indicate that the Sowerbyi-Oolith in the vicinity of the Wochenberg hill belongs to the Discites Zone, as it is the case in all other studied places of the western Swabian Alb (Rieber 1963; Dietze et al. 2019).

# 6.2. Correlation within Germany

North Germany: Hoffmann (1913) described a rich ammonite fauna from the Aalenian of Sehnde near Hannover. The Sehndensis-Subzone of North Germany includes time-equivalent strata of the *latiumbilicus* biohorizon, and the Discoidea-Subzone strata of the *discoidea*  $\alpha$  and  $\beta$  biohorizons.

SW Germany: The crassicostatum biohorizon is widespread in the western Swabian Alb (Rieber 1963). A set of beds occurring a few metres above the (Untere) Wilflingen-Bank in a section at the Wilflinger Steige near Gosheim contain ammonites which could represent the viallii biohorizon; their description is still in progress. In 2020, the discoidea a biohorizon was recorded by the first author for the first time in Gosheim within a c. 1 m thick, probably only locally developed set of arenaceous limestone beds which were temporarily exposed along the connectiong road to the industrial area Sturmbühl. The somewhat deeper occurring "Schichten mit Staufenia sehndensis" ["beds with Staufenia sehndensis"] at Gosheim (Rieber 1963; Dietze 1989a, b), which are very rich in ammonites and shell detritus, are slightly older than the latiumbilicus biohorizon. Since bed-by-bed collections from further localities of the Swabian and Franconian Alb as well as from the Wutach area and the Upper Rhinegraben valley are still lacking, further correlations at the level of biohorizons are impossible.

# 6.3. Correlation outside Germany

France (Franche-Comté): Contini (1969, Tableau I) correlated the ammonite successsion of the French Jura Mountains with the successions of North Germany (Hoffmann 1913) and SW-Germany (Rieber 1963). This correlation was later adopted and revised by Contini et al. (1997, Tableau Va) in a rather confusing way. Different zonal schemes were used for the so-called "biome franco-germanique" [partly inluding the French Jura Mountains] on the one hand and the Submediterranean and Subboreal provinces on the other. Most strangely, the discoidea-Horizont sensu Rieber was totally ignored within these "horizons" of the "biome franco-germanique". The stratigraphic position of the "Horizon à Sehndensis" [biome franco-germanique] was placed between the "Horizon à Obtusiformis" and the "Horizon à Murchisonae" [of the Submediterranean/ Subboreal provinces] in Tableau Va; however, in the corresponding text it was explained that the faunas of the "Horizon à Sehndensis" in the French Jura Mountains and

in SW Germany [biome franco-germanique] are identical with the fauna of the "Horizon à Obtusiformis" [Submediterranen/Subboreal provinces].

This is why we prefer the more consistent and reproducable subdivision of Contini (1969) for our correlation between SW Germany and the French Jura Mountains. Contini's "Horizon à Staufenia sehndensis" with *St. sehndensis* und *Ludwigia obtusiformis* is slightly older than the *latiumbilicus* biohorizon at the Wochenberg hill, where *L. obtusiformis* has not been recorded yet. At Gosheim, only a few kilometres south of the Wochenberg hill, *L. obtusiformis* is recorded and co-occurs with smaller-sized *St. "sehndensis"* (Dietze 1989a, p. 125 figure bottom right, 1989b, p. 172 top left); hence, we suspect these beds correlate with the French Horizon à Sehndensis. The *discoidea* a und *discoidea*  $\beta$  biohorizons correspond to the Horizon à Murchisonae of the French Jura Mountains.

South England (Dorset): Despite of numerous previous studies (Buckman 1887-1907; Callomon and Chandler 1990; Chandler 1982, 1997), a correlation between SW Germany and S England remains problematic. The main reasons are that Staufenia discoidea and St. staufensis do not occur in S England and the corresponding faunas with Ludwigia spp. from England are generally more weakly sculptured and more rounded in ventral aspect than those of SW Germany (Chandler et al. 2012). The faunal horizon of Ludwigia obtusiformis with St. sehndensis, L. obtusiformis and Ancolioceras spp. (Chandler 1982, 1997; Callomon and Chandler 1990, 1997) must be slightly older than the latiumbilicus biohorizon based on the same arguments as explained above for our correlation with the French Jura Mountains. For a correlation of the faunal horizon of L. patellaria only its index L. patellaria can be used (Callomon and Chandler 1990). Since specimens of Ludwigia are extremely rare in the latiumbilicus biohorizon of SW Germany, it is impossible to decide whether both horizons could be time-equivalent or which one is the older. Possibly, the latiumbilicus biohorizon is the younger one of the two, since the few Ludwigia specimens already show a smooth band along the keel; this is not the case in L. obtusiformis. The discoidea α und β biohorizons correlate with the faunal horizon of L. murchisonae. The newly introduced viallii biohorizon is either slightly older or coeval with the comptocostosum horizon of Chandler and Callomon (2010).

**Scotland (Isle of Skye):** Morton and Hudson (1995) divided the rock succession at the type locality of *Ammonites murchisonae* Sowerby, 1827 – the type species of *Ludwigia* Bayle, 1878 – into the same faunal horizons as in South England (Callomon and Chandler 1990). The beds 0.7-0.11 of the Ollach Sandstone Member were assigned to the Murchisonae Subzone, with the two faunal horizons of *L. patellaria* and *L. murchisonae*. These beds correlate with the *latiumbilicus, discoidea* a und *discoidea*  $\beta$  biohorizons in the Wochenberg section.

Switzerland (Central Swiss Jura): Christ (1999, 2000) divided the rock in the central Swiss Jura Mountains into a succession of several ammonite faunas; however, his study is merely hypothetical since it is mostly based on



Staufenia latiumbilicus

**Figure 21.** Evolution of the genus *Staufenia* in the Upper Aalenian of the Swabian Alb. *Staufenia staufensis* originates from the Plettenberg hill (Dietze et al. 2017, pl. 4, fig. 7), all other ammonites from the Wochenberg hill. The *staufensis* biohorizon is not present at the Wochenberg hill due to Quaternary erosion. Scale bar: 3 cm.

imprecisely collected museum material (collection Lieb/ Bodmer). His fauna 6 "murchisonae und ssp." approximately correlates with the discoidea  $\alpha$  und  $\beta$  biohorizons.

In the Aalenian of **Luxembourg**, Sadki et al. (2020) divided the Murchisonae Subzone into biohorizons; however, the few specimens of *Ludwigia* spp. presented in their study do not allow a precise correlation. A high-resolution correlation with **further European regions** is impossible due to the lack of published data.

# 7. Discussion and conclusions

The evolution of the genus *Staufenia* is well-recorded in sections of the Wochenberg and nearby Plettenberg hills (Rieber 1963; Dietze et al. 2017, this study). Although time-equivalent populations show some morphological variation, this variation shifts continuously during evolution. Four evolutionary trends are observed through time (Fig. 21): (1) The umbilical width decreases. (2) The narrowing of the umbilicus is reinforced by a gradual change from a steep to an overhanging umbilical wall during ontogeny. (3) The strength of ribbing decreases and ribbing becomes restricted to earlier and earlier ontogenetic stages. (4)

The suture line becomes simplified. At least the first three evolutionary trends are closely related with each other and occur in many other highly variable ammonite genera. This phenomenon is well-known as "Buckman's rules of covariation" (see Monnet et al. 2015 for more details). Concerning the simplification of the suture line, there is no consistant correlation between complexity of the suture lines and water depth (Lemanis 2020). Therefore, this simplification must be an adaptation to other environmental conditions hardly decipherable without any autecological data.

But why are evolutionary trends in *Staufenia* appear to be continuous and targeted, whereas they are discontinuous and random in *Leioceras/Ancolioceras*? A possible reason could lie in the different distribution ranges of these genera. *Staufenia* is an endemic genus restricted to present-day Germany, E France and S England [only recorded there up to the Obtusiformis Subzone], whereas *Leioceras/Ancolioceras* had a much wider geographic distribution including the entire Tethyan realm. In the latter taxa, different environmental conditions (e.g. water temperature, food supply) in various parts of the distribution area might have led to different adaptations in the various populations. When such temporarily spatially isolated populations of *Leioceras/Ancolioceras* showing an onset of speciation later became reunified, e.g. in the course of a sealevel rise reconnecting neighbouring basins and thus allowing an interbreeding of their populations, this may have resulted in seemingly random developments.

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# Lanternfish otoliths (Myctophidae, Teleostei) from the Miocene of Japan

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# Abstract

Lanternfishes (Myctophidae) are one of the most common groups of fishes in the mesopelagic zone of the world ocean, and their otoliths have been dominant in pelagic sediments since at least Miocene times. Many species have a wide geographic distribution, with several being circumglobal. This wide distribution makes myctophid otoliths potentially useful for supraregional stratigraphic purposes. The Sea of Japan and the Northwest Pacific is an important region for investigations into the diversity and evolution of the Myctophidae. Here, we describe a large collection of myctophid otoliths from the late early to early middle Miocene (late Burdigalian to early Langhian) from six localities on western and central Honshu, which were under warm water influence during that time. A total of 22 species are recognized, of which eight are new. In the order in which they are described, the new species are Bolinichthys higashibesshoensis sp. nov., Ceratoscopelus brevis sp. nov., Lampadena exima sp. nov., Lampanyctus lenticularis sp. nov., Lampanyctus tsuyamaensis sp. nov., Stenobrachius ohashii sp. nov., Diaphus epipedus sp. nov., and Diaphus watatsumi sp. nov. At least nine species are also known from coeval sediments outside of Japan, most notably New Zealand and Europe. This distribution reflects the extraordinary geographic spread of myctophid species already in the early Miocene and indicates the potential for their future use for biostratigraphic purposes. The paleoecological and paleobiogeographical implications of the studied myctophid otolith assemblages are discussed. Furthermore, the stratigraphic ranges of the observed species are discussed and compared with data from other regions of the world in an attempt to outline the potential future application of myctophid otoliths for supraregional biostratigraphic purposes.

# Keywords

North Pacific, Diaphus, biostratigraphy, paleobiogeography, Honshu, new species

# 1. Introduction

During the late early and middle Miocene, much of Japan was submerged under the seas of the Northwest Pacific (Ogasawara 1994). Large parts of the terrain of Honshu were flooded, and extensive neritic to pelagic sediments were deposited in various basins. Fossil otoliths have been collected from these sediments; and these otoliths have been described by Hatai (1965), Ohe and Araki (1973), Ohe (1977, 1981, 1990), Ohe and Yamaoka (1980), and Takahashi (1976). However, much new material has been collected from locations in western and central Honshu since these studies were conducted, and are particularly rich in lanternfish otoliths. Lanternfishes (Myctophidae) are one of the most common groups of fishes in the mesopelagic zone of the world ocean, and they have been so since at least Miocene times. Their otoliths are dominant in pelagic sediments deposited since then. Many species have a wide

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geographic distribution, with several of them being circumglobal, making myctophid otoliths potentially useful for supraregional stratigraphic purposes. Japan and the Northwest Pacific represents an important region in the context of myctophid evolution and is characterized today by a rich community of both circumglobal and regional species. Pliocene and Pleistocene myctophid otoliths from Japan have been reviewed by Schwarzhans and Ohe (2019). Here, we review the rich myctophid otolith assemblages from late Burdigalian to early Langhian of western and central Honshu. In our opinion, this otolith assemblage represents an important cornerstone for both future supraregional correlations of fish faunas in a paleobiogeographic sense as well as potential biostratigraphic purposes.

We recognize 22 myctophid species in this collection, of which eight are new to science and five remain in open nomenclature. At least nine species are also known from coeval sediments outside of Japan, most notably New Zealand and Europe, which reflects the extraordinary geographic spread of these species.

# 2. Geological setting, material, and methods

# 2.1. Sampling localities

The otoliths were obtained from six localities, of which two are located in the western region of Honshu in Okayama Prefecture (Fig. 1), three are onshore from the Ise Bay in Mie and Gifu Prefectures (Fig. 2A–D), and one borders the Sea of Japan in Toyama Prefecture (Fig. 2E, F). The geographic distribution of these sampling localities from the southwest to the northeast are as follows:

- Niimi (Fig. 1A): Road cut on local road near Tesseicho Hattori about 15 km southwest of Niimi Station of the JR Hakubi Line, Niimi City, Okayama Prefecture (PE3102; Fig. 3A). The sampled interval is from the Upper Member (Watanabe and Ishigaki 1986) of the Bihoku Group (Itabashi Formation in Fig. 4; see also Watanabe et al. 1999).
- Tsuyama (Fig. 1B): Exposures along the Miya River (Miyagawa) banks directly east of the Mimasaka University complex up to the bridge of the Chugoku Expressway across the Miya River at Numa and the riverbanks 1,500 m north of the bridge at Oda, Tsuyama City, Okayama Prefecture. The sampled section, which consists of 23 levels and was measured in detail by Ujihara (Fig. 3B), belongs to the Takakura Formation of the Katsuta Group (Fig. 4) (see also Watanabe et al. 1999).
- Makino River (Fig. 2A): Outcrops along the riverbanks of the Makino River (Makinogawa) 1,200 m southwest of Mashino, Iga City, Mie Prefecture. Levels A 1 and A 2 correspond respectively to locations M1 and M2 in Nishimatsu (2019). The section and

sampling intervals have been described in detail by Nishimatsu (2019) and belong to the Makino Formation of the Awa Group (Fig. 4).

- Inabacho (Fig. 2C): Outcrops along the riverbanks of the Nagano River (Naganogawa) at Inabacho, Tsu City, Mie Prefecture. The sampled intervals (ML2304, ML2305, and OA1409; Fig. 3C) are from the Katada Formation, Ichishi Group (Oshida et al. 2018; Fig. 4).
- Mizunami (Fig. 2B): Small exposure at Okuna about 4 km northeast of Mizunami Station of the JR Chuo Line (Fig. 2B), Mizunami City, Gifu Prefecture, corresponding to location 62 in Itoigawa (1980). The samples were obtained from the basal transgressive Nataki Member of the Oidawara Formation, Mizunami Group (Itoigawa 1980; Kawamura et al. 2011; Fig. 4).
- 6. Toyama (Fig. 2E): River floor of the Kubusu River (Kubusugawa) at Kashio (level K 5), Yatsuo machi, Toyama City, Toyama Prefecture; cliff along the Yamada River (Yamadagawa) at Dojima (level H 14), Fuchu machi, Toyama City; and stream beds of a brooklet at Osedani (levels H 20 and H 21), Fuchu machi (Fig. 2E). Levels K 5, H 14, H 20, and H 21 correspond respectively to locations K 5, H 14, H 20, and H 21 in Nishimatsu and Ujihara (2020). The otoliths were obtained from the Kurosedani and Higashibessho formations of the Yatsuo Group (Fig. 4). For a detailed stratigraphic assessment, see Yanagisawa (1999) and Nakajima et al. (2019).

The distribution and abundance of the observed myctophid otoliths are summarized in Table 1.

# 2.2. Stratigraphy and biostratigraphic correlation

The studied myctophid otoliths stem from formations of late Burdigalian to early Langhian age, all within the planktonic foraminifer zone N8 and spanning the range of the northern Pacific diatom zones 2B to 4A of Yanagisawa and Akiba (1998) (Fig. 4). The stratigraphic correlation is based on Yanagisawa (1999), Nakajima et al. (2019), and Irizuki et al. (2021). With respect to the N7/N8 boundary, we follow the geochronological timescale established by Hoshi et al. (2019) in Japan of approximately 17 Ma (compared to 16.39 Ma in GTS 2020; Gradstein et al. 2020). The studied otoliths were obtained from the following stratigraphic units.

# Bihoku Group

The stratigraphy of the Bihoku Group has been studied by, inter alia, Imamura et al. (1953), Itoigawa and Nishikawa (1976), and Ueda (1986). Imamura et al. (1953) subdivided the Bihoku Group in the Miyoshi-Shobara area, Hiroshima Prefecture, into the Lower Sandstone Member and the


Figure 1. Location map for Niimi City (A) and Tsuyama City (B) and index map (C). Based on the topographic map of the Geospatial Information Authority of Japan, 2021.

Upper Shale Member. Ueda (1986) defined the strata corresponding to the Lower Sandstone Member and the Upper Shale Member in the Shobara area as the Korematsu Formation and the Itabashi Formation, respectively.

Watanabe and Ishigaki (1986) subdivided the Bihoku Group in the western part of Niimi City into the Lower, Middle, and Upper members. The otoliths were collected from the Upper Member. The Upper Member is mainly composed of mudstones and is correlated to the Upper Shale Member of the group in the Miyoshi Shobara area. Watanabe and Ishigaki (1986) suggested a continental slope position for the depositional environment of the member based on the molluscan assemblage. Watanabe et al. (1999) assigned the upper part of the Bihoku Group in the Koyamaichi area, Okayama Prefecture, which presumably correlates with the Upper Member of Watanabe and Ishigaki (1986), to diatom zone NPD3A (upper part) to NPD3B (lower part) of Yanagisawa and Akiba (1998).

Localities	Niimi	Tsuyama	Makino R.	Mizunami	Inabacho	Toyama	Toyama	Totals
Diatome Zones	ЗA	3A-3B	(3A)	(4A)	(3A)	(2B-3A)	3A-4A	-
Planktonic Foraminifer Zones	N8	N8 upper	N8 lower	N8 upper	N8 lower	N8 lower	N8 upper	-
Myctophinae								
Diogenichthys aguilerai		1						1
Myctophum murbani		20		1				21
Protomyctophum ahunga		158					2	160
Lampanyctinae								
Bolinichthys higashibesshoensis							2	2
Ceratoscopelus brevis		4					2	6
Lampadena exima		1						1
Lampanyctus lenticularis		33						33
Lampanyctus profestus		1						1
Lampanyctus tsuyamaensis		18						18
Stenobrachius ohashii	4	221				4	5	234
Taaningichthys sp.		1						1
Diaphinae								
Diaphus angulatus					1		1	2
Diaphus epipedus		7					2	9
Diaphus metopoclampoides		6		2			4	12
Diaphus watatsumi		11						11
Diaphus biatlanticus		5		2				7
Diaphus cassidiformis				20		60		80
Diaphus hataii	4	459	243	931	91	2	14	1744
Diaphus sp.2				2				2
Gymnoscopelinae								
Notoscopelus kuboensis		36		3	1		2	42
Totals	8	982	243	961	93	66	34	2389

Table 1. Distribution of myctophid species in the studied samples from the early to middle Miocene of Japan. Sequence from left to right corresponds to sequence of description of localities from southwest to northeast. Two specimens (*Myctophum* sp. and *Diaphus* sp.1) have been obtained form a location not covered in this study and will be described later by one of us (YT) and hence are not shown in this table.

### Katsuta Group

The stratigraphy of the Katsuta Group has been studied by, inter alia, Takeyama (1930), Tamura (1957), Kawai (1957), and Taguchi (2002). Kawai (1957) subdivided the Katsuta Group into the Uetsuki, Yoshino, and Takakura formations in ascending order. The otoliths described here were collected from the Takakura Formation.

The Takakura Formation is mainly composed of mudstones in its lower part and alternating sandstones and mudstones in its upper part. Taguchi (2002) inferred that the lower part of this formation was deposited in an environment with a water depth of about 200 m based on the molluscan assemblage. No macrofossils have been found in the upper part of the Takakura Formation, with the exception of plant fragments. Taguchi (2002) assumed that this section was deposited in an environment with a water depth of over 200 m based on lithofacies. Watanabe et al. (1999) correlated the Takakura Formation with the diatom zone NPD3A (upper part) or NPD 3B (lower part) of Yanagisawa and Akiba (1998).

### Awa Group

The stratigraphy of the Awa Group has been studied by, inter alia, Araki (1960a), Itoigawa (1961), and Fujiwara et al. (2005). According to Fujiwara et al. (2005), the Awa Group consists of the Higashitanihata, Hiramatsu, and Makino formations in ascending order. The otoliths described here were collected from the Makino Formation.

The Makino Formation is mainly composed of pebbly mudstones and more than 50 m thick (Fujiwara et al. 2005). Molluscs (Itoigawa 1961; Shibata 1978) and elasmobranchs (Nishimatsu 2019) have been described from this formation. Shibata (1978) found co-occurring shallow-water and deep-sea molluscs in the pebbly mudstones of the Makino Formation and assumed that the shallow-water elements were transported into a deep-water environment. Yoshida (1987) correlated the Makino Formation with the planktonic foraminifera zone N8 of Blow (1969), and Fujiwara et al. (2005) concluded that this formation lies within the planktonic foraminifera zones N8–9. Fujiwara et al. (2005) also assigned the Makino Formation to the calcareous nannofossil zone CN3 of Okada and Bukry (1980).

### Ichishi Group

The stratigraphy of the Ichishi Group has been studied by, inter alia, Takimoto (1935), Araki (1960b), Shibata (1967), and Yoshida et al. (1995). Shibata (1967) subdivided the Ichishi Group into the Haze, Oi, and Katada formations in ascending order. The otoliths described here were obtained from the Katada Formation.



Figure 2. Location map for Makino, Iga City (A), Okuna, Mizunami City (B), and Inabacho, Tsu City (C) with index map (D), and Yatsuo machi and Fuchu machi, Toyama City (E) with index map (F). Based on the topographic map of the Geospatial Information Authority of Japan, 2021.



Figure 3. Stratigraphic columns of sampled sections in Niimi City (A), Tsuyama City (B), and Tsu City (C).



Figure 4. Stratigraphic correlation chart of sampled intervals. The correlation follows the six locations in the described sequence from southwest to northeast. The chronostratigraphy follows the GTS2020 (Gradstein et al. 2020), with the exception of the N7/N8 boundary, which follows Hoshi et al. (2019). The planktonic foraminifer zones (P.F.) are from Blow (1969). The diatom zones (D.NPD) follow Yanagisawa and Akiba (1998). The stratigraphic correlation is based on Yanagisawa (1999), Nakajima et al. (2019), and Irizuki et al. (2021).

The Katada Formation is mainly composed of sandstones and mudstones, with mudstones being predominant at the sampling locality. This formation is approximately 250 m thick (Shibata 1967). Shibata (1970) described the deepsea molluscan assemblages from the Katada Formation, while Yoshida (1991) and Oshida et al. (2018) assigned the Katada Formation to the planktonic foraminifera zone N8. Hoshi et al. (2019) obtained the U-Pb ages of 17.03±0.11 Ma for the tuff layers in the uppermost part of the Oi Formation which more or less corresponds to the boundary of the planktonic foraminifera zones N7/N8, and 17.09±0.06 Ma for the tuff layer in the upper part of the Katada Formation.

#### Mizunami Group

The stratigraphic classification of the Mizunami Group was established by Itoigawa (1974) and has since been widely referred to; it was partially revised by Irizuki and Hosoyama (2006). Based on these studies, the Mizunami Group consists of the Toki Lignite Bed and the Hongo, Akeyo, Shukunohora, and Oidawara formations in ascending order (Itoigawa 1974; Irizuki and Hosoyama 2006). The otoliths described here were collected from the Oidawara Formation.

The Oidawara Formation is subdivided into the Nataki Member, from which the otoliths were collected, and the Oidawara Member (Itoigawa 1974). The Nataki Member consists of conglomerates and is only a few meters thick. A variety of fossils, including molluscs (e.g., Itoigawa 1960; Itoigawa et al. 1974; Shibata and Itoigawa 1980), benthic foraminifera (Seto 1992), and fish otoliths (Takahashi 1976), have been described from the Nataki Member. Shibata and Itoigawa (1980) noted that the Nataki Member contains many shallow-water molluscs. In contrast, Seto (1992) inferred that the Nataki Member was deposited in a relatively deep environment based on the analysis of benthic foraminifera. Kawamura et al. (2011) considered the Oidawara Member to represent the diatom zone NPD4A (lower part) of Yanagisawa and Akiba (1988) and concluded that it was deposited during a very short time period from 15.7 to 15.8 Ma.

#### Yatsuo Group

Many stratigraphic studies have been conducted on the Yatsuo Group since the original work of Makiyama (1930). Hayakawa and Takemura (1987) considered the Yatsuo Group to be composed of the Nirehara, Iwaine, Iozen, Kurosedani, and Higashibessho formations in ascending order. They subdivided the Higashibessho Formation into the Tochiage, Shiotani, Asatani, and Mitani members. The otoliths described here were collected from the Kurosedani Formation and the Tochiage and Shiotani members of the Higashibessho Formation.

The Kurosedani Formation consists of conglomerates alternating with sandstones and mudstones (Hayakawa and Takemura 1987) and is up to approximately 900 m thick (Hayakawa and Takemura 1987). Mudstones form the predominant lithology at the sampling locality. The Higashibessho Formation conformably overlies the Kurosedani Formation (Hayakawa and Takemura 1987) and is approximately 600 m thick (Nakajima et al. 2019). The Tochiage Member is mainly composed of mudstones, while the Shoitani Member is characterized by sandstones.

The Kurosedani and Higashibessho formations are rich in fossils, such as molluscs (e.g., Tsuda 1960; Shimizu et al. 2000; Amano et al. 2004), benthic foraminifera (e.g., Chiji 1954; Hasegawa and Takahashi 1992), ostracods (Ozawa 2016), and elasmobranchs (e.g., Nishimatsu and Ujihara 2019, 2020). The sampling horizons of the Kurosedani and Higashibessho formations seem to have been deposited in a wide range of sublittoral to bathyal depths based on an analyses of benthic foraminifera, molluscs, and ostracods (Hasegawa and Takahashi 1992; Shimizu et al. 2000; Ozawa 2016).

Yanagisawa (1999) placed the Higashibessho Formation in the diatom zones NPD3A–4A of Yanagisawa and Akiba (1988). Tamaki et al. (2006) correlated a reversed polarity interval in the upper part of the Kurosedani Formation to Chrone C5Cn.2r and reversed polarity intervals in the Higashibessho Formation to chrons C5Cn.2r, C5Cn.1r, and C5Br in correlation with the diatom stratigraphy of Yanagisawa (1999). Yoshida et al. (2019) obtained an <sup>87</sup>Sr/<sup>86</sup>Sr age of 17.02  $\pm$  0.27 Ma for tusk-shell concretions collected from the upper part of the Kurosedani Formation. Using the U-Pb method, Nakajima et al. (2019) obtained an age of 16.6 $\pm$ 0.2 Ma and FT method of 16.4 $\pm$ 1.2 Ma for the Yamadanaka Tuff, which is located in the uppermost part of the Kurosedani Formation.

## 2.3. Methodology and depository

The otoliths were photographed with a Canon EOS 1000D mounted on a Wild M400 photomacroscope; the camera was remotely controlled and the photographs captured from a computer. Individual images of every view of the objects taken at ranges of field of depths were stacked using Heliconsoft's Heliconfocus software. Adjustment of exposure and contrast and retouching were performed in Adobe Photoshop where necessary in order to improve the images without altering any morphological features.

The morphological terminology follows that established by Koken (1884), with amendments by Chaine and Duvergier (1934) and Schwarzhans (1978). The morphometrics were applied as established in Schwarzhans and Aguilera (2013). The abbreviations used are as follows: OL = otolith length, OH = otolith height, OT = otolith thickness, OsL = ostium length, CaL = cauda length, OCL = length of ostial colliculum, and CCL = length of caudal colliculum.

Depository: All type-specimens and figured specimens are deposited in the Senckenberg Museum, Frankfurt am Main, Germany, under the registry SMF PO. 101.112–149.

## 3. Results

## 3.1. Systematics

The classification of the Myctophidae follows Martin et al. (2018).

Division Teleostei Müller, 1846 Order Myctophiformes Regan, 1911 Family Myctophidae Gill, 1893 Subfamily Myctophinae Fowler, 1925 (sensu Martin et al., 2018)

#### Genus Diogenichthys Bolin, 1939

### Diogenichthys aguilerai Schwarzhans, 2013

Fig. 5A-C, Table 1

2013b Diogenichthys aguilerai - Schwarzhans: pl. 2, figs 4-5.

- 2019 *Diogenichthys aguilerai* Schwarzhans, 2013 Schwarzhans: fig. 50.12.
- 2021 Diogenichthys aguilerai Schwarzhans, 2013 Schwarzhans and Nielsen: fig. 7a-d.

**Material.** A single specimen (SMF PO 101.112) from Miya River at Oda, Tsuyama City, Okayama Prefecture, late Burdigalian, diatom zone 3A–3B, Takakura FM, level MS 04.5.

**Discussion.** *Diogenichthys aguilerai* is an unspectacular and small high-bodied myctophid otolith with a ratio OL:OH of 0.95–1.05. Its ventral rim is regularly curved and smooth; the dorsal rim is highest slightly behind its middle. Rostrum, excisura, and antirostrum are all small. The inner face is flat, and the outer face is distinctly convex and smooth. The narrow sulcus exhibits a slightly longer ostium than cauda, with the latter being underlain by a very long, anteriorly extended pseudocolliculum.

Diogenichthys aguilerai was apparently widespread during the early Miocene (Aquitanian and Burdigalian) but usually not common, with the exception of a recent find in the late Burdigalian of Chile (Schwarzhans and Nielsen 2021). It was originally described from Angola (Schwarzhans 2013b) but is also known from New Zealand (Schwarzhans 2019) and possibly also from the Caribbean (as Diogenichthys sp. in Schwarzhans and Aguilera 2013).

### Genus Myctophum Rafinesque, 1810

# Myctophum murbani (Weinfurter, 1952)

Fig. 5D–L, Table 1

1952 Scopelus tenuis murbani - Weinfurter: pl. 2, figs 1, 2.

1976 Myctophum sp. - Takahashi: pl. 17, fig. 4.

- 1994 Hygophum murbani (Weinfurter, 1952) Brzobohatý: pl. 2, figs 10–15.
- 2013 Myctophum murbani (Weinfurter, 1952) Schwarzhans and Aguilera: pl. 4, figs 5–8 (see there for further synonymies).

**Material.** 21 specimens: 20 specimens (figured specimens SMF PO 101.113), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 07, MS 15, MS 27, MS 36, MS 52, MS 70, MS 80, d, gh and h, late Burdigalian, diatom zone 3A–3B; 1 specimen, SMF PO 101.114, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

**Description.** Delicate, moderately large otoliths reaching up to 3.2 mm length (Fig. 5H). OL:OH = 1.15-1.25; OH:OT = 4.0-4.3. Ventral rim well rounded, deep, very regularly curved; dorsal rim much shallower, likewise regularly curved, sometimes with very mild obliquely cut postdorsal section. Rostrum and antirostrum short, of equal length, with very small excisura in between; posterior rim

regularly curved. Rostral tip and posterior tip positioned at lower margin of sulcus and distinctly supramedian. All rims delicately crenulated, ventral rim usually more intensely than dorsal rim.

Inner face distinctly convex, smooth, with distinctly supramedian, long, narrow sulcus. OL:SuL = 1.2; OCL:C-CL = 1.9-2.5. Dorsal margin of ostium slightly oscillating; cauda slightly bent upwards, with angular upper-posterior termination. Caudal colliculum narrower than ostial colliculum but of equal width when incorporating underlying pseudocolliculum. Dorsal depression shallow, indistinct; ventral furrow indistinct, far from ventral rim of otolith. Outer face flat to slightly convex, less than inner face, with short radial furrows near rims and smooth central portion.

Discussion. Myctophum murbani belongs to a group of Myctophum species with oval otoliths that usually also show a strong marginal ornamentation. This group contains the extant species M. lychnobium Bolin, 1946, M. obtusirostre Tåning, 1928, M. orientale (Gilbert, 1913), and M. spinosum (Steindachner, 1867) (see Ohe 1985 and Schwarzhans and Aguilera 2013 for figures). Myctophum murbani is the only fossil representative of this group and differs from all of them in the more gently curving ventral rim (vs. pronounced mid-ventral angle or expansion) and the more regularly curved dorsal rim. In addition, the postdorsal termination of the cauda is less strongly bent upwards and at a less sharp angle than in the extant species. Myctophum murbani (Weinfurter, 1952) is a widely distributed tropical to subtropical species that occurred in the late Burdigalian to Langhian in the Caribbean, the Mediterranean, the Paratethys, and now also in Japan. Thus far, no coeval Myctophum otoliths are known from the southern hemisphere (i.e., New Zealand or Chile; see Schwarzhans 2019 and Schwarzhans and Nielsen 2021).

#### Myctophum sp.

Fig. 5M-O

**Remarks.** An additional, relatively large *Myctophum* species of about 3.5 mm in length is observed in the Ichishi Group and will be described separately by one of us (YT). It is characterized by a regularly rounded outline and a relatively long rostrum.

#### Genus Protomyctophum Fraser-Brunner, 1949

### **Protomyctophum ahunga Schwarzhans, 2019** Fig. 5P–Z, Table 1

2019 Protomyctophum ahunga – Schwarzhans: figs 51.1–5. 2021 Protomyctophum ahunga Schwarzhans, 2019 – Schwarzhans and Nielsen: fig. 7i–m.

**Material.** 160 specimens: 158 specimens (figured specimens SMF PO 101.115), Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 06, MS 07, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70,



**Figure 5.** A–C: *Diogenichthys aguilerai* Schwarzhans, 2013, SMF PO 101.112, Tsuyama City, Takakura Formation, level MS 04.5; D–L: *Myctophum murbani* (Weinfurter, 1952); D–I, K–L; SMF PO 101.113, Tsuyama City, Takakura Formation, levels MS 15, MS 27, MS 52, h, J) SMF PO 101.114 Mizunami City, Oidawara Formation; M–O: *Myctophum* sp., col. Tsuchiya, Ichishi Group; P–Z: *Protomyctophum ahunga* Schwarzhans, 2019, SMF PO 101.115, Tsuyama City, Takakura Formation, levels MS 15, MS 26, h.

MS 80, MS 90, b, d, f9, f10, f40, g, gh, h and j, late Burdigalian, diatom zone 3A–3B; 2 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

**Discussion.** For a detailed description, see Schwarzhans (2019) and the subsequent update in Schwarzhans and Nielsen (2021). *Protomyctophum ahunga* is a typical and rather common species in the late Burdigalian of New Zealand and Chile but has not been found in coeval sediments of the Caribbean (Trinidad or Venezuela). Its common occurrence in late Burdigalian to early Langhian sediments of Japan indicates that it may have had an antitropical distribution in the Pacific Ocean during the late early and early middle Miocene.

#### Subfamily Lampanyctinae Paxton, 1972 Genus Bolinichthys Paxton, 1972

#### Bolinichthys higashibesshoensis sp. nov.

http://zoobank.org/A7B69D07-807A-42AC-AC17-1E9FDBED029D Fig. 6A-D, Table 1

**Etymology.** Named after the type formation Higashibessho FM.

**Holotype.** SMF PO 101.116 (Fig. 6A–D), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

**Paratype.** One specimen, SMF PO 101.149, same location as holotype, level H 21.

**Diagnosis.** OL:OH = 1.25. Ventral rim shallow with 4 denticles anteriorly; dorsal rim shallow, smooth. Rostrum inferior, long, rounded, distinctly longer than antirostrum, 18% of OL. OCL:CCL = 1.85. Inner face flat; outer face convex, smooth.

**Description.** A well preserved and very typical otolith with rounded parallelogram-like outline of 1.8 mm length. OH:OT = 4.0. Ventral rim shallow, anteriorly pronounced and there with 4 broad, rounded denticles; dorsal rim shallow, smooth, with distinct, rounded postdorsal angle at junction with oblique, smooth posterior rim. Rostrum very broad, inferior, with rounded tip, distinctly longer than antirostrum. Antirostrum far dorsally shifted, short, pointed; excisura relatively deep, angular.

Inner face completely flat, with more or less centrally positioned, narrow and relatively shallow sulcus. Ostium nearly twice as long as cauda (OCL:CCL = 1.85). Dorsal margin of ostium straight, oriented slightly upward towards anterior; ventral margin of ostium distinctly concave and curved. Cauda slightly upward oriented; its pseudocolliculum extending forward beyond caudal colliculum. Ventral furrow weak, close to ventral rim of otolith. Dorsal depression large with indistinct boundary except towards sulcus with distinct crista superior. Outer face moderately convex, entirely smooth.

**Discussion.** Bolinichthys higashibesshoensis is a typical species of the genus and cannot be confused with any of the few fossil species of the genus: the late Miocene *B. italicus* (Anfossi & Mosna, 1971) is characterized by a pointed rostrum and the lack of an excisura; B. kreffti Schwarzhans, 1986 from the early Pliocene differs in its outline and the more undulating and extended nature of the ventral rim and also shows a straight ostium. Both species have been found in sediments along the Mediterranean, and B. higashibesshoensis hence represents the only fossil species from the Pacific. Bolinichthys higashibesshoensis resembles extant otoliths of the genus but is more compressed than most of them, with the exceptions of B. distofax Johnson, 1975 (Fig. 6E) and B. supralateralis (Parr, 1928) (see Brzobohatý and Nolf 2000 for figure), from which it differs in the relatively shorter rostrum, the deeper excisura, and the oscillating ventral margin of the ostium. The latter character is found in certain other extant Bolinichthys species, notably B. indicus (Nafpaktitis & Nafpaktitis, 1969) and B. longipes (Brauer, 1906), from which, however, it differs in the other abovementioned characters.

#### Genus Ceratoscopelus Günther, 1864

#### Ceratoscopelus brevis sp. nov.

http://zoobank.org/A593637F-5B26-4AA9-98E6-2E45A98C8B85 Fig. 6F-M, Table 1

**Etymology.** From brevis (Latin) = short, referring to the compressed shape of the otoliths.

**Holotype.** SMF PO 101.117 (Fig. 6J–M); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

**Paratypes.** 3 specimens (SMF PO 101.118), same location as holotype, levels MS 07, MS 22, MS 52.

**Tentatively assigned specimens.** 2 poorly preserved specimens from Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21 may also represent this species and are tentatively assigned.

**Diagnosis.** OL:OH = 1.25-1.35. Rostrum moderately long with rounded tip, 18-22% of OL. Dorsal, posterior and ventral rims all continuously curved. OCL:CCL = 1.8-2.5. Outer face with radial furrows close to rims and smooth, slightly bulged central region set off by circular furrow.

**Description.** Small, delicate otoliths reaching about 2.25 mm in length (holotype 1.8 mm). OH:OT = 3.6–3.8. Dorsal rim gently curving without marked angles, continuously curving into rounded posterior and ventral rims around posterior reaches of otolith. Rostrum massive, broad, moderately long (18–22% of OL), with rounded tip; no or minute antirostrum and excisura. All rims slightly undulating.

Inner face nearly flat, with long, distinctly supramedian, shallow positioned sulcus; OL:SuL = 1.25. Ostium about twice as long as cauda (OCL:CCL = 1.8–2.5), straight and slightly wider. Caudal colliculum oval, underlain by slightly anteriorly shifted pseudocolliculum. Ventral furrow variable in expression and position; dorsal depression narrow, indistinct except towards crista superior. Outer face slightly convex with radial furrows along rims and characteristic smooth central area set off from rest of outer face by distinct circular furrow.



**Figure 6. A–D:** *Bolinichthys higashibesshoensis* sp. nov., holotype, SMF PO 101.116, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; **E:** *Bolinichthys distofax* Johnson, 1975, coll. Schwarzhans, Recent, Walter Herwig R/V, station 459-71; **F–M:** *Ceratoscopelus brevis* sp. nov., Tsuyama City, Takakura Formation; **J–M:** holotype, SMF PO 101.117, level MS 15; **F–I:** paratypes, SMF PO 101.118, levels MS 7, MS 52; **N–Q:** *Lampadena exima* sp. nov., holotype, SMF PO 101.119, Tsuyama City, Takakura Formation, level MS 36; **R–U:** *Lampadena speculigera* Goode & Bean, 1896, Recent; **R:** coll. Schwarzhans, Walter Herwig R/V, 38°S, 54°W; **S:** MCZ 169474; **T–U:** MCZ 96917; **V–X:** *Taaningichthys* sp., SMF PO 101.120, Tsuyama City, Takakura Formation, level MS 27.

Discussion. Otoliths of C. brevis are typical of those of Ceratoscopelus otoliths with the flat inner face and the long rostrum paired with minute antirostrum and excisura. Ceratoscopelus brevis differs from the three extant species by being more compressed and the regularly curving and undulating rims and characteristic aspect of the outer face. Its proportions are similar to those of the earlier C. richardsoni Schwarzhans, 2019 from New Zealand but differ in the very regularly curving posterior rim section of the otolith (vs. presence of a distinct obtuse postdorsal angle). An otolith found in situ and described as C. miocenicus Bedini, Francalacci & Landini, 1986 from the late Miocene of Italy is even more compressed and shows a pointed rostrum. Otoliths described as Ceratoscopelus sp. from the late Burdigalian of Chile (Schwarzhans and Nielsen 2021) differ in the pronounced postdorsal angle at the junction with the posterior rim, the oblique posterior rim, and the lack of any marginal crenulation of the rims. It appears that the Miocene Epoch featured a greater diversity of the genus than that observed today (Linkowski 1997).

#### Genus Lampadena Goode & Bean, 1893

#### Lampadena exima sp. nov.

http://zoobank.org/890977A5-B6AA-4B35-9D76-D47608468C75 Fig. 6N-Q, Table 1

2012 Lampadena sp. - Brzobohatý & Stranik: fig. 7.11.

2015 Lampadena aff. speculigeroides Brzobohatý & Nolf, 1996 – Lin et al.: fig. 2.21.

**Etymology.** From eximus (Latin) = excellent, exemplary, referring to the good preservation and clear allocation of the type specimen.

**Holotype.** SMF PO 101.119 (Fig. 6N–Q); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 36, late Burdigalian, diatom zone 3A–3B.

**Diagnosis (based on holotype and measurements taken from photograph of Lin et al. 2015).** OL:OH = 1.25– 1.30. Rostrum massive, its length 18–22% of OL. Ventral rim broadly rounded with 6 massive denticles; dorsal rim shallow, nearly straight; posterior rim rounded. Ostium slightly inclined, slightly wider than cauda. OCL:CCL = 1.7–1.8. Caudal pseudocolliculum longer than caudal colliculum, extending forward beyond collum.

**Description (based on holotype and measurements taken from photograph of Lin et al. 2015).** Thin, delicate otoliths up to 3.5 mm length (holotype 3.1 mm); OH:OT = 5.2. Rostrum broad, massive, relatively long (18–22% of OL); excisura distinct, but not deep; antirostrum short and high on anterior rim. Ventral rim regularly curving, with 6 evenly spaced, massive and robust denticles; dorsal rim shallow, flat, with distinct angle at junction with regularly curved posterior rim. Posterior rim somewhat undulating but without concavity.

Otolith flat, almost not bent along axis, resulting in nearly flat inner and outer faces. Sulcus large, wide, distinctly supramedian, reaching close to posterior rim of otolith; OL:SuL = 1.1-1.2. Ostium longer and wider than cauda, slightly inclined upwards towards anterior, with ostial colliculum opening towards anterior otolith rim. Cauda short, slightly inclined upwards towards posterior. Caudal colliculum small, OCL:CCL = 1.7-1.8. Caudal pseudocolliculum longer than caudal colliculum and extending forward further than caudal colliculum. Ventral furrow distinct, positioned distant from ventral rim; dorsal depression weak, poorly defined and small. Outer face smooth with few faint, very wide radial depressions along ventral rim.

Discussion. Lampadena exima more closely resembles the extant L. speculigera Goode & Bean, 1896 than the coeval L. speculigeroides Brzobohatý & Nolf, 1996 from the Paratethys. It differs from L. speculigera (Fig. 6R-U) in the more gently curving outline, particularly the ventral and posterior rims (with the latter not being concave, as is characteristic of L. speculigera); the upward inclined ostium (vs. straight); the OCL:CCL relation (1.7-1.8 vs. 2.1-2.3); and the long caudal pseudocolliculum extending forward of the caudal colliculum (vs. similar in length and not forward extended). Lampadena exima differs from L. speculigeroides in being more compressed (OL:OH = 1.25-1.3 vs. 1.35-1.5), the shallower dorsal rim, the smaller number and more robust nature of the denticles along the ventral rim of the otolith (6 vs. 8 or indistinct undulations), and the relatively wide ostium.

Otoliths of *Lampadena* are among the most diverse in the myctophid genera and are relatively easy to identify. The ease with which they can be identified makes them potentially valuable for biostratigraphic purposes, but unfortunately they are also usually very rare. In any case, it is interesting to note that specimens described by Lin et al. (2015) as *L*. aff. *speculigeroides* from the Tortonian of Italy and by Brzobohatý and Stranik (2012) as *Lampadena* sp. from the Langhian of the Czech Republic seem to represent the same species as our holotype of *L*. *exima* from the late Burdigalian of Japan. This finding indicates a relatively wide distribution range and a relatively long stratigraphic range.

#### Genus Lampanyctus Bonaparte, 1840

#### Lampanyctus lenticularis sp. nov.

http://zoobank.org/2B3AE3EF-39C9-4642-B5CE-0CB84A1440AB Fig. 7A-J, Table 1

**Etymology.** From lenticularis (Latin) = lens-shaped, referring to the regular outline and small size of the otoliths.

**Holoytpe.** SMF PO 101.121 (Fig. 7B–D), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level f9, late Burdigalian, diatom zone 3A–3B.

**Paratypes.** 8 specimens (SMF PO 101.122); same data as holotype, levels f9, g, h, j.

Additional material. 24 specimens; same data as holotype, levels MS 15, MS 36, MS 52, MS 70, d, f9, f40, g, gh, h, j.



Figure 7. A–J: Lampanyctus lenticularis sp. nov., Tsuyama City, Takakura Formation; B–D: holotype, SMF PO 101.121, level h; A, E–J: paratypes, SMF PO 101.122, levels f, g, h, j; K–M: Lampanyctus profestus Schwarzhans, 2019, SMF PO 101.123, Tsuyama City, Takakura Formation, level MS 36; N–V: Lampanyctus tsuyamaensis sp. nov., Tsuyama City, Takakura Formation; N–P: holotype, SMF PO 101.124, level MS 15; Q–V: paratypes, SMF PO 101.125, levels MS 15, MS 36, MS 90; W–AJ: Stenobrachius ohashii sp. nov.; W–Y: holotype, SMF PO 101.126, Yatsuo machi, Toyama City, Kurosedani Formation, level K 5; Z–AB, AF–AJ: paratypes, SMF PO 101.127, Tsuyama City, Takakura Formation, levels MS 15, MS 70; AC–AD: paratype, SMF PO 101.128, Niimi City, Bihoku Group; AE: paratype, SMF PO 101.129, Fuchu machi, Toyama City, Higashibessho Formation, level H 21; AK–AM: Stenobrachius leucopsarus (Eigenmann & Eigenmann, 1890), Recent, coll. Schwarzhans, leg. Fitch, off California; AN–AO: Stenobrachius nannochir (Gilbert, 1890), Recent, NSMT-P.63309, 36°28'N, 141°10'E.

**Description.** Small, relatively thin and nearly perfectly round otoliths with smooth rims without angles up to about 1.7 mm in length (holotype 1.55 mm). Rostrum short, rounded, only slightly longer than minute antirostrum, 7–15% of OL. Excisura small.

Inner face nearly flat and smooth, with slightly supramedian positioned, relatively narrow, shallow and straight sulcus. Ostium slightly longer and wider than cauda (OCL:CCL = 1.3-1.6). Ostial and caudal colliculi well marked but caudal pseudocolliculum often very narrow and sometimes indistinct. Ventral furrow closely following ventral rim of otolith; dorsal depression wide, but usually indistinct. Outer face slightly more convex than inner face, smooth.

**Discussion.** The otoliths of most *Lampanyctus* species are small and unspectacular with smooth rims and hence can be easily confused with eroded juvenile otoliths of other myctophids, for instance those of *Diaphus*. It is therefore important to ensure that one is dealing with a sufficient number of well-preserved specimens before attempting a taxonomic classification of *Lampanyctus* otoliths. This is the case here. Even in light of the unspectacular nature of *Lampanyctus* otoliths, those of *L. lenticularis* stand out as particularly poor in traits. *Lampanyctus lenticularis* differs from the coeval *L. profestus* Schwarzhans, 2019 in the regularly rounded dorsal rim (vs. shallow) and the ostial colliculum being relatively little longer than the caudal colliculum (OCL:CCL = 1.3–1.6 vs. 2.0–2.5).

#### Lampanyctus profestus Schwarzhans, 2019

Fig. 7K-M, Table 1

 2019 Lampanyctus profestus – Schwarzhans: figs 54.5–9.
 2021 Lampanyctus profestus Schwarzhans, 2019 – Schwarzhans and Nielsen: fig. 8g.

**Material.** 1 specimen (SMF PO 101.123); Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 36, late Burdigalian, diatom zone 3A–3B.

**Discussion.** A single otolith from the Takakura Formation differs from the much more common *L. lenticularis* described above in the shallower, depressed dorsal rim; the much smaller caudal colliculum expressed in the ratio OCL:CCL of 2.35; and a nearly completely flat inner face. The OL:OH (1.1) and OCL:CCL (2.35) ratios are well within the range of diversity observed in the type specimens from the early Miocene of New Zealand (OL:OH = 1.1-1.25; OCL:CCL = 2.0-2.5). The species has recently also been identified from the Burdigalian of Chile (Schwarzhans and Nielsen 2021) and thus, although generally uncommon, appears to represent another myctophid species with an antitropical distribution pattern in the early to middle Miocene of the Pacific Ocean.

#### Lampanyctus tsuyamaensis sp. nov.

http://zoobank.org/8C5C8DA1-66AA-4B95-971B-4960EE692871 Fig. 7N-V, Table 1

**Etymology.** Named after Tsuyama City, the type-locality, Okayama Prefecture in western Honshu, Japan.

**Holotype.** SMF PO 101.124 (Fig. 7N–P), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

**Paratypes.** 6 specimens (SMF PO 101.125); same data as holotype, levels MS 15, MS 36, MS 90.

Additional material. 11 specimens; same data as holotype, levels MS 15, MS 27, MS 36, f40.

**Diagnosis.** OL:OH = 0.85-0.92. Ventral rim deeply curving, deepest anterior of its middle. Anterior rim slightly inclined, almost straight from broad, inferior rostrum to predorsal angle with minute excisura and antirostrum. Inner face flat, outer face convex, smooth. OCL:CCL = 1.2-1.5.

**Description**. A small, very high-bodied, robust and thick otolith reaching about 1.5 mm in length (holotype); OH:OT = 3.4–3.7. Ventral rim deeply curving, deepest anterior of its middle, curving backwards into a steeply rounded posterior rim. Dorsal rim relatively shallow and nearly flat with distinct postdorsal angle at junction with posterior rim, somewhat irregular. Anterior rim steeply inclined at 75–85° (with sulcus oriented horizontal), nearly straight from distinct, rounded and inferior rostrum to minute antirostrum and predorsal angle at junction with anterior rim. Excisura minute. All rims smooth.

Inner face completely flat, with long, relatively wide, straight, shallow and slightly supramedian positioned sulcus. Ostial colliculum shallow, slightly longer and distinctly wider than caudal colliculum (OCL:CCL = 1.2-1.5; OCH:CCH = 1.25-1.5). Caudal pseudocolliculum as long as caudal colliculum. Ventral furrow distinct, positioned far from ventral rim of otolith. Dorsal depression wide, occupying almost entire dorsal field, but with indistinct margins. Outer face distinctly convex, smooth.

Discussion. Lampanyctus tsuyamaensis resembles L. popoto Schwarzhans, 2019 from the early Miocene of New Zealand and L. latesulcatus Nolf & Steurbaut, 1983 from the late Miocene of Italy but can be readily distinguished from both species by the more high-bodied shape, which is also expressed in the OL:OH ratio of 0.85-0.92 (vs. 0.95-1.05 and > 1.0, respectively). Another distinctive character is the straight, inclined anterior rim and the asymmetrical ventral rim. The known otoliths of extant species of Lampanyctus are usually also less high-bodied, with the exceptions of L. lepidolychnus Becker, 1967 and L. macdonaldi (Goode & Bean, 1896). Otoliths of L. lepidolychnus (see Smale et al. 1995 for figures) differ in the less inclined anterior rim, a more distinct development of a broad excisura, and a more regularly rounded dorsal rim, while those of L. macdonaldi are among the very few myctophid otoliths with fused colliculi (note that the specimens of L. macdonaldi figured in Smale et al. 1995 are erroneously identified). In contrast, the otoliths of the genus Nannobrachium Günther, 1887, which is commonly synonymized with

Lampanyctus, are even more compressed and high-bodied with a near rectangular outline and the sulcus almost reaching the posterior rim of the otolith.

#### Genus Stenobrachius Eigenmann & Eigenmann, 1890

#### Stenobrachius ohashii sp. nov.

http://zoobank.org/B0C99414-2E14-47BC-8DB0-51176BD45B0D Fig. 7W-AJ, Table 1

**Etymology.** Named in honor of Fumitaka Ohashi (Aichi Prefecture, Japan) who collected and donated a large part of the studied otoliths and has undertaken an original thesis on the fossil contents of many of the locations covered in this study.

**Holotype.** SMF PO 101.126 (Fig. 7W-Y), Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5, late Burdigalian, lower part of biozone N8, probably diatom zone 3A.

**Paratypes.** 6 specimens: 6 specimens: 1 specimen (SMF PO 101.128), near Tesseicho Hattori, Niimi City, Okayama Prefecture, Bihoku Group, late Burdigalian, diatom zone 3A–3B; 4 specimens (SMF PO 101.127), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 15, MS 70, h, late Burdigalian, diatom zone 3A–3B; 1 specimen (SMF PO 101.129), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21, late Burdigalian to early Langhian, diatom zone 3A–4A.

Additional material. 227 specimens: 3 specimens, Near Tesseicho Hattori, Niimi City, Okayama Prefecture, Bihoku Group; 217 specimens, Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5, MS 06, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70, MS 80, MS 90, c, d, f9, f10, f40, g, gh, h, j; 3 specimens, Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5; 4 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21.

**Diagnosis.** OL:OH = 1.0-1.15. Rostrum long, massive, with more or less rounded tip, 17-25% of OL. Excisura and antirostrum distinct. Ostium slightly longer than cauda, OCL:CCL = 1.2-1.7. Caudal pseudocolliculum distinct, as long as caudal colliculum or longer. Inner face flat; outer face convex, smooth.

**Description.** A small, roundish, and moderately thick otolith reaching about 2.1 mm in length (holotype); OH:OT = 3.5–4.0. Ventral rim deeply curving, deepest at or anterior of its middle. Dorsal rim relatively shallow, somewhat irregular with distinct postdorsal angle near junction with posterior rim. Anterior rim with long, massive rostrum with usually rounded tip, 17–25% of OL. Antirostrum distinct, about half the length of rostrum. Excisura deep, usually sharp. Posterior rim variably rounded. All rims smooth.

Inner face completely flat, with moderately long, relatively narrow, straight, shallow and nearly axial positioned sulcus. Ostial colliculum shallow, slightly longer and wider

indistinct margins. Outer face distinctly convex, smooth. Discussion. The genus Stenobrachius is today known from two species in the North Pacific: S. leucopsarus Eigenmann & Eigenmann, 1890 (Fig. 7AK-AM) and S. nannochir (Gilbert, 1890) (Fig. 7AN-AO). The fossil S. ohashii differs from the otoliths of the extant S. leucopsarus in the more regularly rounded ventral and posterior rims, the deeper excisura and sharper antirostrum, and the comparatively longer ostium (OCL:CCL = 1.2-1.7 vs. 1.05-1.3). It differs from the second extant species, S. nannochir, in the longer rostrum (vs. rostrum about as long as antirostrum) and the presence of a more or less strongly developed postdorsal angle. Stenobrachius otoliths are also quite similar to certain Lampanyctus otoliths such as those of the extant L. lepidolychnus or the fossil L. tsuyamaensis described above. A consistent difference seems to be that the caudal pseudocolliculum is not reduced in length or expression in Stenobrachius as it is in most Lampanyctus species.

sion wide, occupying almost entire dorsal field, but with

#### Genus Taaningichthys Bolin, 1959

Taaningichthys sp. Fig. 6V-X, Table 1

**Material.** 1 specimen (SMF PO 101.120), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 27, late Burdigalian, diatom zone 3A–3B.

**Discussion.** A single relatively small and slightly eroded otolith of 1.7 mm in length is interpreted as representing an unknown species of the genus *Taaningichthys* and is characterized by a relatively elongate shape (OL:OH = 1.4), a regularly curving ventral rim, a nearly flat dorsal rim, a distinct rostrum and a dorsally shifted posterior tip, and a flat inner face, with a supramedian sulcus with a long ostium and a short cauda (OCL:CCL = 2.0).

# Subfamily Diaphinae Paxton, 1972 (sensu Martin et al. 2018)

Genus Diaphus Eigenmann & Eigenmann, 1890 Diaphus theta Otolith Group after Schwarzhans (2013a)

# Diaphus angulatus Ohe & Araki, 1973

Fig. 8A-F, Table 1

1973 Diaphus angulatus – Ohe & Araki: pl. 49, figs 1–2, 20–21.

Material. 2 specimens; 1 specimen (SMF PO 101.130) Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada FM, level I 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 1 small, tentatively assigned specimen (SMF PO 101.131), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

**Remarks.** *Diaphus angulatus* was described based on a single incomplete specimen from the Yakuoji Formation, a partial lateral equivalent of the Katada Formation (see Oshida et al. 2018). Due to the incomplete preservation, *D. angulatus* was considered a doubtful species by Nolf (2013). Now, we have found a second specimen from the Katada FM which perfectly resembles the holotype but again lacks a rostrum (size 4.3+ mm; Fig. 8A–C). A complete smaller specimen of 2.6 mm in length from the Higashibessho FM (Fig. 8D–F) somewhat deviates from the larger specimens in the shape of the posterior rim and is therefore only tentatively assigned to the species. This difference is here considered to reflect an ontogenetic effect. These new finds are here used to revalidate and redefine the species.

**Diagnosis (emended).** OL:OH = 1.2-1.3. Ventral rim regularly curved with 6 denticles of variable strength. Rostrum long, massive; antirostrum and excisura small. Dorsal rim with prominent postdorsal angle; predorsal portion depressed. Inner face flat. Caudal colliculum shorter and much narrower than ostial colliculum (OCL:C-CL = 1.5-1.8; OCH:CCH = 1.6-1.8).

**Description (emended).** Large, thin otoliths reaching at least 5.5 mm in length (holotype recorded by Ohe and Araki 1973); OH:OT = 4.0 (4.5 in tentatively assigned specimen). Rostrum long, pointed, 20% of OL in tentatively assigned small specimen with completely preserved rostrum (Fig. 8D). Antirostrum distinct, but very short; excisura small. Ventral rim relatively shallow and regularly curved, with 6 denticles of varying strength. Dorsal rim smooth, anteriorly depressed, posteriorly with prominent postdorsal angle positioned above termination of cauda. Posterior rim obliquely cut in large specimens (holotype figured by Ohe and Araki 1973, and Fig. 8A), rounded and without postventral angle in tentatively assigned small specimen of Fig. 8D.

Inner face flat with distinctly supramedian sulcus. Ostial colliculum about twice as long and wide as caudal colliculum; caudal pseudocolliculum long and distinct. Dorsal margin of ostium straight; cauda slightly bent upwards. Ventral furrow distinct, moderately close to ventral rim of otolith; dorsal depression large, rather deep but with indistinct margins except for crista superior towards sulcus. Outer face slightly convex with shallow postcentral umbo, smooth.

**Discussion.** A typical and rather large otolith-based species of the *Diaphus theta* Otolith Group that resembles the coeval *D. haereticus* (Brzobohatý & Schultz, 1978) but differs in the far more backward positioned postdorsal angle and the much narrower caudal colliculum. In the latter aspect, it resembles *D. audax* Schwarzhans, 2019 from the early Miocene of New Zealand and Chile but again differs in the distinctly further backward positioned postdorsal concavity.

#### Diaphus epipedus sp. nov.

http://zoobank.org/FEEDFC9A-53E6-468B-B369-53B3BD7ED6B4 Fig. 8G-N, Table 1

**Etymology.** From epipedos (Greek) = flat, referring to the relatively shallow ventral rim, the main distinguishing character from *D. metopoclampoides*.

**Holotype.** SMF PO 101.132 (Fig. 8G–I), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 15, late Burdigalian, diatom zone 3A–3B.

**Paratypes.** 8 specimens; 6 specimens (SMF PO 101.133), same data as holotype, levels MS 15, MS 27, MS 90, j; 2 specimens (SMF PO 101.134), Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 21, late Burdigalian to early Langhian, diatom zone 3A–4A.

**Diagnosis.** OL:OH = 1.2-1.25. Shape rounded triangular with relatively shallow ventral rim, inferior rostrum and posterior tip and broad mediodorsal bulge. Antirostrum and excisura minute. Ventral rim with 7–9 denticles. Postdorsal rim broadly concave. OCL:CCL = 1.5-1.7.

**Description.** Otoliths with rounded triangular outline, relatively robust, up to 2.8 mm in length (holotype 2.5 mm); OH:OT = 3.4-3.7. Rostrum far inferior, relatively short and pointed, 10-12% of OL. Antirostrum and excisura minute. Dorsal rim with broad, rounded, pronounced mediodorsal bulge, anteriorly steeply inclined, posteriorly inclined with long depressed or concave section. Ventral rim rather shallow, regularly curved, with 7-9 medium strong denticles. Posterior rim curved, slightly projecting behind termination of cauda, its tip centrally or inframedian.

Inner face relatively flat, only slightly bent in horizontal direction. Sulcus terminating relatively far from posterior rim of otolith, straight, narrow. Ostial colliculum distinctly longer than caudal colliculum (OCL:CCL = 1.5–1.7) but only slightly wider (OCH:CCH = 1.2–1.4). Caudal pseudocolliculum distinct, about as long as caudal colliculum. Ventral furrow indistinct, sometimes not discernable, relatively close to ventral rim of otolith; dorsal depression small, ventrally marked by short crista superior. Outer face moderately convex throughout without distinct umbo, with distinct excisural furrow and few other weak and short radial furrows.

**Discussion.** *Diaphus epipedus* is an easily recognizable otolith that shares many features, such as the shape of the dorsal rim and the robust appearance without distinct umbo on the outer face, with *D. metopoclampoides* (see below) but differs in the shallow ventral rim, which results in a higher ratio OL:OH of 1.2-1.25 (vs. 1.05-1.1); the relatively long ostium (OCL:CCL = 1.5-1.7 vs. 1.1-1.4); and the narrower sulcus.

#### Diaphus metopoclampoides Steurbaut, 1983

Fig. 80-T, Table 1

1983 Diaphus metopoclampoides - Steurbaut: pl. 1, figs 22-28.

- 1984 Diaphus metopoclampoides Steurbaut, 1983 Steurbaut: pl. 7, fig. 23.
- 2000 Diaphus metopoclampoides Steurbaut, 1983 Brzobohatý & Nolf: pl. 4, figs 7–14.



Figure 8. A–F: *Diaphus angulatus* Ohe & Araki, 1973; A–C: SMF PO 101.130, Inabacho, Tsu City, Katada Formation, level ML 2305; D–E: SMF PO 101.131, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; G–N: *Diaphus epipedus* sp. nov.; G–I: holotype, SMF PO 101.132, Tsuyama City, Takakura Formation, level MS 15; K–J: paratype, SMF PO 101.133, Tsuyama City, Takakura Formation, level MS 15; L–N: paratype, SMF PO 101.134, Yatsuo, Toyama City, Higashibessho Formation level MS 06, f; U–AB: *Diaphus watatsumi* sp. nov., Tsuyama City, Takakura Formation; U–X: holotype, SMF PO 101.136, level MS 52; Y–AB: paratypes, SMF PO 101.137, levels gh, j; AC–AE: *Diaphus* sp.1, col. Tsuchiya, Ichishi Group.

**Material.** 12 specimens; 6 specimens (figured specimens SMF PO 101.135), Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 06, f40, gh, j, late Burdigalian, diatom zone 3A–3B; 2 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 4 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, late Burdigalian to early Langhian, diatom zone 3A–4A.

**Discussion.** A very characteristic but relatively rare otolith putatively related to *D. epipedus* (see above for distinction) that has thus far only been recorded from the late Burdigalian to Langhian of Europe (stratigraphically younger references in Brzobohatý and Nolf 2000, need verification); however, the records from Japan document a much wider geographical distribution in the northern hemisphere. The systematic positions of both species must be regarded as tentative because they do not clearly align with any of the extant *Diaphus* otolith-based groups.

# *Diaphus splendidus* Otolith Group after Schwarzhans (2013a)

#### Diaphus watatsumi sp. nov.

http://zoobank.org/211177B6-5D3E-4052-808F-C2DC9D55EB37 Fig. 8U-AB, Table 1

**Etymology.** Named after Watatsumi, a Shinto spirit of the sea in Japanese.

**Holotype.** SMF PO 101.136 (Fig. 8U–X), Miya River at Numa, Tsuyama City, Okayama Prefecture, Takakura FM, level MS 52, late Burdigalian, diatom zone 3A–3B.

**Paratypes.** 3 specimens (SMF PO 101.137), same data as holotype, levels gh, h, j.

Additional material. 7 specimens, same data as holotype, levels MS 15, MS 22, MS 27, MS 36, MS 70, f9, j.

**Diagnosis.** OL:OH = 1.35–1.45; OH:OT = 3.8–4.5. Dorsal rim with distinct postdorsal angle above central position of cauda, slightly concave postdorsal section and depressed predorsal section. Rostrum moderately long, 16–18% of OL. Ventral rim with 13–15 feeble denticles. Sulcus long, relatively narrow, slightly bent; OCL:CCL = 2.0.

**Description.** Slender, thin and relatively large otoliths reaching about 4.1 mm in length (holotype 3.8 mm). Rostrum moderately long and pointed; excisura mostly shallow and narrow, antirostrum much shorter than rostrum. Dorsal rim anteriorly depressed, ascending to distinct postdorsal angle positioned relatively forward above center of cauda; postdorsal section inclined, slightly concave. Ventral rim rather shallow and very regularly bent, with 13–15 feeble denticles which erode easily and are rarely completely preserved like in holotype. Posterior rim gently and regularly curved, slightly crenulated.

Inner face slightly bent in horizontal direction, relatively smooth, with long, slightly supramedian and slightly bent, shallow sulcus. Ostium about as wide as cauda but twice as long. Ostial colliculum only slightly wider than caudal colliculum (OCH:CCH = 1.1-1.3). Caudal pseudocolliculum distinct, long, fine. Dorsal margin of ostium slightly oscillating. Ventral furrow very indistinct; dorsal depression large, well marked towards crista superior. Outer face nearly flat except slightly thickened central and postcentral region, with numerous rapidly fading radial furrows on dorsal and ventral fields.

Discussion. Diaphus watatsumi is superficially an inconspicuous Diaphus otolith but can be relatively easily identified by its proportions and the shape and number of delicate denticles along the ventral rim. It resembles D. marwicki (Frost, 1933), a common species in the early and middle Miocene of the southern Pacific in New Zealand and Chile (see Schwarzhans 2019 and Schwarzhans and Nielsen 2021), but differs in the more elongate shape (OL:OH = 1.35-1.45 vs. 1.25-1.35), the thin appearance (OH:OT = 3.8-4.5 vs. 3.5-3.6), the larger number of denticles on the ventral rim (13-15 vs. 10-13), and the anteriorly depressed dorsal rim. Diaphus watatsumi resembles even more closely D. sulcatus (Bassoli, 1906) from the middle and late Miocene of Europe and the extant D. splendidus (Brauer, 1904), which is known since at least the early Pliocene, and is therefore associated with the Diaphus splendidus Otolith Group. Diaphus watatsumi differs from D. sulcatus in the rostrum being much longer than the antirostrum (vs. slightly longer to equal length) and the more depressed and longer predorsal region. It differs from D. splendidus in the relatively higher ratio OCL:CCL (2.0 vs. 1.6-1.8) and the higher number of denticles on the ventral rim (13-15 vs. 9-13). Diaphus watatsumi also resembles otoliths of the extant Lobianchia gemellarii (Cocco, 1838) (see Schwarzhans and Ohe 2019 for figures) but differs in the higher number of denticles along the ventral rim (13-15 vs. 5-9), the more regularly rounded posterior rim and the many radial furrows on the outer face.

#### Diaphus sp.1

Fig. 8AC-AE

**Remarks.** An additional relatively large *Diaphus* species of about 6.0 mm in length is observed in the Ichishi Group and will be described separately by one of us (YT). It also belongs to the *Diaphus splendidus* otolith group and is characterized by a relatively long and sharp rostrum, a high postdorsal angle, and the lack of a postdorsal concavity.

# Diaphus garmani Otolith Group after Schwarzhans (2013a)

## Diaphus biatlanticus (Weiler, 1959)

Fig. 9AD-AG, Table 1

1959 Nyctophus biatlanticus - Weiler: figs 9, 10.

2013 Diaphus biatlanticus (Weiler, 1959) – Schwarzhans and Aguilera: pl. 11, figs 1–8 (see there for further synonymies).

**Material.** 7 specimens; 5 specimens (figured specimen SMF PO 101.145), Miya River at Numa, Tsuyama City,

D

 $\cap$ 





F

Figure 9. A-I: Diaphus cassidiformis (Frost, 1933), SMF PO 101.138, Yatsuo, Toyama City, Kurosedani Formation, level K 5; J-AC: Diaphus hataii Ohe & Araki, 1973; J-L: SMF PO 101.139, Mizunami City, Oidawara Formation; M-N, Q-V: SMF PO 101.140, Tsuyama City, Takakura Formation, levels MS 06, MS 07, MS 52, MS 90; O-P: SMF PO 101.141, Fuchu machi, Toyama City, Higashibessho Formation, level H 20; W-AA: SMF PO 101.142, Makino River, Iga City, Makino Formation, level A 1; AB-AC: SMF PO 101.143, Inabacho, Tsu City, Katada Formation, level ML 2305; AD-AG: Diaphus biatlanticus (Weiler, 1959); AD-AF: SMF PO 101.144, Mizunami City, Oidawara Formation; AG: SMF PO 101.145, Tsuyama, Takakura Formation, level h; AH-AJ: Diaphus sp.2, SMF PO 101.146, Mizunami City, Oidawara Formation.

Okayama Prefecture, Takakura FM, levels MS 27, MS 52, h, late Burdigalian, diatom zones 3A-3B; 2 specimens (SMF OP 101.144), Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

Discussion. Diaphus biatlanticus has thus far only been reported from the early to middle Miocene of tropical America (Trinidad and Venezuela). Its otoliths are characterized by a very regular oval outline, a short rostrum, a short antirostrum and a minute excisura, a relatively long ostium compared to the cauda (OCL:CCL = 2.0-2.4), and a convex inner face combined with a flat to slightly concave outer face. The rare occurrence of the species in the middle Miocene of Japan indicates that it had a much wider geographical distribution than previously believed.

#### Diaphus cassidiformis (Frost, 1933)

Fig. 9A-I, Table 1

1933 Scopelus cassidiformis - Frost: figs 17, 18.

1980 Diaphus cassidiformis (Frost, 1933) – Schwarzhans: figs 176–177, 597.

1992 Diaphus sp. 6 - Radwanska: pl. 4, figs 1-3, textfig. 33.

- 2013b Diaphus cassidiformis (Frost, 1933) Schwarzhans: pl. 4, figs 4–7.
- 2019 Diaphus cassidiformis (Frost, 1933) Schwarzhans: figs 58.8–10.

**Material.** 80 specimens; 20 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 60 specimens (figured specimens SMF PO 101.138), Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosednai FM, level K 5, late Burdigalian, lower part of planktonic foraminifera biozone N8.

**Discussion.** *Diaphus cassidiformis* is easily recognized by its small, round otoliths. It was widely geographically distributed during the middle Miocene from New Zealand to Gabon (West Africa) and is now also recorded from Japan. It is also here interpreted to be present in the Paratethys based on an ongoing review of the myctophid otoliths originally described by Radwanska (1992). Its occurrence is rather irregular, as it may occur in large numbers at one location and in one formation (e.g., in Japan in the Oidawara and Kurosedani formations), while it may be completely missing from other locations. The reason for this unusual distribution pattern is unknown but most likely has to do with the species' ecological adaptation or with a specific lifestyle (e.g., a pseudoceanic occurrence).

#### Diaphus hataii Ohe & Araki, 1973

Fig. 9J–AC, Table 1

1973 Diaphus hataii - Ohe & Araki: pl. 49, figs 3, 4.

- 1976 Diaphus sp. Takahashi: pl. 17, fig. 5.
- 1980 Diaphus hataii Ohe & Araki, 1973 Ohe and Yamaoka: figs 7(?) 8–13.
- 1980 Diaphus sp. Ohe & Yamaoka: fig. 14.
- 2000 Diaphus regani Tåning, 1932 Brzobohatý & Nolf: pl. 3, figs 15–20.
- 2013 Diaphus hataii Ohe & Araki, 1973 Schwarzhans and Aguilera, pl. 10, figs 9–16, 17(?) (see there for further synonymies).

**Material.** 1744 specimens (figured specimens SMF PO 101.139-143): 4 specimens near Tessicho Hattori, Niimi

City, Okayama Prefecture, Bihoku Group, late Burdigalian, diatom tone 3A-3B; 459 specimens, Miya River at Oda and Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5, MS 06, MS 07, MS 15, MS 22, MS 27, MS 36, MS 52, MS 70, MS 80, MS 90, b, c, d, f9, f10, f40, g, gh, h, j, early Burdigalian, diatom zone 3A-3B; 243 specimens, Makino River SW of Mashino, Iga City, Mie Prefecture, Makino FM, levels A 1, A 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 91 specimens, Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada FM, levels I 1, I 2, OA1409, late Burdigalian, lower part of planktonic foraminifera biozone N8; 931 specimens, Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 2 specimens, Kubusu River at Kashio, Toyama City, Toyama Prefecture, Kurosedani FM, level K 5, late Burdigalian, lower part of planktonic foraminifera biozone N8; 14 specimens, Yamada River at Dojima and Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, levels H 14, H 20, H 21, late Burdigalian to early Langhian, diatom zone 3A-4A.

Discussion. Diaphus hataii is by far the most common myctophid otolith-based species throughout the early and early middle Miocene (late Burdigalian and early Langhian) of Japan, and it represents about 73% of all myctophid otoliths studied here. It is characterized by a short rostrum, which is not or only a fraction longer than the antirostrum; a convex inner face; a ratio OL:OH of 1.20-1.35 (adjusted from Schwarzhans and Aguilera 2013); a ratio OCL:CCL of 1.7-2.0; an oscillating dorsal rim of the ostium; 8-12 fine denticles along the ventral rim (adjusted from Schwarzhans and Aguilera 2013); and a more or less strongly developed predorsal lobe. Schwarzhans and Aguilera (2013) used the latter character as an important means by which to distinguish D. hataii from the contemporaneous D. austriacus (Koken, 1891), but the newly available material shows a certain degree of variability, as most species show such predorsal lobe (Fig. 9J, M, O, Q, R), while others show a moderately developed predorsal lobe (Fig. 9T, V, W); there are also specimens with a rather regularly curved dorsal rim (Fig. 9Z, AA, AB). We could not recognize sufficient consistency or additional characters that would warrant splitting of D. hataii into separate species. However, this also means that the distinction between D. hataii and D. austriacus becomes less clear. However, the specimens with a regularly curving dorsal rim are also slightly more elongate than the specimens with a distinct predorsal lobe (OL:OH = 1.25-1.35 vs. 1.20-1.25), while specimens of D. austriacus do not exhibit a predorsal lobe and are more compressed (OL:OH = 1.1-1.2, rarely to 1.25). In addition, D. hataii is thinner than D. austriacus (OH:OT = 3.5-4.0 vs. 3.0-3.5) and shows more denticles along the ventral rim of the otolith (8-12 vs. 6-8). We maintain the view that two separate species existed during the late early Miocene (Burdigalian) and middle Miocene (chiefly Langhian), with D. hataii being widely distributed in the tropics and the northern hemisphere from Europe through Central America and Japan, while D. austriacus appears to have been geographically

restricted to Europe and the tropical Atlantic. A further potential vicariant species could be *D. curvatus* Schwarzhans, 1980 in the early and middle Miocene of the South Pacific (New Zealand and Chile; see Biostratigraphic Evaluation chapter).

### Diaphus sp. 2

Fig. 9AH-AJ, Table 1

**Material.** 2 specimens (figured specimen SMF PO 101.146), Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A.

**Discussion.** Two very compressed, nearly round otoliths differ from the common *D. hataii* in the low index OL:OH of 1.1 and the distinctly widened ostium. The specimens share with *D. hataii* the short rostrum, the number of denticles along the ventral rim (9), and the expanded predorsal lobe. It most likely represents a separate species, but more specimens will have to be obtained before a reliable diagnosis can be established.

### Subfamily Gymnoscopelinae Paxton, 1972 (sensu Martin et al. 2018) Genus Notoscopelus Günther, 1864

Notoscopelus kuboensis (Ohe & Araki, 1973) Fig. 10A–N, Table 1

1973 Lampanyctus kuboensis - Ohe & Araki: pl. 49, figs 7-11.

1977 Lampanyctus sp. – Takahashi: pl. 25, fig. 4.

1981 Lampanyctus parvicauda Parr, 1931 – Ohe: pl. 3, fig. 12.

2019 Notoscopelus kuboensis (Ohe & Araki, 1973) – Schwarzhans and Ohe: fig. 13K-M.

**Material.** 40 specimens (figured specimens SMF PO 101.147-148): 36 specimens, Miya River at Oda and

Numa, Tsuyama City, Okayama Prefecture, Takakura FM, levels MS 04.5, MS 05, MS 05.5. MS 06, MS 15, MS 22, MS 27, MS 36, MS 70, MS 80, MS 90, f10, f40, gh, h, j, late Burdigalian, diatom zone 3A–3B; 1 specimen, Nagano River at Inabacho, Tsu City, Mie Prefecture, Katada FM, level I 2, late Burdigalian, lower part of planktonic foraminifera biozone N8; 3 specimens Okuna, Mizunami City, Gifu Prefecture, Oidawara FM, early Langhian, diatom zone 4A; 2 specimens, Osedani, Toyama City, Toyama Prefecture, Higashibessho FM, level H 20, late Burdigalian to early Langhian, diatom zone 3A–4A.

Discussion. Notoscopelus kuboensis is a wide-ranging species in the late early and middle Miocene to early Pleistocene of Japan and belongs to the lineage leading to the extant N. japonicus (Tanaka, 1908) (see Schwarzhans and Ohe 2019). The new data document a rather large variability of the ratio OL:OH ranging from 1.65 to 1.9, with a single large specimen reaching a ratio of 2.0 (corrected for erosion along the central portion of the ventral rim). This wide range appears to be mostly ontogenetically driven, with specimens up to 3 mm in length having a ratio OL:OH of 1.65–1.7 (Fig. 10J, K, M), those of 3 to 4 mm in length a ratio OL:OH of 1.75-1.85 (Fig. 10E, G, H), and the largest specimens reaching 4.85 mm in length with a ratio OL:OH of 1.9-2.0 (Fig. 10A, B). The specimens described from the Pliocene and early Pleistocene by Schwarzhans and Ohe (2019) are of larger size (4.4-5.0 mm in length) and show a similar ratio of 1.85-1.95. Notoscopelus kuboensis differs from the middle Pleistocene N. praejaponicus Schwarzhans & Ohe, 2019 and the extant N. japonicus (Tanaka, 1908) primarily by the not extended posterior tip of the otolith, the postdorsal angle being positioned further backward on the dorsal rim in comparison to the two other species, and the lack of the distinctive and long postdorsal concavity developed in N. praejaponicus and N. japonicus.



Figure 10. A–N: Notoscopelus kuboensis (Ohe & Araki, 1973); A: SMF PO 101.147, Inabacho, Tsu City, Katada FM, level ML 2305; B–N: SMF PO 101.148, Tsuyama City, Takakura Formation, levels MS 15, MS 36, MS 80, MS 90, j.

### 3.2. Faunal evaluation

### 3.2.1. Paleoecology

The late early and middle Miocene was a phase characterized by widespread transgression and submergence of the Japanese Archipelago. A paleogeographic reconstruction of Japan and its vicinity at 16 Ma (base Langhian) by Ogasawara (1994; Fig. 11) shows that large parts of the terrain of the main island, Honshu, were flooded. A broad and mostly deep water strait crossed southern Honshu through the region now occupied by Okayama, Tottori, and Hyogo Prefectures; today's Ise Bay was much wider, occupying terrain across Mie, Aichi, and Gifu Prefectures, and much of the northern area of Honshu and Hokkaido was flooded, with only occasional islands emerging (Fig. 11). Another broad and deep water way existed in the northern part of central Honshu over Toyama and Ishikawa Prefectures. The myctophid otoliths studied here stem from locations in Okayama, Mie, Gifu, and Toyama Prefectures (see Materials and Methods chapter). Some of them were deposited in upper bathyal environments with a shallowing upward tendency such as the Kurosedani and Higashibessho formations in Toyama Prefecture (Nishimatsu and Ujihara 2020). According to Taguchi (2002), the Takakura Formation of Okayama Prefecture was deposited in an upper bathyal to lower shelf environment. In the paleo-lse Bay, the Makino Formation of Mie Prefecture was deposited on the lower shelf to upper slope at about 200 m water depth (Nishimatsu 2019) and the Katada Formation at Inabacho in Mie Prefecture probably in an upper bathyal position. The rich myctophid association sampled from the basal transgressive Nataki Member of the Oidawara Formation at Okuna, Mizunami City, Gifu Prefecture, was deposited at a relatively shallow shelf environment but with access to the open sea.

Diaphus hataii is a ubiquitous myctophid species in all locations and samples studied and is also the most common species throughout. It dominates the myctophid associations of the Oidawara Formation of Mizunami City, the Makino Formation of Iga City, and the Katada Formation at Inabacho of Tsu City. The paleoenvironment ranges from rather shallow water at Mizunami City to deep shelf and upper slope in Iga and Tsu cities. Diaphus hataii is essentially the only myctophid species at Iga, Tsu and Mizunami cities is associated with rare Diaphus cassidiformis. Elsewhere, D. hataii is also very common in the Higashibessho Formation and the Takakura Formation at Tsuyama City but is associated with a richer myctophid assemblage. Such rich myctophid assemblage is particularly obvious in the Takakura Formation, which commonly yields Stenobrachius ohashii, Protomyctophum ahunga and less common but still significant, species of Lampanyctus, Myctophum murbani, and Notoscopelus kuboensis. Thus, the Takakura Formation is the most myctophid species-rich location of the entire study. It should be noted, however, that the Takakura Formation has also yielded more myctophid specimens in total

than all other locations, with the exception of Mizunami City (just under 1,000 specimens). More significant is the greater myctophid diversity observed in the Takakura Formation of Tsuyama City when compared with the rather uniform assemblage in the Oidawara Formation of Mizunami City.

### 3.2.2. Paleobiogeography

Lanternfishes of the family Myctophidae belong to the most abundant and widespread high oceanic mesopelagic fishes (Hulley 1981). They have dominated all pelagic otolith communities on a worldwide basis since at least Miocene times, but they probably became already common in the Oligocene (Schwarzhans and Carnevale 2021). Today, myctophid fishes occur in very large swarms offshore in high oceanic regions, where most of them undertake vertical diel migrations; they live at about 1,000 m water depth or more during the day and ascend to near the ocean surface at night together with the oceanic zooplankton on which they feed. These myctophid species are often very widely distributed geographically, with their range often being limited by climate belts and current regimes, and some are indeed circumglobal (Froese and Pauly 2021). Other extant myctophid species live pseudoceanic (sensu Hulley and Lutjeharms 1989) and may have a more disjunctive or regionally restricted distribution pattern. Selected myctophid species are known to have been distributed on a superregional basis during the early Miocene between Chile and New Zealand (Schwarzhans and Nielsen 2021) or in the late Miocene and Pliocene across the Atlantic (Schwarzhans and Aguilera 2013). The late Burdigalian to Langhian time interval is among the best known for pelagic otolith communities on a worldwide basis. Myctophid otoliths are known from the time interval between 17 and 14 Ma from various European Basins, Central America (Caribbean), tropical West Africa, southwest America (Chile), New Zealand, and now also Japan (Fig. 12). With respect to otoliths of a specific environment, it is the first time interval with such widespread occurrence available for analysis and comparison with the extant situation.

Regarding the fauna from the late Burdigalian to early Langhian of Japan described here, the most obvious correlation options in the absence of adequate data from northwestern America are across the equator to the South Pacific (i.e., New Zealand [Schwarzhans 2019] and Chile [Schwarzhans and Nielsen 2021]). Five of the 22 myctophid species identified in the early to middle Miocene of Japan are also known from comparable time intervals from New Zealand, while three are also known from Chile. This is a reasonable correlation, albeit much lower than that between New Zealand and Chile, as 12 of 13 myctophid species identified in Chile are also known from New Zealand. This correlation shows that some exchange took place between the antitropical open ocean environments in the southern and northern Pacific. The



Figure 11. Paleogeographic situation of Japan and sampled locations at about 16 Ma. Based on Ogasawara (1994).

species found in Japan and shared with New Zealand are Diogenichthys aguilerai, Protomyctophum ahunga, Lampanyctus profestus, Diaphus cassidiformis, and Notoscopelus kuboensis (Fig. 13). Of these, Diogenichthys aguilerai and Diaphus cassidiformis appear to have been distributed on a global basis at the time, with D. aguilarai also known from West Africa and D. cassidiformis from West Africa and Europe. There are also myctophid species from the early to middle Miocene of Japan that possibly had a circumglobal distribution in the northern hemisphere. *Myctophum murbani* and *Diaphus hataii*, which are both also known from Europe and Central America, seem to fall into this category. *Diaphus hataii* is of particular interest, as it forms a group of closely related species with



**Figure 12.** Knowledge base of early to middle Miocene myctophid otoliths based on this work for Japan, Brzobohatý and Nolf (2000, modified) for the Mediterranean, Brzobohatý and Nolf (2000, modified) and ongoing research for Paratethys, Steurbaut (1984, modified) for the northeast Atlantic, Schwarzhans (2010) for the North Sea Basin, Schwarzhans (2013b) for West Africa, Schwarzhans and Aguilera (2013) for the Caribbean, Schwarzhans (2019) for New Zealand, and Schwarzhans and Nielsen (2021) for Chile. Paleogeo-graphic reconstruction based on Blakey (2021).



**Figure 13.** Correlation of myctophid species from the early and middle Miocene across three studied areas around the Pacific based on this work, Schwarzhans (2019), and Schwarzhans and Nielsen (2021). Numbers at regions represent number of myctophid species recognized; number on arrows indicate shared species between regions. Paleogeographic reconstruction based on Blakey (2021).

*D. austriacus* (Koken, 1891) and *D. curvatus* Schwarzhans, 1980. *Diaphus hataii* appears to have been distributed circumglobally in the northern hemisphere and is known from Japan, the Caribbean, Atlantic Europe, the Western Tethys, and Paratethys (the northern Indian Ocean is inferred, as no data are available as yet) (Fig. 14). *Diaphus austriacus*, however, appears to have been restricted to the Atlantic, including the North Sea Basin, and the Western

ern Tethys and Paratethys (Fig. 14). In these areas it is the dominant species of the group, whereas *D. hataii* is much rarer. In the South Pacific, the group is represented by *D. curvatus* in New Zealand and Chile (Fig. 14). There are no data yet from the South Atlantic or the southern Indian Ocean, and therefore we do not yet know whether *D. curvatus* actually was a circumglobal species in the southern hemisphere.



**Figure 14.** Interpolated biogeographic distribution of the related species *D. hataii*, *D. austriacus*, and *D. curvatus* during the early to middle Miocene. See Fig. 12 for database and paleogeographic reconstructions.



**Figure 15.** Biostratigraphic and biogeographic distribution of *Diogenichthys aguilerai* Schwarzhans, 2013. See Fig. 12 for database and paleogeographic reconstructions.

# 3.2.3. The use of myctophid otoliths in biostratigraphy

Myctophid otoliths are easy to recognize as such, although morphological differences between species are often subtle. The fact that they are largely composed of aragonite (like all other teleost otoliths) make them less resistant to diagenesis, leaching, and other syn- and post-depositional effects, but they are also not as easily affected by reworking, as is the case for many more robust constructed microfossils that are used for biostratigraphic purposes. In particular, the delicate denticles along the ventral rim of many myctophid otoliths are easily affected by even brief exposure to erosional abrasion. Therefore, otoliths have the benefit of being mostly autochthonous where preserved (see Carnevale and Schwarzhans 2022). This aspect, in combination with their abundance in pelagic sediments since at least the early Miocene, their diversity, and their often very wide geographical distribution make them potential candidates for biostratigraphic use. Of course, we are currently at the very early stages of using myctophid otoliths for this purpose, but an initial stratigraphic correlation between the Navidad Formation and its equivalents from Chile with the well-known myctophid assemblages of New Zealand has yielded promising results (Schwarzhans and Nielsen 2021). Therefore, in the following, we discuss a number of myctophid otolith-based species observed in the middle Miocene of Japan that appear to have some potential for biostratigraphic purposes in the future.

Diogenichthys aguilerai (Fig. 15) was apparently a very widespread species but, with the exception of the Navidad Formation in Chile (Schwarzhans and Nielsen 2021), has never been found in great quantities. It also



Figure 16. Biostratigraphic and biogeographic distribution of *Myctophum murbani* (Weinfurter, 1952). See Fig. 12 for database and paleogeographic reconstructions.



**Figure 17.** Biostratigraphic and biogeographic distribution of *Protomyctophum ahunga* Schwarzhans, 2019. See Fig. 12 for database and paleogeographic reconstructions.

shows a rather long stratigraphic range from the Aquitanian to the late Burdigalian, with the specimens from Japan described here representing the youngest record. However, *Diogenichthys* otoliths show only a low morphological complexity, and species recognition and distinction by means of otoliths are therefore likely to prove difficult in the future. Therefore, we do not expect *Diogenichthys* otoliths to become prime candidates for biostratigraphic applications despite the seemingly wide geographic distribution that some of the *Diogenichthys* species may exhibit.

In contrast, *Myctophum murbani* (Fig. 16) belongs to a genus the otoliths of which exhibit a relatively larger spectrum of morphological characteristics, which eases their differentiation. Some *Myctophum* species have already been used as stratigraphic indicators (e.g., in tropical America) (Schwarzhans and Aguilera 2013). However, *Myctophum* otoliths are usually not very common, and its fossil species do not seem to be very widely distributed. *Myctophum murbani* may have been more extensively distributed geographically, at least in the northern hemisphere. Furthermore, it has thus far only been positively identified from the late Burdigalian and Langhian, chiefly biozones N8 and N9, and may thus prove to be biostratigraphically useful.

*Protomyctophum ahunga* (Fig. 17) appears to represent an antitropical transpacific species during the late Burdigalian and Langhian and therefore could prove to be of some regional stratigraphic value.

*Ceratoscopelus* species are today few, very widely distributed, and common (Froese and Pauly 2021). They would thus seem to be near optimal for superregional stratigraphic purposes. The fossil record in the Miocene, however, has thus far exhibited a much more fractionated distribution pattern as different species are found in different ocean basins, for example tropical West Atlantic (Schwarzhans and Aguilera 2013), the Mediterranean (Bedini et al. 1986), New Zealand (Schwarzhans 2019), and now also Japan with *Ceratoscopelus brevis*. More research will be required to decipher their evolution and to determine their potential for stratigraphic purposes in the Neogene.



Figure 18. Biostratigraphic and biogeographic distribution of *Diaphus metopoclampoides* Steurbaut, 1983. See Fig. 12 for database and paleogeographic reconstructions.

Otoliths of *Lampadena* are among the most morphologically diverse among the myctophids. They are also often relatively large, which makes identifying them relatively easy and would also make them good candidates for biostratigraphic purposes, as has been demonstrated by Girone and Nolf (2002) with the Pleistocene species *Lampadena ionica* Girone & Nolf, 2002. The here described *L. exima* is known from very few specimens from the late Burdigalian to early Langhian of Japan and the Tortonian of Italy. It also represents an easily recognizable species, but, like so many other species in the genus, it is rare in the fossil record and thus of limited practical value for biostratigraphic purposes.

Lampanyctus otoliths are often difficult to recognize and exhibit little morphological diversity. The Japanese collection described here is the richest in terms of otolith-based Lampanyctus species, but mostly lacks potential for comparison with other coeval associations. Future research should evaluate the biostratigraphic potential of Lampanyctus otoliths.

*Diaphus* otoliths are often the most common in Neogene sediments, including the samples described here from Japan, and certainly represent the most taxonomically diverse group. Species are not always easy to distinguish, and identification usually depends on the presence of well-preserved specimens with intact denticles along the ventral rim (which erode easily). Their biostratigraphic usefulness has been postulated several times (e.g., Brzobohatý and Nolf 1995, 2000; Schwarzhans and Aguilera 2013; Schwarzhans 2019; Schwarzhans and Nielsen 2021), and indeed they may represent the prime candidate for such purposes among myctophids. Below, we focus on three species that have been identified in the late Burdigalian to early Langhian of Japan.

Diaphus metopoclampoides (Fig. 18) is one of the most readily recognizable fossil species in the genus Diaphus, but its generic allocation is in fact not entirely certain. Brzobohatý and Nolf (2000) stated that it occurred in the Mediterranean from the late Burdigalian until the Messinian. Ongoing research by one of us (WWS), however, has failed to identify this species in the late Miocene (Tortonian and Messinian) of the Mediterranean based on a very large collection. As Brzobohatý and Nolf mentioned, *D. metopoclampoides* bears some resemblance to *Benthosema* otoliths, and it is possible that these researchers mistook late Miocene specimens of *Benthosema taurinense* Carnevale & Schwarzhans, 2022 for *Diaphus metopoclampoides*. If that is true, it would leave a stratigraphic range of the species from the late Burdigalian to Langhian and possibly Serravallian. Furthermore, the species appears to be a temperate to subtropical northern hemisphere species, and its geographic distribution is yet to be investigated. In Japan, *Diaphus epipedus* represents a related coeval species.

Diaphus cassidiformis (Fig. 19) is a small species but is nevertheless relatively easy to recognize by its very compressed shape with an index OL:OH of 1.0-1.1. It was originally described from New Zealand and has subsequently also been identified in West Africa (Schwarzhans 2013b), the Paratethys (following an ongoing review of myctophid otoliths described by Radwanska 1992), and now Japan. Its occurrence is somewhat irregular and disjunctive, which may point to a pseudoceanic rather than high oceanic lifestyle. Thus far, it has not been identified from the Americas. Stratigraphically, it appears to be indicative for the middle Miocene with a confirmed range from the latest Burdigalian (in Japan) through Serravallian (in West Africa). We consider Diaphus cassidiformis to be relatively valuable for superregional biostratigraphic correlation.

Diaphus hataii (Fig. 20) was extensively discussed in the previous chapter, which focused on the paleobiogeography of early to middle Miocene myctophids. It is a very common species, particularly in Japan, but is also found in certain basins in Europe and Central America. Its recognition and distinction from other *Diaphus* species, however, are still not well understood and so is its stratigraphic range that seems to be confirmed throughout the Burdigalian and Langhian but could reach into Serravallian or even Tortonian. Tentatively assigned specimens from the early



Figure 19. Biostratigraphic and biogeographic distribution of *Diaphus cassidiformis* (Frost, 1933). See Fig. 12 for database and paleogeographic reconstructions.



Figure 20. Biostratigraphic and biogeographic distribution of *Diaphus hataii* Ohe & Araki, 1973. See Fig. 12 for database and paleogeographic reconstructions.

Pliocene of Central America in Schwarzhans and Aguilera (2013) likely represent a different species. Nevertheless, despite this species abundance and wide geographic distribution, its practical biostratigraphic value is still problematic and requires further investigation.

# Conclusions and outlook

The late Burdigalian to early Langhian sediments of western and central Honshu, Japan, have yielded a rich association of myctophid otoliths. This is the first sizeable assemblage so far reported from the Miocene of the North Pacific, with the exception of a study by Ohe and Araki (1973), which, however, was less rich in myctophids. The main results of this study are as follows:

 The myctophid assemblage from the late Burdigalian-early Langhian of Japan fills an important geographic gap and provides initial evidence concerning the composition of mesopelagic fishes at the time from the region.

- A superregional comparison of the early-middle Miocene myctophid assemblage from Japan with faunas from Europe, Central America, and New Zealand indicates that a varied set of shared species existed, which, similarly to the contemporary situation, allows for a direct correlation of mesopelagic fishes from the time across large geographical distances.
- The late early to middle Miocene now harbors the most complete record of fossil myctophids on the globe and indicates the potential of myctophid otoliths with regard to superregional biostratigraphic purposes in the Neogene.

The study of Neogene myctophid otoliths has begun to yield a picture that seems very promising for a variety of future applications, not least the use of these otoliths as an additional tool for superregional biostratigraphy. Otoliths may be less common than planktonic foraminifera or nannoplankton, and they may also be less resistant to destruction by different causes, but they have the advantage of being usually autochthonous due to their vulnerability to erosion. However, much work will be required before a reliable biostratigraphic scheme can be established based on otoliths. Formulating such a scheme will require sampling many more regions of the world and performing detailed stratigraphic sampling. The present study does not really offer much more beyond a glimpse into their potential application. We hope that other researchers will be inspired by the potential of otoliths and thus pay attention to them while conducting their research.

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# A possible terrestrial egg cluster in driftwood from the Lower Jurassic (Late Pliensbachian) of Buttenheim (Franconia, Germany)

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# Abstract

Our paper shows several clusters of circular fossil egg capsules from the Franconian Amaltheenton Facies (Lower Jurassic, Upper Pliensbachian), mostly found in the clay pit south of Buttenheim. The egg capsules are scatteredly and irregularly arranged on various substrates like calcareous nodules, mollusk shells, or sunken driftwoods. Marine gastropods have been presumed as their producers spawning their eggs autochthonous. Only one specimen exhibits a regular honeycomb-like pattern of small pyritized eggs deposited seemingly within driftwood but originally lead in a small deadwood break. We interpret it as representing a possible allochthonous insect spawn drifted off from the about 70 km removed coastal region.

# Keywords

Liassic, egg capsules, gastropods, insects

# Introduction

In the fossil record, non-vertebrate eggs have been described in all ages (for review, see Zatoń et al. 2009; Boucot and Poinar 2010). For instance, authors interpreted Ediacaran fossils as "resting zygotes within egg cases" (Xiao et al 1998, p. 557) or "animal-like eggs" (Willman et al. 2020, p. 1) and Cambrian fossils as "eggs containing identifiable embryos of metazoans" (Bengtson and Zhao 1997, p. 1645). For example, the phosphatized (Orsten type preservation) Cambrian egg like *Markuelia* has been interpreted as an embryo of stem-priapulid worms (Dong et al. 2010). In rare cases, fossils show eggs in combination with putative producers as shown for the eggs of the bradoriid arthropod *Kunmingella* from the Lower Cambrian (Shu et al. 1999). Some fossilized egg producers indicate parental brood care, for example, Silurian ostracods (Siveter et al. 2007) or Carboniferous both spinicaudatans (Vannier et al. 2003) and syncarid crustaceans (Perrier et al. 2006). Late Carboniferous fossils also revealed the first gastropod egg capsules, attached to bivalve shells (Emrich et al. 2017), and the first insect egg clusters, oviposited on or in plants (Béthoux et al. 2004; Laaß and Hauschke 2019). Mesozoic ages added annelid egg cases (Late Triassic, Manum et al. 1991) and ammonite egg sacs (Late Jurassic, Etches et al. 2009) to the known fossil record. With the increasing occurrences of Mesozoic and particularly Cenozoic amber Lagerstätten, many ovipositions of insects became available (e.g., Xing et al. 2021), preserved often jointly with their producers (e. g., Keupp 2021d). However, "most of these cases could reflect false oviposition due to death stress" (Hörnig et al. 2019, p. 123).

Beside the below mentioned findings in the clay pit south of Buttenheim, fossil record of gastropod egg capsules is

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"extremely poor due to their low fossilization potential" (Zatoń and Mironenko 2015b, p. 1). The known findings include imprints on bivalve shells, on gastropod shells or on ammonite body chambers from the Lower Jurassic (Kaiser and Voigt 1977; Kaiser and Voigt 1983), the Upper Jurassic (Zatoń and Mironenko 2015b) or the Cretaceous (Zatoń et al. 2013; Zatoń et al. 2017) as well as one three-dimensional record in mid-Cretaceous amber (Xing et al. 2021). To our knowledge, there are only two examples of pyritized gastropod eggs on driftwood (Riegraf and Schubert 1991; Schubert et al. 2008).

Analysis of fossil evidence for insect oviposition has shown that "almost all fossil structures on plants, which have been identified as oviposition, are of the endophytic mode" (Laaß and Hauschke 2019, p. 1). That is, there are scars as ovipositional records on plant fossils, very most of which are on leaves (e.g., Moisan et al. 2012; Gnaedinger et al. 2014; Laaß and Hauschke 2019). In contrast to the scars on leaves, to our knowledge, fossil record shows only one endophytic ovipositional scar on a fruit (Middle Jurassic, China; Meng et al. 2019) and very few scars on stems (e.g., Béthoux et al. 2004). Exophytic oviposition is a large minority on plant fossils, for instance, on a Cordaites leaf (Upper Carboniferous, Germany, Laaß and Hauschke 2019). Additionally, there are three ichnogenera of fossil insect egg clusters that are not attached to specific plant fossils and interpreted as eggs of aquatic insects, for instance, Monilipartus (Upper Buntsandstein, France; Gall and Grauvogel 1966).

In our paper, we summarize previous findings of autochthonous non-vertebrate eggs in the clay pit south of Buttenheim (Lower Jurassic, Germany), describe new egg findings, and discuss their relevance for the fossil record of non-vertebrate eggs.

## The clay pit south of Buttenheim

Lower Jurassic strata occur in northern Bavaria along the mountainside of the Franconian Alb. The clay pit of the LIAPOR Company Altendorf south of Buttenheim (49°47'34"N, 11°02'30"E) lies about 8 km south-eastwards of Bamberg and crop out both, the Lower Jurassic Amaltheenton Formation (Upper Pliensbachian) and the Posidonia Shale (Lower and Middle Toarcian) (Fig. 1). The about 35 m thick section of the Amaltheenton Formation is characterized by homogenous dark clay intercalated with irregularly distributed calcareous concretions. The profile can be subdivided by four thin horizons that represent short phases of reworking by high water energy settings due to sea level low stands, resulting in the winnowing of smaller grain sizes and enrichment of the reworked concretions (Keupp and Schobert 2015; Keupp et al. 2016a, 2016b). The stratigraphic boundary between the top of the Margaritatus ammonite zone (Gibbosus subzone) and the basal Spinatum ammonite zone (Apyrenum subzone) is marked by the 'pyrite-bed' containing up to 600 mm large ammonites of Amaltheus margaritatus and the first Amaltheus salebrosus and Pleuroceras solare. It is further characterized by an enrichment of small calcareous nodules of 10-40 mm in diameter exhibiting bioerosion scratch marks on its surface. The second reworking horizon, the 'Quellhorizont' (spring horizon), marks the stratigraphic boundary between the Apyrenum subzone and the Hawskerense subzone, bearing the first Pleuroceras spinatum. The third reworking horizon, the socalled echinid-pectinid-bed (EPH), is characterized by pebbly coquina and by largely reworked calcareous nodules



Figure 1. Map of Germany (Bavaria coloured) with the position of the clay pit south of Buttenheim (left) and its schematized profile (right): The red lines mark the four reworking horizons.

which are synsedimentarily settled by a diverse association of hardground settlers (Keupp 2021c). The fourth reworking horizon, the so-called 'Bollernbank' marks the Pliensbachian top and represents a sedimentary gap of about 150 ky (Keupp 2021a). The more or less condensed sections between the first three reworking horizons are fossil rich comprising mass occurrences of ammonites and other fossils. They represent sea level highs with reduced sedimentation rates and faunal immigration from the Tethyan Ocean in the south (Keupp and Schweigert 2017). The section above the 'pyrite-bed' of about 6 m thickness corresponds with the Apyrenum subzone and contains aragonitic shells of a diverse ammonite association, often preserved with color patterns. Above the 'Quellhorizont' the increasing fossil enrichment culminates in a mass occurrence of Pleuroceras spinatum about 6 m below the 'Bollernbank'.

# Autochthonous non-vertebrate eggs from the Amaltheenton Facies of Buttenheim

Keupp et al. (2016b) described for the first time pyritized remnants of a presumed molluscan spawn (pyritized fixation bases and flattened egg capsules) from the Late Pliensbachian sediments of the Buttenheim clay pit. They discussed *Hayamia reticulata*, a gastropod found in the same outcrop, as the originator, owing to comparisons with similar findings of the Lower Jurassic of Poland and the Early Cretaceous of Daghestan (Zatoń et al. 2009; Zatoń and Mironenko 2015a) as well as modern spawns of neritimorph gastropods. The loosely arranged cluster of about 40 egg capsules is attached to the surface of a calcareous nodule (75 × 32 mm) of EPH and occupies an area of about 300 mm<sup>2</sup> (Fig. 2A, B). Calcareous nodules of this horizon were synsedimentarily washed out from the muddy sediment. Afterward, mostly all sides were settled by hard ground colonizers and at least enriched with coarse shell chills.

The second report is given by Keupp and Doppelstein (2018). The authors figured a presumed gastropod spawn, which was fixed at the navel of a large ammonite shell (*Pseudamaltheus engelhardti*) found in the EPH. More than 100 irregularly arranged circular egg capsules of about 1 mm in diameter cover an area of about 900 mm<sup>2</sup> (Fig. 2D).

The third report presented two additional findings (Keupp 2021b): First, a couple of nine scatteredly arranged and three-dimensionally preserved pyritized egg capsules are fixed on the surface of a *Pleuroceras spinatum*, which are included in the private collection of Bernd Doppelstein, Berlin. The diameter range is also about 1 mm. Their slightly wrinkled surface indicates a taphonomic shrinkage process (Fig. 2C). Size and preservation correspond with the



**Figure 2.** Autochthonous clusters of probable gastropod spawns with pyritized egg capsules, each of about 1 mm in diameter, found in the Late Pliensbachian claystones (Amaltheenton Facies) of Buttenheim. **A**, **B**: Attached on the surface of a carbonatic concretion of the EPH (from Keupp et al. 2016b, SNSB-BSPG 2014 XXV 332). **C**: Three-dimensional preserved egg capsules on the shell of *Pleuroceras spinatum*, image width 11 mm (from Keupp 2021b). **D**: Covering the navel of *Pseudamaltheus engelhardti* from the EPH (from Keupp and Doppelstein 2018). **E**, **F**: On the belemnite rostrum of *Passaloteuthis* sp., at the transverse fracture of the surrounding concretional limestone, the lens-shaped configuration of the egg capsules is visible (arrow) (from Keupp 2021b, SNSB-BSPG 2011 XI 1333).



**Figure 3.** Hitherto unpublished presumed gastropod spawn (red arrow) from the Late Pliensbachian of the clay pit south of Buttenheim (leg. J. Schobert, SNSB-BSPG 2011 XI 1334) fixed on the surface of 88 mm long driftwood piece (left). Right: Irregular cluster of pyritized, circular, and scatteredly arranged egg capsules of about 0.9 mm diameter.

probable gastropod spawn described by Schubert et al. (2008) which was attached to the surface of a driftwood from the Late Pliensbachian of northern Germany. Second, an about 70 mm long belemnite phragmocone (*Passaloteuthis*), collected by one of us (J. S.), is partly covered by thin relicts of the rostrum. On its surface, one can see imprints of a cluster of circular and irregularly arranged egg capsules of 1 mm diameter, along a 35 mm long and 10 mm brought stripe (Fig. 2E). Within the transverse fracture of the concretion surrounding the belemnite rest, the lens-shaped outlines of the slightly compressed pyritized egg capsules are visible (arrow in Fig. 2F).

# Hitherto unpublished egg findings

First, a pyritized 88 mm long piece of driftwood shows a spawn of about 16 scatteredly arranged circular egg capsules of about 0.9 mm diameter. The three-dimensional preserved pyritized eggs are partly shrunk, partly hemispherical with smooth surfaces (Fig. 3). The center of each egg bears a small, about 0.25 mm broad pore. Arrangement, settlement on a pyritized driftwood, habitus and dimensions of the eggs correspond with the presumed gastropod spawn described by Riegraf and Schubert (1991) and also the example described by Schubert et al. (2008), besides of the egg diameters (0.9 mm vs. 0.35 mm). Both stem from the contemporaneous sediments of northern Germany.

Second, one of us (J. S.) found an additional hitherto unpublished specimen from the Amaltheenton facies from Buttenheim. A cluster of pyritized egg capsules attached to the inside of a small, 3 mm long pectinid bivalve fragment has been identified among the sieve residues of micropaleontological samples of the EPH (Fig. 4). With irregularly and scatteredly arranged egg capsules, the pattern corresponds with the examples from the same locality described above, but their diameters of 0.5 mm reach only half the size. Also, the egg capsules described by Kaiser and Voigt (1977) inside of a pectinid bivalve from the



Figure 4. A: Fragment of a pectinid bivalve (3 mm) showing inside attached pyritized egg capsules of about 0.5 mm in diameter (B). Late Pliensbachian (EPH) of the clay pit south of Buttenheim (collected by J. Schobert, SNSB-BSPG 2011 XI 1332).



**Figure 5.** Adhesive rings of presumed gastropod egg capsules of about 0.36 mm in diameter inside a *Pleuroceras* body chamber, Late Pliensbachian of Hummeltal-Creez SW of Bayreuth (leg. F.-J. Scharfenberg, SNSB-BSPG 2022 I 2).

Late Pliensbachian of northern Germany are significantly larger, reaching diameters of 1.3–1.5 mm.

Third, one of us (F.-J. S.) identified adhesive rings of scatteredly arranged egg capsules inside a *Pleuroceras* body chamber from the Late Pliensbachian Amaltheenton facies (Fig. 5), found in a small creek ("Mistel") near Creez-Hummeltal southwestern of Bayreuth (49°52'34"N, 11°30'4"E). Their diameter only reaches 0.36 mm.

We conclude that the dimensions of presumed gastropod egg capsules found in Late Pliensbachian marine sediments differ between 0.35 and 1.5 mm. Their shape is primarily hemispherical with or without a visible central pore. They are always arranged scatteredly, touch each other only occasionally, and do not exhibit any regular geometrical patterns.

# Egg capsules with honeycomb-like arrangement

In 2008, one of us (F.-J.S.) found a non-bed-by-bed collected piece of a fossil driftwood in the Amaltheenton facies of the LIAPOR Company's claypit south of Buttenheim. The about 80 × 30 mm large wood fragment is preserved partly as black glittering jet coal, partly pyritized exhibiting excellent cellular structures (Fig. 6). Enclosed into the wood is a crescent-shaped area of 8 × 2.5 mm showing a crescent-sized cluster of densely, nearly seamless packed pyritized egg capsules of 0.4–0.5 mm in diameter (Fig. 7A). The reniform to polygonal egg capsules exhibit their basal side upwards tracing the fibrous wood structure (Fig. 7B). At the one end of the spawn area, 13 egg capsules are broken out. Their molds reveal the smooth convex upper side of the egg capsules, each bearing a circular central opening of 90 µm width (Fig. 7C). The position of the egg cluster seemingly enclosed within the wood is difficult to explain. The imprints of wood fibers on the base of the egg capsules prove that the eggs have been laid on a flat wood level probably of a torn deadwood break casting its structure similar to bioimmuration process (Voigt 1979). This basic wood layer changed during fossilization into jet coal. The wood surface and the attached egg cluster are covered by a thin massive pyrite layer bridging the distance of 1 to 1.5 mm to the next layer of woody matter. During egg-laying, the break was probably wider and was afterward reduced due to taphonomic processes. Therefore, the upper side of the spawn did not originally have direct contact with wood material, as shown by its smooth surfaces without any signs of casted wood structure. Zatoń and Mironenko (2015b) figured similar egg capsules,



**Figure 6.** Fragment of driftwood from the Upper Pliensbachian of Buttenheim. The red arrow marks the enclosed spawn with pyritized egg capsules on the 80 × 30 mm large find (SNSB-BSPG 2022 I 1).



**Figure 7.** Basal surface of the honeycomb-like arranged pyritized egg capsules cluster enclosed in driftwood from Late Pliensbachian of Buttenheim (SNSB-BSPG 2022 I 1). **A:** Complete crescent-sized cluster. The original wood basis changed due to fossilization processes into jet coal (on the picture above left). **B:** On the egg bases, the fine wood fibers of the original basement are preserved by bioimmuration and, therefore, visible. **C:** The molds of broken-out egg capsules exhibit their smooth surfaces with a small central pore. Scale bars 500 μm.

but they were irregularly attached inside of ammonite body chambers from Russian Late Jurassic sediments.

The new finding differs from the hitherto described presumed gastropod spawns from Late Pliensbachian strata of Buttenheim and other localities for three reasons (Kaiser and Voigt 1977, 1983; Riegraf and Schubert 1991; Schubert et al. 2008):

- 1) It is positioned in a small slit of the woody matter.
- Its regular pattern forms a honeycomb-like arrangement.
- The dimensions of the individual egg capsules are in the lower range of most of the clusters of scatteredly arranged presumed gastropod egg capsules.
### Discussion

Deposition of egg capsules on the driftwood could have happened on land, during marine drifting or after they sank on the ground. Besides of gastropod eggs, only few reports exist about fossile egg clusters of other marine non-vertebrate animals. Etches et al. (2009) described presumed cephalopod (ammonites) egg-sacs from the Upper Jurassic Kimmeridge Clay. They represent three-dimensional accumulations of irregularly arranged 1-2 mm sized subspherical eggs with a pimpled surface texture. Authors still speculate about the egg-laying behavior of ammonites, discussing three possible options (De Baets et al. 2015): (1) the laying of eggs at the bottom of the sea (Tanabe et al. 1993), (2) the gelatinous pseudoplanktonic formation of eggs, and (3) the floating of egg sacs (Westermann 1996). Mesozoic ammonitic eggs had dimensions of at least 1 mm generally due to the corresponding diameter of ammonitella. The differences in terms of position in a deadwood break of a driftwood, small size and reqular arrangement of eggs suggest that other organisms as marine molluscs and/or another environment originated the new finding of an egg cluster. That is, our fossil contrasts to the presumed gastropod spawns attached on the surfaces of mollusk shells and driftwoods hitherto known from contemporaneous marine sediments. Therefore, we discuss marine gastropods vs. possible terrestial organisms like pulmonate gastropods and insects as producers.

The oviposition within a small deadwood break by marine gastropods would be very unusual because all hitherto known egg clusters have been laid on open surfaces (e.g., mollusk shells) and larger cavities respectively (e.g., ammonite body chambers). Kaiser and Voigt (1983) described a unique partly net-like arrangement of 1.2 to 1.5 mm large circular egg capsules inside a body chamber of a representative of Pleuroceras from Haverlahwiese near Salzgitter (marine facies, northern Germany). These circular egg capsules were located among several gastropod egg clusters of the same locality, which show a similar irregularly arranged pattern like most of the findings from Franconia do. However, the eggs of the partly net-like arranged cluster are three times larger than the eggs of our new finding from Buttheim are. Thus, we presume that the eggs were probably laid in the wood on land before they drifted into the marine environment. We know some recent pulmonate freshwater gastropods laying their eggs outside the water (e.g., Burks et al. 2010) as well as various landsnails laying their eggs in deadwood (Strätz 2006), for instance the tropical Camenidae Amphidromus (e.g., Schilthuizen 2013) - But the egg depositions of pulmonate gastropods always form irregular bunches and do not show geometrically arranged clusters (see Figure, Schilthuizen 2013).

On the other hand, regular patterns of epiphytic oviposition are well known and widely distributed among fossil and modern insects, particularly roaches and many butterflies. Roaches (Blattodea) are one of the oldest insect orders known since the Carboniferous, while the radiation of Lepidoptera started during the Late Triassic (Van Eldijk et al. 2018). Laaß and Hauschke (2019) described the oldest exophytic oviposition of insect eggs on Carboniferous *Cordaites* leaves. The individual circular eggs show diameters of nearly half a millimeter ( $388-482 \mu m$ ) forming curved arcs of net-like densely packed clusters. The authors presume insects with short abdomens and ovipositors like roaches as producers. Some extant Lepidopterans produce mono-layered and crescent-sized egg clusters which are similar in size of their egg capsules and in shape of the cluster to our fossil, for example, *Spodoptera frugiperda* (see fig. 02(f), Kasige et al. 2022).

## Conclusion

The producer of the regular honeycomb-like pattern of egg capsules found within a Pliensbachian piece of driftwood from Buttenheim (Figs 6, 7) still remains enigmatic. We cannot completely exclude marine or terrestrial gastropods as possible producers of this fossil. However, owing to the corresponding dimension and similar patterns of their arrangement with Carboniferous blattoidean eggs (Laaß and Hauschke 2019), as well as their deposition within a small deadwood break, we presume rather a terrestrial origin by unknown insects than a marine deposition by gastropods. Fossil driftwoods are often responsible for allochthonous depositions of organisms that settle on their surface and therefore they causes taphocoenoses of heterogenous environments (Keupp et al. 2018).

The specimens figured on Fig. 2A, B, E, F and Figs 3–6 are housed at the Bavarian State Collection, Munich (SNSB-BSPG), specimens figured on Fig. 2C, D at the private collection of Bernd Doppelstein, Berlin.

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## An unusual specimen of the enigmatic fungal reproductive unit *Windipila spinifera* from the Lower Devonian Rhynie cherts of Scotland

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## Abstract

Windipila spinifera from the Rhynie cherts is a spheroidal microfossil enveloped in a hyphal mantle from which extend prominent spines and otherwise shaped projections. It is believed to be a reproductive unit of a fungus in the Glomeromycota or zygomycetes, but features to determine the systematic affinities have not hitherto been documented. This study describes a new specimen of *W. spinifera* that contains a single spherical structure from which a hypha arises that extends outside and terminates in what appears to be a sporangium. The specimen is reminiscent of germinated zygospores of the germ-sporangial type, and thus may suggest affinities of *W. spinifera* to the zygomycetes. However, the interior sphere and its outgrowth could also be a part of another organism that had invaded *W. spinifera*.

## Keywords

fossil fungi, Glomeromycota, intrusive organisms, zygomycetes, zygospore germination

## 1. Introduction

The Lower Devonian Rhynie cherts (including the Rhynie and Windyfield cherts) of Scotland give detailed insights into fungal diversity in a terrestrial ecosystem c. 410 Ma ago (Taylor et al. 2015; Krings et al. 2017a; Strullu-Derrien et al. 2019). One important proxy indicator of this diversity is the morphological variety of fungal propagules and microscopic reproductive units, both of which are present in virtually every thin section of the cherts. However, dealing with these fossils is difficult because they mostly occur detached from the systems on or in which they were produced, and thus do not provide an inclusive comparison with present-day equivalents to determine their systematic affinities (Krings and Harper 2020). Several types of fungal reproductive units have been described from the Rhynie cherts that all possess an ancillary covering in the form of a hyphal investment or mantle. Mantle morphology varies (considerably) among the different types, and thus renders them easy to distinguish from one another (Krings and Taylor 2013, 2014, 2015a, 2015b; Krings et al. 2014, 2016, 2017b; Krings and Harper 2017, 2018, 2020). One of these fossils is *Windipila spinifera* (Fig. 1A), a walled spheroid less than 150 µm in diameter that is enveloped in circumferential hyphae from which extend prominent, thin-walled spines and otherwise shaped projections (Krings and Harper 2017, 2018).

Most mantled fungal reproductive units from the Rhynie cherts, including *Windipila spinifera*, are believed to belong to either the Glomeromycota or the zygomycete fungi based on similar features in modern

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lineages known to produce spores or sporangia with hyphal mantles (e.g., Krings et al. 2016, 2017a; Krings and Harper 2020). The occurrence of several specimens on what appear to be simple, tubular subtending hyphae has been used to suggest that *W. spinifera* developed asexually by blastic inflation and thickening of a hyphal tip, rather than sexually and following gametangial fusion, and for this reason might be a glomoid chlamydospore (Krings and Harper 2017). However, structural features to more precisely delimit the nature and systematic affinities of this fossil have not been documented to date.

This study describes a new specimen of *Windipila spinifera* from the Windyfield chert that contains a single spherical structure from which an unbranched hypha is given off that evidently passes through the wall and mantle and terminates in what appears to be a sporangium with a distal discharge papilla. While this specimen does also not clarify the affinities of *W. spinifera*, it resembles a germinated zygospore or azygospore with a tubular sporangiophore and distal germ sporangium, and thus is suggestive of affinities to the zygomycetes.

## 2. Geological setting

The Rhynie chert Lagerstätte is located in the northern part of the Rhynie outlier of Lower Old Red Sandstone in Aberdeenshire, Scotland, in an extensive sequence of sedimentary and volcanic rocks. The cherts occur in the Rhynie Block of the Dryden Flags Formation located northwest of the village of Rhynie. The Lagerstätte is made up of fossiliferous beds containing lacustrine shales and chert that have been interpreted as a series of ephemeral pools within a geothermal wetland, with alkali-chloride hot springs that were part of a complex hydrothermal system in a region affected by volcanic activity (Rice et al. 2002; Rice and Ashcroft 2004; Trewin and Fayers 2016; Channing 2017). The Windyfield chert site occurs ~700 m to the northeast of the original Rhynie chert site (Trewin and Rice 1992; Fayers 2003; Garwood et al. 2020). It was deposited in an area of hot-spring feeder activity based on the hydrothermally altered nature of its associated fluvio-lacustrine shales and sandstones; paleoenvironments ranged from terrestrial, vegetated aprons of laminated and brecciated sinter to low-temperature pools and marginal aquatic settings (Rice et al. 2002; Fayers 2003; Fayers and Trewin 2004). The Rhynie and Windyfield cherts are regarded as broadly coeval, i.e., 411.5±1.3 to 407.6±2.6 million years old according to Mark et al. (2011, 2013) and Parry et al. (2011), Pragian-earliest Emsian according to Wellman (2006, 2017) and Wellman et al. (2006). For details on the geology and development of the Rhynie chert Lagerstätte, as well as on the paleontology, refer to Trewin and Kerp (2017), Garwood et al. (2020), and the Rhynie chert volume edited by Edwards et al. (2018).

## 3. Material and methods

The specimen described below was identified in a thin section prepared by cementing a wafer of the Windyfield chert to a microscope slide, and then grinding the rock slice until it was sufficiently thin (i.e. c. 60–80 µm thick) to transmit light (for details on thin section preparation, refer to Hass and Rowe 1999). The slide is deposited in the SNSB-Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich, Germany, under accession number SNSB-BSPG 2016 VII 117. The specimen was studied using normal transmitted light microscopy; digital images were captured with a Leica DFC-480 camera and processed in Adobe Photoshop CS5. For comparison, another specimen of *Windipila spinifera* from the holdings of the SNSB-BSPG (accession number SNSB-BSPG 2016 VII 82) has also been illustrated.

## 4. Results

The specimen (Fig. 1B<sub>1</sub>) is located in the chert matrix, within silicified litter comprised predominantly of fragmented and mostly heavily degraded land plant axes, dispersed land plant spores, unidentifiable debris, and fungal hyphae. The reproductive unit is spherical, roughly 145 µm in diameter (including mantle but excluding projections), and composed of a central cavity bounded by a non-hyphal wall up to 2 µm thick. No evidence has been found of pores or otherwise shaped orifices in the wall. The reproductive unit is enveloped in a hyphal mantle composed of 1-3 layers of tightly interlaced hyphae extending along the outer surface of the non-hyphal wall. Prominent projections, irregularly distributed over the entire surface, are given off from the circumferential hyphae in an outward direction. However, there are fewer projections in this specimen as compared to the specimens described previously (Fig. 1A<sub>1.2</sub>; Krings and Harper 2017, 2018). The structure in vivo was probably positioned terminally on a lateral branch or outgrowth of a tubular hypha (see below). However, the attachment site is obscured by the mantle hyphae and most of the hyphal nexus is not recognizable due to the plane of the section through the specimen.

The reproductive unit contains a single, more or less spherical structure (henceforth called interior sphere) that is c. 55 µm in diameter, lacks structured contents, and is delineated by a smooth wall up to 0.75 µm thick. Its position within the cavity is highly eccentric in such a way that it comes into contact with, and in vivo perhaps adhered to, the inner surface of the non-hyphal wall of the reproductive unit. The interior sphere is somewhat flattened where it is in physical contact with this wall. No evidence of a subtending hypha or any other kind of parental structure has been found. However, the cavity of the reproductive unit contains shrivelled fragments of thin-walled hyphae or filaments (Fig. 1B<sub>2</sub>). Arising from roughly the center of the flattened portion of the interior sphere is a narrow hypha 1-2 µm wide (arrows in Fig. 1C), which evidently passes through the non-hyphal wall of the repro-



**Figure 1.** *Windipila spinifera* from the Lower Devonian Rhynie cherts (Windyfield chert).  $A_{1,2}$ . Well preserved specimen in two different focal planes ( $A_1$ : median optical section,  $A_2$ : section off center), with prominent spines and otherwise shaped projections extending from mantle (focal plane  $A_1$  previously published by Krings and Harper 2018: fig. 1A). Slide SNSB-BSPG 2016 VII 82. **B–F.** New specimen. Slide SNSB-BSPG 2016 VII 117. **B**<sub>1</sub>. Overview (median optical section), showing interior sphere in highly eccentric position and stalk-like hypha (arrow) terminating in exterior sphere. **B**<sub>2</sub>. Second exterior structure in different plane; note attached fragment of putative parental hypha (arrow). **B**<sub>3</sub>. Shrivelled hyphae or filaments in cavity of reproductive unit. **C.** Hypha arising from interior sphere (arrows). **D.** Stalk-like hypha becoming wider in periphery of mantle (arrow), and extending in outward direction. **E.** Papilla-like, distal putative discharge apparatus of exterior sphere. **F.** Hypha (rh) with three attached *W. spinifera* reproductive units (labeled 1–3), of which the one in the lower right of the image (labeled 1) is magnified in Fig. 1B<sub>1</sub>; specimen 2 occurs on a lateral branch (lb) and 3 at the tip of the hypha. Scale bars: 10 µm (**B**<sub>4</sub>, **C**, **E**); 20 µm (**B**<sub>2</sub>, **D**); 50 µm (**A**<sub>1</sub>, **A**<sub>2</sub>, **B**<sub>1</sub>); 100 µm (**F**).

ductive unit and proceeds on the outside into the mantle. Unfortunately, the exact path of the hypha through the wall and mantle is not traceable. The hypha reappears in the periphery of the mantle where it expands to up to  $6.5 \,\mu m$  wide (arrow in Fig. 1D) and becomes tubular (stalk-like), and from there runs outwards c. 40  $\mu m$  into the ambience

(arrow in Fig. 1B<sub>1</sub>). The hypha is unbranched and terminates in another spherical structure (henceforth called exterior sphere), which is 46  $\mu$ m in diameter, bounded by a smooth wall, and does also not have structured contents. The exterior sphere is characterized by a single, distal, thin-walled papilla-like projection 8.5  $\mu$ m high (Fig. 1E). A second exterior structure, c. 38  $\mu$ m in diameter and somewhat asymmetrical or distorted, occurs in close proximity to the exterior sphere in a different plane of the specimen (Fig. 1B<sub>2</sub>). This structure, which is partially embedded in the mantle of the reproductive unit, is subtended by a short fragment of what appears to be a hypha (arrow in

the interior sphere cannot be determined. The hypha (rh in Fig. 1F) that gives rise to the specimen described above (labeled 1 in Fig. 1F) bears two further *Windipila spinifera* reproductive units (labeled 2 and 3 in Fig. 1F), one of which occurs on a lateral branch (lb in Fig. 1F), while the other (partially degraded) appears to be positioned at the tip of the hypha itself. Because these latter specimens do not exhibit any new or unusual features, they will not be discussed here any further.

Fig. 1B<sub>2</sub>). As to whether this hypha also originates from

## 5. Discussion

Eight morphologically different types of mantled fungal reproductive units have so far been described from the Rhynie cherts, of which *Windipila spinifera* with its prominent mantle spines certainly is one of the more peculiar ones (Krings and Harper 2017, 2018). A similar, albeit less impressive mantle occurs in the little-known *W. pumila* (Krings and Harper 2018). A third type attributed to *Windipila*, *W. wimmervoecksii*, is characterized by mantle hyphae with vesicle-like inflations from which extend needle-like processes that connect the inner mantle tier with an outer tier of irregularly inflated and interwoven hyphae (Krings and Harper 2020).

Windipila has been suggested to have affinities to either the Glomeromycota or the zygomycete fungi (Krings and Harper 2020). One of the key features distinguishing these two groups of fungi is the sexual stage of the life cycle, which occurs in zygomycetes as a result of zygosporogenesis following gametangial fusion, but has not been observed in Glomeromycota (Benjamin 1979; Benny et al. 2001, 2012). Mature zygosporangia or zygospores with attached gametangia and/or suspensors are therefore the most important component of the zygomycete life cycle that can be used to positively identify a fossil member in this group of fungi (Krings et al. 2012, 2013). However, none of the Windipila species can presently be positively identified as a zygomycete because there is no evidence of gametangia and/or suspensors. Rather, several specimens of W. spinifera (Krings and Harper 2017: fig. 2) and W. wimmervoecksii (Krings and Harper 2020: figs 2d, 3a) appear to have developed on simple, tubular subtending hyphae. Moreover, hyphal anastomoses and H-branching, which are common in several lineages of glomeromycotan fungi (Walker et al. 2018) but believed to be lacking or rare in zygomycetes (Gregory 1984; Glass and Fleissner 2006; Ivarsson et al. 2015), have been documented in *W. wimmervoecksii* (Krings and Harper 2020: figs 4a, b, 5).

The most interesting structural element of the only known specimen of Windipila pumila is a walled spherical structure that occurs in the cavity of this fossil (Krings and Harper 2018: fig. 2). Similar spheres have not hitherto been recorded in W. spinifera or W. wimmervoecksii, but they have been described in other Rhynie chert mantled fungal reproductive units, including Scepasmatocarpion fenestrulatum (Krings and Taylor 2015a: figs 1e, 2c) and Zwergimyces vestitus (Krings et al. 2016: pl. III, 2-8). The interior spheres have been used to speculate that these reproductive units could be sporangia or sporangiola, perhaps comparable to the zygosporangia of zygomycetes or the sporangial or sporangiolar layer(s) of certain glomeromycotan spore walls (see Walker et al. 2021: fig. 1), and the interior spheres either the zygospore or the sporangiospore proper (e.g., Krings and Harper 2018).

The fossil presented in this study provides the first evidence of the occurrence of interior spheres also in Windipila spinifera. Moreover, it exhibits several structural features pertaining to the interior sphere that have not been documented in any other Rhynie chert mantled reproductive unit. Said interior sphere gives off a hypha that exits the reproductive unit and terminates in another spherical structure, which is characterized by a papilla-like protrusion that most likely functioned as a discharge apparatus. There is a certain level of morphological correspondence between the fossil and certain zygomycetes of the order Mucorales in which zygospore germination entails the formation of a germ sporangium (e.g., Brefeld 1872; De Bary 1884; Blakeslee 1906; Gauger 1961: figs 1-3; Hocking 1967). During the sexual stage of the life cycle, these fungi produce zygosporangia (zspo in Fig. 2) containing single zygospores (zsp in Fig. 2) following gametangial fusion, and sometimes azygosporangia containing azygospores, which are similar to zygospores but form parthenogenetically without gametangial fusion (e.g., Benjamin and Mehrotra 1963; O'Donnell et al. 1977). The zygosporangium wall eventually ruptures and the zygospore germinates. If germination is of the germ-sporangial type (sensu Guo and Michailides 1998), then the zygospore produces a tube-like structure termed a sporangiophore or promycelium (sph in Fig. 2), on the tip of which a germ sporangium develops (spo in Fig. 2). After maturation of the spores (called germ sporangiospores), the germ sporangium ruptures and liberates the spores, which, if they fall on a suitable substrate, germinate and develop into a new mycelium (e.g., Cerdá-Olmedo 2001: fig. 1). It is conceivable that the W. spinifera specimen described above represents a zygosporangium or azygosporangium containing a zygospore or azygospore (i.e. the interior sphere), which has germinated and produced a sporangiophore (i.e. the stalk-like hypha) with a terminal germ sporangium (i.e. the exterior sphere). The second exterior



**Figure 2.** Germinated zygospore of *Mucor mucedo* (Mucorales); zspo = zygosporangium, zsp = zygospore, sph = sporangiophore or promycelium, spo = germ sporangium (modified from De Bary 1884: fig. 71C).

structure, which occurs partially embedded in the hyphal mantle of the reproductive unit, could be another germ sporangium. Germinated zygospores with two sporangiophores, each bearing a terminal sporangium, have also been reported in certain present-day zygomycetes (e.g., Michailides and Spotts 1988).

One might counter this comparison by pointing out that no evidence of gametangia and suspensors has been found in any of the *Windipila spinifera* specimens. It is possible, however, that these structures were small, inconspicuous, and entirely embedded in the mantle. For example, the zygosporangia of certain present-day *Mortierella* (Mortierellaceae, Mucorales) species are surrounded by extensive hyphal coverings arising from the suspensors or from hyphae at the base of the suspensors (Brefeld 1881: pl. V, figs 12, 14, 15; Kuhlman 1972; Ansell and Young 1983) that render the gametangia and suspensors very difficult to recognize. It can also be argued

that the interior sphere in W. spinifera is too small to be a zygospore or azygospore because zygosporogenesis involves the development of a complex, multi-layered wall (i.e. the combined sporangium and spore wall) in which newly deposited wall layers follow exactly the shape of the previously deposited layers (e.g., Brefeld 1872: pl. II, fig. 20; Hawker and Gooday 1968; Hawker and Backett 1971; O'Donnell et al. 1978). Rather, the interior sphere is somehow reminiscent of the single oil globules that are visible in the zygospores of, for instance, certain representatives of the mucoralean genera Radiomyces (Radiomycetaceae; e.g., Embree 1959: figs 12, 13; Benny and Benjamin 1991: figs 8, 16, 18, 29h, i) and Dichotomocladium (Lichtheimiaceae; e.g., Benny and Benjamin 1993: fig. 4b). However, it seems unlikely that oil globules would become preserved in a recognizable form. It can also not be ruled out that the spore proper in W. spinifera has shrunken during germination, and again during the silicification process. One must furthermore take into account the possibility that entirely fossil lineages of zygomycete fungi, as well as fossil representatives of present-day lineages, have existed that were characterized by traits unknown in any present-day representative. For example, the germ sporangium in present-day Mucorales ruptures at maturity to release the spores, while the fossil spores likely were liberated through a distal discharge papilla.

An alternative hypothesis views the interior sphere in Windipila spinifera as a part or life cycle stage of some other fungus or fungus-like organism that had invaded and colonized the reproductive unit, and reproduced by producing a sporangium (or sporangia?) outside of the host. Two lines of evidence seem to support this hypothesis. First, co-occurring with the interior sphere in the cavity of the W. spinifera specimen are fragments of hyphae or filaments, which indicate that, at some point, another fungus has been present in this structure, unless the mantle hyphae had invaded the cavity from the circumference (see below). Second, several different types of small spherules occurring singly or in groups, and probably representing the reproductive units of intrusive fungi, have been reported in the cavity of Zwergimyces vestitus (Krings et al. 2016), and thus indicate that mantled fungal reproductive units in the Rhynie paleoecosystem have been invaded by other microorganisms and used as a habitat. On the other hand, there is no evidence of a physical connection between the interior sphere in W. spinifera and any system on which it could have developed. This argues against the hypothesis that the sphere belongs to an intrusive organism. It is also possible that the W. spinifera specimen had already fulfilled its function, namely to produce a spore that subsequently germinated, and, consequently, was in the process of natural decay at the time of fossilization. If this is the case, then the hyphae inside the cavity could belong to saprotrophic fungi or even be outgrowths from the mantle hyphae that invaded the senescing reproductive unit and participated in its degradation.

## 6. Conclusions

The fossil record rarely gives comprehensive insights into the life history of fungi, which is unfortunate because life history stages can provide valuable information to assess the systematic affinities of fossil fungi in the absence of molecular data (Taylor et al. 2015). The affinities of the organism that produced *Windipila spinifera* mantled reproductive units remain conjectural, in spite of the fact that the fossil detailed above shares certain features with germinated zygospores of the germ-sporangial type. I hope that specimens showing these features in greater detail become available as exploration of the Rhynie cherts continues, and that these fossils will clarify the nature of the interior sphere and reveal hitherto unknown aspects, which can then be used to determine the systematic position of *W. spinifera*.

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# Jurassic bivalves from the Spiti area of the Himalayas, northern India

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## Abstract

The present study describes and illustrates six bivalve taxa from the Early Bathonian to Early Callovian Ferruginous Oolite Formation and 24 taxa from the Callovian to basal-most Cretaceous Spiti Shale Formation of the Spiti and Zanskar areas in the Indian Himalayas. The Spiti Shale Formation contains a low-diversity bivalve fauna that is concentrated in few horizons, particularly in the lower member of the formation. With few exceptions, the bivalves are poorly preserved. Bivalve taxa recorded by earlier studies are revised wherever possible. Several of the taxa, most of which are from mid- to outer shelf environments, are characteristic of the south-eastern margin of the Neotethys, but some are also closely related to forms occurring in Kachchh, a rift basin situated at the western margin of the Indian Craton.

## Zusammenfassung

In der vorliegenden Arbeit werden sechs Muscheltaxa aus der Ferruginous Oolite Formation (unteres Bathonium bis unteres Callovium) und 24 Taxa aus der Spiti Shale Formation (Callovium bis unterste Kreide) im Gebiet von Spiti und Zanskar im indischen Himalaya beschrieben und abgebildet. Die Spiti Shale Formation enthält eine niedrig-diverse Muschelfauna, die nur in wenigen Lagen, vor allem im lower member der Formation auftritt. Die Muscheln sind bis auf wenige Ausnahmen schlecht erhalten. Frühere Bestimmungen der Muschelfauna werden revidiert wo immer möglich. Mehrere Taxa, die in Sedimenten des mittleren bis tieferen Schelf vorkommen, sind für den Südostrand der Neotethys charakteristisch. Andere sind eng verwandt aber nicht identisch mit Formen, die im Riftbecken von Kachchh am Westrand des indischen Kratons auftreten.

## Keywords

Bivalvia, offshore shelf, Spiti Shale, taxonomy, Tethys Himalayas

## Introduction

The Spiti Shale Formation of the Tethys Himalaya is a package of black shales with minor sandstone intercalations, which extends from northern Pakistan, via northern India and Nepal to southern Tibet (Fig. 1a). The rocks represent mainly outer shelf to upper slope deposits of the southern margin of the Neotethys. Macroinvertebrate assemblages are dominated by ammonites and belemnites that commonly occur in claystone concretions. Benthic macroinvertebrates (bivalves, gastropods, brachiopods) are restricted to a few widely spaced layers, while large parts of the formation do not contain any macrobenthos. In the Spiti area, the formation is dominated by dark-grey to black and often shaly argillaceous silt to silty clay with minor sandstone intercalatations. The Callovian

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to lowermost Cretaceous Spiti Shale Formation is underlain by the Ferruginous Oolite Formation, a unit of variable lithology (sandstones, shelly limestones, Fe-ooid bearing limestones). It contains a much richer benthic macrofauna, which is, however, usually difficult to extract from the well-cemented rocks. Here we describe bivalves, mainly from the Spiti Shale Formation, collected during two field trips to the area (2016, 2018). Although first documentations of bivalves from these Jurassic rocks reach back to the early nineteenth century (Herbert 1831; Everest 1833), they received further attention only in the mid-sixties of that century when Blanford (1864), Salter and Blanford (1865), and Stoliczka (1866) described a number of bivalve species. Holdhaus (1913) provided the first comprehensive treatment of the bivalve fauna, recording altogether 39 taxa. Since then only one further study dealt with this fossil group (Kanjilal and Pathak 1998). The latter authors recorded ten previously described taxa and updated their taxonomy. The purpose of the present study is to revise the bivalve fauna as a prerequisite for a palaeoecological study (Fürsich et al. 2021) aiming to document the benthic fauna inhabiting the mid to outer shelf regions of the southern Neotethys. Moreover, the present study permits the comparison of the poorly known deep shelf benthic bivalve fauna with the shallow shelf Jurassic fauna of the Kachchh Basin at the western margin of the Indian Craton and thus between the benthic fauna of shallow and deep shelf environments, the latter very poorly known.

## Material and localities

The Spiti area, situated in northern Himachal Pradesh, contains extensive outcrops of the Jurassic sedimentary succession on top of the eastern shoulder of the Spiti Valley (Fig. 1b). Due to the gentle morphology, fresh outcrops are, however, rare being usually restricted to road cuts or cliffs of small streams. Most bivalve fossils come from the lower member of the Spiti Shale Formation, where they weather out from the soft shales or occur in thin shell beds. Very few specimens have been collected from the Ferruginous Oolite Formation. The co-ordinates of the localities from which bivalves have been collected are given in Table 1.

In the Middle member, bivalves are very scarce and usually found in mudrock concretions where they commonly form small clusters. In the Upper member, bivalves locally form loosely packed concentrations, in which the fossils are poorly preserved. Apart from some large and comparatively thick-shelled bivalves such as *Pruvostiella*, bivalves are well preserved only in concretions where they occur as composite moulds. Shells occurring in unconsolidated sediment are usually strongly crushed and fragmented by compaction and tectonic stress, which in some cases renders their identification difficult.

In contrast, the Spiti Shale Formation of the Zanskar Valley in northwestern Ladakh is almost barren of benthic fossils and only few bivalve specimens could be collected from the underlying Ferruginous Oolite Formation near the village of Zangla.



**Figure 1.** Outcrop belt of Tethyan strata in the Himalayas (a) and map of localities in the Spiti area that have been investigated (b).

Altogether more than 240 specimens have been collected from the localities shown in Figure 1b (see also Table 1). After washing them, they have been mechanically prepared where necessary. Before photography, the specimens have been coated with magnesium oxide. The material has been deposited in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (prefix: SNSB-BSPG 2020 XCIX).

## Stratigraphy

The first stratigraphic subdivision of the Jurassic strata of the Indian Himalayas was published by Stoliczka (1866), who distinguished Lower and Upper Tagling Limestone (according to him Lower Jurassic), Clayey Slates, Spiti Shales (according to him Middle Jurassic), and Gieumal Sandstone (Upper Jurassic). Diener (1895: 583), based on 
 Table 1. Localities and their co-ordinates in the Spiti area and the

 Zanskar Valley, from which bivalves have been collected.

Co-ordinates	Stratigraphy
32°20'40.6"N, 77°57'59"E	lower member
32°20'40.6"N, 77°58'04"E	Ferruginous Oolite
	Formation
32°16'16"N, 78°04'12"E	lower member
32°16'08"N, 78°04'31"E	lower member
32°16'03"N, 78°04'43"E	lower member
32°16'04"N, 78°04'35"E	Ferruginous Oolite Formation
32°14'34.6"N, 78°05'07.6"E	lower member
32°14'19.6"N, 78°04'43.6"E	base of lower member
32°09'02"N, 78°10'29"E	upper member
32°14'16"N, 78°06'21"E	middle member
32°09'07"N, 78°10'19"E	upper member
32°19'28"N, 78°00'26"E	lower member
32°17'44"N, 78°02'05"E	lower member
33°41'09.9"N, 76°58'17"E	Ferruginous Oolite
	Formation
	Co-ordinates 32°20'40.6"N, 77°57'59"E 32°20'40.6"N, 77°58'04"E 32°16'16"N, 78°04'12"E 32°16'08"N, 78°04'31"E 32°16'03"N, 78°04'33"E 32°16'04"N, 78°04'35"E 32°14'34.6"N, 78°05'07.6"E 32°14'19.6"N, 78°05'07.6"E 32°14'19.6"N, 78°06'21"E 32°09'02"N, 78°10'19"E 32°19'28"N, 78°00'26"E 32°17'44"N, 78°02'05"E 33°41'09.9"N, 76°58'17"E

Griesbach (1891), subdivided the Spiti Shales in Belemnites gerardi Beds, Chidamu Beds, and Lochambel Beds. The intensively folded and faulted succession made it virtually impossible to measure a single continuous section, which nearly a hundred years later led to disputes of the correct lithostratigraphic composition of the Spiti Shale Formation. Thus, Krishna (1983) distinguished only a lower and an upper member, whereas Pathak (1993) and Pandey et al. (2013) recognised three informal members named the lower, middle, and upper member, respectively (Text-fig. 2), a view followed here. Due to the lack of a continuous section, these members and their boundaries are, at present, very poorly defined. The lower member is characterized by argillaceous silt and silty clay containing common belemnites and bivalves, the latter occasionally concentrated in shell beds. At the base, the bivalve Bositra is abundant, followed by a low-diversity fauna dominated by Palaeonucula, Pruvostiella, and Indogrammatodon. In the middle member silt- and sandstones and some glauconitic shales with phosphorite nodules locally occur and the predominant

Li	thostratigraphy	Metres	Age
Gi	umal Formation	~400	Albian –Berriasian
e Fm	upper member (Lochambel Beds)	<300	?Berriasian –Early Tithonian
Shale	middle member (Chidamu Beds)		Early Tithonian –Kimmeridgian
Spiti	lower member (B. gerardi Beds)		Late Oxfordian –Middle Callovian
Ferr	uginous Oolite Fm	0-20	Early Callovian –Early Bathonian
Та	gling & Para Fm	~600	?Middle Jurassic –Late Triassic

**Figure 2.** Jurassic stratigraphy of the Spiti area (modified from Alberti et al. 2021).

lithology, silty clay/argillaceous silt, contains abundant mudrock concretions arranged in layers. Fossils are occasional ammonites and rare bivalves (*Retroceramus, Australobuchia*). The upper member is characterized by monotonous, unfossiliferous black shales, shales with mudrock concretions, ammonites and belemnites, and some loosely packed bivalve concentrations composed of *Australobuchia, Retroceramus*, and *Malayomaorica*. At the top, the succession coarsens into siltstones and fine- to coarse-grained sandstones. The contact to the overlying Lower Cretaceous sandstone-dominated Giumal Formation is gradual. The thickness of the Spiti Shale Formation is difficult to establish, but judging from the sections measured, which correspond only to segments of the complete succession, the formation is at least 110 m thick (Fürsich et al. 2021).

Based on ammonites, the Spiti Shale Formation in the Spiti area has been thought to range from the Oxfordian to the top of the Tithonian (e.g., Pathak 1993; Pandey et al. 2013), but according to Cariou et al. (1996) the age of the lower member is Callovian–Oxfordian. A more detailed discussion of the existing stratigraphic problems is found in Fürsich et al. (2021).

### Taxonomy

We follow the classification scheme of Bouchet et al. (2010) and Carter et al. (2011). Size measurements were taken with a Vernier caliper. Length was abbreviated L, height H, right valve RV, and left valve LV. The synonymy lists contain, apart from the original combination, for the most part only occurrences documented from the Ethiopian faunal province and from other areas of the Himalayas.

Class Bivalvia Linnaeus, 1758 Subclass Protobranchia Pelseneer, 1889 Order Nuculida Dall, 1889 Family Nuculidae J. Gray, 1824

Genus Palaeonucula Quenstedt, 1930

Type species. Nucula hammeri Defrance, 1825.

#### Palaeonucula cuneiformis (J. de C. Sowerby, 1840) Plate 1, figs 1-2

1831 Modiola – Herbert: 272, pl. 17, fig. 5.

- 1833 Modiola Everest: 114: pl. 2, fig. 28a-c.
- \*1840 Nucula? cuneiformis J. de C. Sowerby: pl. 22, fig. 4 and explanation.
- 1864 Nucula cuneiformis, Sowerby Blanford: 135.
- 1908 Nucula cuneiformis, J. de C. Sowerby Newton and Crick: 7, pl. 1, figs 5–7.
- 1913 Nucula spitiensis sp. nov. Holdhaus: 428, pl. 95, figs 11–13.
- 1913 Nucula hyomorpha sp. nov. Holdhaus: 430, pl. 95, figs 14-17.

1929 Nucula cuneiformis Newton – Weir: 5, pl. 4, figs 2–4.

?1930 Nucula cuneiformis Newton - Basse: 108. pl. 5, fig. 5.

?1939 Nucula cuneiformis Sow. - Stefanini: 219, pl. 24, fig. 3.

- 1940 Nucula (Palaeonucula) cuneiformis J. de C. Sowerby Cox: 13, pl. 1, figs 5–10.
- 1940 Nucula (Palaeonucula) kaoraensis sp. nov. Cox: 15, pl. 1, figs 11–14.
- 1956 Nucula (Palaeonucula) kaoraensis Cox Agrawal: 51, pl. 7, fig. 3a.
- 1959 Nucula cuneiformis Sowerby Jaboli: 46, pl. 6, fig. 3.
- 1980 Palaeonucula kaoraensis Cox Kanjilal: 335, pl. 1, figs 8–10. 1980 Palaeonucula cuneiformis (J. de C. Sowerby) – Kanjilal: 334, pl. 1, figs 4–7.
- 1995 Palaeonucula cuneiformis (J. de C. Sowerby 1840) Jaitly et al.: 155, pl. 1, figs 9–11, 13–17, text-figs 6–9 (pars). [non pl. 1, figs 8, 12, pl. 2, figs 1–2]
- 1998 Palaeonucula cuneiformis (J. de C. Sowerby 1840) Kanjilal and Pathak: 30, pl. 1, fig. 1.

Material. Nine articulated specimens and two left valves from the lower member at Langza (SNSB-BSPG 2020 XCIX 26), 30 articulated specimens, one right and two left valves from the lower member along the Kaza - Hikkim road (SNSB-BSPG 2020 XCIX 27), four articulated specimens from the lower member at Langza (road side exposure) (SNSB-BSPG 2020 XCIX 28), four articulated specimens from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 29), three articulated specimens and one right valve from the lower member near Kibber (SNSB-BSPG 2020 XCIX 30), two articulated specimens from the Ferruginous Oolite Formation near Chichim (SNSB-BSPG 2020 XCIX 31), and three articulated specimens and one right and three left valves from the lower member at Langza locality 3 (SNSB-BSPG 2020 XCIX 32). The shells, several of which are fragmented, invariably suffered compactional and tectonic distortion.

Description. Shell relatively large for genus (H: ~26 mm, L: 32.2 mm), thick-shelled, elongated-oval, strongly inequilateral, moderately inflated. Umbo broad, well-developed, terminal to subterminal, close to posterior end, opisthogyrate. Anterior end narrow to well-rounded, posterior end straight to slightly curved forming a blunt angle with the ventral margin, which describes a wide asymmetric curve with the ventral-most point of shell well anterior of mid-line. Anterodorsal margin straight, sloping; posterodorsal margin short, almost straight to slightly curved, passing gradually into posterior margin. Broad rounded ridge running from the umbo to the anterodorsal end, separating flank from flat, narrow anterodorsal part of shell. Lunule shallow, narrow, lanceolate. Second, equally rounded umbonal ridge running to the posteroventral corner of shell. Area heart-shaped slightly concave in articulated specimens. Surface of shell smooth except for growth lines, which vary in strength. Hinge poorly preserved, with characteristic taxodont teeth.

**Remarks.** As nearly all specimens are crushed to some extent, the original outline and inflation only rarely can be observed. Everest (1833), Blanford (1864), and Stoliczka (1866) regarded the common nuculid in the lower mem-

ber of the Spiti Shale Formation as the species figured by J. de C. Sowerby (1840) as Nucula? cuneiformis, a highly variable species occurring from the Bathonian to the Kimmeridgian in the Kachchh Basin. Subsequent workers, however, followed a much narrower species concept and regarded the forms from the Spiti Shale Formation as different species. Holdhaus (1913) placed the bivalves in two new species, Nucula spitiensis and N. hyomorpha. He realised that the specimens were generally distorted, but argued that N. hyomorpha was always dorso-ventrally compressed, whereas N. spitiensis was laterally compressed. In this way, he clearly related the diagnostic features of the two species to their preservational state. According to Holdhaus (1913), the two species also differ in the shape of their anterodorsal shell portion, which is, however, influenced by the compaction styles. In the case of laterally flattened shells, this part usually cannot be observed. In fact, the style of distortion depends on the final burial position of the shells; they either became dorso-ventrally shortened when buried in growth position, or laterally flattened when post-humously they were reoriented by burrowers or excavated by currents, post-mortem. All intermediate preservational stages occur. In the former case, the inflation was artificially increased and in the latter case the length-height ration was decreased. All intermediate preservational stages occur. Cox (1940) regarded N. spitiensis and N. hyomorpha as synonyms and as a "linear descendent of P. cuneiformis. He followed a narrow species concept recognising two further similar species, P. kaoraensis and P. blanfordi in the Kachchh Basin, which were regarded junior synonyms of P. cuneiformis by Pandey and Agrawal (1984) and Jaitly et al. (1995).

The species is widespread in the Ethiopian faunal province, occurring from Madagascar to the Arabian Peninsula and from the Kachchh Basin to Rajasthan and the Himalayan shelf of the Indian Craton.

#### Palaeonucula stoliczkai Cox, 1940

Plate 1, fig. 3a, b

- \*1940 Nucula (Palaeonucula) stoliczkai sp. nov. Cox: 20, pl. 1, figs 21–23.
- 1956 Nucula (Palaeonucula) stoliczkai Cox Agrawal: 52, pl. 7, fig. 3b.
- 1980 Palaeonucula stoliczkai Cox Kanjilal: 339, pl. 1, figs 13-14.
- 1995 Palaeonucula stoliczkai Cox 1940 Jaitly et al.: 158, pl. 2, figs 7–8.

**Material.** One flattened articulated specimen from the Ferruginous Oolite Member at Langza (SNSB-BSPG 2020 XCIX 34).

**Description and remarks.** The laterally strongly compressed specimen (H: 8.6 mm, L: 11.9 mm) is rounded trigonal in outline and longer than high. The ventral margin is strongly convex, the anterior margin obliquely truncated, forming a blunt angle with the ventral margin and a very obtuse angle with the faintly convex anterodorsal margin. The posterior margin is narrowly rounded. The umbo is prominent. The rounded anterior umbonal ridge extends to the anteroventral margin. Due to the compressed nature of the shell, features such as lunule could not be observed. The surface of the shell is covered with fine commarginal growth lines. Internal features not seen.

Although the hinge could not be observed, the specimen can be safely placed in *P. stoliczkai* as it closely resembles Cox' species in outline.

Subclass Autobranchia Grobben, 1894 Order Arcida Gray, 1854 Family Cucullaeidae Stewart, 1930

#### Genus Megacucullaea Rennie, 1936

Type species. Cucullaea kraussii Tate, 1867.

#### Megacucullaea cf. kraussii (Tate, 1867)

Plate 1, fig. 4a, b

- cf. 1850 *Cucullaea cancellata* Krauss: 452, pl. 48, fig. 2a, b (non Phillips, 1829)
- \*cf. 1867 Cucullaea kraussii Tate: 161.
- cf. 1882 *Cucullaea Kraussi* Tate Holub and Neumayr: 375, pl. 2, fig. 2a-c.
- cf. 1940 Cucullaea (Megacucullaea) kraussii Tate Cox: 57, pl. 4, figs 3-4.
- cf. 1998 Megacucullaea kraussi (Tate, 1867) Kanjilal and Pathak: 34, pl. 1, fig. 6.

**Material.** A single poorly preserved articulated internal mould with remains of shell from the lower member of the Spiti Shale Formation (Oxfordian) near Chichim (SNSB-BSPG 2020 XCIX 1).

**Description.** Specimen large, longer than high (L ~79 mm, H ~60 mm, I ~70), thick-shelled, strongly inflated. Maximum inflation at around one-third of shell height from umbo. Ventral margin faintly arched, anterior margin convex, forming an angle of ~90° with hinge margin. Posterior margin straight, oblique, posteroventral corner rounded. Umbones only partly preserved, prominent, straight, incurved, situated anterior of mid-line of shell. Posterodorsal carina distinct but rounded, posterodorsal area flat to slightly convex. Cardinal area large, largest width anterior of umbo, slightly concave. Ornamentation poorly preserved; there are at least four widely spaced, strong, rounded radial ribs with concave interstices. Hinge line straight, dentition and other internal features not seen.

**Remarks.** The two valves are sligthly laterally sheared. Moreover, the specimen may be somewhat compressed dorso-ventrally. In this case, the inflation would be lower and the height greater than decribed above, and the point of maximum inflation would also be slightly off. The umbones are only partly preserved.

The various Jurassic species of Megacucullaea, i.e. M. eminens Cox (1940, p. 59, pl. 4, figs 5-7), M. kraussii (Tate 1867, p. 161), and "M. sp. nov. aff. C. (M.) eminens Cox" of Agrawal (1956 p. 14, pl. 1, fig. 1) differ in outline and the number of radial ribs (M. kraussii: 6-8; M. eminens: 16-19; Agrawal's specimen: approximately 10). The present specimen is closest to M. kraussii, having a similar number of ribs, whereas in the other two species the number of ribs is distinctly higher. Due to the poor preservation of the specimen, a detailed comparison with M. kraussii is not possible. The material of Cox (1940, p. 57, pl. 4, figs 3-4) exhibits eight radial ribs, of which three are only faintly developed on one out of two specimens. Interestingly, M. eminens and M. kraussii co-occur in Upper Tithonian rocks of the Kachchh Basin. M. eminens Cox (1940, p. 59, pl. 4, figs 5–7) is shorter, carries about 16 radial ribs differing in strength (weak close to the umbonal carina and strong on the remainder of the shell), and the area posterior of the umbonal ridge is distinctly concave. "Cucullaea Kraussi Tate" of Barrabé (1929, p. 147, pl. 8, fig. 13) has more radial ribs and resembles M. eminens. The early Tithonian specimen figured as Megacucullaea kraussii by Kanjilal and Pathak (1998) has seven ribs.

#### Family Parallelodontidae Dall, 1898 Genus Grammatodon Meek & Hayden, 1861

#### Subgenus Indogrammatodon Cox, 1937

Type species. Cucullaea virgata J. de C. Sowerby, 1840.

#### Grammatodon (Indogrammatodon) egertonianus (Stoliczka, 1866)

Plate 1, figs 5-7; Fig. 3

- 1831 Arca sp. Herbert: 272, pl. 17, fig. 6.
- 1833 Arca sp. Everest: 114, pl. 2, fig. 27.
- 1864 Cucullaea virgata Blanford: 136 (non J. de C. Sowerby, 1840).
- \*1866 Macrodon Egertonianum Stol. Stoliczka: 89, pl. 8, fig. 7.
- non 1908 Parallelodon egertonianus, Stoliczka Newton and Crick: 5, pl. 1, figs 1–4.
- 1913 Arca (Cucullaea) egertoniana, Stoliczka Holdhaus: 434, pl. 95, figs 1–10.
- non 1935 Parallelodon egertonianus (Stoliczka) Cox: 160.
- non 1937 Grammatodon (Indogrammatodon) egertonianus (Stoliczka) – Cox: 196, pl. 15, figs 10–11. (= G. (I.) virgatus J. de C. Sowerby, 1840)
- non 1939 Grammatodon egertonianus (Stol.) Stefanini: 222, pl. 24, figs 7–10. (= G. (I.) virgatus J. de C. Sowerby, 1840)
- non 1959 Grammatodon (Indogrammatodon) egertonianus (Stoliczka) – Jaboli: 48, pl. 5, fig. 12.
- non 1976 Cucullaea egertoniana (Stoliczka) Gu et al.:125, pl. 45, figs 1–6.
- non 1983 Grammatodon (Indogrammatodon) egertonianus (Stoliczka) – Gou and Li: pl. 2, fig. 6.



Plate 1. (1, 2) Palaeonucula cuneiformis (J. de C. Sowerby, 1840). 1. Left valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 26a). 2. Left valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 26b). (3) Palaeonucula stoliczkai Cox, 1940. Laterally crushed articulated specimen, lower member at Langza (SNSB-BSPG 2020 XCIX 34); a, left valve view; b, right valve view. (4) Megacucullaea cf. *kraussii* (Tate, 1867). Internal mould of articulated specimen with remains of shell from the lower member near Chichim (SNSB-BSPG 2020 XCIX 1); a, right valve view; b, dorsal view. (5–7) Grammatodon (Indogrammatodon) egertonianus (Stoliczka, 1866). 5. Articulated specimen from the lower member near the pass to Tashigeng (SNSB-BSPG 2020 XCIX 4). a, left valve view; b, dorsal view. 6. Laterally crushed articulated specimen from the lower member along the Kaza–Hikkim road (SNSB-BSPG 2020 XCIX 3b); right valve view. 7. Dorso-ventrally compacted articulated specimen from the lower member along the Kaza–Hikkim road. 8. Right valve (SNSB-BSPG 2020 XCIX 2a). 9. Right valve (SNSB-BSPG 2020 XCIX 2b). a, lateral view; b, dorsal view. (10) Anopaea? Fragmented right valve from the upper? member at Langza (SNSB-BSPG 2020 XCIX 67).

non 1997 Grammatodon (Indogrammatodon) egertonianus (Stoliczka) – Gardner and Campbell: 495, fig. 5l.

1998 Indogrammatodon egertonianus (Stoliczka, 1865) – Kanjilal and Pathak: 34, pl. 1, fig. 3.

**Material.** Six right and four left valves and 18 articulated specimens in shell preservation from the lower member of the Spiti Shale Formation at Langza (SNSB-BSPG 2020 XCIX 5, 6, 8, 9), Kazam-Hikkim road (SNSB-BSPG 2020 XCIX 3), Kibber (SNSB-BSPG 2020 XCIX 7), and near the pass to Tashigeng (SNSB-BSPG 2020 XCIX 4). The specimens are invariably distorted due to compaction and partly incomplete.

Dimension. See Table 2.

Description. Shell rhomboidal to trapezoidal in outline, much longer than high (Fig. 3). Ventral margin straight to slightly sinuous, grading smoothly into curved anterior margin, which forms an angle of 80-90° with the hinge line. Posterior margin convex ventrally and straight, oblique dorsally, forming an angle of ~130° with hinge line. Hinge line straight. Posterodorsal carina pronounced near umbo, becoming rounded and indistinct towards posteroventral margin. Area posterior of umbonal ridge concave. Umbo situated one-third to two-fifths of hinge length from anterior end, forward directed and incurved. Ornamentation of right valve slightly differing from that of left valve. Number of radial ribs of right valve (16-19) larger than that of left valves (12-17). Radial ribs present only on flank and not posterior of the umbonal ridge, equally spaced except for the anteriormost part of shell where their distance is much wider. Rib density greatest at middle of flank. Ribs of left valve of equal strength, slightly stronger than those of right valve. No intercalatory ribs present. Ribs of right valve widely spaced, with intercalations of 1-2 weak secondaries towards posterior. Both valves with distinct commarginal growth rugae; at intersections of growth rugae and radial ribs small nodes are developed.

Ligament area long, relatively narrow, with numerous chevron-shaped grooves. Except for fragments of hinge

**Table 2.** Dimensions (in mm) and number of ribs of Grammatodon (Indogrammatodon) egertonianus (Stoliczka, 1866).

oncoimon	Longth	Hoight	N ribo (D\/)	N ribo (IV)
specimen	Lengui	пеідії	NTIDS (RV)	N HDS (LV)
SNSB-BSPG 2020 XCIX 5a	84.8	-	-	-
SNSB-BSPG 2020 XCIX 5b	62.8	-	-	-
SNSB-BSPG 2020 XCIX 5c	63.2	>25.5	-	-
SNSB-BSPG 2020 XCIX 4	74.5	>30.6	18	14
SNSB-BSPG 2020 XCIX 3	54.8	-	19	14
SNSB-BSPG 2020 XCIX 6a	42.7	-	16	-
SNSB-BSPG 2020 XCIX 6b	35.6	-	15	-



**Figure 3.** Length plotted against height of *Grammatodon* (*Indo-grammatodon*) virgatus (J. de C. Sowerby, 1840) from the Callovian of Kachchh and *G.* (*I.*) egertonianus (Stoliczka, 1866) from the Spiti Shale Formation. Due to the distorted nature of nearly all specimens from the Spiti area, only two specimens yielded reasonable values.

no internal features seen. Hinge with 3–4 moderately long anterior teeth, arranged parallel to hinge margin anteriorly, converging towards ventral margin of hinge plate posteriorly. Posterior teeth longer, subparallel to dorsal margin of hinge. All teeth serrated. short central teeth not seen.

**Remarks.** Nearly all specimens are distorted by compaction. Commonly, the dorso-ventral axis has been shortened suggesting that the individuals are preserved in growth position. Due to this distortion, the length-height ratio could not be calculated and the inflation could not be measured. *G. (1.) egertonianus* is closely related to *G. (1.) virgatus* (J. de C. Sowerby, 1840), which is widespread within the Ethiopian faunal province. It differs from the present species by being less elongated, having far more radial ribs on both valves, and the difference in ribbing between right and left valve is much more pronounced (see, for example, the specimens figured by Cox 1940, pl. 2, figs 22–30 from the Jurassic of Kachchh). These differences have already been noted by Stoliczka (1865). The specimens recorded as

Parallelodon egertonianus Stol. by Basse (1930, p. 109, fig. 3a, b) from Ethiopia, Newton and Crick (1908, p. 5, pl. 1, figs 1–4) from the Arabian Peninsula, Stefanini (1925, p. 171, pl. 31, figs 6–7) from Somalia, and Weir (1930, p. 81, pl. 9, figs 12, 12a) from Kenya are generally much shorter and more densely ribbed and belong to *G*. (*I.*) virgatus or related forms. This is probably also true of the material listed by Cox (1935) from the Kimmeridgian–Tithonian of Somalia The specimen of *P. egertonianus* Stoliczka figured by Trechmann (1923, p. 263, pl. 14, fig. 8) from the Jurassic of New Zealand is too poorly preserved to warrant a precise identification.

#### Subgenus Cosmetodon Branson, 1942

Type species. Arca keyserlingii d'Orbigny, 1850.

#### Grammatodon (Cosmetodon) sp.

Plate 1, figs 8, 9

?1998 ?Parallelodon sp. indet. - Kanjilal and Pathak: 33, pl. 1, fig. 2.

**Material.** Two right valves from the lower member at the Kaza–Hikkim road (SNSB-BSPG 2020 XCIX 2).

**Description.** Shell strongly elongated, hinge line long, straight, position of umbo distinctly anterior of mid-line of the shell. Shallow umbonal sulcus widening ventrally and resulting in slight indentation of ventral margin. Umbonal ridge broadly rounded, area posterior of umbonal ridge concave. Surface covered with numerous delicate radial riblets and fine commarginal growth lines and, towards ventral margin, with several commarginal grooves corresponding to growth halts. Cardinal area narrow, attaining its greatest width below umbo. Posterior teeth long, extending parallel to dorsal margin of hinge plate, anterior teeth shorter, oblique, and directed posteriorly towards point below the hinge line.

**Remarks.** The specimens, in which the anterior and posterior ends are missing, has been dorso-ventrally compacted. As a result, the two valves have become separated and slightly distorted so that the inflation has been artificially increased. Due to its poor preservation, an identification at the species level is not possible. However, the specimen exhibits the characteristic features of the subgenus *Cosmetodon*, such as a strongly elongated shell, long, straight hinge line, a position of the umbo distinctly anterior of the mid-line of shell, and a shallow umbonal sulcus that widens ventrally and is responsible for a slightly indented ventral margin.

#### Order Myalinida Paul, 1939 Family Inoceramidae Giebel, 1852

#### Genus Anopaea Eichwald, 1861

Type species. Inoceramus lobatus Auerbach & Frears, 1846.

Anopaea? sp.

Plate 1, fig. 10

**Material.** Fragmented right valve from the upper? member at Langza (SNSB-BSPG 2020 XCIX 67).

**Description and remarks.** The specimen represents a poorly preserved, nearly flat posterior fragment of a right valve. It is ornamented with broad, irregular growth folds and superimposed fine commarginal growth lines. Two oblique shallow grooves extend for some distance towards the ventral margin.

As the outline of the specimen is not clear, its identification is questionable. *Inoceramus stoliczkai* Holdhaus (1913, p. 418, pl. 98, figs 10–11) from the Niti Pass, according to Crame (1981) and Zell et al. (2015) an *Anopaea*, differs in outline and in having well-spaced, far more acute commarginal folds.

#### Family Retroceramidae Koschelkina, 1980 Genus Retroceramus Koschelkina, 1959

Subgenus Retroceramus Koschelkina, 1959

Type species. Inoceramus retrorsus Keyserling, 1848.

# Retroceramus (Retroceramus) haasti (Hochstetter, 1863)

Plate 2, figs 1, 2

- 1863 Inoceramus haasti sp. nov. Hochstetter: 473, pl. 20, figs 1–2.
- 1982 Retroceramus (Retroceramus) haasti (Hochstetter, 1863) Crame: 569, pl. 57, figs 1–4.

**Material.** Numerous fragments of internal moulds of single valves with remains of shell from the upper member, road cut close to Demul Pass (SNSB-BSPG 2020 XCIX 60–63).

**Description and remarks.** The specimens occur in loosely packed matrix-supported shell concentrations. The umbonal areas are not preserved, but the specimens are apparently quite large, the largest fragment measuring 135 mm in height. Preserved parts of moulds are more or less flat, with spaced commarginal folds, the distance between folds increasing ventrally. The folds are slightly asymmetric in cross-section, the ventral flank being steeper. Areas with preserved shell material show that the shells were very thin.

Despite the fragmentary nature of the material, the specimens can be safely referred to *Retroceramus (R.) haasti*, originally described by Hochstetter (1863) from Kimmeridgian strata of New Zealand, based on their large size, nearly flat shells, broad ventral area, and characteristic ornamentation. The species has been recorded in the past from the Kimmeridgian of New Zealand and Antarctica (Hochstetter 1863; Crame 1982; Crampton 1988).

Inoceramus hookeri of Salter (1865: 95, pl. 23, fig. 1 only) exhibits a similar ornamentation but differs in



Plate 2. (1, 2) *Retroceramus* (*Retroceramus*) *haasti* (Hochstetter, 1863). 1. Fragment of internal mould of single valve with remains of shell from the upper member, road cut close to Demul Pass (SNSB-BSPG 2020 XCIX 62a). 2. Fragment of external mould of single valve with remains of shell from the upper member, road cut close to Demul Pass (SNSB-BSPG2020 XCIX 62b). (3, 4) *Retroceramus* (*Retroceramus*) everesti (Oppel, 1863). Fragmented internal moulds from the upper member near Demul. 3. Right valve (SNSB-BSPG 2020 XCIX 65). (4. Right valve (SNSB-BSPG 2020 XCIX 64). (5, 6) Gryphaeidae indet. from the upper member close to the Demul Pass 5. Right valve (SNSB-BSPG 2020 XCIX 37). 6. Right valve (SNSB-BSPG 2020 XCIX 38).

outline being rounded-rectangular. *Inoceramus haasti*, Hochstetter, 1863 has been transferred to *Retroceramus* (*Retroceramus*) by Crame (1982). The latter author regarded the species as characteristic of the Kimmeridgian – Early Tithonian.

#### Retroceramus (Retroceramus) everesti (Oppel, 1863) Plate 2, figs 3, 4

1831 Ostrea?, Inoceramus? - Herbert: 272, pl. 17, fig. 7.

- ?1833 Inoceramus(?) Everest: 114, pl. 2, fig. 29.
- \*1863 Inoceramus Everesti Opp. Oppel: 298.
- ?1865 Inoceramus Hookeri-N.Sp. var. crenatulinus Salter: 95, pl. 23, fig. 2.
- 1913 Inoceramus Everesti, Oppel Holdhaus: 415, pl. 98, figs 12–14.
- 1913 Inoceramus gracilis sp. nov. Holdhaus: 417, pl. 98, fig. 15.
- 1982 Retroceramus (Retroceramus) everesti (Oppel, 1865) Crame: 576: pl. 58, figs 5–11, pl. 59, figs 1–11.

**Material.** Internal mould of a left valve, locality and horizon unknown (SNSB-BSPG 2020 XCIX 66), and two internal moulds of right valves from the upper member near Demul (SNSB-BSPG 2020 XCIX 64–65). All specimens are fragmentary.

**Description.** Specimens small- to large-sized (H of largest specimen >70 mm), posteroventrally elongated but of variable obliquity, umbonal area well-inflated. Hinge line straight, moderately long; anterior margin weakly convex to straight, posterior margin gently curved, ventral margin well-rounded. Umbonal area narrowly rounded in cross-section, umbo small, prosogyrate. Posterodorsal area nearly flat; angle between dorsal and anterior margin approximately 90°. Valves ornamented with commarginal folds, asymmetric in cross-section with steeper dorsal flank. Folds regular to irregular, generally increasing in strength and distance towards ventral margin. Hinge features not seen.

**Remarks.** The species has been transferred to the genus and subgenus *Retroceramus* by Crame (1982). Crame (1982) regarded *Inoceramus hookeri* Salter, 1865 and *I. gracilis* Holdhaus, 1913 as junior synonyms, a view followed here. The species does not only occur on the northern shelf of the Indian craton but also in western Australia, New Zealand, Antarctica, and southern Chile (Crame 1982). According to Crame (1882), *R.* (*R.*) *everesti* has a stratigraphic range from the Upper Tithonian to Lower Berriasian. In the Spiti area, it occurs in the Upper Tithonian.

Holdhaus (1913) described four species of *Inoceramus*, of which only *R. everesti* (Oppel, 1863) and *R. haasti* ((Hochstetter, 1863) are recorded here. *I. gracilis* Holdhaus, 1913 is regarded synonymous with *R. everesti*, and *I. stoliczkai* Holdhaus and has been included in the genus *Anopaea* by Crame (1982). *Inoceramus* cf. *sularum* Boehm, 1907 of Holdhaus (1913: 420, fig. on p. 421) is too poorly preserved to be positively identified (see also Crame 1982).

#### Order Ostreida Férussac, 1822 Family Gryphaeidae Vyalov, 1936

#### Gryphaeidae indet.

Plate 2, figs 5, 6

**Material.** Four single valves, partly preserved as internal moulds, from the upper member close to the Demul Pass (SNSB-BSPG 2020 XCIX 37–38).

**Description and remarks.** The comparatively small (H: 11–19 mm), poorly preserved specimens are nearly flat and covered with irregular growth rugae. The available features preclude a precise identification. Possibly, they belong to the common Jurassic genus *Liostrea* Douvillé, 1904.

#### Family Aulacomyellidae Ichikawa, 1958

#### Genus Bositra De Gregorio, 1886

**Type species.** *Posidonia ornati* Quenstedt, 1851 (= *Posidonia Buchii* Roemer, 1836).

#### Bositra buchii (Roemer, 1836)

Plate 3, figs 1, 2

\*1836 Posidonia Buchii Nob. - Roemer: 81, pl. 4, fig. 8.
1930 Posidonia ornati Quenstedt - Weir: 83, pl. 10, figs 14-21.
?1935 Posidonia somaliensis sp. nov. - Cox: 166, pl. 15, figs 7-8.
1938 Posidonia ornati Quenstedt - Weir: 45, pl. 3, fig. 6.
1940 Posidonia ornati Quenstedt - Cox: 103, pl. 7, figs 10-11.
?1965 Bositra somaliensis (Cox) - Cox: 50, pl. 6, fig. 2.
1994 Bositra buchii - Oschmann: 424, fig. 9b-d.
1995 Bositra buchii - Oschmann: 33, fig. 10b-e.
1995 Bositra buchi (Roemer 1836) - Jaitly et al.: 175, pl. 8, figs 6-9.

**Material.** Numerous composite moulds from the basal silty black shales of the lower member at Langza (SNSB-BSPG 2020 XCIX 18–20).

**Description.** Small-sized, feebly inflated, generally longer than high, obliquely ovate but occasionally suborbicular composite moulds. Dorsal margin short, straight, remaining margins well-rounded. Umbo inconspicuous, not protruding beyond dorsal margin and situated slightly anterior of mid-line of shell. Surface covered with 16–18 broad, rounded commarginal ribs, separated by narrow interstices.

**Remarks.** Bositra buchii is a very widespread opportunistic byssate bivalve able to tolerate dysoxic conditions (Oschmann 1994). It occurs profusely in black silty shales at the base of the lower member at Langza, where it forms near-monospecific assemblages.

The species is morphologically quite variable in outline, as has been documented by Conti and Monari (1992). Whether the more orbicular *Bositra somaliensis* (Cox, 1935) from the Kimmeridgian of Somalia falls within the range of variation of *B. buchii* requires a study of the type material of that species.

#### Order Pectinida Gray, 1854 Family Buchiidae Cox, 1953

#### Genus Australobuchia Zakharov, 1981

#### Type species. Aucella plicata Zittel, 1864.

Remarks. The generic assignment of the two species described below is still under discussion. Most recent authors (e.g., Crame 1990; Hikuroa and Grant-Mackie 2008) follow Zakharov (1981), who regarded buchiids from high latitudes of the southern hemisphere as belonging to a different lineage than those from the northern hemisphere and therefore included them in his new genus Australobuchia. Other authors (e.g., Crame 1986, 1993) argue that more research is needed to understand the origin and evolution of the bipolar benthic faunas, which may have resulted from fragmentation of an originally wide distribution or by dispersal. The Spiti area at the northern margin of the Indian craton bordering the Neotethys during the Late Jurassic occupied a southern palaeolatitude between 20-30° according to the Paleolatitude Calculator of van Hinsbergen et al. (2015). The occurrence of high latitude southern taxa at relatively low latitudes can be explained by their restriction to outer shelf and slope environments where, due to upwelling, lower water temperatures prevailed (compare Alberti et al. 2021; Fürsich et al. 2021). In this context, isothermal submergence may explain the way polar faunas were able to cross the tropics (e.g., Crame 1993).

#### Australobuchia spitiensis (Holdhaus, 1913)

Plate 3, fig. 3

- \*1913 Aucella spitiensis n.sp. form. typ. Holdhaus: 410, pl. 97, fig. 8–11.
- ?1913 Aucella spitienis grandis nov. form. Holdhaus: 411, pl. 97, fig. 7.
- ?1913 Aucella spitiensis superba nov. form. Holdhaus: 411, pl. 97, fig. 13.
- ?1913 Aucella spitiensis extensa nov. form. Holdhaus: 411, pl. 97, fig. 12.
- 1959 Buchia spitiensis (Holdhaus) Fleming: 898, figs 15, 16, 20C, D
- 1976 Buchia spitiensis (Holdhaus) Wen: 85, pl. 21, fig. 1.
- 1976 Buchia spitiensis (Holdhaus) Gu et al.: 151, pl. 46, figs 3–7.
- 1988 Buchia spitiensis Holdhaus 1903 Li and Grant-Mackie: 253, fig. 2A, B.

**Material.** Composite moulds of one articulated and one right valve and external moulds of fragments of one right

and one left valve from the middle member, roadside close to Komic (SNSB-BSPG 2020 XCIX 43) and from the upper member close to Demul Pass (SNSB-BSPG 2020 XCIX 43).

**Description.** Poorly preserved composite and external moulds, some with remains of shell, obliquely elongated, higher than long (H: 25.8 mm, L: 23.1 mm). Mould of right valve moderately inflated, with distinctly sloping anterior and posterior flank and inconspicuous umbo; mould of left valve strongly inflated, umbo prominent, beak incurved, prosogyrate. Anterior and posterior margins sub-parallel, weakly convex, ventral margin strongly convex. Surface covered with numerous growth folds of varying strength. Anterior auricle of right valve concave, tongue-like, not level with commissure but directed slightly towards left valve.

**Remarks.** Most specimens are strongly flattened and fragmentary so that diagnostic features are difficult to observe. *Australobuchia spitiensis* as described by Holdhaus (1913) varies considerably in outline and degree of obliquity. Holdhaus (1913) distinguished altogether four varieties (forma *typica*, forma *grandis*, forma *extensa*, and forma *superba*). Due to the limited information from the present specimens, we cannot evaluate these varieties. Our material corresponds most closely to his forma *typica*. The species is also common in the Mt. Everest region (e.g., Wen 1976).

#### Australobuchia blanfordiana (Stoliczka, 1866) Plate 3, figs 4–5

1864 Monotis concentricus Blanford – Blanford: 136, pl. 4, figs 6–7.

non 1865 Monotis concentricus Blanford – Salter: 91, pl. 22, fig. 4. \*1866 Ancella [sic] Blanfordiana, Stol. – Stoliczkai: 88.

- 1913 Aucella blanfordiana, Stolczkai Holdhaus: 412, pl. 98, figs 1–9.
- 1976 Buchia blanfordiana (Stoliczka) Wen: 86, pl. 20, figs 1–6.
- 1976 Buchia blanfordiana (Stoliczka) Gu et al. 150, pl. 46, figs 17–25.
- 1988 Buchia blanfordiana (Stoliczka 1866) Li and Grant-Mackie: 252, fig. 2J–K.
- 2005 Buchia blanfordiana (Stoliczka) Xia and Bai: 502, pl. 1, figs 5, 7, 8.

**Material.** One internal mould of a left valve from the middle? member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 44); one right valve, two right valve internal moulds, five left valveinternal moulds, and one crushed articulated specimen from the upper member close to the pass to Demul (SNSB-BSPG 2020 XCIX 44–46).

**Description and remarks.** The species differs from *A. spitiensis* in being less strongly oblique and less posteroventrally elongated. According to Holdhaus (1913, p. 413), the species is quite variable with respect to shape and ornamentation. Whether it is, in fact, conspecific with *A. spitiensis* cannot be evaluated with the present poorly preserved material.



Plate 3. (1, 2) Bositra buchii (Roemer, 1836). Composite moulds from the lower member at Langza. 1. a, articulated specimen in butterfly position, dorsal view (SNSB-BSPG 2020 XCIX 18a); b, c, single valves, lateral view (SNSB-BSPG 2020 XCIX 18b). 2. External mould of right valve (SNSB-BSPG 2020 XCIX 19). (3) Australobuchia spitiensis (Holdhaus, 1913). Composite mould of articulated specimen from the middle member, roadside close to Komic; right valve view (SNSB-BSPG 2020 XCIX 43). (4–5) Australobuchia blanfordiana (Stoliczka, 1866). upper member close to Demul Pass. 4. Right valve (SNSB-BSPG 2020 XCIX 46). 5. Right valve (SNSB-BSPG 2020 XCIX 45). (6–10) ?Malayomaorica sp. upper member close to Demul Pass. 6. Left valve (SNSB-BSPG 2020 XCIX 51a). 7. Right valve interior (SNSB-BSPG 2020 XCIX 51b). 9. Left valve (SNSB-BSPG 2020 XCIX 51c). 10. Fragment of right valve (SNSB-BSPG 2020 XCIX 51b). 9. Left valve (SNSB-BSPG 2020 XCIX 51c). 10. Fragment of right valve (SNSB-BSPG 2020 XCIX 51b). (11) Entolium (Entolium) corneolum (Young & Bird, 1822). Internal mould of a left valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 15). (12) Propeamussium (Propeamussium) sp. Internal mould of a small fragment from the lower member at Langza (SNSB-BSPG 2020 XCIX 12). a, natural size; b, enlarged. (13) Camptonectes (Camptochlamys) obscurus (J. Sowerby, 1818). Left valve interior from the lower member near the pass to Tashigeng (SNSB-BSPG 2020 XCIX 13).

#### Genus Malayomaorica Jeletzky, 1963

Type species. Aucella malayomaorica Krumbeck, 1923.

#### Malayomaorica? sp.

Plate 3, figs 6-10

**Material.** Numerous right and left valves preserved as composite moulds or with remains of shell, generally strongly compacted and often fragmented, from the upper member close to Demul Pass (SNSB-BSPG 2020 XCIX 51–52).

**Description and remarks.** The poorly preserved specimens are characterized by a feebly inflated right valve and a strongly inflated left valve. The height distinctly exceeds the length of the shell, which is slightly oblique, the ventralmost part being posterior of the mid-line. The anterior margin is well-rounded, the posterior margin sub-straight, the ventral margin strongly curved. The right valve anterior auricle is directed towards the left valve; the byssal notch is well-developed. The surface of the shell is covered with faint radial riblets in addition to faint commarginal growth rugae.

The different outline and the radial riblets distinguish the material from *Buchia*. Due to the poor preservation and lack of detailed hinge information the specimens are only tentatively placed in *Malayomaorica*. This is the first documentation of the genus from the Indian Himalayas.

#### Family Oxytomidae Ichikawa, 1958

#### Genus Meleagrinella Whitfield, 1885

Type species. Avicula curta Hall, 1852.

#### Meleagrinella? sp.

**Material.** A single right valve from the top of the lower member at Komic (SNSB-BSPG 2020 XCIX 16).

**Description and remarks.** The small, slightly crushed specimen (H: 3.5 mm) is suborbicular and nearly flat. The dorsal margin is long and straight, the anterior, posterior and ventral margins are well rounded. There is no sign of a posterior wing, the dorsal margin forming a blunt angle with the posterior margin. The umbo is small, more or less mesial, and not protruding beyond the dorsal margin. The

shell thin, and ornamented with remains of spaced commarginal riblets. The annterior auricle is small but has a deep byssal notch.

Right valves of *Meleagrinella* are generally regarded as having a small pointed posterior wing (Cox 1969), which is apparently lacking in the present specimen. For this reason, it is referred to the genus *Meleagrinella* with reservation. The *Meleagrinella* sp. indet. of Kanjilal and Pathak (1998, p. 35, pl. 1, fig. 4) is difficult to evaluate and comes from the upper part of the Spiti Shale Formation.

#### Family Entoliidae Teppner, 1922 Genus Entolium Meek, 1865

#### Subgenus Entolium Meek, 1865

**Type species.** *Pecten demissus* Phillips, 1829 (= *Entolium demissum* Meek, 1865).

#### Entolium (Entolium) corneolum (Young & Bird, 1828) Plate 3, fig. 11

\*1828 Pecten corneolus - Young and Bird: 234, pl. 9, fig. 5.

- 1924 Pecten (Entolium) demissum Phillips Hennig: 14, pl. 2, figs 1–2.
- 1933 Pecten (Entolium) solidus Roemer Dietrich: 65, pl. 8, figs 118, 119.
- 1938 Entolium demissum (Phillips) Weir: 46, pl. 3, fig. 8.
- 1939 Entolium demissum (Phillips) Stefanini: 179, pl. 22, figs 2-3.
- 1965 Entolium corneolum (Young & Bird) Cox: 1965: 51.
- 1981 Entolium (Entolium) corneolum (Young & Bird) Kanjilal: 265, pl. 1, fig. 1.
- 1995 Entolium (Entolium) corneolum (Young & Bird, 1828) Jaitly et al.: 193: pl. 18, figs 8–9.

**Material.** Internal mould of a left valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 15).

**Description.** Disc subovate, smooth, poorly inflated. Length 21.7 mm, height >25 mm. Auricles well demarcated from disc, only partly preserved, anterior auricle apparently larger than posterior one. Anterior, posterior, and ventral margin forming a semi-circle.

**Remarks.** The specimen can be referred to *Entolium* (*E.*) *corneolum* without doubt, based on its outline,

even though no shell is preserved. Left valves of *E. corneolum, E. lunare* (Roemer, 1839), and *E. orbiculare* (J. Sowerby, 1817) are very similar, but differ with respect to stratigraphic and/or geographic distribution (Johnson 1984).

#### Family Pectinidae Rafinesque, 1815 Genus Camptonectes Agassiz in Meek, 1864

#### Subgenus Camptochlamys Arkell, 1930

Type species. Pecten intertextus Roemer, 1839.

# *Camptonectes (Camptochlamys) obscurus (J. Sowerby, 1818)*

Plate 3, fig. 13

\*1818 Pecten obscura – J. Sowerby: 3, pl. 205, fig. 1.

- 1852 Camptonectes indicus sp. nov. Cox: 25, pl. 3, figs 1-4.
  ?1939 Camptonectes Germaniae (d'Orb.) Stefanini: 171, pl. 19, fig. 11.
- 1956 Camptonectes indicus Cox Agrawal: 77, pl. 9, fig. 5.

1968 Camptonectes indicus Cox - Maithani: 505, pl. 33, fig. 6.

- 1979 Camptonectes (Indonectes) obscurus (J. Sowerby) subgen. nov. – Kanjilal: 120, fig. 6.
- 1983 Camptonectes (Indonectes) obscurus (J. Sowerby) Singh and Jaitly: 47, pl. 1, fig. 5.
- 1995 Camptonectes (Camptochlamys) obscurus (J. Sowerby, 1818) Jaitly et al.: 196, pl. 19, figs 7–8.

**Material.** A single left valve partly in shell preservation, seen from the interior, from the lower member near the pass to Tashigeng (SNSB-BSPG 2020 XCIX 13).

**Description.** Shell suboval, higher than long (H: 22.2 mm, L: ~20 mm), moderately inflated, anteroventral, posteroventral and ventral margins rounded and regularly curved; antero- and posterodorsal margins of disc sub-straight. Anterior auricle large, distinctly set off from anterodorsal flank, which is more steeply sloping than posterodorsal flank. Tip of umbo and posterior auricle missing, anterior and posterior margin of disc also not fully preserved. Disc ornamented with thin, sharp, regularly spaced commarginal ribs and numerous thin divaricate radial grooves, separated by smooth, flat intervals about twice the width of the grooves. Umbonal area with thin radial riblets. Anterior auricle covered with spaced commarginal riblets intersected by thin radial riblets, creating a reticulate pattern.

**Remarks.** The specimen closely corresponds to the diagnosis of *Camptonectes* (*Camptochlamys*) obscurus as given by Johnson (1984). So far, the species has not been recorded from the Himalayan shelf of the southern Tethys, but it occurs in the Callovian of the Kachchh Basin further south (Cox 1952; Jaitly et al. 1995) and possibly also in other parts of the Ethiopian faunal province (e.g., as *Camptonectes germaniae* (d'Orbigny, 1850) in Somalia; Stefanini 1939 p. 171, pl. 19, fig. 11).

Genus Chlamys Röding, 1798

#### Subgenus Chlamys Röding, 1798

Type species. Pecten islandicus Müller, 1776.

#### Chlamys (Chlamys) cf. textoria (Schlotheim, 1820) Plate 4, fig. 2

- cf. 1820 Pectinites textorius Schlotheim, p. 229.
- cf. 1952 Chlamys (Chlamys) ambigua (Münster) Cox: 4, pl. 1, figs 2–4.
- cf. 1965 Chlamys subtextoria (Münster) Cox: 55, pl. 7, fig. 8.
- cf. 1984 Chlamys (Chlamys) textoria (Schlotheim 1820) Johnson: 163, pl. 6, figs 10–12, pl. 7, figs 1–21, pl. 8, figs 1–3, 5–20, ?4, text-figs 146–157.
- cf. 1995 Chlamys (Chlamys) textoria (Schlotheim 1820) Jaitly et al.: 197, pl. 20, figs 3–7.

**Material.** A single, incomplete right valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 11).

**Description.** Somewhat abraded right valve with ventral part missing. Early disc suborbicular, equilateral, poorly inflated. Auricles well-demarcated from disc. Posterior auricle relatively small, forming obtuse angle with disc. Disc with ~19 radial plicae plus some very faint ones near anterior and posterior end. Number of plicae increasing ventrally by bifurcating. No growth lines or commarginal lamellae seen due to poor preservation.

**Remarks.** The poorly preserved specimen can be placed in *Chlamys* (C.) *textoria* with reservation only.

#### Genus Spondylopecten Roeder, 1882

Subgenus Plesiopecten Munier-Chalmas, 1887

Type species. Pectinites subspinosus Schlotheim, 1820.

#### Spondylopecten (Plesiopecten) subspinosus (Schlotheim, 1820)

Plate 4, fig. 3

1820 Pectinites subspinosus - Schlotheim: 223.

- 1938 Plesiopecten subspinosus (Schlotheim) Weir: 50, pl. 3, fig. 18.
- 1952 Chlamys (Plesiopecten) subspinosa (Schlotheim) Cox: 18, pl. 1, figs 9–12.
- 1995 Spondylopecten (Plesiopecten) subspinosus (Schlotheim 1820) Jaitly et al.: 194, pl. 18, figs 14–15.

**Material.** One composite mould of a right valve and one external mould from the upper part of the lower member at the Hikkim-Kaza road (SNSB-BSPG 2020 XCIX 23).

**Description.** Specimens small (H: 5.4 mm; K: 5.8 mm), suborbicular, equilateral, weakly inflated. Auricles large, distinctly separated from disk, anterior one incomplete.

Surface of composite mould covered with 11–13 positive radial structures interpreted herein as corresponding to radial ribs, which are angular and show a tendency to bi-furcate towards the ventral margin.

**Remarks.** Despite the poor preservation of the specimens (lack of shell), they can be safely assigned to *S*. (*Plesiopecten*) *subspinosus*, based on the number and angularity of their ribs (compare Johnson 1984, p. 84).

#### Genus Radulopecten Rollier, 1911

Type species. Pecten hemicostatus Morris & Lycett, 1853.

#### Radulopecten cf. fibrosus (J. Sowerby, 1816)

Plate 4, fig. 4a, b

cf. 1816 Pecten fibrosus - J. Sowerby: 84, pl. 136, figs 1-2.

**Material.** A single fragment of a right valve from the lower? member near Demul (SNSB-BSPG 2020 XCIX 39).

**Description and remarks.** Although the specimen does not allow to infer the shape of the bivalve, the ornamentation is so characteristic that it can be placed in the genus *Radulopecten* without any doubt. The shell is covered with broad, nearly flat-topped radial plicae, separated by much narrower shallow sulci. The radial plicae are crossed by spaced, narrow commarginal lamellae. The ornamentation closely resembles that of *Radulopecten fibrosus* (J. Sowerby, 1816). For this reason, the specimen is tentatively placed in that species.

#### Pectinidae indet.

Plate 4, fig. 5

**Material.** Slightly distorted fragment of a single valve from 5–8 m below the top of the lower member along the Kaza-Hikkim road (SNSB-BSPG 2020 XCIX 17).

**Description.** Specimen small (H: 9.6 mm), higher than long. Disc moderately inflated, rounded triangular; auricles distinctly set off from disc, large, incomplete. Disc covered with approximately 12 coarse, rounded radial ribs, differing in strength.

**Remarks.** The poor preservation (incomplete shell, compactional/tectonic distortion) precludes a more precise identification of the specimen, which to some extent resembles *Spondylopecten*, the ribbing of which is, however, far more regular.

#### Family Propeamussiidae Abbott, 1954 Genus Propeamussium De Gregorio, 1884

#### Subgenus Propeamussium De Gregorio, 1884

**Type species.** *Pecten (Propeamussium) ceciliae* De Gregorio, 1884.

#### Propeamussium (Propeamussium) sp. Plate 3, fig. 12

**Material.** One internal mould of a single valve (SNSB-BSPG 2020 XCIX 12) and several small fragments from the lower member at Langza.

**Description and remarks.** The internal mould of a fragment displays seven radial grooves, which correspond to internal ribs. The complete shell might have carried 8–9 ribs. These ribs end just before the ventral margin.

While the specimen undoubtedly can be referred to *P*. (*Propeamussium*), identification at the species level is impossible. The only Upper Jurassic species recognized by Johnson (1984) is *P*. (*P*.) nonarium (Quenstedt, 1858, p. 795, pl. 98, fig. 4), which is restricted to Europe and differs from the present specimen by relatively short internal ribs, which end well before the ventral margin.

#### Order Limida Moore, 1952 Family Limidae Rafinesque, 1815

Genus Plagiostoma J. Sowerby, 1814

Type species. Plagiostoma giganteum J. Sowerby, 1814.

#### Plagiostoma? sp. A

Plate 4, fig. 7a, b

**Material.** A strongly crushed single valve with remains of shell from the lower member at Langza (SNSB-BSPG 2020 XCIX 35).

**Description and remarks.** The very poorly preserved specimen cannot be identified with certainty. The surface of the apparently rounded triangular-ovate specimen is covered with numerous faint, rounded, radial riblets.

#### Plagiostoma? sp. B

Plate 4, fig. 6

**Material.** A fragmented left internal mould with remains of the inner shell layer from the Ferruginous Oolite Formation near Zangla (SNSB-BSPG 2020 XCIX 36).

**Description and remarks.** As the ventral part of the specimen is missing, its outline remains unknown, but most likely was obliquely triangular-ovate. The hinge line is short and straight, the umbo orthogyrate, the posterior auricle distinctly set off from the flank. The shell surface is ornamented with indistinct remnants of radial ribs. It differs from *Plagiostoma*? sp. A in outline and style of ribbing. The few features that can be observed all support the placement of the specimen in *Plagiostoma* or a related genus.

#### Genus Ctenostreon Eichwald, 1862

Type species. Ostracites pectiniformis Schlotheim, 1820.



Plate 4. (1) *Camptonectes* (*Camptochlamys*) sp. from the upper member close to Demul Pass (SNSB-BSPG 2020 XCIX 14). (2) *Chlamys* (*Chlamys*) cf. *textoria* (Schlotheim, 1820). Incomplete right valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 11). (3) *Spondylopecten* (*Plesiopecten*) *subspinosus* (Schlotheim, 1820). Internal mould of right valve from the lower member at the Kaza–Hikkim road (SNSB-BSPG 2020 XCIX 23). (4) *Radulopecten* cf. *fibrosus* (J. Sowerby, 1816). a, b, Fragment of a right valve from the ?lower member near Demul (SNSB-BSPG 2020 XCIX 39). (5) Pectinidae indet. Slightly distorted internal mould of a single valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 39). (5) Pectinidae indet. Slightly distorted internal mould of a single valve from the lower member along the Kazan–Hikkim road (SNSB-BSPG 2020 XCIX 39). (5) Pectinidae indet. Slightly distorted internal mould of a single valve with remains of shell from the lower member at Langza (SNSB-BSPG 2020 XCIX 39). (7) *Plagiostoma*? sp. B. Strongly crushed single valve with remains of shell from the lower member at Langza (SNSB-BSPG 2020 XCIX 35). (7) *Plagiostoma*? sp. A. a, b, Fragmented left internal mould with remains of the inner shell layer from the Ferruginous Oolite Formation near Zangla (SNSB-BSPG 2020 XCIX 36). (8) Trigonia? sp. Right internal mould from the top of the Ferruginous Oolite Formation at Zangla (SNSB-BSPG 2020 XCIX 24). (9) *Vaugonia* (*Orthotrigonia*) sp. Poorly preserved right valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 25). (10–13) *Pruvostiella* (*Pruvostiella*) *hermanni* (Oppel, 1863). 10. Hinge of left valve from the lower member close to the pass to Tashigeng; Aa, anterior adductor scar; Apr,

anterior pedal retractor scar (SNSB-BSPG 2020 XCIX 54b). **11.** Hinge of left valve from the lower member at the Kaza–Hikkim road cut; Cpr, central pedal retractor scar (SNSB-BSPG 2020 XCIX 59). **12.** Hinge of right valve from the lower member close to the pass to Tashigeng; Apr, anterior pedal retractor scar. a, lateral view; b, dorsal view (SNSB-BSPG 2020 XCIX 54b). **13.** Articulated specimen from the lower member at Langza (SNSB-BSPG 2020 XCIX 59a). a, left valve view; b, dorsal view.

#### Ctenostreon sp.

**Material.** One small fragment from the Ferruginous Oolite Formation near Chichim (SNSB-BSPG 2020 XCIX 21).

**Description and remarks.** The very small fragment of a thick shell carries large, rounded, somewhat irregular radial ribs. The fragment can be differentiated from the genus *Trichites* by lacking the prismatic shell structure of the latter, and from large ribbed oysters such as *Actinostreon marshii* by the rounded nature of the ribs. The fragment is too small to warrant photographic documentation.

#### Infraclass Heteroconchia Hertwig, 1895 Order Trigoniida Dall, 1889 Family Trigoniidae Lamarck, 1819

#### Genus Trigonia Bruguière, 1789

Type species. Venus sulcata Hermann, 1781.

#### Trigonia? sp.

Plate 4, fig. 8

**Material.** A single right internal mould from the top of the Ferruginous Oolite Formation at Zangla (SNSB-BSPG 2020 XCIX 24).

**Description and remarks.** The internal mould shows the typical commarginal ribs of the flank and a weak sulcus anterior of the marginal carina. As no information about the area is available, it cannot be decided whether the specimen belongs to *Trigonia* s.s. or to the genus *Indotrigonia*.

#### Family Myophorellidae Kobayashi, 1954 Genus Vaugonia Crickmay, 1930

Subgenus Orthotrigonia Cox, 1952

Type species. Trigonia duplicata J. Sowerby, 1819.

### Vaugonia (Orthotrigonia) sp.

Plate 4, fig. 9

**Material.** A single poorly preserved right valve from the lower member at Langza (SNSB-BSPG 2020 XCIX 25).

**Description and remarks.** The specimen (H: 22.7 mm, L: 24.5 mm) exhibits the typical ornamentation of *Orthotrigonia* such as steep subvertical tuberculated ribs on the flank, commarginal tuberculated to spinose ribs in the umbonal area, a tuberculated marginal carina, and a commarginally striated area. The specimen resembles *V. (Orthotrigonia) kutchensis* (Kitchin, 1903: 84, pl. 8, figs 7–9) from the Kachchh Basin, but due to its poor preservation an identification at the species level is not possible.

#### Clade Heterodonta Neumayr, 1884 Order Carditida Dall, 1889 Family Astartidae d'Orbigny, 1844

#### Genus Pruvostiella Agrawal, 1956a

**Emended diagnosis.** Equivalve, inequilateral shell, generally longer than high, thick-shelled. Inner shell margin crenulated; umbonal area depressed and ornamented with spaced, well-developed, commarginal ribs asymmetric in cross-section; remaining shell smooth except for growth lines. Hinge with serrated teeth. Right valve with 2–3 cardinals and 1 anterior and 1 posterior lateral. Left valve with 2–3 cardinals and 1 anterior and 1 posterior lateral. Left eral. Distinct pedal retractor muscle scar developed below the hinge line and close to the anterior adductor muscle scar. Inner shell margin crenulated.

**Remarks.** *Pruvostiella* was erected by Agrawal (1956a: 435) as a subgenus of *Neocrassina* for specimens from the Oxfordian Dhosa Oolite of Kachchh, western India. The main diagnostic feature of his new subgenus is the umbonal region, which is distinctly depressed, with small beaks and ornamented with spaced, well-developed commarginal ribs, which are asymmetric in cross-section with a steeper slope dorsally. The ribs fade after 10–15 mm to be replaced by irregular growth lines. Agrawal (1956a)

 Table 3. Species included in the genus Pruvostiella (\* previously included by Agrawal 1956a).

Species included in the genus Pruvostiella	occurrence	age
*Astarte unilateralis J. de C. Sowerby,	Kachchh	Callovian-
1840a: 327, pl. 21, fig. 14		Oxfordian
*Astarte major J. de C. Sowerby, 1840b: 718	Kachchh	Kimmeridgian-
pl. 61, fig. 1		Tithonian
*Astarte hermanni Oppel, 1863: 273, 297	Himalayas	Oxfordian
*A <i>starte scytalis</i> Holdhaus, 1913: 444, pl. 100, figs 2–3	Himalayas	Oxfordian
*Astarte spitiensis Stoliczka, 1866: 91, pl. 9, fig. 1.	Himalayas	Oxfordian
Astarte hiemalis Stoliczka: 91, pl. 9, figs 2–3.	Himalayas	Oxfordian
*Astarte muelleri Daqué, 1910: 31, pl. 4, fig. 5	East Africa	?Callovian- ?Kimmeridgian
*Astarte stefanini Basse, 1930: 110, pl. 5, fig. 9	Ethiopia	Kimmeridgian
Astarte krenkeli Dietrich, 1933: 40, pl. 4, figs 62. 64. 66	East Africa	Tithonian
* <i>Astarte</i> sp. A Nicolai, 1950–1951: 45, pl. 4. fig. 11	Madagascar	Late Oxfordian
Astarte sp. B Nicolai, 1950–1951: 45, pl. 5, fig. 1	Madagascar	Late Oxfordian
*Astarte freneixae Agrawal, 1956a: 436, pl. 21, figs 5–6	Kachchh	Oxfordian
Seebachia (Eoseebachia) elongata Fürsich, Heinze & Jaitly, 2000: 96, pl. 6, fig. 25, pl. 8, figs 2–7, pl. 9, fig. 2, pl. 10, fig. 1, text-figs 16–18	Kachchh	Kimmeridgian– Tithonian
Seebachia (Eoseebachia) sowerbyana (J. de C. Sowerby, 1840) – Fürsich et al. 2000: 92, pl. 6, fig. 24, pl. 7, figs 1–5, pl. 8, fig. 1, pl. 10, fig. 5, text-figs14–16	Kachchh	Kimmeridgian– Tithonian

included a number of astartids in *Pruvostiella* (Table 3). *Pruvostiella* is here elevated to generic rank.

Fürsich et al. (2000: 92; 2019, p. 174) created *Eoseebachia* as a subgenus of *Seebachia* Holub & Neumayr, 1881 and accommodated *Astarte major* J. de C. Sowerby, 1840 and their new species *elongata* in this subgenus. Although these species are related to *Seebachia*, they are clearly more closely related to *Pruvostiella*, as the former genus is strongly elongated, wedge-shaped and has a distinct posterior umbonal ridge. *Eoseebachia* is, therefore, moved from *Seebachia* to *Pruvostiella*.

Gardner and Campbell (2002, p. 328) regarded *Pruvostiella* as a junior synonym of *Neocrassina* Fischer, 1886, a view not followed here. The depressed, flattened umbo, the corresponding distinct break in the growth spiral of the shell, and the distinctly serrated cardinal teeth are consistent features of many large astartids from the Ethiopian faunal province (Table 3).

*Pruvostiella* (*Pruvostiella*) appears to be restricted to the Callovian–Oxfordian time interval of the Ethiopian Faunal Province (Madagascar, East Africa, India) and possibly occurs also in the Kimmeridgian of New Zealand (Trechman 1923; Marwick 1953), whereas *Pruvostiella* (*Eoseebachia*) occurs from the Late Oxfordian to the Late Tithonian (and probably earliest Cretaceous) in the same area (e.g., Dietrich 1933; Cox 1965). *Eoseebachia* differs from *Pruvostiella* s.s. by being up to three times larger, generally more elongated and by having a lunule with a lower length-width ratio.

J. de C. Sowerby (J. de C. Sowerby, 1840, pl. 61, fig. 1) erected Astarte major for the large astartids from the Upper

Jurassic of Kachchh. Blanford (1864), Stoliczka (1866), and Holdhaus (1913) regarded moderately-sized astartids from the Himalayas also as Astarte major J. de C. Sowerby, 1840. Whereas Blanford (1864, p. 135, ..."undoubtedly identical") was quite confident, Holdhaus only tentatively regarded the large astartids from Spiti to belong to Sowerby's Astarte major from Kachchh. Holdhaus (1913) erroneously regarded that Sowerby's name was preoccupied by Astarte elegans major Zieten (1833: 82, pl. 62, fig. 1). Therefore, Holdhaus (1913, p. 443) erected the replacement name Astarte sowerbyana for the forms from the Himalayas and Kachchh. It is clear that the Kachchh species differs from the Spiti material. The specimens from the Spiti Shale are placed herein in P. (Pruvostiella) hermanni (Oppel, 1863). The large astartid from Kachchh represents Sowerby's A. major and the species is assigned to Pruvostiella (Eoseebachia), because it is much closer to Pruvostiella than to Seebachia (see above). Thus, in the Kachchh Basin four species of Pruvostiella occur: P. (Eoseebachia) major (J. de C. Sowerby, 1840), P. (Eoseebachia) elongata Fürsich, Heinze & Jaitly, 2000, P. (Pruvostiella) unilateralis (J. de C. Sowerby, 1840), and P. (Pruvostiella) freneixae Agrawal, 1956a. In the Himalayas, in contrast, the species group is represented by P. (Pruvostiella) hermanni (Oppel, 1863).

#### Subgenus Pruvostiella Agrawal, 1956a

**Type species.** Astarte (Pruvostiella) freneixae Agrawal, 1956a.

Emended diagnosis. As for genus.

#### Pruvostiella (Pruvostiella) hermanni (Oppel, 1863)

Plate 4, figs 10-13, Plate 5, figs 1-6; Fig. 4

- 1831 Unio? and Trigonia? Herbert 272, pl. 17, fig. 4, 4a.
- 1833 Unio? Everest: 114, pl. 2, fig. 26.
- \*1863 Astarte hermanni Opp. Oppel: 273, 297.
- 1865 Astarte unilateralis Sow. Salter: 97, pl. 23, fig. 10. (non Sowerby, 1840).
- 1866 Astarte unilateralis, Sow. 1840 Stoliczka: 90. (non Sowerby, 1840).
- 1866 Astarte spitiensis Stol. Stoliczka: 91, pl. 9, fig. 1.
- 1866 Astarte hiemalis Stol. Stoliczka: 91, pl. 9, figs 2-3.
- 1913 Astarte scytalis sp. nov. Holdhaus: 444, pl. 100, figs 2-3.
- 1913 Astarte sowerbyana sp. nov. Holdhaus: 443, pl. 99, figs 12, 13, 15, pl. 100, fig. 1.
- 1913 Astarte spitiensis Stoliczka Holdhaus: 444, pl. 100, figs 4–8.
- 1913 Astarte hermanni Oppel 1863 Holdhaus: 440, pl. 99, figs 7–11, 14.
- 1923 Astarte spitiensis Stol. Trechmann: 279, pl. 13, fig. 1.
- 1923 Astarte cf. scytalis Holdhaus Trechmann: 280, pl. 13, fig. 3.
- 1923 Astarte cf. sowerbyana Holdhaus Trechmann: 280, pl. 13, fig. 2.
- ?1929 Astarte scytalis Holdhaus Weir: 5, pl. 3, fig. 20.
- 1935 Astarte scytalis Holdhaus Cox: 180, pl. 19, figs 4-5.
- 1953 Astarte spitiensis Stol. Marwick: 107, pl. 11, figs 13, 15.

- non 1956b Astarte (Pruvostiella) spitiensis Stoliczka Agrawal: 109, pl. 10, fig. 3. (non Stoliczka).
- ?1959 Astarte scytalis Holdhaus Jaboli: 49, pl. 6, fig. 6.
- 1998 Neocrassina (Pruvostiella) unilateralis (J. de C. Sowerby, 1840) – Kanjilal & Pathak: 35, pl. 1, fig. 8. (non Sowerby, 1840).
- 1998 Neocrassina (Pruvostiella) sowerbyana (Holdhaus, 1913) Kanjilal & Pathak: 35, pl. 1, fig. 9.

**Material.** Three right valves, four left valves, 16 articulated specimens, and two hinge fragments from the lower member at Langza (SNSB-BSPG 2020 XCIX 53, 57, 58, 59), two right valves, one left valve, 17 articulated valves, and six hinge fragments from the lower member at the Kaza– Hikkim road cut (SNSB-BSPG 2020 XCIX 55a, b), and two right valves, one left valve, nine articulated specimens and six hinge fragments from the lower member close to Tashigeng (SNSB-BSPG 2020 XCIX 54a, b).

#### Dimensions. See Fig. 4.

**Description.** Shell highly variable in outline, longer than high (Fig. 4), moderately inflated. Anterodorsal margin concave, anteroventral margin convex, grading smoothly into the broadly arched ventral margin. Posteroventral margin well-rounded, posterodorsal margin faintly convex. Umbo prosogyrate, distinctly depressed, situated approximately one-fifth to one-eighth of shell length from the anterior end. Beaks small, lunule elongated, deep, bordered by sharp ridge (Plate 5); escutcheon lanceolate, bordered by distinct ridge. Ligament opisthodetic. Ornamentation consisting of widely spaced commarginal ribs in umbonal area only and extending for 10–15 mm ventrally. Remaining surface covered with irregular growth lines.

Hinge of right valve with three cardinals, 3b thin and inconspicuous, and one posterior lateral. Left valve with two cardinals and one short anterior and posterior lateral,



**Figure 4.** Length plotted against height of *Pruvostiella* (*P.*) *hermanni* from the Spiti Shale Formation and of the holotypes of *P.* (*P.*) *unilateralis* (J. de C. Sowerby, 1840) and *P.* (*Eoseebachia*) *major* (J. de C. Sowerby, 1840) (= *Seebachia* (*E.*) *sowerbyana* (J. de C. Sowerby, 1840) in part).

respectively. Two pedal retractor muscle scars developed right underneath hinge plate, one more or less mesial, the second one close to the anterior adductor muscle scar. Inner shell margin strongly crenulated.

Remarks. Due to their high morphological variability the specimens from the Spiti Shale Formation have been accommodated in several species in the past. Stoliczka (1866) recognised Astarte spitiensis, A. unilateralis, and A. hiemalis and Holdhaus (1913) A. sowerbyana, A. hermanni, A. scytalis and A. spitiensis, all occurring in the lower member where they form a characteristic association together with Palaeonucula cuneiformis and Grammatodon (Indogrammatodon) egertonianus (Fürsich et al. 2021). Apart from the fact that intermediate forms exist between these species, usually two to four of these morphotypes co-occur within individual horizons. On ecological grounds it is highly unlikely that several closely related species with a more or less identical mode of life repeatedly co-occur within a community, and we therefore regard these forms as representing a single species, even though the end members of the morphological range are quite disparate. The oldest available name is Pruvostiella (P.) hermanni (Oppel, 1863).

Several authors (e.g., Cox 1965: 88; Stoliczka 1866; Holdhaus 1913; Gardner and Campbell 2002) assumed that the species occurs also in the Kachchh Basin on the western margin of the Indian Craton where it has been named Astarte major by J. de C. Sowerby (1840). However, the Kachchh specimens, although undoubtedly closely related, are more than three times the size of the Himalayan forms and thus unlikely conspecific. Gardner and Campbell (2002, p. 346) placed most of the large astartids from the Tethys Himalaya in *Neocrassina unilateralis* (J. de C. Sowerby, 1840), a view not followed here. *Pruvostiella* (*P*.) *hermanni* occurs from the Tethys Himalaya to New Zealand (Trechmann 1923; Marwick 1953).

The record of Astarte scytalis Holdhaus from the Kimmeridgian? of East Africa (Weir 1929, p. 5, pl. 3) is doubtful. The specimen may represent a juvenile *Pruvostiella* (*Eoseebachia*) major.

#### Genus Nicaniella Chavan, 1945

#### Subgenus Nicaniella Chavan, 1945

Type species. Astarte communis Zittel & Goubert, 1861.

# Nicaniella (Nicaniella) cf. polymorpha (Contejean, 1860)

Plate 5, fig. 7a-d

cf. 1860 Astarte polymorpha Contej. – Contejean: 266, pl. 11, figs 13–16.

**Material.** A single articulated specimen from the lower member, Kaza–Hikkim road (SNSB-BSPG 2020 XCIX 42).



Plate 5. (1–6) *Pruvostiella* (*Pruvostiella*) *hermanni* (Oppel, 1863). 1. Crushed articulated specimen from the lower member at Langza (SNSB-BSPG 2020 XCIX 53). a, left valve view; b, dorsal view. 2. Crushed articulated specimen from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 54a). a, left valve view; b, right valve view. 3. Crushed articulated specimen from the lower member at Langza (SNSB-BSPG 2020 XCIX 54a). a, left valve view; b, right valve view. 3. Crushed articulated specimen from the lower member at Langza (SNSB-BSPG 2020 XCIX 55b). a, right valve view; b, left valve view. 5. Articulated specimen from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 54b). a, right valve view; b, dorsal view; c, left valve view. 6. Crushed articulated specimen from the lower member at the Kaza–Hikkim road cut (SNSB-BSPG 2020 XCIX 55b). (7) *Nicaniella* (*Nicaniella*) cf. *polymorpha* (Contejean, 1860). Articulated specimen from the lower member at the Kaza–Hikkim road cut (SNSB-BSPG 2020 XCIX 55b). (7) *Nicaniella* (Nicaniella) cf. *polymorpha* (Contejean, 1860). Articulated specimen from the lower member at the Kaza–Hikkim road cut (SNSB-BSPG 2020 XCIX 42). a, right valve view, natural size; b, enlarged; c, dorsal view; d, left valve view. (8) *Cryptocardia* sp. Right internal mould with remains of shell from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 40). (9) *Integricardium* (*Integricardium*) *bannesianum* (Contejean, 1860). Right internal mould with remains of shell from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 40). (9) *Integricardium* (Integricardium) bannesianum (Contejean, 1860). Right internal mould with remains of shell from the Ferruginous Oolite Formation near Zangla (SNSB-BSPG 2020 XCIX 41). a, lateral view; b, dorsal view.

**Description.** Specimen small-sized (H: 9.1 mm; L: 9.7 mm), rounded-triangular, slightly longer than high, moderately inflated. Anterodorsal margin concave, anteroventral margin convex, ventral margin faintly curved, posterodorsal margin long, straight, sloping, forming a rounded angle with the slightly truncated posteroventral margin. Umbones mesial, conspicuous, prosogyrate. Lunule oval, deeply sunk, bordered by sharp carina. Escutcheon long, lanceolate, sharply demarcated, extending to posterior end. Ventral shell margin strongly crenulated. Shell surface covered with 22 closely set, sharp commarginal ribs which are more widely spaced in the umbonal area. Internal features not seen.

**Remarks.** Among the numerous Jurassic species of *Nicaniella*, the specimen is closest to *Nicaniella polymorpha* (Contejean, 1860: 266, pl. 11, figs 13–16) from the Kimmeridgian of eastern France in outline and ornamentation, but that species is known only from its drawings. Therefore, we place our specimen in this species with reservation.

#### Order Cardiida Ferrusac, 1822 Family Cardiidae Lamarck, 1809

Genus Cryptocardia Palmer, 1974

Type species. Cryptocardia bajocensis Palmer, 1974.

#### Cryptocardia sp.

Plate 5, fig. 8

**Material.** A single right valve internal mould with remains of shell from the lower member close to the pass to Tashigeng (SNSB-BSPG 2020 XCIX 40).

**Description.** Specimen small, subequilateral, well-inflated, nearly as long as high (H: 17.2 mm; L: 16.6 mm). Umbo mesial, prominent, broad, protruding beyond hinge line, orthogyrate; beaks slightly prosogyrate and distinctly incurved. Anterior margin convex, ventral margin broadly arched, posterodorsal margin oblique, nearly straight, grading smoothly into rounded posteroventral margin. Posterodorsal margin forming a rounded shoulder with posterior margin. Two narrow parallel grooves, separated by equally narrow shell interval, extending from posterior side of umbo to posteroventral end of shell. Shell surface covered with fine, dense, commarginal striae. Hinge features not seen. **Remarks.** The diagnostic feature of *Cryptocardia*, two parallel radial ridges on the inside of the right valve, are clearly seen in the present internal mould as grooves. The genus has been erected by Palmer (1974) based on material from Pliensbachian to Callovian strata. Palmer established four new species based on differences in the outline of the shell and the size of the umbones. The present specimen cannot be accommodated in any of the four species, but is closest to his *C. morrisi* from the Callovian of Tanzania. As only a single specimen is available, we refrain from creating a new species and, instead, keep it in open nomenclature.

#### Genus Integricardium Rollier, 1912

#### Subgenus Integricardium Rollier, 1912

Type species. Cardium dupinianum d'Orbigny, 1844.

# Integricardium (Integricardium) bannesianum (Contejean, 1860)

Plate 5, fig. 9

1860 Cardium bannesianum Contej. – Contejean: 276, pl. 15, figs 1–5.

1959 Cardium bannesianum Contejean – Jaboli: 59, pl. 7, fig. 9.

1995 Integricardium (Integricardium) bannesianum (Contejean 1860) – Jaitly et al.: 115, pl. 12, figs 14–18, text-figs 27–28.

**Material.** A single right internal mould with remains of shell from the Ferruginous Oolite Formation near Zangla (SNSB-BSPG 2020 XCIX 41).

**Description.** Specimen relatively small for the species (H: 32 mm), suborbicular, nearly equilateral, moderately inflated. Margins slightly damaged but anterior and posterior margins apparently regularly rounded, ventral margin broadly curved. Umbo mesial, orthogyrate. With very faint posterior umbonal ridge. Shell surface covered with commarginal growth lines but lacking posterior radial striae.

**Remarks.** The latter feature distinguishes species the genus *Integricardium* from *Protocardia*. The specimen falls in the range of variation of *I*. (*I*.) *bannesianum* and therefore has been placed in that species. According to Dietrich (1933), the closely related *I*. (*I*.) *propebanneianum* (Dietrich, 1933, p. 50, pl. 6, figs 92–93) differs in possessing, in contrast to *I*. (*I*.) *bannesianum*, a pallial sinus, a stronger

**Table 4.** List of bivalve taxa encountered in the Spiti Shale Formation of the Spiti area.

Palaeonucula cuneiformis (J. de C. Sowerby, 1840)
Palaeonucula stoliczkai Cox, 1940
Megacucullaea cf. kraussii (Tate, 1867)
Grammatodon (Indogrammatodon) egertonianus (Stoliczka, 1865)
Grammatodon (Cosmetodon) sp.
Meleagrinella? sp.
Bositra buchii (Roemer, 1836)
Australobuchia spitiensis (Holdhaus, 1913)
Australobuchia blanfordiana (Stoliczka, 1865)
Malayomaorica? sp.
Retroceramus (Retroceramus) haasti (Hochstetter, 1863)
Retroceramus (Retroceramus) everesti (Oppel, 1863)
Anopaea? sp.
Entolium (Entolium) corneolum (Young & Bird, 1828)
Pectinidae indet.
Propeamussium (Propeamussium) sp.
Chlamys (Chlamys) cf. textoria (Schlotheim, 1820)
Radulopecten cf. fibrosus (J. Sowerby, 1816)
Spondylopecten (Plesiopecten) subspinosus (Schlotheim, 1820)
Camptonectes (Camptochlamys) obscurus (J. Sowerby, 1818)
Gryphaeidae indet.
Plagiostoma? sp. A
Plagiostoma? sp. B
Ctenostreon sp.
Trigonia? sp.
Cryptocardia sp.
Nicaniella (Nicaniella) polymorpha (Contejean, 1860)
Pruvostiella (Pruvostiella) hermanni (Oppel, 1863)

**Table 5.** List of bivalves described by Stoliczka (1866) from the Spiti Shale Formation. Where possible, the taxonomic name has been revised.

Stoliczka (1866)	present taxonomic name
Ostrea sp. (aff. flabelloides	Actinostreon
Lam.)	
Pecten lens	Camptonectes (C.) lens
Amusium sp. cf. Pecten solidus Trautsch.	Entolium (E.) corneolum
Aucella blanfordiana Stol.	Australobuchia blanfordiana (Stoliczka)
Aucella leguminosa Stol.	Australobuchia leguminosa (Stoliczka)
<i>Lima</i> sp. (like <i>L. rigida</i> )	Plagiostoma
Inoceramus hookeri Salter	Retroceramus
Macrodon egertonianum Stol.	Grammatodon (Indogrammatodon) egertonianus (Stoliczka)
Nucula sp. (resembling N. subovalis Goldf.)	Palaeonucula
Nucula cuneiformis Sow.	Palaeonucula cuneiformis (J. de C. Sowerby)
Cyprina trigonalis Blanf.	?
Trigonia costata	Trigonia (Trigonia)
Astarte unilateralis	Pruvostiella (P.) hermanni (Oppel)
Astarte major Sow.	Pruvostiella (P.) hermanni (Oppel)
Astarte spitiensis Stol.	Pruvostiella (P.) hermanni (Oppel)
Astarte hiemalis Stol.	Pruvostiella (P.) hermanni (Oppel)
Homomya tibetica Stol.	Arcomya?

**Table 6.** List of bivalve taxa described by Holdhaus (1913) from the Spiti Shale Formation. Where possible, the present taxonomic status has been added. Where no material was available to us, often only a new generic assignment is proposed.

Holdhaus (1913)	present taxonomic status
Avicula spitiensis Oppel, 1863	Oxytoma
Pseudomonotis inornata sp. nov.	?
Pseudomonotis amoena sp. nov.	?
Aucella leguminosa Stoliczka, 1866	Australobuchia leguminosa (Stoliczka, 1866)
Aucella spitiensis sp. nov.	Australobuchia spitiensis (Holdhaus, 1913)
Aucella spitiensis form. typ.	Australobuchia spitiensis (Holdhaus, 1913)
Aucella spitiensis grandis nov. form.	Australobuchia spitiensis? (Holdhaus, 1913)
Aucella spitiensis superba nov. form.	Australobuchia spitiensis? (Holdhaus, 1913)
Aucella blanfordiana Stoliczka, 1866	Australobuchia blanfordiana (Stoliczka, 1866)
Aucella? formosa sp. nov.	Australobuchia?
Inoceramus everesti Oppel, 1863	Retroceramus everesti (Oppel, 1863)
Inoceramus gracilis sp. nov.	Retroceramus everesti (Oppel, 1863)
Inoceramus stoliczkai sp. nov.	Anopaea stoliczkai (Holdhaus, 1913)
Inoceramus cf. sularum Boehm, 1907	?
Lima melancholica sp. nov.	Limatula?
Lima tristicula sp. nov.	?
Lima roberti Oppel, 1863	Plagiostoma
Lima spitiensis sp. nov.	Plagiostoma
Pecten inertulus sp. nov.	?
Pecten sp.	?
Ostrea sp.	Actinostreon
Nucula spitiensis sp. nov.	Palaeonucula cuneiformis (J. de C. Sowerby, 1840)
Nucula hyomorpha sp. nov.	Palaeonucula cuneiformis J. de C. Sowerby, 1840)
Nucula kibberiana sp. nov.	Palaeonucula stoliczkai Cox, 1940
Nucula sp.	Palaeonucula
Nucula dieneri sp. nov.	Rollieria
Leda sp.	?
Leda? sp.	?
Arca (Cucullaea) egertoniana	Grammatodon (Indogrammatodon)
Stoliczka, 1866	egertonianus (Stoliczka, 1866)
Trigonia spitiensis sp. nov.	Trigonia (Trigonia)
Astarte hermanni Oppel, 1863	Pruvostiella (P.) hermanni (Oppel, 1863)
Astarte sowerbyana sp. nov.	Pruvostiella (P.) hermanni (Oppel, 1863)
Astarte scytalis sp. nov.	Pruvostiella (P.) hermanni (Oppel, 1863)
Astarte spitiensis Stoliczka, 1866	Pruvostiella (P.) hermanni (Oppel, 1863)
Pleuromya spitiensis sp. nov.	Pleuromya
Cosmomya egregia sp. nov.	Cosmomya egregia Holdhaus, 1913
Homomya tibetica Stoliczka, 1866	Arcomya?
Goniomya uhligi sp. nov.	Goniomya
Pholadomya? problematica sp. nov.	?

posterior umbonal ridge and a less strongly curved ventral margin. A detailed investigation of the type material is required to clarify the relationship of the two species.

## Concluding remarks

Most parts of the nearly exclusively siliciclastic Spiti Shale Formation in the Spiti area represent middle to to outer shelf environments. Benthic macroinvertebrates are absent from large parts of the succession, and in other parts they are very rare. The reason are unsuitable conditions at the sea floor, in particular the lack of oxygen, partly caused by upwelling (Fürsich et al. 2021). Most of the fossils occur in the lower member, where a near-monospecific Bositra buchii association and a low-diversity association dominated by *Palaeonucula cuneiformis*, *Grammatodon* (*Indogrammatodon*) egertonianus, and *Pruvostiella* (*P*.) *hermanni* are common (Fürsich et al. 2021). All in all, relatively few bivalve taxa occur in the formation, which spans the time interval between the Callovian and the earliest Cretaceous. In the present account, 24 taxa are described from the Spiti Shale Formation (Table 4), six additional ones from the Ferruginous Oolite Formation. Stoliczka (1866) described 17 bivalve taxa from the two formations, whereby after taxonomic revision only 13 remain valid (Table 5). In the most extensive account published so far, Holdhaus (1913) described 37 bivalve taxa from the Indian Himalayas, chiefly from the Spiti area, of which around 30 remain after sorting out synonymies (Table 6). Some faunal elements, such as Australobuchia, Malayomaorica, and Retroceramus, are also known from the southeastern margin of the Neotethys (e.g., New Zealand, Indonesia). Others, in particular Provostiella (P.) hermanni and Grammatodon (Indogrammatodon) egertonianus, are closely related but not identical to forms from the Kachchh Rift Basin situated at the western margin of the Indian Craton.

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## Late Jurassic (Upper Kimmeridgian) Heterobranchia (Gastropoda) of the coral-facies of Saal near Kelheim and the viciniy of Nattheim (Germany)

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### Abstract

Forty gastropod species of the subclass Heterobranchia are described from the Upper Jurassic (Upper Kimmeridgian) reefal limestones of South Germany, including ten species in open nomenclature and further ten species of uncertain identity. Six species are new to science: *Ceritella convexa* **sp. nov.**, *Nerinea donosa* **sp. nov.**, *Endoplocus acutus* **sp. nov.**, *Endoplocus acutus* **sp. nov.**, *Endoplocus acutus* **sp. nov.**, *Pseudonerinea? pseudomelaniformis* **sp. nov.**, and *Itieroptygmatis cylindrata* **sp. nov.** A lectotype is designated for *Ptygmatis? tornata* (Quenstedt, 1852). With this final part of the study of the Late Jurassic gastropods from Saal and the Nattheim area, a total of 156 species have been reported. Of these species, 125 have been reported from Saal and 54 from the Nattheim area. Only 23 species occur in both Saal and the Nattheim area. The sample sizes (number of specimens) from Saal and the Nattheim area differ considerably and few species are shared. Diversity metrics suggest the same high diversity at both sites. The gastropod fauna from the Saal quarry has yielded particularly much new information – all new species are based on specimens from Saal. With 125 gastropod species from a single outcrop, the diversity at the Saal quarry is the highest from the Kimmeridgian worldwide. In total, up to 300 species of marine macro-invertebrates have been reported from this quarry, which is a very high point diversity. Gastropods are by far the most diverse group from Saal, which is a modern aspect of this fauna.

### Keywords

Gastropoda, Heterobranchia, Southern Germany, Kimmeridgian, coral reef facies, taxonomy

### Introduction

This is the fourth and final part of the description of the Late Jurassic (Upper Kimmeridgian) gastropods from the reefal limestones of South Germany (Saal und Nattheim) (Gründel et al. 2015, 2017, 2019). Meanwhile, an additional private collection from Saal (collection Sylla) has been obtained by the Bavarian State Collection (SNSB-BSPG)

in 2017 (Werner et al. 2017). It yields numerous not yet studied gastropod specimens that potentially could complement our knowledge of the gastropods from Saal and also yields additional undescribed species, but the study of this collection will need time.

Nerineoidea probably originated in the Early Jurassic (Tracey et al. 1993) and were comparatively rare and of low diversity until the Callovian. They diversified from the

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Oxfordian onward and continued to do so in the Kimmeridgian. They became extinct at the end-Cretaceous mass extinction event.

Generally, gastropods from Saal are re-crystallized and lack the early ontogenetic shell including the protoconch. The specimens from Nattheim are silicified, but the silicification is rather coarse. However, many species could be characterized in sufficient detail so that 156 species could be described making this fauna one of the most diverse known Late Jurassic gastropod faunas.

### Geological setting

The geological setting for the studied Late Jurassic gastropod fauna is provided by Gründel et al. (2015) in German. A complemented translation is provided herein: The gastropod faunas come from Upper Jurassic reefal limestones from the localities of Saal near Kelheim, Lower Bavaria and Nattheim in Baden-Württemberg. Almost all finds from Württemberg published to date are listed under the locality name "Nattheim". This information is a collective name for finds from small quarries that no longer exist and finds from fields in the wider area of Nattheim. The exact fossiliferous localities can no longer be determined. Today, most finds are made in the Gerstetten area (see below).

#### Saal

By far most of the studied gastropod material comes from a quarry near Saal near the Danube River. The quarry of the Fels-Werke GmbH (right-high value: 4495500/5417000) exposes a more than 100 m thick section of massive limestone of Middle and Late Kimmeridgian age which possibly extends into the basal Tithonian (Meyer in Weber et al. 1978; Meyer and Schmidt-Kahler 1983). The massive limestones are unconformably overlain by sediments of the Danubian Cretaceous Group (Niebuhr and Pürner 2009). Up to 80 m deep karst fissures, which formed during the Early Cretaceous, are filled with colourful, terrestrial sediments, the pre-Cenomanian Schutzfelsschichten (kaolinite-bearing clays, sands and fine gravel). The erosive surface of the Upper Jurassic massive limestones (in some places with borings of lithophagous bivalves), together with its filled carst fissures, is transgressively overlain by marine sands of the Regensburg Formation (Gümbel 1854; Trusheim 1935). In the Regensburg-Kelheim area, this succession is up to 16 m thick, contains glauconite, fossil-bearing sandstones (Upper Cenomanian Unterer Grünsandstein (Lower Greensandstone): Saal-Member) with a glauconite content of over 30% (Meyer and Schmidt-Kahler 1983; Wilmsen et al. 2009). At the contact between to the Cretaceous Schutzfelsschichten, the otherwise very dense Upper Jurassic massive limestones have been intensively weathered in a zone of usually only a few millimetres to up to 60 mm in some cases. From this highly porous weathering layer, small fossils, in particular gastropods, bivalves, echinoderms, brachiopods, corals, etc.,

can be carefully washed out. The acidic karst waters have gently and meticulously etched the fossils free. In 2003 and 2014, one of the authors (Fritz Lang) was able to isolate more than 300 and 1,000 gastropods, respectively, by washing the loose material carefully scraped off the karst surfaces.

The massive Upper Jurassic limestones are subject to rapid vertical and lateral facies changes. The deeper part of the section (up to approximately 300 m above sea level) exposed in the quarry is dominated associations of siliceous sponges and microbes. Then, platy corals (Microsolena) are increasingly intercalated during the Upper Kimmeridgian until a continuous transition into a pure coral reef facies is reached at the middle quarrying level, about 380 m above sea level (Meyer in Weber et al. 1978). In the upper 40-50 meters of the reef limestone from which the gastropod fauna was retrieved, the switch from the deeper-water association dominated by siliceous sponges to a shallow water coral facies is completed. The reefal facies consist of individual in situ reef bodies vielding a highly diverse coral fauna, as well as reef debris limestone and typical lagoon sediments (facies with coated grains, dasycladaceans, gastropods: "Breistein"="Porridge-Stone") containing pocket-like shell accumulations dominated by terebratulid brachiopods.

The stratigraphic age of the massive limestones is disputed. Rare ammonite finds reported by Schairer and Sylla (1996) from different levels of the Saal guarry confirmed a Late Kimmeridgian age, supported by finds of Hybonoticeras beckeri, Sutneria subeumela and a Virgataxioceras that cannot be determined in more detail between 335 and 415 m above sea level, i.e., up to the upper quarry level. From the top 15 meters of the reef limestone exposed in the quarry, no exactly localized ammonites have been described so far. Meyer (in Weber et al. 1978) assumed that the highest proportions of the Kelheim reef limestone reach into the basal Tithonian. However, direct evidence of this (Lithacoceras cf. ulmensis) is not available from Saal, but from the abandoned guarry near Ofenstetten, about 10 km SW. Meyer and Schmidt-Kaler (1983) base the presumed Lower-Tithonian age of the highest reefal limestones at Saal on the alleged occurrence of Neochetoceras steraspis with the unspecified locality information "above the middle working level." This ammonite is also a characteristic faunal element of the Obere Schiefer (Upper Slate) of the Solnhofen Plattenkalke (Solnhofen Lithographic Limestone) (Schweigert 2007).

#### Gerstetten

The fossils from the Nattheim coral facies are silicified, i.e., originally aragonitic and calcitic shells were diagenetically converted into siliceous material. Thus, fossils can be freed from the dense limestone with acetic or formic acid. In addition to a very diverse coral association comprising more than 130 species, the massive limestones contain an equally rich reef dwelling fauna consisting of coralline sponges, tube worms, brachiopods, molluscs and echinoderms (e.g., Benz 1979; Reif 1988; Sauerborn 1988). During the 19<sup>th</sup> century, in the course of bean ore mining, numerous outcrops on the Swabian Jura in the Nattheim/ Blaubeuren/Gerstetten area were sampled for fossils. Today, finds are essentially limited to cobbles from fields or to temporary outcrops in connection with construction work. In the older descriptive literature (Goldfuss 1844; Quenstedt 1856–1858, 1881–1884; Brösamlen 1909) usually only "Nattheim" is mentioned as a locality name.

The massive coral facies in that area is part of the more than 120 m thick Mergelstetten Formation. It lies at the border to the Unterer Massenkalk (Lower Massive Limestone) that underlies the Mergelstetten Formation. It can thus be regarded as a chronological equivalent of the Liegende Bankkalk-Formation (Schweigert and Franz 2004). The Mergelstetten Formation is bounded by sedimentary discontinuities and may interfinger with the Brenztal-Trümmerkalken (Brenztal Debris-Limestones) in the East and with the bedded units of the Liegende Bankkalke (Lying Bedded Limestones) or the Zementmergel-Formation (Cement-Marl Formation) in the West (Reif 1988; Schweigert and Franz 2004; Schmid et al. 2005). As the rare finds of ammonites show, the Mergelstetten Formation belongs stratigraphically to the uppermost Kimmeridgian (Beckeri Zone, Ulmense Subzone) and is therefore contemporaneous with the Nusplinger Plattenkalk (Nusplingen Lithographic Limestone). Fischer and Weber (1997) erroneously considered the occurrences of Nattheim to be contemporaneous with the Transversarium to Bimammatum (Middle to Upper Oxfordian) zone – a range from which d'Orbigny (1851–1860) has described numerous species.

### Repository

Most of the illustrated and type material is reposited at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (SNSB-BSPG) (collections by Lang, Schäfer, Neubauer, and Keupp). Material from the Lang collection that has been examined but not figured herein has been returned to this collector. However, not illustrated specimens that are designated as type specimens of new taxa is also reposited at SNSB-BSPG. The material from the collection Sauerborn remains entirely in his private collection. The collection of Quenstedt is housed at the Universität Tübingen (Fachbereich Geowissenschaften, Paläontologische Forschungs-, Schau- und Lehrsammlung).

### Systematic palaeontology

Shell shape, ornament, number and morphology of plaits, ontogenetic change of shell morphology, and other shell characters have been used for taxonomy in Nerineoidea. However, the various authors used these characters in an inconsistent way, and thus the supraspecific classification is commonly also inconsistent. Due to a lack of a consistent concept, the generic or family assignments of species may differ strongly from author to author. Taxonomy and systematics of Nerineoidea are obviously still unstable. The most recent comprehensive treatment on the family level is that by Kollmann (2014). The present taxonomical treatment and classification is largely based on the contributions by Gründel and Nützel (2012), Kollmann (2014), and Bouchet et al. (2017).

The identification and systematics of the present Nerineoidea turned out to be especially challenging and needs further study. The preservation of nerineoid specimens is commonly insufficient and poorer than in other taxa. This is true of both the calcareous re-crystallized specimens from Saal and the silicified ones from Nattheim. Commonly, the ornamentation of the whorls is not or insufficiently preserved in Nerineoidea. Many Nerineoidea are relatively large and slender (turreted), and specimens are present as fragments of a few whorls only. Since both ornamentation and inner plaits are commonly subject to ontogenetic change, it was often impossible to attribute these fragments to any taxon with higher resolution. Previous students of these gastropods faced the same problems and therefore some of the species are characterized in a contradictionary way in the literature (see e.g., 'Remarks' for Cossmannea desvoidyi).

#### Subclass Heterobranchia Gray, 1840 Superfamily Nerineoidea Zittel, 1873 Family uncertain

#### Genus Cossmannea Pchelintsev, 1927

**Type species.** *Nerinea desvoidyi* d'Orbigny, 1851; OD, Middle Oxfordian; France.

Remarks. Again declared as new by Pchelintsev (1931).

#### Cossmannea desvoidyi (d'Orbigny, 1851) Plate 1: figs 1-3

?\*1836 - Nerinea grandis Voltz in litt. - Bronn: 549, pl. 6, fig. 1.

\*1851 – Nerinea desvoidyi d'Orbigny – d'Orbigny: 107, pl. 261, figs 1–3.

\*1858 - Nerinea grandis concava - Quenstedt: 766, pl. 94, fig. 3.

v1881-1884 - Nerinea grandis concava - Quenstedt: 524, pl. 205, fig. 60.

part1901 - Nerinea desvoidyi d'Orb. - Geiger: 283, pl. 11, fig. 5.

- 1979 Cossmannea desvoidyi desvoidyi (d'Orbigny, 1850) Wieczorek: 321, fig. 11, pl. 7, figs 1, 4; pl. 8, figs 1, 6.
- 1997 Cossmannea desvoidyi (d'Orbigny, 1851) Fischer and Weber: 42, pl. 11, figs 1–3.
- 1997 Cossmannea (Cossmannea) desvoidyi (d'Orbigny, 1850) Hägele: 129, fig. p. 129 upper left.
- 2014 Cossmannea desvoidyi (d'Orbigny, 1850) Kollmann: 354, fig. 2B.

**Material.** A specimen from the area near Nattheim (collection Sauerborn) and a specimen from the Quenstedt collection, possibly the specimen figured by Quenstedt (1858, pl. 94, fig. 3) from Nattheim.



Plate 1. (1–3) Cossmannea desvoidyi (d'Orbigny, 1851). (1–2) collection Sauerborn, Nattheim area; (1) lateral view, height 23.8 cm;
(2) last whorls with aperture, height 8 cm. (3) University Tübingen, collection Quenstedt), Nattheim, lateral view, height 130 mm (original of Quenstedt 1881–1884, pl. 205, 60). (4–6) Aptyxiella planata (Quenstedt, 1858), SNSB-BSPG 2021 XV 1, Nattheim–Rinderberg;
(4–5) lateral views, height 70 mm; (6) aperture, height of detail 70 mm. (7) Aptyxiella quenstedti Geiger, 1901, Nattheim, lateral view (copy from Geiger 1901, pl. 11, fig. 1).

**Description.** The specimen from the Sauerborn collection is 23.8 cm high. The shell is slender with relatively high whorls. The whorl face is concave and lacks any visible ornament. The suture is distinct but shallow, situated at the lower side of an abapical, rounded bulge forming the transition to the flat, seemingly smooth base. The periphery is situated directly above abapical suture. The aperture is rhomboid with a large, oblique siphonal canal. Two columellar plaits are visible.

**Remarks.** According to Fischer and Weber (1997), *Cossmannea desvoidyi* has a long range from the middle Oxfordian to lower Portlandian. The type specimen is from the middle Oxfordian of France. Considering this long range, *Nerinea grandis* Voltz in Bronn, 1836 (Portlandian?) and *Nerinea grandis concava* Quenstedt, 1858 (upper Kimmeridgian) could represent *C. desvoidyi*. If true, then *Nerinea grandis* would be the oldest available name for this species.

The identity of *C. desvoidyi* is unclear, especially regarding the plaits, because there are conflicting reports in the literature: According to Geiger (1901), Cox (1947), and Fischer and Weber (1997), *C. desvoidyi* has a single columellar and a single palatal plait. In the present specimen from Nattheim, two columellar plaits are visible. The outer lip is not sufficiently well-preserved to show or exclude the presence of palatal plaits. Bronn (1836) and Kollmann (2014) mention the presence of only a single columellar plait. It is unclear whether these differences are results of variability, preservation, ontogenetic change, or whether two or more species are present.

There are also contradictory statements about the morphology of the aperture of *C. desvoidyi*. Kollmann (2014) reported that a siphonal canal is absent in specimens from the type locality of St. Mihiel. However, Fischer and Weber (1997: pl. 11, fig. 1) figured a specimen from the same locality that has a siphonal canal. The present specimen from Nattheim (Sauerborn collection) has a very distinct oblique canal. Furthermore, this species is generally said to lack ornamentation, but the illustration by Geiger (1901: pl.11, fig. 5) shows numerous spiral cords covering the entire whorls, which is, however, not mentioned in Geiger's (1901) description of this species.

The present contribution cannot solve these problems. We assume that the upper Kimmeridgian specimens described herein represent the same species as the middle Oxfordian holotype of *C. desvoidyi* from France. In order to avoid nomenclatorial confusion, we include only the reference to the type material and to Kimmeridgian material in the synonymy and chresonymy list.

#### Genus Aptyxiella P. Fischer, 1885

**Type species.** *Nerinea sexcostata* d'Orbigny, 1852; Oxfordian-Kimmeridgian; France.

#### Aptyxiella planata (Quenstedt, 1858)

Plate 1: figs 4-6

\*1858 – Nerinea planata – Quenstedt: p. 770, pl. 94, figs 31, 32. v1881–1884 – Nerinea planata Qu. – Quenstedt: p. 554, pl. 207, figs 5–7, 8?

1901 - Aptyxiella planata Quenstedt - Geiger: p. 276.

1997 – Aptyxiella planata (Quenstedt) – Hägele: p. 133, fig. p. 133 upper right.

**Material.** One specimen (SNSB-BSPG 2021 XV 1) and four questionable fragments from Nattheim (Tübingen, Quenstedt collection).

**Description.** The shell is high-spired and very slender. It is 70 mm high (apex missing). The whorls are high with a straight to slightly concave whorl face and slowly increasing in width. The suture is oblique and situated on a slightly elevated bulge formed by two adjoined whorls. No ornament is visible (due to preservation?). The base is flat and demarcated from whorl face by a sharp angulation, and lacks visible ornament. The aperture is elongated, higher than wide, rhomboid, and has a distinct, oblique siphonal canal (partially broken). Plaits are absent.

**Remarks.** The four fragments from the Tübingen collection are poorly preserved and might represent different species. According to Geiger (1901, p. 277), the whorls are ornamented with numerous spiral cords of various strength which are, however, destroyed by the coarse silicification of the specimens from Nattheim (if they were present at all).

Aptyxis planata Quenstedt sensu Schlosser (1882) differs from the studied specimens by having spiral cords, a broader shape, lower whorls and more oblique sutures. According to Schlosser (1882, p. 77) "the only specimen housed in the Munich Museum" shows ornamentation. However, our study of the specimen could not confirm this. The very similar (identical?) *Cossmannea? quenstedti* Geiger, 1901 has a columellar plait.

#### Aptyxiella quenstedti Geiger, 1901

Plate 1: fig. 7

- part v1858 Nerinea grandis nuda Quenstedt: 766, pl. 94, fig. 4 (non fig. 5).
- part v1881–1884 Nerinea grandis nuda Quenstedt: p. 553, pl. 207, fig. 2 (non fig. 1).
- \*1901 Aptyxiella quenstedti sp. nov. Geiger: p. 278, pl. 11, fig. 1.
- 1997 Aptyxiella quenstedti Geiger, 1901 Hägele: 133, fig. p. 133 lower right.

**Material.** One specimen from Nattheim (Tübingen: Quenstedt collection).

**Description.** The specimen illustrated by Quenstedt (1881–1884: pl. 207, fig. 2) is a 29 mm high fragment consisting of three whorls. Geiger (1901, pl. 11, fig. 1; copied herein in Plate 1: fig. 7) used another, better preserved specimen. In Quenstedt's (1881–1884) specimen, approximately half of shell wall is broken off. The flanks are straight. The suture is slightly impressed. No ornament is visible. The base is anomphalous. The aperture has a weak columellar plait.

**Relationships.** *Nerinea grandis nuda* Quenstedt, 1858 is much larger and has seemingly no plaits. The very similar and maybe identical *Aptyxiella planata* (Quenstedt) lacks a columellar plait. Hägele (1997) also claimed that *Aptyxiella quenstedti* has a more convex whorl face, but the specimen illustrated by Geiger (1901) does not show this.

#### Family Pseudonerineidae Pchelintzev, 1965

#### Genus Pseudonerinea Loriol in Loriol & Koby, 1890

**Type species.** *Pseudonerinea blauensis* Loriol in Loriol & Koby, 1890; Oxfordian; France.

#### Pseudonerinea? pseudomelaniformis sp. nov.

https://zoobank.org/0A09158-5B82-45A5-B516-C04A5FF7943D Plate 2: figs 1-7

**Derivatio nominis.** For being similar to *Pseudomelania* Pictet & Campiche, 1862 in regard to shell shape.

Holotype. SNSB-BSPG 2021 XV 23 (collection Lang).Locus typicus. Saal quarry near Kelheim.Stratum typicum. Upper Kimmeridgian.

**Paratypes.** Thirty-three specimens from Saal, collection Lang: SNSB-BSPG 2021 XV 24–26, 183–212.

Additional material. Three specimens from Saal, without type status (collection Lang).



Plate 2. (1–7) Pseudonerinea? pseudomelaniformis sp. nov. (1–3) Holotype, SNSB-BSPG 2021 XV 23, Saal (collection Lang); (1) lateral view, height 22 mm; (2) aperture, height 8.5 mm; (3) base, width 6.5 mm. (4–5) Paratype, SNSB-BSPG 2021 XV 24, Saal (collection Lang); (4) lateral view, height 13.7 mm; (5) apex, height 2.8 mm. (6) Paratype, SNSB-BSPG 2021 XV 25, Saal (collection Lang), last whorl with aperture, height 10 mm. (7) Paratype, SNSB-BSPG 2021 XV 26, Saal (collection Lang); aperture, height 7 mm.

**Diagnosis.** Shell slender; spire high in relation to last whorl; whorl face straight with narrow ramp; weak spiral furrow present below ramp; aperture with distinct siphonal canal, two columellar, and one parietal plait.

**Description.** The holotype is 22 mm high. The shell is slender, high-spired, and consists of many whorls. The whorl face is straight. The sutures are accentuated by a narrow ramp. The early whorls are poorly preserved, seemingly with two spiral cords near sutures and having a concave whorl face between the cords. Later whorls have a subsutural bulging spiral cord (weakly nodular?) that is demarcated by an abapical spiral furrow. This furrow is rarely distinct or frequently not visible at all probably due to preservation. No other ornament is present. The transition from whorl face to the strongly convex base is evenly rounded. The base has several, weakly defined, bulging spiral cords. It is anomphalous. The growth lines are indistinct; they are strongly curving backward adapically. The aperture is narrow with a weakly convex outer lip; parietal and columellar lip meet at an angle. The aperture has a distinct siphonal canal, a distinct parietal and two columellar plaits. The columellar plaits are commonly weak or not visible even in seemingly well-preserved specimens (variability or due to preservation).

**Remarks.** It is possible that the studied material represent two species. The type species of *Pseudonerinea* lacks plaits. Therefore, the generic assignment of *P*? *pseudomelaniformis* is tentative.

**Relationships.** *Phaneroptyxis fusiformis* (d'Orbigny) sensu Gemmellaro (1870), Blake and Hudleston (1877), Cossmann (1898), Loriol in Loriol and Koby (1895), and Fischer and Weber (1997) is less slender, has a higher last whorl in relation to spire height, a narrow umbilicus, and only a single columellar plait is visible. Cerithium pellati Loriol in Loriol & Pellat, 1874 is very similar but lacks plaits and the siphonal canal is less pronounced. Itieria melanioides Zittel, 1873 has only a single columellar plait as well as one parietal and one palatal plait; it lacks a siphonal canal, and its whorl face is weakly convex with impressed sutures. Phaneroptyxis sulejovensis Wieczorek, 1979 is larger, has a more pronounced ramp and deeper sutures, its base is demarcated by an edge, and it has a single columellar plait. Nerinea eichwaldiana d'Orbigny, 1845 has only a single columellar plait and a palatal plait; it lacks a ramp and the sutures are barely impressed. Phaneroptyxis grayensis Maire, 1927 is larger, its whorls are lower and increase more rapidly in width, and it has only a single columellar plait.

#### Family Ceritellidae Wenz, 1938

Kollmann (2014) used a broad concept of the family Ceritellidae, and besides Ceritella included also closely related genera, even those that deviate considerably, such as Cossmannea Pchelintsev, 1931, Aptyxiella P. Fischer, 1885, Aphanoptyxis Cossmann, 1896, and others. Guzhov (2017) included only the genera Ceritella Morris & Lycett, 1851 and Ceritellopsis Fischer, 1961. Until recently, Ceritellidae have been considered to represent basal Nerineoidea (e.g., Kollmann 2014; Bouchet et al. 2017). However, according to Guzhov (2017), the genera Ceritella and Ceritellopsis belong to Acteonoidea d'Orbigny, 1843. We cannot contribute to this debate because the present material attributed to this family is too fragmentary. The species assigned to Ceritellidae and Nerineidae commonly appear as pairs of species lacking plaits (Ceritellidae) and having plaits (Nerineidae): Ceritellopsis gramanni/Nerinea donosa, Ceritella sp. 1/ Endoplocus acutus, Ceritella convexus/Endoplocus inflatus. This could indicate that both families are closely related to each other or share similar environmental requirements. However, the species in question differ strongly from each other in size, i.e., Ceritellidae being small and Nerineidae large.

#### Genus Ceritellopsis J.-C. Fischer, 1961

**Type species.** Cerithium petri d'Archiac, 1843; Bathonian; France.

#### Ceritellopsis gramanni Huckriede, 1967

Plate 3: figs 1-4

- ?1895 *Ceritella plicata* Zittel and Goubert Cossmann: 102, pl. 4, figs 66, 67.
- \*1967 Ceritella (Ceritellopsis) gramanni sp. nov. Huckriede: 198, pl. 19, figs 4–9.

**Material.** Twenty-five specimens from Saal (collection Lang), three of which are illustrated herein: SNSB-BSPG 2021 XV 2–4.

**Description.** A large specimen is 3.2 mm high. The shell is fusiform, relatively slender with a high spire. The whorls are rather high and have a distinct, oblique ramp, demarcated from whorl face by a spiral cord. The whorl face is straight. The suture is distinct and is accentuated by the ramp. The whorls are ornamented with straight, slightly opisthocline, rounded axial ribs separated by wide interspaces. The ribs become weaker and may fade entirely on the last preserved whorl. The transition from whorl face to base is evenly rounded. The ribs do not continue onto the smooth base. The aperture is oval, higher than wide, with a weak, short canal and an acute posterior part. The inner lip is reflexed in the columellar portion. **Remarks.** Most of the specimens of *Ceritellopsis* gramanni figured by Huckriede (1967) have a broader shell. However, in general the present specimens fall into the variation of this species as reported by Huckriede (1967: figs 7 and 8 on pl. 19).

**Relationships.** The differences to *Ceritellopsis plicatula* are discussed under the treatment of that species. *Actaeonina plicata* Zittel & Goubert, 1861 has a broader, stouter shell and its spire is not as slender and with a lower whorl face of the spire whorls. *Ceritella rissoides* Buvignier sensu Cossmann (1895) has a broader shell, its last whorl is higher in relation to the spire height and its ramp is not as sharply demarcated. *Cerithium lorteti* Loriol sensu Loriol and Pellat (1874) has more axial ribs, the whorl face of the spire whorls is higher and the aperture is narrower. *Ceritellopsis huckriedei* Gründel & Kaim, 2006 is slenderer, its spire is distinctly higher than the last whorl, and it has more axial ribs bent backwards adapically.

#### Ceritellopsis plicatula Huckriede, 1967

Plate 3: figs 5, 6

\*1967 – Ceritella (Ceritellopsis) plicatula sp. nov. – Huckriede: 197, pl. 18, figs 31–50.

?1971 - Ceritella elata Loriol, 1889 - Dmoch: 17, pl. 2, fig. 1.

Material. Five specimens from Saal (collection Lang), two of which are illustrated herein: SNSB-BSPG 2021 XV 5, 6.

**Description.** The largest specimen is 5.3 mm high. The shell is slender with a high and acute spire. The whorls are high and have a distinctly oblique ramp accentuating the sutures. The ramp is demarcated from whorl face by an angulation. The whorls are ornamented with broad axial ribs, that are fading on the last preserved whorls. The transition from whorl face to base is evenly rounded. The base is smooth. The damaged aperture is oval, acute adapically, and has a siphonal canal.

**Relationships.** Ceritellopsis gramanni Huckriede, 1967 is much stouter, has lower whorls and a nearly horizontal ramp. Ceritellopsis huckriedei Gründel & Kaim, 2006 has lower whorls, a horizontal ramp and its axial ribs are bent backward adapically. Orthostoma longiscata Buvignier sensu Buvignier (1852) is distinctly slenderer. The species with the same name, Orthostoma longiscata, sensu Buvignier (1843) resembles C. plicatula more closely in shape but has a horizontal ramp and more axial ribs. Ceritella elata de Loriol var. striata Maire, 1927 has a spiral ornament and lower whorls.

#### Genus Ceritella Morris & Lycett, 1851

Type species. Ceritella acuta Morris & Lycett, 1851; Bathonian; England.



Plate 3. (1–4) Ceritellopsis gramanni Huckriede, 1967. (1) SNSB-BSPG 2021 XV 2, Saal (collection Lang), lateral view, height 2.5 mm. (2, 4) SNSB-BSPG 2021 XV 3, Saal (collection Lang); (2) lateral view, height 2.7 mm; (4) base, width 1.3 mm. (3) SNSB-BSPG 2021 XV 4; Saal (collection Lang), aperture, height of detail 1.3 mm. (5–6) Ceritellopsis plicatula Huckriede, 1967. (5) SNSB-BSPG 2021 XV 5, Saal (collection Lang), lateral view, height 3.3 mm. (6) SNSB-BSPG 2021 XV 6, Saal (collection Lang), lateral view, height 4.8 mm.

#### Ceritella convexa sp. nov.

https://zoobank.org/154A9E44-1AEB-42FC-B0B6-0526AA853724 Plate 4: figs 1–5

**Derivatio nominis.** Lat. *convexus* – convex; for the convex, somewhat inflated whorls.

Holotype. SNSB-BSPG 2021 XV 9, collection Lang.

Locus typicus. Quarry Saal near Kelheim.

Stratum typicum. Upper Kimmeridgian.

**Paratypes.** Twenty-two mostly juvenile specimens from Saal (collection Lang) SNSB-BSPG 2021 XV 8, 147–167.

Additional material. Three specimens from Saal, without type status (collection Lang).

**Diagnosis.** Shell broadly fusiform; whorls with distinctly oblique ramp; larger specimens have a somewhat inflated last whorl; early whorls with axial ribs changing to strengthened growth lines in later whorls; ribs curve backward below ramp edge; spiral cords absent.

Description. A large specimen is 4.3 mm high. The shell is broadly oval, fusiform with an acute spire. The shell width is variable. Larger specimens have a somewhat inflated last whorl. The sutures are distinct. The whorls have a relatively broad, strongly oblique ramp, demarcated from whorl face by an edge. The spire whorls are broad and low. The early whorls have opisthocline axial ribs which weaken during ontogeny and finally change to strengthened growth lines. The ribs or strengthened growth lines run prosocyrt opisthocline from edge near ramp to base, and curve strongly backward at the edge that demarcates the ramp. The course of the growth lines is not visible on the ramp. Spiral ornament is absent. The base is strongly convex and smooth except of growth lines. The aperture is narrow and acute adapically. It has a short, oblique siphonal canal.

**Relationships.** Ceritella pupoides (d'Orbigny) sensu Fischer and Weber (1997) is slenderer, has a higher spire, and lacks axial ribs. Ribs are also absent in Ceritella lauretana Guirand and Ogérien, C. dolium Loriol (both sensu Cossmann 1895), Orthostoma granum Loriol in Loriol and Pellat (1866), and Acteonina lauretana Guirand and Ogérien sensu Loriol in Loriol and Bourgeat (1886– 1888). Acteonina terebra Étallon sensu Loriol in Loriol and Bourgeat (1886–1888) is slenderer, lacks an oblique ramp, has a higher spire and its axial ribs are not reduced during ontogeny. Ceritella (Ceritellopsis) parvula (F. A. Roemer) sensu Huckriede (1967) has a horizontal ramp and therefore a gradate spire; it has fewer axial ribs that are stronger and not bent backward adapically.

Ceritella sp. 1 Plate 4: figs 6–8

**Material.** Nine specimens from Saal (collection Lang), one of which is illustrated herein: SNSB-BSPG 2021 XV 7.

**Description.** The illustrated specimen is 3.2 mm high. The shell is moderately slender with high, acute spire. The whorls are distinctly broader than high. The sutures are impressed. The whorls have a strongly inclined ramp, separated from whorl face by a spiral cord. The growth lines are strengthened and weakly prosocyrt from ramp to base. The base and aperture are as in *Ceritella convexa* sp. nov.

**Relationships.** The shell of *Ceritella convexa* sp. nov. is broader than that of *Ceritella* sp. 1. *Ceritella convexa* sp. nov. has axial ribs whereas *Ceritella* sp. 1 lacks ribs. *Ceritella lorteti* Loriol sensu Cossmann (1895) has a higher last whorl in relation to the spire and its ramp is less pronounced. *Ceritella pupoides* (d'Orbigny) sensu Fischer and Weber



Plate 4. (1-5) Ceritella convexa sp. nov. (1-2) Paratype, SNSB-BSPG 2021 XV 8, Saal (collection Lang), lateral views, height 4.3 mm.
(3-5) Holotype, SNSB-BSPG 2021 XV 9, Saal (collection Lang); (3-4) lateral views, height 3.5 mm; (5) apical view, width 1.8 mm.
(6-8) Ceritella sp. 1, SNSB-BSPG 2021 XV 7, Saal (collection Lang); (6-7) lateral views, height 3.2 mm; (8) apical view, width 1.3 mm.

(1997) and Actaeonina lauretana Guirand and Ogérien. sensu Loriol in Loriol and Bourgeat (1886–1888) have a distinctly stouter shell and a less pronounced ramp. Actaeonina miliola d'Orbigny sensu Loriol in Loriol and Bourgeat (1886–1888) is broader and lacks a ramp entirely.

#### Family Nerineidae Zittel, 1873

#### Genus Nerinea Deshayes, 1827

**Type species.** *Nerinea mosae* Deshayes, 1827; Oxfordian; France.

#### Nerinea donosa sp. nov.

https://zoobank.org/0351A026-965F-4B49-8FEB-714BAEF2B779 Plate 5: figs 1-5

2017 - Nerineoidea Nr. 7 - Gründel: 33, pl. 14D.

**Derivatio nominis.** Anagram of Latin *nodosa*, referring to the subsutural rows of nodes.

Holotype. SNSB-BSPG 2021 XV 11, collection Lang.

Locus typicus. Quarry Saal near Kelheim. Stratum typicum. Upper Kimmeridgian.

**Paratypes.** Six incomplete or juvenile specimens from Saal: five specimens collection Lang (SNSB-BSPG 2021 XV 10, 13, 168–170), one specimen collection Keupp (SNSB-BSPG 2021 XV 12).

Additional material. Three specimens without type status from Saal (collection Lang).

**Diagnosis.** Shell moderately slender; subsutural row of strong nodes forming distinct ramp; spire gradate; transition from whorl face to base at distinct spiral, crest-like cord; base convex, with narrow umbilicus; aperture with two columellar plaits, one strong parietal and partly a palatal plait; with siphonal canal.

**Description.** The largest specimen is 20 mm high. The shell is moderately slender with relatively rapidly increasing whorls. The whorls are more than twice as wide as high. The whorls are ornamented with a subsutural row of strong nodes (8–10 nodes per whorl) occupying 1/2 to 2/3 of whorl height. The nodes demarcate the distinct ramp producing a gradate spire. The suture is accentuated by the ramp. The transition from whorl face to base is marked by a distinct, crest-like spiral cord which is not nodular, and is covered by the following whorls in spire whorls. The incompletely



Plate 5. (1-5) Nerinea donosa sp. nov. (1) Paratype, SNSB-BSPG 2021 XV 10, Saal (collection Lang), lateral view, height 18 mm.
(2-4) Holotype, SNSB-BSPG 2021 XV 11, Saal (collection Lang);
(2) lateral view, height 8.8 mm; (3) base, width 4.5 mm; (4) last whorl, height 4.5 mm. (5) Paratype, SNSB-BSPG 2021 XV 11, Saal (collection Keupp), lateral view, height 20 mm.

preserved aperture is narrow and has a siphonal canal. It has two columellar plaits, 1-2 parietal plaits and in some specimens a palatal plait. If two columellar plaits are present, the adapical one is weaker as the abapical. The outer lip is not preserved. The base is distinctly convex.

**Relationships.** Nerinea mosae Deshayes, 1827 has weaker subsutural nodes and lacks a strong spiral cord at the transition to the base. Nerinea (respectively Ptygmatis) nogreti Guirand & Ogérien, 1865 has, according to these authors and according to Loriol in Loriol and Bourgeat (1886–1888), a similar shape but is larger and lacks a nodular ornament. *Cerithium kelheimense* Schlosser, 1882 lacks plaits and a spiral cord at the transition to the base. *Itieria* (respectively *Nerinea*) *moreana* d'Orbigny sensu Buvignier (1852) and Schlosser (1882) has a higher last whorl in relation to the spire height and it lacks a spiral cord at the transition to the base. *Nerinea margaritifera* d'Archiac, 1843 and *Itieria multicoronata* Zittel, 1873) lack a spiral cord at the transition to the base. *Nerinea catalloi* Gemmellaro, 1870 is broader and stouter and has a higher last whorl in relation to the spire.

#### Genus Acrostylus Cossmann, 1896

Type species. Nerinea trinodosa Voltz, 1836; Portlandien.

Acrostylus? sp. 1 Plate 6: figs 1, 2

v2017 - Nerineoidea Nr. 1 - Gründel: 33, pl. 13, fig. 13 C.

**Material.** Two specimens from Saal, collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 73).

**Description.** The present material is poorly preserved and only fragmentary. The illustrated specimen is 23 mm high. The whorl face is weakly concave. The whorls are ornamented with a subsutural row of knobs and two strong, knobby spiral cords below it, followed by one or two weak spiral cords and a strong, knobby suprasutural spiral cord. The knobby sub- and suprasutural cords form a bulge on which the suture is situated. The base is flat and its



Plate 6. (1-2) Acrostylus? sp. 1., SNSB-BSPG 2021 XV 73, Saal (collection Lang), (original to Gründel 2017, fig. 13 C); (1) section of shell, height 23 mm; (2) lateral view, height 23 mm.

transition to the whorl face is angulated. A distinct umbilicus is present. The aperture is rhomboid. It is unclear whether a siphonal canal is present. The aperture has a parietal, a columellar, and a palatal plait.

Relationships. Nerinella subscalaris Münster sensu Schlosser (1882) has bulges that lack knobs and lacks an umbilicus. Nerinea danubiensis Zittel sensu Schlosser (1882) has lower whorls, the bulges have stronger knobs, and it lacks distinct spiral cords between the bulges. Nerinella subtricincta (d'Orbigny) sensu Fischer and Weber (1997) has an almost straight whorl face, its bulges are weaker and only weakly knobby (Fischer and Weber 1997, p. 54: "faiblement granuleux"). Nerinella (cf.) laufonensis Thurmann sensu Loriol in Loriol and Koby (1895) and Hägele (1997) is slenderer and has weaker bulges. Nerinea chantrei Loriol and Nerinea ornata d'Orbigny, both sensu Loriol in Loriol and Bourgeat (1886-1888), have a slenderer shell with higher and more concave whorls. Nerinea hoheneggeri Peters sensu Zittel (1873) has a slenderer shell, more spiral cords on the whorl face between the bulges, and lacks an umbilicus. Nerinea roemeri Philippi sensu Goldfuss (1844) is slenderer, has higher whorls; its whorls are not concave and the bulges are rather weak.

#### Genus Endoplocus Cox, 1954

**Type species**. Actaeon staszycii Zeuschner, 1849; Tithonian; Poland.

**Remarks.** Cox (1954) reported that this genus is characterized by having 4–5 plaits (2 columellar, 1 parietal, and 1–2 palatal plaits). The present species assigned to *Endoplocus* shows only three plaits: two columellar and one parietal plait. The apparent lack of palatal plaits could be due to preservation.

#### Endoplocus acutus sp. nov.

https://zoobank.org/3FF77922-9E93-4BA4-9B75-0176AAE61CA4 Plate 7: figs 1-7

part?1898 – *Phaneroptyxis clymene* d'Orbigny – Cossmann: 16, questionable pl. 8, fig. 35, non pl. 1, figs 23, 24.

**Derivatio nominis.** Latin *acutus* – acute; because of the acute spire.

Holotype. SNSB-BSPG 2021 XV 14 (collection Lang). Locus typicus. Saal quarry near Kelheim.



Plate 7. Endoplocus acutus sp. nov. (1–3) Holotype, SNSB-BSPG 2021 XV 14, Saal (collection Lang); (1) apical whorls in lateral view, height 11 mm; (2) lateral view, height 29 mm; (3) aperture, height 14 mm. (4) Paratype, SNSB-BSPG 2021 XV 15, Saal (collection Keupp), lateral view, height 18.5 mm. (5) Paratype, SNSB-BSPG 2021 XV 16, Saal (collection Lang), base, width 11 mm. (6–7) Endoplocus acutus sp. nov. var., paratype, SNSB-BSPG 2021 XV 17, Saal (collection Lang); (6) lateral view, height 23 mm; (7) last whorl, height 10 mm.



Plate 8. Endoplocus inflatus sp. nov. (1-3) Holotype, SNSB-BSPG 2021 XV 20, Saal (collection Lang); (1) lateral view, height 16 mm;
(2) aperture, height 6.5 mm; (3) base, width 9 mm. (4) Paratype, SNSB-BSPG 2021 XV 108, Saal (collection Lang), juvenile specimen showing ramp on early whorls, height 9 mm.

Stratum typicum. Upper Kimmeridgian.

**Paratypes.** Thirteen specimens from Saal, collection Lang and Keupp: SNSB-BSPG 2021 XV 15–19, 171–178.

Additional material. Three specimens from Saal, without type status (two specimens collection Neubauer, one specimen collection Lang).

**Diagnosis.** The shell has a high, multi-whorled, acute spire; last whorl of large specimens distinctly lower than spire; last whorl somewhat constricted (slightly pupoid outline); no ornament visible.

**Description.** The holotype is 29 mm high. The shell has a high, multi-whorled, acute spire. The whorls are low with a slightly convex to straight whorl face. The sutures are somewhat impressed. In some specimens, a narrow ramp accentuates the sutures. The whorls lack visible ornament. The last whorl of large specimens is slightly tapering in an abapical direction resulting in a slightly pupoid shell shape. The last whorl is distinctly lower than the spire. The transition from whorl face to the strongly convex base is fluent and evenly rounded. The base is smooth and has a distinct umbilicus that is surmounted by an indistinct cord. The aperture is narrow. The inner lip has a strong parietal and two columellar plaits. The adapical columellar plait is weaker than the abapical one.

Remarks. The specimen illustrated by Cossmann (1898, pl. 8, fig. 35; specimens in pl.1, figs 23, 24 dif-

fer more strongly) as *Phaneroptyxis clymene* d'Orbigny from the Rauracien resembles *Endoplocus acutus* sp. nov. However, the specimen illustrated by Cossmann (1898) differs from *Endoplocus acutus* sp. nov. by having a slenderer shell, a higher last whorl in relation to the spire height, and by having only a single columellar plait. Fischer and Weber (1997) illustrated the holotypes of *Phaneroptyxis moreana* (d'Orbigny, 1851) (Fischer and Weber 1997, pl. 13, fig. 4) and of *P. clymene* (d'Orbigny, 1851) (Fischer and Weber 1997, pl. 13, fig. 5). These taxa were interpreted to represent a single variable species by Fischer and Weber (1997), both differ significantly from *Endoplocus acutus* sp. nov. and are not conspecific with the specimen illustrated by Cossmann (1898, pl. 8, fig. 35) as *Phaneroptyxis clymene*.

Endoplocus acutus sp. nov. var. (Plate 7: figs 6, 7): Two specimens from Saal agree with *E. acutus* in shell shape, size (specimen illustrated in Plate 7: figs 6, 7 is 23 mm high), and in the morphology of the plaits. However, these specimens have a subsutural spiral cord which accentuates the sutures. These specimens are considered to represent a variant of *Endoplocus acutus* sp. nov.

**Relationships.** Endoplocus staczycii (Zeuschner, 1849) has a stouter shell, more strongly convex whorls, deeper sutures, and the last whorl is higher in relation to spire height. Endoplocus staczycii sensu Hägele (1997) shows the same differences. Endoplocus staczycii is very variable according to Peters (1855). The specimen illustrated by Peters (1855, pl. 2, fig. 6) most closely resembles Endoplocus stactus sp. nov.. However, this specimen has a stouter shell, a less slender spire, and the last whorl is higher in relation to spire height. Nerinea clymene d'Orbigny sensu Gemmellaro (1870, pl. 4, fig. 4, 5; non fig. 3) is much larger and has deep sutures that are accentuated by a narrow ramp; its shell is slenderer and has higher whorls.

#### Endoplocus inflatus sp. nov.

https://zoobank.org/03411E75-CB23-4ADB-B736-262D700F4E2E Plate 8: figs 1-4

**Etymology.** Latin *inflatus* – inflated, according to the inflated last whorls of large specimens.

Holotype. SNSB-BSPG 2021 XV 20, Lang collection.

Locus typicus. Saal Quarry near Kelheim.

Stratum typicum. Upper Kimmeridgian.

**Paratypes.** Seven specimens from Saal, collections Lang and Keupp: SNSB-BSPG 2021 XV 21, 22, 108, 179–182.

Additional material. Two specimens from Saal, without type status (one specimen collection Neubauer, one specimen collection Lang).

**Diagnosis.** Spire conical, acute, coeloconoid, consisting of numerous whorls with low whorl face; last whorl of larger specimens inflated with convex whorl face; nodes absent.

**Description.** The holotype is 15 mm high. The early teleoconch is conical, acute, coeloconoid, slender, and consists of numerous very low whorls. A relatively well-preserved juvenile paratype (Plate 8: fig. 4) has a flat ramp demarcated by a distinct angulation. Later whorls

increase more rapidly in width producing coeloconoid shape. The last part of the last whorl is deflected downward so that the height of the whorl increases more rapidly. The transition from whorl face to the strongly convex base is evenly rounded. The last whorl is strongly convex and somewhat inflated. The shell is smooth, except in rare cases (due to preservation?) with a narrow subsutural spiral furrow. The base is narrowly phaneromphalous. The aperture is strongly damaged in all specimens; it has a strong parietal plait and two columellar plaits (adapical one weaker).

**Relationships.** *Phaneroptyxis proboscidea* Cossmann, 1898 has an even more inflated last whorl and is ornamented with nodes. *Phaneroptyxis* cf. *nogreti* (Guirand and Ogérien) sensu Hägele (1997) has fewer and higher whorls, a narrow ramp that accentuates the sutures, and its last whorl is not inflated. *Phaneroptyxis obtusiceps* Zittel sensu Hakobjan (1962) has a nodular ornament. *Endoplocus staczycii* (Zeuschner) sensu Wieczorek (1998) is similar but is slenderer, its last whorl is not as inflated, and its whorls are higher. According to Wieczorek (1998) this species is very variable. *Nerinea clymene* d'Orbigny sensu Gemmellaro (1870: pl. 4, fig. 3, non figs 4, 5) has a higher and less inflated last whorl and higher spire whorls.

#### Family Ptygmatididae Pchelintsev, 1960 Subfamily Ptygmatidinae Pchelintsev, 1960

Genus Ptygmatis Sharpe, 1850

**Type species.** *Nerinea bruntrutana* Thurmann, 1832; Oxfordian; Switzerland.

#### Ptygmatis mandelslohi (Bronn, 1836)

Plate 9: figs 1-5

- \*1836 Nerinea mandelslohi sp. nov. Bronn: 553, pl. 6, fig. 26. 1844 – Nerinea mandelslohi Bronn – Goldfuss: 39, pl. 175, fig. 4. non v1881–1884 – Nerinea mandelslohi Bronn – Quenstedt: 535, pl. 206, figs 11, 12.
- ?1882 Ptygmatis mandelslohi Bronn Schlosser: 81, pl. 11, fig. 14.
- 1893 Ptygmatis bruntrutana (Thurmann), Zittel Loriol in Loriol and Lambert: 25, pl. 2, figs 6, 7.
- ?part1979 Ptygmatis bruntrutana (Thurmann, 1832) Wieczorek: 324, pl. 8, figs 2–5, 7; textfig. 10, 14, 19–21.
- 1997 Nerinea bruntrutana (Thurmann, 1832) Hägele: 128, fig. p. 128 upper left.
- part 1997 Cryptoplocus depressus (Bronn ex Voltz, 1836) -Fischer and Weber: 41, pl. 10, fig. 5 (non fig. 4).
- 2017 Nerineoidea Nr. 6 Gründel: 33, pl. 14C.

**Material.** Four specimens from Saal: three specimens, collection Lang, two of which are illustrated (SNSB-BSPG 2021 XV 27, 28), one specimen collection Keupp, SNSB-BSPG 2021 XV 29, and one additional questionable specimen from Saal (collection Lang).



Plate 9. *Ptygmatis mandelslohi* (Bronn, 1836). (1–4) SNSB-BSPG 2021 XV 27, Saal (collection Lang); (1) base, width 15 mm; (2–3) lateral views, height 35 mm; (4) last whorl with aperture, height 12 mm (original to Gründel 2017, fig. 14 C). (5) SNSB-BSPG 2021 XV 28, Saal (collection Lang), last whorl with aperture, width 10 mm.

**Description.** The illustrated specimen (Plate 9: figs 1–4) is 35 mm high. The shell is moderately wide. The early whorls increase more rapidly in width than later ones producing slightly cyrtoconoid outline. The whorls are much wider than high. The whorl face is straight to slightly concave. The sutures are hardly impressed but visible. The whorls have a weak subsutural spiral furrow; apart from that, the whorls are smooth. The base is weakly convex and demarcated from whorl face by a sharp, almost rectangular edge. The base is smooth and narrowly phaneromphalous. The aperture is rhomboid. The inner lip has a strong parietal plait and two columellar plaits. The adapical columellar plait is visible.

**Remarks.** According to Fischer and Weber (1997), *P. mandelslohi* is a junior synonym of *P. bruntrutana*. The specimen figured as *P. bruntrutana* by Fischer and Weber

(1997, pl. 10, fig. 6) is slenderer and has higher whorls than *Ptygmatis mandelslohi*. Regarding these characters, this specimen agrees with *Nerinea bruntrutana* as illustrated and described by Thurmann and Étallon (1861–1864).

The cyrtoconoid shape (produced by slower increase in width during ontogeny) is particularly characteristic of *P. mandelslohi*. This character is absent in most otherwise similar species. However, it is commonly unclear whether the lack of a cyrtoconoid shape is real or has not been recognized (e.g., due to preservation). This makes the differentiation of *P. mandelslohi* from similar species difficult. Otherwise similar species that also have a cyrtoconoid shape may have an entirely different plait-pattern in the aperture, i.e., having only a single, strong parietal plait as is typical for the genus *Cryptoplocus* (for instance *Cryptoplocus picteti* Gemmellaro, 1870: 39, pl. 6, fig. 8). As a consequence, a correct generic assignment of such species is impossible if the plait-pattern is unknown.

**Relationships.** *Cryptoplocus depressus* (Voltz, 1836) is distinctly larger, has whorls that are regularly increasing in width so that the shell is not cyrtoconoid, a wider umbilicus, and only a single parietal plait. *Ptygmatis carpathica* Zeuschner sensu Zeuschner (1850) and Zittel (1873) has a distinct bulge at the transition from whorl face to base, a wider umbilicus, and a weakly concave whorl face. *Ptygmatis carpathica* (Zeuschner) and *P. salomoniana* Cotteau, both sensu Loriol in Loriol and Lambert (1893), are slenderer, have a distinct bulge at the transition from whorl face to base, and a more or less distinctly concave whorl face.

Ptygmatis carpathica (Zeuschner) sensu Gemmellaro (1870) shows similar differences. Moreover, it is distinctly larger and the abapical spiral bulge is visible distinctly above the suture. Nerinea carpathica Zeuschner sensu Thurmann and Étallon (1861–1864) is slenderer and has a concave whorl face. Cryptoplocus depressus (Bronn ex Voltz, 1836) sensu Fischer and Weber (1997: pl. 10, fig. 5, non fig. 4) is slenderer and has higher whorls. Cerithium climax Zittel sensu Blaschke (1911) has more and lower whorls; its transition to the base is seemingly more strongly rounded. Ptygmatis submirabilis Pchelintsev, 1965 is larger and slenderer, its spiral bulge at the transition from whorl face to base is more pronounced and visible above the suture.

#### Ptygmatis? tornata (Quenstedt, 1852)

Morphotype 1 Plate 10: figs 1–10

\*1830–1833 – Nerinea terebra Schübler – Zieten: 48, pl. 36, fig. 2.
 \*1836 – Nerinea incavata sp. nov. – Bronn: 553, pl. 6., fig. 22.

- 1836 Nerinea terebra Schübl. Bronn: 557.
- v\*1852 Nerinea tornata Quenstedt: 429, pl. 34, fig. 36.
- 1852 Nerinea constricta Quenstedt: pl. 34, fig. 32.
- 1858 Nerinea tornata Quenstedt: 757, pl. 94, figs 12, 13.
- v 1881–1884 Nerinea tornata Quenstedt: 527, pl. 205, figs 67, 68.
- v1881–1884 Nerinea cochlearis Quenstedt: 556, pl. 207, figs 14, 15.
- 1901 Nerinea tornata Quenst. Geiger: 295.

- 1997 Nerinella tornata (Quenstedt, 1852) Hägele: 132, fig. p. 132 lower left.
- 1997 Nerinella partschi (Peters, 1855) Hägele: 132, pl. 13, fig. 2; fig. p. 132 upper left.
- 2017 Nerineoidea Nr. 3 Gründel: 33, pl. 13E.

Lectotype designation. Quenstedt (1852) based Nerinea tornata on a specimen from Nattheim (Quenstedt 1852, pl. 34, fig. 36). This illustration is somewhat schematic. It is probably the same specimen that was illustrated by him elsewhere (Quenstedt 1881–1884, pl. 205, fig. 67) and that is also illustrated herein (Plate 10: figs 8, 9). This specimen is herewith designated as the lectotype.

**Material.** Thirty-one specimens representing the typical form from Saal (collection Lang) of which five specimens are illustrated (SNSB-BSPG 2021 XV 32–36) and seven specimens representing the morphotype 2 from Saal: five specimens collection Lang of which two are illustrated (SNSB-BSPG 2021 XV 37, 38), one specimen collection Keupp (SNSB-BSPG 2021 XV 39), one specimen collection Neubauer); three specimens from Nattheim: *Nerinea tornata*, Tübingen (collection Quenstedt); two fragments from Nattheim: *Nerinea cochlearis*, Tübingen (collection Quenstedt).

Description. The shell is very slender; a fragmentary specimen (incomplete ad- and abapically) is 62 mm high; the shell illustrated in Plate 10: fig. 6 is ca. 50 mm high. If the assignment of the specimen illustrated in Plate 10: fig. 1 is correct, then the juvenile shell is very long, slender, and consists of numerous whorls. The whorls are generally wider than high but the height/width ratio varies. The whorls increase only slowly in width. The whorl face is concave. The only recognizable ornament is a subsutural bulge forming the whorl periphery. The subsutural bulge forms a sharp crest and ramp in well-preserved specimens. The whorls have a subsutural bulge bordered by the adapical suture. The base is flat, smooth and joins the whorl face at an angular edge. The base has a narrow umbilicus. The growth lines are generally opisthocline and curve backward strongly immediately below the adapical suture. The damaged aperture has a rhomboid outline and an oblique siphonal canal, two columellar plaits, one parietal, and one palatal plait.

#### Ptygmatis? tornata (Quenstedt, 1852)

Morphotype 2 Plate 10: figs 11, 12

2017 - Nerineoidea Nr. 2 - Gründel: 33, pl. 13D.

**Note.** In some specimens, the ramp is not bordered by a sharp crest, but by a more or less pronounced band that is demarcated from the concave part of the whorl face by another edge; there seem to be transitions between both varieties.

**Remarks.** Two poorly preserved fragments of *Nerinea cochlearis* Quenstedt, 1881–1884 are present in the Quenstedt collection (Tübingen), both probably representing juveniles. Shape and ornament match the description



Plate 10. Ptygmatis? tornata (Quenstedt, 1852). (1–10) Ptygmatis? tornata (Quenstedt, 1852) morphotype 1. (1) SNSB-BSPG 2021 XV 32; Saal (collection Lang); lateral view, height 14 mm. (2) SNSB-BSPG 2021 XV 33, Saal (collection Lang), lateral view, height 65 mm (original to Gründel 2017, fig. 13 E). (3–4) SNSB-BSPG 2021 XV 34, Saal (collection Lang); (3) lateral view, height 20 mm; (4) base, width 7 mm). (5) SNSB-BSPG 2021 XV 35, Saal (collection Lang), lateral view, height 19 mm. (6–7) SNSB-BSPG 2021 XV 36, Saal (collection Lang); (6) lateral view, height ca. 50 mm; (7) aperture, width 15 mm. (8–9) Lectotype; University Tübingen (collection Quenstedt), Nattheim, shell in lateral view, height ca. 30 mm (original Quenstedt 1881–1884, pl. 205, fig. 67). (10) University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 45 mm (original Quenstedt 1881–1884, pl. 206, fig. 68). (11–12) Ptygmatis? tornata (Quenstedt, 1852) morphotype 2; (11) SNSB-BSPG 2021 XV 37, Saal (collection Lang), lateral view, height 29 mm. (12) morphotype 2, SNSB-BSPG 2021 XV 38, Saal (collection Lang), lateral view, height 42 mm (original 2017, fig. 13 D).

of *Ptygmatis tornata* given above, as does the number and position of the plaits. Their base is umbilicated. However, these two specimens are too poorly preserved for a safe identification as *Ptygmatis tornata*.

It remains unclear whether *N. terebra* Schübler in Zieten and *N. incavata* Bronn are conspecific with *N. tornata* Quenstedt. At least for *N. terebra* this is likely, because this species was described from Nattheim as is also the case for *Nerinea cochlearis*. Both, *N. terebra* and *N. incavata*, would have priority over *N. tornata* Quenstedt.

**Relationships.** Numerous similar species have been described which are hardly distinguishable based on study of the literature alone. In the following, differences to middle Oxfordian and to early Tithonian taxa are discussed.

Nerinea mandelslohi Bronn sensu Zeuschner (1850) has higher whorls that are more rapidly increasing in width. Nerinea suevica Quenstedt sensu Schlosser (1882) has higher whorls, and only 3 apertural plaits are known for this species. Aptyxis paradoxa Schlosser, 1882 lacks plaits and also shows other differences. Bactroptyxis cassiope d'Orbigny sensu Fischer and Weber (1997) has higher whorls, its whorl face is less concave and it has less pronounced bulges; its sutures are situated on the bulge. Nerinea partschi Peters, 1855 closely resembles Ptygmatis? tornata but has higher whorls and lacks an open umbilicus. Nerinea gosae Roemer sensu Goldfuss (1844) resembles the present material in shell shape but its sutures are situated on the bulge. The latter is also the case in Nerinea acteon d'Orbigny sensu Cossmann (1898), Nerinea baillei Maire, 1913, and N. castor d'Orbigny sensu Maire (1927). Nerinea bruntrutana Thurmann sensu Goldfuss (1844) resembles Ptygmatis tornata morphotype 2 in having a band-like, broadened bulge; however, its whorls increase more rapidly in width so that its shape is more broadly conical and it has two palatal plaits.

#### Ptygmatis nodosa (Voltz, 1836)

Plate 11: figs 1-15

- \*1836 Nerinea nodosa (Voltz) Voltz: 542.
- 1836 Nerinea nodosa Voltz Bronn: 561, pl. 16, fig. 9.
- 1851 Nerinea nodosa Voltz d'Orbigny: 95, pl. 254, figs 3-5.
- \*1852 Nerinea calypso d'Orbigny d'Orbigny: 136, pl. 274, figs 4–6.
- \*1852 Nerinea elegans Thurm. d'Orbigny: 146, pl. 278, figs 4-6.
- ?1870 Nerinea plassenensis Pet. Gemmellaro: 25, pl. 4, figs 14, 15.
- 1889 Nerinea nodosa Voltz Loriol in Loriol and Koby: 32, pl. 4, figs 5–11.
- 1997 *Ptygmatis nodosa* (Bronn ex Voltz, 1836) Fischer and Weber: 37, pl. 11, figs 4–6.
- 1997 *Ptygmatis nodosa* (Bronn ex Voltz, 1836) Fischer and Weber: 54.
- ?1997 Nerinella elegans (Bronn ex Thurmann, 1836) Fischer and Weber: 58, pl. 8, fig. 5.
- 2017 Nerineoidea Nr. 8 Gründel: 33, pl.15A.

**Material.** 142 fragments and juvenile specimens from Saal: 138 specimens collection Lang, of which eight are illustrated (SNSB-BSPG 2021 XV 40–45, 47, 48), four specimens collection Keupp (SNSB-BSPG 2021 XV 46, 49–51).

Description. The present material consists of fragments of larger specimens and juvenile specimens. The largest specimen is 32 mm high. The apical whorls are not preserved. The shell is slender with a somewhat variable apical angle. The ornament consists of a nodular adapical bulge forming a narrow ramp. The suture is situated on the adapical portion of the bulge. The nodular spiral cord (in some specimens only very weakly developed) is mostly close to the abapical suture or - more rarely - about half way between adapical bulge and abapical suture. The number of nodes per whorl is strongly variable (only in part due to preservation). In few specimens, an additional weakly nodular spiral cord is present between the nodular spiral cord and the adapical bulge. The base is weakly convex with a pronounced spiral cord at the almost rectangular transition to the whorl face. This bordering spiral cord is sometimes nodular. The base is covered with spiral cords. The aperture has a rhomboid outline and a distinctly oblique siphonal canal. The plait pattern is only visible in few specimens. It consists of one or two columellar plaits, one strong parietal plait, while a palatal is plait very rarely visible - perhaps due to the preservation.

**Remarks.** In the present material, some specimens have one and others have two columellar plaits. The references listed in the chresonymy and synonymy list above probably refer to material from older strata (Oxfordian, with the exception of Gründel 2017). These references note the presence of four plaits (two columellar plaits, one parietal and one palatal plait).

Relationships. See Remarks for Eunerinea sp. 1 for relationships with Ptygmatis nodosa. Ptygmatis nodosa Voltz sensu Cossmann (1898) has higher whorls, its whorl face is more concave, its basal spiral rib is not as pronounced and widened, and it has three spiral cords on the base. Nerinea danubiensis Zittel sensu Schlosser (1882) has more rapidly increasing whorls in width, its second nodular spiral cord is situated directly above the suture and forms the basal spiral cord at the transition from whorl face to base instead of having a non-nodular bulge/cord at this position. Moreover, this spiral cord is stronger than the subsutural row of knobs. Nerinea plassenensis Peters, 1855 has a more convex base and stronger subsutural knobs and therefore a more concave whorl face. In Nerinea nodosa Voltz sensu Thurmann and Étallon (1861-1864), the spiral cord at the transition from whorl face to base is distinctly knobby. Ptygmatis nodosa Voltz sensu Maire (1913, 1927) has fewer but larger subsutural knobs, the edge from whorl face to base is at least partly knobby (Maire emphasized the great variability of this species), and it has some spiral cords on the base. Nerinea paronae Stefano, 1884 has more and smaller subsutural knobs, more weak, knobby spiral cord on the whorl face, knobs on the edge demarcating whorl face and base and it has spiral cords on the base.



Plate 11. *Ptygmatis nodosa* (Voltz, 1836). (1–3) SNSB-BSPG 2021 XV 40, Saal (collection Lang); (1) lateral view, height 22 mm; (2) last whorl with aperture, width 6.6 mm; (3) base, width 6.6 mm. (4–5) SNSB-BSPG 2021 XV 41; Saal (collection Lang); (4) lateral view, height 9 mm; (5) base, width 3.5 mm. (6) SNSB-BSPG 2021 XV 42, Saal (collection Lang), aperture, width of whorl 3.7 mm. (7–8) SNSB-BSPG 2021 XV 43, Saal (collection Lang); (7) lateral view, height 11.5 mm; (8) last two whorls in lateral view, width 4.2 mm. (9) SNSB-BSPG 2021 XV 44, Saal (collection Lang); base, width 6 mm. (10–11) SNSB-BSPG 2021 XV 45, Saal (collection Lang); (10) lateral view, height 16 mm; (11) last whorls in lateral view, width 5.2 mm. (12–13) SNSB-BSPG 2021 XV 46, Saal (collection Lang); (12) lateral view, height 9 mm; (13) apex in lateral view, height 2.9 mm. (14) SNSB-BSPG 2021 XV 47, Saal (collection Lang), lateral view, height 10 mm. (15) SNSB-BSPG 2021 XV 48, Saal (collection Lang), last whorls with aperture, width 7.8 mm.

#### Ptygmatis clio (d'Orbigny, 1852)

Plate 12: figs 1-3

\*1852 - Nerinea clio d'Orbigny - d'Orbigny: 139, pl. 275, figs 3-5.
1886-1888 - Ptygmatis clio d'Orbigny - Loriol in Loriol and Bourgeat: 84, pl. 7, figs 1-3.

1898 – Ptygmatis clio d'Orbigny – Cossmann: 72, pl. 6, figs 18, 19.
1997 – Polyptyxisella clio (d'Orbigny, 1852) – Fischer and Weber: 55, pl. 12, figs 9, 10.

**Material.** Two illustrated specimens (SNSB-BSPG 2021 XV 59, 60) and a questionable one, all from Saal, collection Lang.

**Description.** The largest specimen (Plate 12: fig. 3) is 108 mm high. The shell is slender. The whorl face is straight. The last whorl of the largest specimen has a weak, indistinctly delimited subsutural furrow. The sutures are distinct. The whorls lack visible ornament. The basal edge is pronounced and forms an angular transition to the base. The base is incompletely preserved, and is seemingly smooth with a distinct umbilicus. The aperture is not preserved. A columellar section shows the presence of a parietal, two columellar, and one palatal plaits.

**Remarks.** Fischer and Weber (1997) designated a lectotype (section of a shell, Fischer and Weber 1997: pl. 12, fig. 9) that agrees well with the sectioned shell illustrated herein (Plate 12: figs 1, 2). The lateral view provided by Fischer and Weber (1997: pl. 12, fig. 10) also agrees well with the present material. The specimens illustrated by Fischer and Weber (1997) are from the middle Oxfordian of St. Mihiel, but these authors noted that the species is also present in the Kimmeridgian. The illustration given by d'Orbigny (1852: pl. 275, figs 3–5) deviates more strongly from our specimens: the shell is slenderer and the whorl face is distinctly concave.

**Relationships.** Aptyxiella planata (Quenstedt) sensu Hägele (1997), A. quenstedti Geiger, 1901, and A. ewaldi Geiger, 1901 lack plaits. Cossmannea nantuacensis (d'Orbigny) sensu Fischer and Weber (1997) is much larger, lacks an umbilicus and columellar and parietal plaits. Megaptyxis caucasica Pchelintsev, 1965 has a concave whorl face and more oblique sutures.

#### Ptygmatis? polyspira (Quenstedt, 1884)

Plate 12: fig. 4

v\*1881–1884 – Nerinea polyspira – Quenstedt: 554, pl. 207, fig. 3. 1901 – Aphanoptyxis polyspira Quenstedt – Geiger: 301.

1997 – Aphanoptyxis polyspira (Quenstedt, 1884) – Hägele: 133, fig. p.133, lower left.

**Material.** Quenstedt's (1881–1884) figured specimen (holotype by monotypy) from Nattheim (Tübingen, Quenstedt collection).

**Description.** The specimen consists of 7 whorls and is 32 mm high (apex missing). The shell is moderately slender and the whorls are increasing regularly in width. The sutures are somewhat pronounced by a subsutural bulge. The whorl face is straight and entirely covered by spiral cords (7–8 spiral cords on last whorl). The transition from whorl face to base is angular. The aperture is not preserved, plaits are not visible.

**Remarks.** The studied holotype of *Nerinea polyspira* Quenstedt, 1884 is a poorly preserved specimen. Its systematic and taxonomic position remain unclear because aperture and plaits are unknown.

**Relationships.** Nerinea ursicina Thurmann, 1861 (in Thurmann and Étallon 1861–1864) differs in having a strong adapical bulge, making the whorl face distinctly concave, fewer spiral cords, and four apertural plaits. Nerinea punctata Voltz sensu Bronn (1836) has a narrow but distinct ramp, and only three spiral cords on its whorl face. Nerinella calliope d'Orbigny sensu Cossmann (1898) has 5–6 spiral cords on the whorl face, some of them having fine knobs. Its aperture has three plaits. Nerinella turritella Voltz sensu Cossmann (1898) lacks a bulge and has four strong, knobby spiral cords on the whorl face and additional weaker cords between them. Nerinella cyane Loriol in Loriol & Pellat, 1874 has higher whorls with a smooth portion above the suture.

# *Ptygmatis? ursicina* (Thurmann, 1861 in Thurmann and Étallon 1861–1864)

Plate 12: figs 5-7

- ?1844 Nerinea visurgis Röm. Goldfuss: 44, pl. 176, fig. 6.
- 1852 Nerinea visurgis Roemer, 1836 d'Orbigny: 122, pl. 268, figs 5-7.
- \*1861–1864 Nerinea ursicina Th. Thurmann and Étallon: 103, pl. 8, fig. 50.
- ?1872 Nerinea pseudospeciosa P. de Loriol, 1871 Loriol, Royer and Tombeck: 89, pl. 6, fig. 7.
- 1889 Nerinea ursicina Thurmann Loriol and Koby: 37, pl. 6, figs 1–8.
- 1898 Nerinea ursicinensis Thurmann Cossmann: 37, pl. 3, figs 11, 12.
- 1927 Nerinea ursicinensis Thurmann Maire: 142, pl. 7, figs 15, 16.
- 1997 Cossmannea (Eunerinea) ursicina (Thurmann, 1861) Fischer and Weber: 40, pl. 9, fig. 2.

**Material.** Nineteen juvenile specimens from Saal (collection Lang), of which two are illustrated (SNSB-BSPG 2021 XV 30, 31).

**Description.** The largest specimen from Saal is 9 mm high. The shell is slender to very slender. The whorls are regularly increasing in width. The whorl face is concave, with a strong, sometimes ramp-like bulge. The bulge is formed at the suture by both whorls. The suture is situated somewhat above the middle of the bulge. The whorl face between the bulges is initially ornamented with one spiral cord, later whorls with 4–5 spiral cords: two of these spiral cords may be stronger than the others. The bulges and stronger spiral cords are possibly nodular (unclear



Plate 12. (1–3) Ptygmatis clio (d'Orbigny, 1852). (1–2) SNSB-BSPG 2021 XV 59, Saal (collection Lang); (1) section of fragment, height 21 mm; (2) detail, height 3.7 mm. (3) SNSB-BSPG 2021 XV 60, Saal (collection Lang), lateral view, height 108 mm. (4) Ptygmatis? polyspira (Quenstedt, 1881–1884), holotype, collection University Tübingen (collection Quenstedt); Nattheim, lateral view, height 32 mm (original to Quenstedt 1881–1884, pl. 207, fig. 3. (11–12) Bactroptyxis teres (Münster in Goldfuss, 1844), collection Sauerborn, Nattheim area. (5–7) Ptygmatis? ursicina (Thurmann in Thurmann & Étallon, 1861). (5–6) SNSB-BSPG 2021 XV 30, Saal (collection Lang); (5) last whorl with aperture, height 4 mm; (6) lateral view, height 9.5 mm. (7) SNSB-BSPG 2021 XV 31, Saal (collection Lang), aperture and ornament of base, width 2.5 mm.

due to preservation). The base is flat, with an almost rectangular transition to the whorl face. The transition has a strong, protruding bulge that is largely covered by the following whorls of the spire. The base is densely covered with weak spiral cords. The aperture has an approximately rectangular outline and distinct oblique siphonal canal. The aperture has a single parietal plait, two columellar plaits, and a palatal plait.

**Remarks.** The identity of the present juvenile shells with much larger growing taxa is uncertain (see synonymy list). Thurmann in Thurmann and Étallon (1861–1864) reported that *Nerinea ursicina* has distinct knobs on the bulges and partly also on the spiral cords between the bulges. Such a knobby ornament could not be substantiated for the present material, due perhaps to preservation.

**Relationships.** Differences to *Ptygmatis? polyspira* (Quenstedt, 1881–1884) are herein discussed in the treatment of this taxon. *Nerinea subscalaris* Münster in Goldfuss (1844) has higher whorls in relation to whorl width and it has more oblique sutures. *Nerinea? lafayettensis* Imlay, 1945 has, among other differences, only two spiral cords between the bulges. *Nerinea speciosa* Voltz sensu Maire (1927) has a broader shell with lower whorls and its bulges

are not as much protruding. *Nerinea mariae* d'Orbigny sensu Cossmann (1898) is slenderer and has higher whorls.

#### Genus Bactroptyxis Cossmann, 1896

**Type species.** *Nerinea implicata* d'Orbigny, 1851; Bathonian; France.

#### Bactroptyxis teres (Münster in Goldfuss, 1844) Plate 13: figs 1, 2

\*1844 - Nerinea teres Münster - Goldfuss: 43, pl. 176, fig. 3.

?1997 – Nerinea teres (Münster, 1844) – Hägele: 136, fig. p. 136 lower left, pl. 13, fig. 6.

**Material.** Two specimens from the Nattheim area (collection Sauerborn).

**Description.** A specimen is 28 mm high. The shell is very slender. The sutures are indistinct and hardly recognizable. The whorl face is straight. The ornament is weak (due to preservation?) consisting of four spiral cords on



Plate 13. (1–2) Bactroptyxis teres (Münster in Goldfuss, 1844), from the Nattheim area (collection Sauerborn); (1) last whorl with aperture, height 11 mm; (2) lateral view, height 29 mm. (3–5) Bactroptyxis cf. fasciata (Voltz, 1836), SNSB-BSPG 2021 XV 56, Saal (collection Lang); (3) detail of ornament, width 4.5 mm; (4) lateral view, height 36 mm; (5) aperture, width of whorl 4.6 mm. (6–8) Bactroptyxis? subcochlearis (Münster in Goldfuss, 1844). (6–7) SNSB-BSPG 2021 XV 57, Saal (collection Neubauer); (6) detail of ornament, height 11.5 mm; (7) lateral view, height 55 mm. (8) SNSB-BSPG 2021 XV 58, Saal (collection Lang), lateral view, height 29 mm. (9–10) Bactroptyxis? tricincta (Münster in Goldfuss, 1844). (9) SNSB-BSPG 2021 XV 52, Saal (collection Lang), lateral view, height 48 mm (original to Gründel 2017, fig. 14 B). (10) SNSB-BSPG 2021 XV 52, Saal (collection Lang), detail of shell in lateral view, height 21 mm. (11–16) Bactroptyxis? tricincta (Münster) sensu Quenstedt (1881–1884). (11–12) Collection University Tübingen (collection Quenstedt); Nattheim, lateral view, height 29 mm (original to Quenstedt 1881–1884), pl. 207, fig. 9). (13) SNSB-BSPG 2021 XV 53, Saal (collection Lang), lateral view, height 55 mm. (15–16) SNSB-BSPG 2021 XV 55, Saal (collection Lang); (15) lateral view, height 72 mm; (16) last whorl, width 17 mm.

the whorl face at about same distance to each other. Two spiral cords are situated directly near the sutures, two other cords are in the middle portion of the whorl face. The transition from whorl face to base is angular. The aperture has two columellar, two palatal plaits, and one parietal plait.

**Remarks.** *Bactroptyxis teres* (Münster) sensu Hägele (1997) is probably identical but has three columellar and three palatal plaits according to Hägele (1997).

Relationships. Bactroptyxis? tricincta Goldfuss sensu Quenstedt (1881-1884) is distinctly larger, not as slender and has only three spiral cords (suprasutural spiral cord lacking). Bactroptyxis sp. cf. fasciata (Voltz, 1836) (see below) is very similar to Bactroptyxis teres but has much more distinct spiral cords. However, this could be due to preservation and both taxa could represent a single species. Nerinella bipunctata (Quenstedt) sensu Hägele (1997) has nodular spiral cords and it has only one columellar and one parietal plait. Aptyxiella ewaldi Geiger, 1901 closely resembles Bactroptyxis teres in shape and ornament but lacks plaits in the aperture according to Geiger (1901). Nerinea vallonia Loriol in Loriol and Cotteau (1868) differs by having 7-8 spiral cords on the whorl face and only a weak columellar plait. Aptyxiella inornata d'Orbigny sensu Maire (1913) has an ornament of five spiral cords of unequal strength and lacks plaits in the aperture.

#### Bactroptyxis cf. fasciata (Voltz, 1836)

Plate 13: figs 3-5

?1836 - Nerinea fasciata Voltz - Bronn: 554, pl. 16, fig. 21.

**Material.** One specimen (SNSB-BSPG 2021 XV 56) and one questionable specimen, both from Saal, collection Lang.

**Description.** The bona fide specimen is 36 mm high. The shell is very slender. The whorl face is straight. The sutures are not impressed and only occasionally visible. The ornament is only preserved on the last whorl. It consists of four spiral cords of equal strength that are equally distant from each other. A knobby ornament is absent. An abapical spiral cord, probably representing the bordering spiral cord, is visible above the suture and marks the angular transition to the flat base. Only the inner lip of the aperture is preserved; it shows one parietal plait and two columellar plaits.

**Remarks.** *Nerinea fasciata* sensu Bronn (1836) has the same shell shape as the present species and it has also four spiral cords, which are, however, of unequal strength.

**Relationships.** Bactroptyxis teres (Münster in Goldfuss, 1844) differs from Bactroptyxis cf. fasciata by having four strong spiral cords of equal strength and at equal distances. Bactroptyxis teres (Münster) sensu Hägele (1997) has more and weaker spiral cords of unequal strength. Aptyxiella rupellensis d'Orbigny sensu Pchelintsev (1965) has higher whorls and more spiral cords. Aptyxiella inornata d'Orbigny sensu Maire (1913) has five spiral cords on the whorl face and a subsutural bulge; apertural plaits are not visible. Nerinea quadricincta Münster sensu Maire (1913, pl. 11, fig. 7) has two stronger spiral cords on the

whorl face (unlike in Maire's 1913, p. 93 description) and allegedly additional weak spiral cords that are unrecognizable, and it shows swellings near the sutures. These swellings form bulges on which the sutures are situated.

## Bactroptyxis? subcochlearis (Münster in Goldfuss, 1844)

Plate 13: figs 6-8

- \*1844 Nerinea subcochlearis Münster Münster in Goldfuss: 42, pl. 175, fig. 14.
- 1858 Nerinea subcochlearis Goldfuss Quenstedt: 769, pl. 94, fig. 24.
- v1881–1884 Nerinea subcochlearis Goldf. Quenstedt: 555, pl. 207, figs 12, 13.
- non1997 *Aptyxiella subcochlearis* (Münster, 1844) Hägele: 134, fig. 134 upper right.

**Material.** One relatively large specimen (collection Neubauer) and four fragments (collection Lang), of which two are illustrated (SNSB-BSPG 2021 XV 57, 58) from Saal; two specimens from Nattheim (Tübingen: collection Quenstedt).

**Description.** The large specimen is 55 mm high. The shell is slender. The whorls increase regularly in width. The sutures are hardly recognizable. The whorl face is or namented with two strong spiral cords lacking knobs. The upper spiral cord is in directly subsutural position. The lower spiral cord lies somewhat above the abapical suture. The adapical spiral cord is somewhat stronger than the abapical one. At least on the last whorl, another much weaker spiral cord is intercalated. The base and the aperture are not preserved. The base has a narrow umbilicus.

**Relationships.** In *Aptyxiella nattheimensis* (d'Orbigny) sensu Hägele (1997), the suture lies on a bulge formed by adapical and abapical swelling of neighbouring whorls; its whorl face has two spiral cords. *Nerinea quadricincta* Münster sensu Geiger (1901) has a gradate spire, a subsutural bulge and at least two distinct spiral cords on the whorl face. The ornament reported by Geiger (1901: 293) cannot be seen in the illustration provided by this author. *Nerinea sulcata* Schübler in Zieten 1830 has whorls that are more rapidly increasing in width (conical shape), higher whorls and more distinct sutures. *Nerinea bicostata* Gemmellaro, 1870 has a broader shell and lacks an umbilicus.

#### Bactroptyxis? tricincta (Münster in Goldfuss, 1844) Plate 13: figs 9, 10

- \*1844 Nerinea tricincta Münster Münster in Goldfuss: 42, pl. 176, fig. 1.
- 2017 Nerineoidea Nr. 5 Gründel: 33, pl. 14 B.

Material. One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 52.

**Description.** The specimen is 47 mm high. The apical whorls, aperture, and base are missing. The shell is very slender. The whorl face is concave. The sutures are indistinct. The earliest preserved whorls have three spiral cords: a strong subsutural cord and a pair of closely spaced, somewhat weaker spiral cords below mid-whorl, close to the abapical suture. The area between the upper cord and the lower pair of cords is strongly concave. On late whorls, a fourth, weak spiral cord is intercalated between the upper cord and the lower pair of cords. The subsutural spiral cord is strong and crest-like on the latest preserved whorls. The base has an umbilicus.

**Remark.** The aperture as well as number and arrangement of the plaits are unknown, therfore the generic assignment is doubtful.

#### Bactroptyxis? tricincta (Münster) sensu Quenstedt, 1881–1884

Plate 13: figs 11-16

1844 - Nerinea turritella Voltz - Goldfuss: 43, pl. 176, fig. 5.
1852 - Nerinea nattheimensis sp. nov. - d'Orbigny: 144.
v1881-1884 - Nerinea tricincta Goldfuss - Quenstedt: 555, pl. 207, fig. 9.

**Material.** Three specimens from Saal, collection Lang: SNSB-BSPG 2021 XV 53–55, one specimen from Nattheim (Tübingen: collection Quenstedt).

**Description.** The largest specimen is 72 mm high. The shell is slender. The whorl face is straight. The suture is weakly impressed. The whorls are ornamented with a strong subsutural spiral cord, two somewhat weaker spiral cords at mid-whorl which are close to each other. The adapical cord of this pair is either weaker or both cords have about the same strength. The spiral cords are weakly knobby (knobby ornament indistinct due to preservation). The base is flat. The transition from base to whorl face is sharply angular at a pronounced bordering spiral cord. The base is umbilicated. Other details are not preserved.

**Relationships.** *Bactroptyxis? tricincta* (Münster in Goldfuss, 1844) is smaller. It has four spiral cords on the whorl face. As in the present material, two of these cords are close to each other, of which the adapical one is stronger, and both are close to the abapical suture. *Nerinella subtricincta* (d'Orbigny) sensu Fischer and Weber (1997: 54, pl. 5, figs 21, 22) is slenderer and has two spiral cords at mid-whorl that are distinctly nodular. *Nerinella* cf. *laufonensis* (Thurmann, 1859) and *N. subtricincta* (d'Orbigny, 1850) sensu Hägele (1997) are both slenderer and have higher, more concave whorls, and their nodular ornament is more pronounced.

#### Subfamily Cryptoplocinae Pchelintsev in Pchelintsev & Korobkov, 1960

#### Genus Cryptoplocus Pictet & Campiche, 1861

Type species. Nerinea depressa Voltz, 1836; Kimmeridgian?

Cryptoplocus depressus (Voltz, 1836) Plate 14: figs 1-5

\*1836 – Nerinea depressa Voltz – Voltz: 540.

- 1836 Nerinea depressa Voltz Bronn: 549, fig. 17.
- ?1858 Nerinea depressa Voltz Quenstedt: 765, pl. 94, figs 1, 2.
- 1874 *Trochalia depressa* (Voltz) Sharpe Loriol in Loriol and Pellat: 312, pl. 7, fig. 2.
- v1881-1884 Nerinea depressa Voltz, 1836 Quenstedt: 546, pl. 206, figs 48-53.
- 1898 *Cryptoplocus depressus* Voltz Cossmann: 158, pl. 11, figs 33, 34; pl. 12, figs 3, 4, 7, 11, 12.
- non 1997 Cryptoplocus depressus (Bronn ex Voltz, 1836) Fischer and Weber: 41, pl. 10, figs 4, 5.
- ?1998 Cryptoplocus cf. picteti Gemmellaro, 1864 Wieczorek 316, pl. 1, fig. 5.

**Material.** Seven fragments from Nattheim (Tübingen, collection Quenstedt), three specimens from the vicinity of Nattheim (collection Sauerborn) and three specimens from Saal (collection Lang), one of which illustrated herein (SNSB-BSPG 2021 XV 106).

**Description.** The largest specimen is 96 mm high. The shell is moderately broad. The whorls are regularly increasing in width throughout ontogeny. They are distinctly wider than high. The whorl face is straight. The sutures are not impressed and hardly visible. No ornament is visible on whorl face. The base is weakly convex. The transition from base to whorl face forms a pronounced angular edge. The base has a wide umbilicus that is surmounted by a bulge. The base is otherwise smooth. The aperture is strongly damaged in all studied specimens, only a strong parietal plait is visible.

**Remarks.** Quenstedt's (1881–1884) material of *Cryptoplocus depressus* from Nattheim consists of seven poorly preserved fragments. Their shell shape is mostly not recognizable. The specimen illustrated by Quenstedt (1881–1884: pl. 206, fig. 52) (here: Plate 14: figs 3, 4) is a fragment of 37 mm height. It has a strong parietal plait.

**Relationships.** Differences to *Ptygmatis mandelslohi* are discussed where that species is treated. *Nerinea depressa* Voltz sensu Zeuschner (1850) has a distinct subsutural furrow, and its whorl face has a concave zone in lateral view. *Cryptoplocus depressus* Voltz sensu Yin (1931) is slenderer and has lower whorls. *Ptygmatis meneghini* Gemmellaro sensu Yin (1931) is slenderer and has a suprasutural bulge that is delimited adapically by a furrow. *Nerinea terebra* Schübler in Zieten, 1830 is slenderer, has a bulge at the sutures and its whorl face is concave.

# Cryptoplocus subpyramidalis (Münster in Goldfuss, 1844)

Plate 14: fig. 6

<sup>1844 –</sup> Nerinea subpyramidalis Münster – Münster in Goldfuss: 40, pl. 175, fig. 7.

- 1882 Cryptoplocus subpyramidalis Münster Schlosser: 86, pl. 12, fig. 10.
- ?1931 Cryptoplocus pyramidalis Münster Yin: 66, pl. 7, figs 11–15.

1931 - Cryptoplocus subpyramidalis Münster - Yin: 67, pl. 8, fig. 1.

**Material**. Three specimens from Saal: two specimens collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 61), one specimen collection Keupp: SNSB-BSPG 2021 XV 62).

**Description.** The larger specimen (composed of numerous fragments) is incomplete and is 103 mm high. The shell is conical with regularly increasing whorls. The whorls are very low in relation to their height. The whorl

face is weakly concave. A weak subsutural bulge with narrow ramp accentuates the sutures. No ornament is visible on the whorls. The base is moderately convex. The transition from base to whorl face forms a distinct edge. No other morphological details are preserved.

**Relationships.** Cryptoplocus pyramidalis (Münster in Goldfuss) sensu Yin (1931) and Trochalia subpyramidalis Sharpe sensu Loriol in Loriol and Pellat (1874) lack a subsutural bulge. Nerinea pyramidalis Münster in Goldfuss, 1844 has a distinctly concave whorl face. In Trochalia engeli Geiger sensu Geiger (1901) and Hägele (1997), Nerinea pyramidalis sensu Quenstedt (1881–1884), Peters (1855), Gemmellaro (1870), and Münster in Goldfuss (1844) the bulge is situated above the suture (not subsutural).



Plate 14. (1–5) *Cryptoplocus depressus* (Voltz, 1836). (1–2) Collection Sauerborn, Nattheim area; (1) lateral view, height 78 mm; (2) base, width 29 mm. (3–4) University Tübingen (collection Quenstedt), Nattheim; (3) lateral view, height 37 mm; (4) last whorls with aperture, width 25 mm. (5) SNSB-BSPG XV 106, Saal (collection Lang), columellar section, height 47 mm. (6) *Cryptoplocus subpyramidalis* (Münster in Goldfuss, 1844), SNSB-BSPG 2021 XV 61, Saal (collection Lang), lateral view, height 103 mm.

#### Family Nerinellidae Pchelintsev in Pchelintsev & Korobkov, 1960

#### Genus Nerinella Sharpe, 1850

**Type species.** *Nerinea dupiniana* d'Orbigny, 1842–1843; Lower Cretaceous; France.

#### Nerinella ornata (d'Orbigny, 1852)

Plate 15: figs 1-5

- \*1852 Nerinea ornata d'Orbigny d'Orbigny: 135, pl. 274, figs 1–3. v1881–1884 – Nerinea ornata Orb. – Quenstedt: 528, pl. 205, figs 74, 75.
- 1997 Nerinella subtricincta (d'Orbigny, 1852) Fischer and Weber: 54, pl. 5, figs 21, 22.

**Material.** Two specimens from Nattheim (Tübingen: collection Quenstedt), one specimen certainly representing this species (SNSB-BSPG 2021 XV 72) and a questionable juvenile specimen from Saal (both collection Lang).

**Description.** The specimen illustrated in Plate 15: figs 1–3 is 33 mm high and that in Plate 15: fig. 4 is 18 mm high. The shell is very slender and consists of many whorls. The whorls are high with concave whorl face. The most conspicuous sculptural feature is a bulge lacking knobs (or weakly knobby?) forming the periphery which is formed by two neighbouring whorls. The suture is not clearly visible on this bulge. A weak spiral cord is present directly below the bulge followed by two stronger spiral cords in abapical direction. All spiral cords are knobby. Base and aperture are incompletely preserved. At least one columellar and a parietal plait are present. The aperture seemingly has an abapical canal.

**Remarks.** Fischer and Weber (1997) designated a neotype for *N. ornata* and illustrated it (pl. 5, fig. 22). They considered this species to represent a synonym of *Nerinella subtricincta* d'Orbigny, 1852.

Relationships. Nerinella elatior d'Orbigny juv. sensu Fischer and Weber (1997) has more concave whorls, only a single strong, knobby spiral cord at mid-whorl and a distinctly weaker one above it. Nerinella chantrei Loriol sensu Cossmann (1898) is similar and has the same ornamentation but differs in having higher whorls, the whorl face is more concave, and besides knobby spiral cords it also has smooth ones. Nerinea satagea Loriol in Loriol and Pellat (1874) has a knobby bulge, the spiral cords on the whorls are of approximately equal strength, and the whorls are higher. Nerinea greppini Loriol, 1889 (in Loriol and Koby 1889-1892) has two knobby and two smooth spiral cords. Nerinea sp. sensu Hudleston (1880) has three approximately equally strong knobby spiral cords and its shell is slenderer. Nerinea punctata Quenstedt sensu Fiebelkorn (1893) has higher and more concave whorls; the knobs on the spiral cords are weaker (due to preservation?). Nerinea subscalaris Münster sensu Schlosser (1882) has a stronger bulge (knobby?), a more concave whorl face and two knobby spiral cords. Nerinella subtricincta (d'Orbigny) sensu Hägele (1997) has a weaker but knobby bulge and three equally strong knobby spiral cords. *Nerinea ornata* d'Orbigny sensu Loriol in Loriol and Lambert (1893) is slenderer and has higher whorls and the abapical spiral cord is weakest. *Nerinea fasciata* Voltz sensu Fiebelkorn (1893) has lower whorls that increase more rapidly in width, and it has more spiral cords.

#### Nerinella? subscalaris (Münster in Goldfuss, 1844) Plate 15: figs 6–12

- \*1844 Nerinella subscalaris Münster Goldfuss: 41, pl. 175, fig. 12.
- \*v1852 Nerinea uniplicata Quenstedt: 429, pl. 34, fig. 22.
- ?1852 Nerinea suprajurensis Quenstedt: 429, pl. 34, fig. 24.
- v part1858 *Nerinea punctata* Voltz, 1836 Quenstedt: 767, pl. 94, figs 7–9 (original of fig. 8 seen).
- v1858 Nerinea uniplicata Quenstedt: 766, pl. 94, fig. 6.
- v\*1858 Nerinea suevica Quenstedt: 767, pl. 94, fig. 10.
- v1881-1884 Nerinea suevica Quenstedt Quenstedt: 525, pl. 205, figs 63-64.
- v1881-1884 Nerinea uniplicata Quenstedt: 526, pl. 205, fig. 65.
- v1881–1884 Nerinea subscalaris Goldfuss Quenstedt: 526, pl. 205, fig. 66.
- vpart1881–1884 *Nerinea punctata* Bronn, 1836 Quenstedt: 527, pl. 205, figs 69–73 (original to fig. 73 seen).
- 1997 Cossmannea (Eunerinea) subscalaris (Münster, 1844) Hägele: 130, pl. 12, fig. 6 left, p. 130 fig. lower left.
- 1997 Nerinella suevica (Quenstedt, 1858) Hägele: 132, fig. p. 132 left middle.

**Material.** Thirteen specimens from Nattheim/Rinderberg, eight of which housed at BSPG (SNSB-BSPG 2021 XV 63–70), six specimens Tübingen: collection Quenstedt).

**Description.** A large specimen is 63 mm high. The shell is very slender. The whorls are high and separated by oblique sutures. They have a broad, nearly horizontal ramp that is demarcated from whorl face by a sharp edge forming the periphery. The whorl face is straight, somewhat tapering abapically. The details of the ornament are commonly obscured by poor preservation. The whorls are ornamented by a spiral cord at about mid-whorl. The originals of Quenstedt (1881–1884) show further spiral cords. The transition from whorl face to base is demarcated by a rounded bulge that is covered by the following whorl of the spire whorls. The base is moderately convex. The aperture is elongated, rhomboid with a long, almost vertical canal. The aperture has a strong parietal plait, one somewhat weaker columellar plait, and one palatal plait.

**Remarks.** Quenstedt (1858) erected Nerinea constricta suevica as a subspecies separate from Nerinea suevica that was introduced in the same year and in the same publication. The latter species, Nerinea suevica, is considered to represent a synonym of Nerinella subscalaris (Münster in Goldfuss, 1844) as is indicated in the synonymy list, whereas Nerinea constricta suevica is seen as a nomen dubium herein (see Nerinea constricta dubia Quenstedt).

Relationships. Eunerinea sp. 1 differs from Nerinella? subscalaris by having lower whorls, a row of stronger



Plate 15. (1–5) Nerinella ornata (d'Orbigny, 1852). (1–3) SNSB-BSPG 2021 XV 72, Saal (collection Lang); (1) lateral view, height 33 mm; (2) detail of ornament, height 10 mm; (3) whorl with plait, height 3 mm. (4) University Tübingen (collection Quenstedt), Nattheim, lateral view, height 18 mm (original Quenstedt 1881–1884, pl. 205, fig. 74). (5) University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 14 mm (original to Quenstedt 1881–1884, pl. 205, fig. 75). (6–12) Nerinella? subscalaris (Münster in Goldfuss, 1844). (6–7) SNSB-BSPG 2021 XV 63, Nattheim–Rinderberg; (6) lateral view, height 64 mm; (7) last whorls with aperture, height 38 mm. (8) University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 40 mm (original Quenstedt 1881–1884, pl. 205, fig. 63). (9) University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 30 mm (original Quenstedt 1881–1884, pl. 205, fig. 64). (10–11) Collection University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 30 mm (original to Quenstedt 1881–1884, pl. 205, fig. 64). (10–11) Collection University Tübingen (collection Quenstedt), Nattheim; (10) lateral view, height ca. 38 mm (original to Quenstedt 1881–1884, pl. 205, fig. 66); (11) last whorls with aperture, height ca. 20 mm. (12) Collection University Tübingen (collection Quenstedt), Nattheim, 26 mm, lateral view, height ca. 26 mm (original Quenstedt 1881–1884, pl. 205, fig. 73). (13–15) Nerinella? sp. 1, SNSB-BSPG 2021 XV 78, Saal (collection Lang); (13) lateral view, height 43 mm; (14) whorl with plaits, width 17 mm; (15) detail of ornament, height 17 mm.

nodes at mid-whorl, a less pronounced ramp and a more pronounced spiral cord at the transition from whorl face to base. *Nerinella turriculata* d'Orbigny sensu Cossmann (1898) has higher whorls in relation to their width, lacks a pronounced spiral cord at mid-whorl and also lacks a palatal plait. *Nerinella jollyana* d'Orbigny sensu Cossmann (1898) has four stronger and additional weak spiral cords on the whorl face. *Nerinella subelegans* Étallon sensu Cossmann (1898) has lower whorls and its whorl face is ornamented by alternating weak and strong spiral cords.

Nerinella? sp. 1

Plate 15: figs 13-15

Material. One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 78.

**Description.** The specimen is 45 mm high and has a moderately broad shape. The whorls increase regularly in width. They are distinctly wider than high. The sutures are hardly visible. The whorls are ornamented with three spiral cords. The subsutural spiral cord is the most prominent one. All spiral cords bear small knobs. The largest knobs are on the subsutural spiral cord. In the last whorls, the knobs on the middle and suprasutural spiral cord become weaker. The base is flat and has an angular transition to the whorl face which is demarcated by a spiral cord that is probably not knobby. The growth lines on the base are prosocyrt. The aperture is not preserved. Only a strong palatal plait can be recognized.

**Relationships.** Aphanoptyxis polyspira (Quenstedt) sensu Hägele (1997) has spiral cords of equal strength on the whorl face, the aperture lacks plaits, and the ornament does not become weaker during ontogeny. *Nerinea nodospira* Quenstedt, 1881–1884 has four spiral cords on the whorl face, the knobby ornament is stronger, and the ornament does not become weaker during ontogeny. *Nerinea punctata* Voltz sensu Bronn (1836) has a weak ramp so that the whorls are well separated from each other and its ornament does not become weaker during ontogeny.

#### Family Eunerineidae Kollmann, 2005

#### Genus Eunerinea Cox, 1947

**Type species.** Nerinea castor d'Orbigny,1852; middle Oxfordian; France.

#### *Eunerinea? sequana* (Bronn ex Thirria, 1836) Plate 16: figs 1, 2

\*1836 - Nerinea sequana Thirr. - Bronn: 561, pl. 6, fig. 6.
?1852 - Nerinea speciosa Voltz - d'Orbigny: 123, pl. 269, figs 1, 2.
?1997 - Cossmannea (Eunerinea) sequana (Bronn ex Thirria, 1836) - Fischer and Weber: 49.

Material. One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 74. **Description.** The almost complete specimen is 42 mm high. The shell is slender. The whorls are regularly increasing in width forming an acutely conical shell. The whorls are relatively low with concave whorl face. The earliest whorls are poorly preserved. Later whorls seem to have a subsutural, weakly knobby bulge. The suture is barely visible. One or two weak knobby spiral cords below the bulge are present. The knobs of the bordering spiral cord emerge from the abapical suture. The whorl face is ornamented with broad, barely visible axial ribs. The base is flat and its transition to the whorl face is almost rectangular with a distinctly knobby bodering spiral cord. The base is entirely covered with numerous densely spaced, fine spiral cords. The aperture is not preserved; it probably has at least a columellar and a parietal plait.

**Relationships.** Nerinea visurgis Roemer sensu Bronn (1836) lacks a subsutural bulge, the knobs on the bordering spiral cord are smaller, the base is more convex and seemingly devoid of any ornament. Nerinea tuberculosa Defrance sensu Cossmann (1896) has a slenderer shell with higher whorls, lacks a weakly knobby spiral cord at mid-whorl, the knobs on the bordering spiral cord are smaller but more numerous and its base is smooth. Nerinea speciosa Voltz sensu Cossmann (1898) is slenderer, its whorls increase less rapidly in width and are higher and it has five spiral cords on the whorl face. Nerinea posthuma Zittel sensu Cossmann (1898) is much larger, its whorls are higher and its base lacks spiral cords.

#### Eunerinea? biplicata (Quenstedt, 1858)

Plate 16: figs 3-9

- \*1858 Nerinea biplicata Quenstedt: 766, pl. 94, fig. 11.
- 1881-1884 Nerinea biplicata Quenstedt: 529, pl. 205, figs 76-77.

**Material.** Five specimens from Saal, collection Lang, four of which are illustrated (SNSB-BSPG 2021 XV 75–77, 107).

**Description.** The largest fragment is 58 mm high. The shell is slender. The whorls increase regularly in width. The sutures are situated in the middle of a bulge that is formed by two neighbouring whorls. The whorl face is distinctly concave. The whorl face is ornamented with broad, orthocline axial ribs that reach from suture to suture in early whorls but may be reduced on late whorls except of nodes. They are thickened and node-like near the sutures. The whorl are deepened and pit-like between the axial ribs at mid-whorl. Juvenile specimens have two spiral cords between the nodes. The base is flat, smooth, and distinctly umbilicated. The transition from base to whorl face is sharply angulated. Sections show that the aperture is rhomboid and has two columellar plaits, a parietal, a palatal, and a basal plait.

**Relationships.** Nerinea or else Cossmannea (Eunerinea) sculpta Étallon sensu Loriol in Loriol and Bourgeat (1886– 1888), Cossmann (1898) and Hägele (1997) has stronger and probably also more axial ribs, a more strongly concave whorl face and, according to Loriol, lacks an umbilicus.



Plate 16. (1–2) Eunerinea? sequana (Bronn ex Thirria, 1836), SNSB-BSPG 2021 XV 74, Saal (collection Lang); (1) lateral view, height 42 mm; (2) base, width 13 mm. (3–9) Eunerinea? biplicata (Quenstedt, 1858). (3–4) SNSB-BSPG 2021 XV 75, Saal (collection Lang); (3) lateral view, height 36 mm; (4) shell detail, height 17 mm. (5) SNSB-BSPG 2021 XV 76, Saal (collection Lang), oblique view of base, width 16 mm. (6–7) SNSB-BSPG 2021 XV 77, Saal (collection Lang), lateral view and section, height 58 mm. (8–9) SNSB-BSPG 2021 XV 107, Saal (collection Lang), height 57 mm; (8) columellar section; (9) lateral view showing concave whorl face encrusted by colonial coral. (10–13) Eunerinea sp. nov. 1. (10–11) collection Sauerborn, Nattheim area; (10) lateral view, height 46.5 mm; (11) aperture, width 10 mm. (12–13) Collection Sauerborn, Nattheim area; (12) lateral view, height 120 mm; (13) detail of ornament, height 26 mm. (14) Eunerinea sp. 2; SNSB-BSPG 2021 XV 79 (collection Lang), lateral view, height 32 mm.

Nerinea bicincta Bronn sensu Goldfuss (1844) has stronger axial ribs, lacks spiral cords and seemingly also lacks an umbilicus. Nerinea wosinskiana Zeuschner, 1849 has lower whorls, stronger nodes and it allegedly has only two plaits. Nerinea wosinskiana Zeuschner sensu Gemmellaro (1870) has an only weakly concave whorl face, lacks spiral cords and has only a columellar plait. Nerinea haidingeri Peters, 1855 is slenderer, has higher whorls which increase less rapidly in width, lacks spiral cords, has stronger knobs, and lacks an umbilicus. Nerinea incisa Étallon sensu Cossmann (1898) has a slenderer shell, higher whorls, a more distinctly concave whorl face, and more spiral cords; the presence of an umbilicus was not mentioned for that species.

Eunerinea sp. nov. 1

Plate 16: figs 10-13

**Material.** Three certain and a questionable specimen from the Nattheim area (all from the collection Sauerborn).

**Description.** A specimen is 120 mm high. The shell is very slender, needle-shaped. The shell has a pronounced bulge at the suture that is formed by two neighbouring whorls. The suture lies on this bulge. The whorl face is distinctly concave between the bulges where it is entirely covered with numerous weak spiral cords. Details of this ornament cannot be recognized because of insufficient preservation. The base is flat with an angular transition to the whorl face. The aperture is damaged in all specimens; it probably has a rhomboid outline and a distinct siphonal canal, a columellar plait that forms the adapical border of the canal, and a parietal plait.

**Remarks.** The illustrated specimen of *Nerinea terebra* Schübler sensu Goldfuss (1844) derives from Nattheim and could be identical with *Eunerinea* sp. nov. 1. The lack of spiral ornament in the specimen illustrated by Goldfuss (1844) and the lack of a palatal plait in *Eunerinea* sp. nov. 1 could be due to preservation. *Nerinea terebra* as described by Schübler (in Zieten 1830: pl. 36, fig. 3) is, however, not identical with the specimen figured by Goldfuss (1844): its shell is much broader, it has lower whorls and only a single, strong parietal plait in the aperture.

**Relationships.** Nerinea contorta Buvignier sensu Cossmann (1898) is even slenderer, has higher whorls, and its whorl face is more concave. Its whorl face is ornamented with four strong spiral cords and weaker ones between them. Nerinella bononiensis Loriol sensu Cossmann (1898) is somewhat less slender, its whorls are higher and the suture is not situated on the bulge. Aptyxiella cottaldina d'Orbigny sensu Cossmann (1898) has lower whorls and it lacks plaits in the aperture. Nerinea contorta Buvignier var. sesostris Krumbeck sensu Delpey (1939) has higher whorls, its whorl face is more concave, and it lacks distinct plaits.

#### Eunerinea sp. 2

Plate 16: fig. 14

?part 1882 – Aptyxis kelheimensis sp. nov. – Schlosser: 77, ?pl. 11, figs 3, 7; non pl. 11, figs 4–6. **Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 79.

**Description.** The specimen is 32 mm high. The early whorls are lacking. The shell is very slender. The whorls are very broad in relation to their height. The whorl face is concave. The suture is situated on a bulge that is formed by two neighbouring whorls. The bulge is demarcated abapically by a furrow-like deepening. There is no other ornament. The base and aperture are not preserved. Within the last preserved whorl, there are at least two columellar plaits. The aperture probably has a siphonal canal.

Relationships. Aptyxis kelheimensis Schlosser, 1882 is quite similar in part and possibly conspecific to the present specimen (Schlosser 1882, pl. 11, figs 3, 7; non figs 4-6). However, this species has several spiral cords and allegedly lacks plaits in the aperture. Nerinea cincta Münster in Goldfuss, 1844 is very similar but much younger (Gosau-Cretaceous) and has more concave whorls. Nerinea goldfussi d'Orbigny sensu Schlosser (1882) is much larger, has higher whorls and a spiral cord at mid-whorl. Nerinea petersi Gemmellaro, 1870 has a rounded transition from whorl face to base, the whorls are higher and the whorl face is less concave; the situation of the suture is unclear in this species. Nerinea curmontensis Loriol in Loriol, Royer and Tombek (1872) lacks a bulge, has a suprasutural row of knobs and a straight whorl face. Nerinea cincta Münster sensu Schafhäutl (1863) is much larger and has higher whorls. Ptygmatis intermedia Pchelintsev, 1926 and P. exelsa Pchelintsev, 1926 have higher whorls and a more convex base. Nerinea bruntrutana Thurmann sensu Zeuschner (1849) is larger, has a distinct umbilicus and its whorls increase more rapidly in width.

#### Eunerinea sp. 1

Plate 17: figs 1-8

non1836 - N. punctata Voltz in litt. - Bronn: 559, pl. 6, fig. 23.

- 1886–1888 Nerinea subelegans Étallon Loriol in Loriol and Bourgeat: 110, pl. 11, figs 4–6.
- 1997 Nerinella elatior (d'Orbigny, 1852), forme juvenile Fischer and Weber: 52, pl. 5, fig. 5.

**Material.** Seven specimens from the Nattheim area (five specimens collection Quenstedt/Tübingen, two specimens collection Sauerborn), four specimens from Saal, collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 71).

**Description.** A large specimen is 30 mm high. The shell is very slender. The whorls are slowly increasing in width. The apical angle is somewhat variable. The whorl face is concave and ornamented with a subsutural bulge (smooth or knobby), with a strong and distinctly knobby spiral cord at approximately mid-whorl, and a narrow projecting bordering spiral cord that emerges above the suture. This cord demarcates the flat base from whorl face. Only very well preserved specimens show further weak spiral cords between adapical bulge and median spiral cord, and another between median spiral cord and abapical suture.



**Plate 17.** *Eunerinea* sp. 1. (1–3) SNSB-BSPG 2021 XV 71, Saal (collection Lang); (1) lateral view, height 15 mm; (2) last two whorls, height 4 mm; (3) base, width 3.7 mm. (4–5) Collection Sauerborn, Nattheim area; (4) lateral view, height 10.5 mm; (5) last whorls with aperture, height 3.4 mm. (6–8) Collection Sauerborn; Nattheim area; (6) last whorl with aperture, height of detail 6.5 mm; (7–8) lateral views, height 26 mm.

They are at least partly knobby. The base lacks ornament. The rhomboid aperture has a siphonal canal. It shows a columellar, a parietal, and a palatal plait.

**Remarks.** The present material assigned to this species is somewhat variable. The subsutural bulge is of various strength and, even if well preserved, is either smooth respectively knobby (in silicified specimens). It is possible that two very similar species are present. A possible identity with *Nerinella nodosa* (Voltz, 1836) remains unclear. This species differs from *Nerinella* sp. 1 by having a broader shell and more rapidly increasing whorls, an always knobby adapical bulge, a knobby spiral cord that is situated in most cases below mid-whorl, and a less projecting bordering spiral cord at the transition to the base. It is unclear whether these differences reflect preservation differences or not.

Relationships. Differences to Nerinella subscalaris (Münster in Goldfuss, 1844) are discussed under this taxon. Nerinea punctata Voltz, as described by Bronn (1836), with which Quenstedt (1881-1884) identified his species (Nerinea punctata Voltz sensu Quenstedt, 1858 and 1881-1884), has three knobby spiral cords of about equal strength and lacks the pronounced projection of the bordering spiral cord. Nerinea ornata d'Orbigny sensu Loriol in Loriol, Royer and Tombeck (1872) is similar but its subsutural bulge is less pronounced. Nerinea hoheneggeri Peters, 1855 has a row of knobs directly above the abapical suture and several crenulated, relatively weak spiral cords between the suprasutural row of knobs and a knobby spiral cord situated somewhat above mid-whorl. Eunerinea hoheneggeri Peters sensu Wieczorek (1998) has distinct knobs on the bulges. Nerinea ornata d'Orbigny and N. tricincta d'Orbigny sensu Cossmann (1898) have three strong knobby spiral cords as well as weaker not knobby spiral cords in their interspaces.

#### Family Itieriidae Cossmann, 1896

#### Genus Itieroptygmatis Charvet & Termier, 1971

**Type species.** *Itieroptygmatis ellipticata* Charvet & Termier, 1971; Jurassic/Cretaceous transition; Bosnia–Herzegovina.

#### Itieroptygmatis cylindrata sp. nov.

https://zoobank.org/05FC3FC9-3FBE-4EE3-8FA8-0B64093E42EA Plate 18: figs 1-14

?1882 – *Itieria austriaca* Zitt. – Schlosser: 84, pl. 12, figs 8, 9. 2017 – Nerineoidea Nr. 9a, b – Gründel: 33, pl. 15B–C.

**Derivatio nominis.** Latin *cylindratus* – cylindrical; according to the approximately cylindrical shell shape of the late teleoconch of this species.

Holotype. SNSB-BSPG 2021 XV 80, collection Lang. Locus typicus. Saal Quarry near Kelheim. Stratum typicum. Upper Kimmeridgian.

**Paratypes.** 45 specimens from Saal (43 specimens collection Lang, BSPG (SNSB-BSPG 2021 XV 81–84, 86, 109–146); one specimen collection Keupp, SNSB-BSPG 2021 XV 87, one specimen collection Schäfer, BSPG SNSB-BSPG 2021 XV 85; additional specimens on block with *Cassianopsis quenstedti* SNSB-BSPG 2015 VII 58.

**Material.** A total of 56 specimens from Saal, 46 types (see above) and 10 specimens without type status from private collections: 6 specimens collection Lang, 4 specimens collection Schäfer.

**Diagnosis.** The adapical part of the shell is slender with many whorls lacking a ramp. Later whorls are broad in relation to their height and have a ramp which becomes broader from whorl to whorl in most specimens. Below the



Plate 18. (1–10) Itieroptygmatis cylindrata sp. nov., morphotype 1. (1–2) Holotype, SNSB-BSPG 2021 XV 80, Saal (collection Lang); (1) lateral view, height 15 mm; (2) oblique view, width 5.5 mm (Gründel 2017, fig. 15 B). (3–4) Paratype, SNSB-BSPG 2021 XV 81, Saal (collection Lang), apical and lateral views, width 14 mm. (5–6) Paratype, SNSB-BSPG 2021 XV 82, Saal (collection Lang), apical and lateral views, width 16 mm (original Gründel 2017, fig. 15 C). (7–8) Paratype, SNSB-BSPG 2021 XV 83, Saal (collection Lang), basal and lateral views, width 15 mm. (9–10) Paratype, SNSB-BSPG 2021 XV 84, Saal (collection Lang); (9) columellar section, height 16 mm; (10) detail of (9), height 7.5 mm. (11) Itieroptygmatis cylindrata sp. nov., transition from morphotype 1 to morphotype 2, paratype, SNSB-BSPG 2021 XV 85, Saal (collection Schäfer), lateral view, height 33 mm. (12–14) Itieroptygmatis cylindrata sp. nov., morphotype 2, paratype, SNSB-BSPG 2021 XV 86, Saal (collection Lang), (12) lateral view, height 27 mm; (13) apex in lateral view, height 12 mm; (14) apical, width 13 mm. (15–16) Itieroptygmatis sp. 1. (15) SNSB-BSPG 2021 XV 88, Saal (collection Lang), lateral view, height 47 mm. (16) SNSB-BSPG 2021 XV 89, Saal (collection Lang), base, width 21 mm.

ramp, a weak concavity (lateral view) is developed; rarely, the ramp remains narrow and the concavity is lacking. The last whorls of large specimens increase only slowly in width and this part of the shell is more or less cylindrical. The transition from whorl face to base is evenly rounded without edge or spiral cord. Aperture with two columellar and palatal plaits and one parietal plait.

This species is present in two morphotypes and specimens that are intermediate:

- Morphotype 1: Plate 18: figs 1–10;
- Transition from morphotype 1 to morphotype 2: Plate 18: fig. 11;
- Morphotype 2: Plate 18: figs 12–14.

**Description.** A large specimen (early whorl missing) is 33 mm high. The early shell is very slender consisting of at least eight smooth whorls having a weakly convex whorl face and somewhat impressed sutures. The following 2–3 whorls increase rapidly in width and are very wide in relation to their height. As a result, the spire is coeloconoid. In the mentioned 2–3 whorls following the slender spire whorls, a broad, distinctly concave, funnel-shaped ramp is formed. From now on, the ontogenetic evolution of the shell follows different pathways leading to two varieties (morphotype 1 and 2 as well as to intermediate forms).

In morphotype 1 (much more abundant than morphotype 2), the wide ramp continues and becomes wider. It is delimited from whorl face by a broad concavity with indistinct borders. Initially, the whorls continue to rapidly increase in width. In large, more or less fully grown specimens, the increase in width decelerates, the last whorls are high and almost cylindrical in shape. The edge of the ramp is projecting abaxially and forms the whorl periphery.

In the other extreme form, morphotype 2, the rapid increase of the width of the whorls and the formation of a broad ramp is confined to 2–3 whorls. Afterwards, the whorls become wider and increase in width only slow-ly, but considerably increase in height. The ramp forms only a narrow band. The whorl face is straight and lacks a concavity below the ramp so that this part of the shell is almost cylindrical. As mentioned, there are transitional forms between varieties 1 and 2 (Plate 18: fig. 11).

All individuals have a continuous, rounded transition from whorl face to the strongly convex base. Base and whorl face are smooth. The base has a distinct umbilicus. The growth lines run straight and somewhat opisthocline on the whorl face and curve strongly backward below the ramp. The aperture is very narrow, adapically acute and has a weakly developed siphonal canal. The inner lip is broadened and detached in the columellar area; it partly covers the umbilicus. The inner lip bears a strong parietal and two columellar plaits. The adapical columellar plait is weaker than the abapical one. The aperture has two palatal plaits which are, however, rarely recognizable.

**Remarks.** Itieria austriaca Zittel as described by Schlosser (1882) closely resembles morphotype 2 of Itieroptygmatis cylindrata sp. nov. However, it has a distinctly lower last whorl in relation to its spire height. The real *Itieria austriaca* Zittel, 1873 differs distinctly from *Itieroptygmatis cylindrata* sp. nov. by lacking a ramp and by having a subsutural row of knobs.

**Relationships.** Itieria (Campichia) pellati Cossmann and Itieria (Campichia) truncata Pictet and Campiche, both sensu Cossmann (1916), resemble morphotype 1 of Itieroptygmatis cylindrata sp. nov. However, their spire is lower and has not as many whorls, the last whorl is much broader than the spire (having wide ramp only on a single whorl). Itieria obtusiceps Zittel, 1873 resembles morphotype 2 of Itieroptygmatis cylindrata. However, I. obtusiceps has a less distinct ramp, the spire is blunter, and the shell outline is more oval-shaped. Phaneroptyxis nogreti Guir. and Ogérien sensu Cossmann (1898) differs from morphotype 1 of Itieroptygmatis cylindrata sp. nov. by having a lower last whorl (in relation to spire height) in large specimens, lacking a wide ramp, and not having a cylindrical shape of the last whorl.

#### Itieroptygmatis sp. 1

Plate 18: figs 15, 16

**Material.** Two juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 88, 89.

**Description.** A specimen is 47 mm high. The shell is moderately high-spired and coeloconoid. At least the first six whorls are moderately slender with whorls increasing slowly in width. The sutures are impressed. The whorls are smooth. The last two preserved whorls increase rapidly in width and at the same time, a furrow-like ramp is forming. The whorl face below the ramp is straight and the transition to the moderately convex base is evenly rounded. The base is smooth and has a wide umbilicus. The aperture is not preserved and it is unknown whether it has plaits.

**Remarks.** This incompletely preserved species shows the same ontogenetic change in shell shape as *l. cylindra-ta* sp. nov. but is distinctly larger.

**Relationships.** Itieroptygmatis cylindrata sp. nov. is considerably smaller and more gracile. *Phaneroptyxis* cf. *nogreti* sensu Hägele (1997) has whorls that are more regularly increasing in width across the entire shell and lacks a distinct ramp.

# Insufficienty known or problematic species of Nerineoidea

## Nerinea constricta suevica Quenstedt, 1858 nomen dubium

1852 – Nerinea constricta Roemer, 1836 – Quenstedt: 429, pl. 34, fig. 32.

\*1858 - Nerinea constricta suevica - Quenstedt: 769, pl. 94, fig. 25.
\*1881-84 - Nerinea columelloides - Quenstedt: 556, pl. 207, figs 16, 17.

**Remarks.** Two small fragments from the Nattheim area labelled *Nerinea constricta suevica* were found in the

collection of Quenstedt (1881–1884) of the Tübingen Institute. They probably represent two species because they have different apical angles (one very slender, the other distinctly broader). The slender specimen is probably the one illustrated by Quenstedt (1852: *N. constricta* Roemer, 1836; 1858: *Nerinea constricta suevica*; 1881– 1884: *N. columelloides* Quenstedt). Because the original material is fragmentary, poorly preserved and probably represents two species, *N. constricta suevica* is herein considered a *nomen dubium*. It is (even according to Quenstedt 1881–1884) not identical with *Nerinea suevica* Quenstedt, 1858 (see under *Nerinella subscalaris* Münster, 1844 in Goldfuss).

## *Nerinea grandis nuda* Quenstedt, 1858 nomen dubium

part v\*1858 – Nerinea grandis nuda – Quenstedt: 766, pl. 94, fig. 5 (non fig. 4).

part v1881-1884 - Nerinea nuda - Quenstedt: 553, pl. 207, fig. 1 (non fig. 2).

Material. One specimen (Tübingen: collection Quenstedt).

**Description.** The specimen illustrated by Quenstedt (1881–1884, pl. 207, fig. 1) is 77 mm high. It consists of well over two whorls. Half of the shell wall is broken off. The whorls are high, the whorl face is straight. The surface



Plate 19. (1–2) Nerinea bruntrutana Thurmann, 1832 sensu Quenstedt (1881–1884); University Tübingen (collection Quenstedt), Nattheim; (1) aperture, height ca. 22 mm; (2) lateral view (original Quenstedt 1881–1884, pl. 206, fig. 2). (3–4) Nerinea mandelslohi Bronn sensu Quenstedt (1881–1884); (3) University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height ca. 31 mm (original Quenstedt 1881–1884, pl. 206, fig. 11). (4) University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height ca. 21 mm (original Quenstedt 1881–1884, pl. 206, fig. 12). (5) Nerinea teres (Goldfuss, 1844) sensu Quenstedt (1881–1884), collection University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height 12 mm (original to Quenstedt 1881–1884, pl. 206, fig. 26). (6–8) Nerinea? sp. 1; (6) SNSB-BSPG 2021 XV 90, Saal (collection Lang), lateral view, height 67 mm. (7–8) SNSB-BSPG 2021 XV 91, Saal (collection Schäfer); (7) lateral view, height 21 mm; (8) detail of ornament, width 8.5 mm. (9–11) Gen. et sp. Indet, SNSB-BSPG 2021 XV 92, Saal (collection Lang); (9) lateral view, height 19 mm; (10) base, width 9 mm; (11) last whorls with aperture, height 12 mm.

of the whorls is completely encrusted. No ornament is visible. The suture is indicated with red ink but it is unclear whether this interpretation of the situation of the suture is correct. No plaits are visible inside the shell. Aperture and base are not preserved.

**Remarks.** Quenstedt (1858, 1881–1884) assigned two specimens to *Nerinea grandis nuda* which differ strongly from each other: a large and a small one. However, he considered only the specimen illustrated by him (Quenstedt 1858, pl. 94, fig. 5) as the "real grandis nuda" (p. 766). Referring to that, Geiger (1901) based *Aptyxiella quenstedti* Geiger, 1901 on the smaller specimen (see also treatment of that taxon herein). *Nerinea grandis nuda*, which is based on a fragment, cannot be sufficiently characterized and is here regarded as a *nomen dubium*. Geiger (1901) assigned this specimen to *Nerinea nantuacensis* d'Orbigny, 1851.

#### Nerinea bruntrutana Thurmann, 1832 sensu Quenstedt (1881–1884)

Plate 19: figs 1, 2

v1881–1884 – Nerinea bruntrutana Thurmann – Quenstedt: 534, pl. 206, fig. 2.

**Remarks.** The fragmentary specimen from Nattheim that was assigned to *N. bruntrutana* by Quenstedt (1881–1884) consists of a single complete whorl and two whorls that are partially preserved. The shell is slender. The whorl face is weakly convex, without visible ornament. The sutures are weakly impressed. The base is not preserved. The aperture is strongly damaged. An umbilicus is present and filled with quartz. A strong and a weak columellar, a strong parietal, and a palatal plait are visible. A safe identification of this specimen is impossible. *Nerinea bruntrutana* Thurmann (in Thurmann and Étallon 1861–1864) differs significantly in having lower whorls that increase more rapidly in width, a straight whorl face, and weakly impressed suture.

## Nerinea dilatata d'Orbigny sensu Quenstedt (1881–1884)

1881–1884 – *Nerinea dilatata* d'Orbigny – Quenstedt: 550, pl. 206, fig. 61.

**Remarks.**Two indeterminable columella remains from Nattheim are present in the Quenstedt collection (Tübingen) and were assigned to *Nerinea dilatata* d'Orbigny. The whereabouts of the specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 61) is unknown.

## Nerinea fasciata Bronn, 1836 sensu Quenstedt (1858)

1858 - Nerinea fasciata Bronn, 1836 - Quenstedt: 770, pl. 94, fig. 18.

v1881-1884 - Nerinea fasciata Bronn - Quenstedt: 529, pl. 205, figs 78-81.

**Remarks.** Quenstedt's (1858, 1881–1884) material consists of four moderately to poorly preserved fragments that represent at least two to possibly three species. This material cannot be identified.

# Nerinea mandelslohi Bronn, 1836 sensu Quenstedt (1881–1884)

Plate 19: figs 3, 4

- vpart 1858 Nerinea mandelslohi Bronn, 1836 Quenstedt: 767, pl. 94, figs 14, 15 (specimen in fig. 15 not seen).
- v1881–1884 Nerinea mandelslohi Bronn Quenstedt: 535, pl. 206, figs 11, 12.

**Remarks.** The following statements are based on the study of the material from Nattheim figured by Quenstedt (1858, 1881–1884). The specimen illustrated by Quenstedt (1858, pl. 94, fig. 14 and 1881–1884, pl. 206, fig. 12) (herein Plate 19: fig. 4) is a fragment consisting of about two whorls. The shell wall is broken off at one side so that the columella with two plaits and a parietal plait are visible. The specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 11 (herein Plate 19: fig. 3) is a columellar fragment of about 2.5 whorls. Both mentioned specimens are undeterminable.

## Nerinea pyramidalis Münster in Goldfuss, 1844 sensu Quenstedt (1881–1884)

vpart 1881–1884 – Nerinea pyramidalis Münster in Goldfuss – Quenstedt: 549, pl. 206, figs 59, 60.

**Remarks.** Quenstedt (1881–1884) illustrated two specimens from Nattheim and assigned them to *Nerinea pyra-midalis* Münster, 1844 in Goldfuss. The specimens illustrated by Quenstedt (1881–1884, pl. 206, fig. 59) could not be found. The other specimen is an undeterminable cast of an umbilicus.

### Nerinea teres Goldfuss, 1844 sensu Quenstedt (1881–1884)

Plate 19: fig. 5

v1881–1884 – Nerinea teres Goldfuss – Quenstedt: 540, pl. 206, fig. 26.

**Remarks.** The material representing *Nerinea teres* studied by Quenstedt (1881–1884) consists of five poorly preserved fragments. The best preserved one is figured here in Plate 19: fig. 5 (Quenstedt 1881–1884, pl. 206, fig. 26). It consists of about three whorls and is 12 mm high. Its whorl face is straight and ornamented with four equally strong spiral cords without knobs. The distance between the second and

third spiral cord is larger than the distance between the other cords. The sutures are barely impressed. The specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 25), which is of uncertain species identity, has a canal, two columellar plaits, and a parietal plait. The morphology of the outer lip is unknown. The fragment illustrated cannot be assigned with certainty to any of the species described herein.

#### Nerinea? sp. 1

Plate 19: figs 6-8

**Material.** Two incomplete specimens from Saal (one specimen collection Lang, SNSB-BSPG 2021 XV 90, one specimen collection Schäfer, SNSB-BSPG 2021 XV 91).

**Description.** The larger specimen is 67 mm high. The multi-whorled shell is slender. The apical whorls are missing. The whorl height is about one third of its width. The whorl face is weakly convex to straight. The sutures are somewhat impressed. The early whorls are ornamented with 2–3 distinct spiral cords. The subsutural spiral cord is weakly knobby. Later whorls have numerous rather weak spiral cords (respectively lirae). Weak axial ribs emerge from the adapical suture and fade rapidly in an abapical direction. The base is flat with an angular transition to the whorl face. Other details are not preserved.

**Remarks.** The present material is too poorly preserved and cannot be identified.

**Relationships.** *Ptygmatis crassa* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888) has higher whorls, a more distinct ramp and smaller knobs. *Nerinea guirandi* Loriol in Loriol & Bourgeat, 1886–1888 has higher whorls, a more distinct ramp and, at least on the early whorls, more distinct knobs. *Ptygmatis guirandi* Loriol sensu Cossmann (1898) has higher whorls, a more concave whorl face, and knobs are restricted to the early whorls.

#### Gen. et sp. indet.

Plate 19: figs 9-11

Material. One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 92.

Description. The shell fragment is 19 mm high. The whorls are relatively high. The whorl face is straight. The sutures are indistinct. The whorls are ornamented with a subsutural row of axially elongated, opisthocline knobs. Below it, the whorl face is ornamented with three spiral cords: a weak upper one, then a stronger one and again a weak spiral cord. All spiral cords are knobby. The size of the knobs corresponds to the strength of the spiral cords. The knobs of the bordering spiral cord emerge from the abapical suture. The bordering spiral cord is strong and marks the angular transition from whorl face to the weakly convex base. The base is ornamented with at least one distinct spiral cord and possibly with additional weaker ones. The growth lines are weakly prosocyrt on the base and almost straight orthocline on the whorl face. They curve strongly backward immediately below the adapical suture. The aperture is rhomboid and has a siphonal canal. Only a single strong parietal plait is visible.

**Relationships.** *Nerinea binodosa* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888: pl. 9, fig. 6) is larger, the adapical knobs are prosocline, it lacks a distinct row of knobs below mid-whorl, the knobs on the bordering spiral are larger, less numerous, almost fully exposed above the abapical suture, and the base is covered with distinct spiral cords. *Nerinea oppeli* Gemmellaro, 1870 is larger, the knobs on the bordering spiral are larger, almost fully exposed above the abapical suture, and the subsutural knobs are smaller and not as distinctly elongated. *Nerinea loreti* nom. mut. sensu Cossmann (1898) has higher whorls, a concave whorl face, the subsutural knobs are smaller and not elongated, the knobs on the bordering spiral are larger and almost fully exposed above the abapical suture, and its whorl face is covered with numerous spiral cords.

#### Infraclass Euthyneura Spengel, 1881 Superfamily Acteonoidea d'Orbigny, 1843 Family Cylindrobullinidae Wenz, 1938

#### Genus Rugalindrites Gründel & Nützel, 2012

**Type species.** Acteon cuspidatus Sowerby, 1824; Bathonian; England.

#### **Rugalindrites cylindracea (Cornuel, 1841)** Plate 20: figs 1–9

- \* 1841 Melania cylindracea sp. nov. Cornuel: 289, pl. 15, fig. 14.
- 1852 Actaeonina cylindracea (Cornuel). d'Orbigny: 179, pl. 288, fiq. 9?
- 1874 Acteonina cylindracea d'Orbigny (Cornuel) Loriol in Loriol and Pellat: 295, pl. 6, fig. 7.
- 1895 Cylindrobullina cylindracea Cornuel Cossmann: 57, pl. 3, fig. 1, pl. 4, fig. 1, 2.
- 1997 Cylindrobullina cylindracea (Cornuel, 1841) Fischer and Weber: 69.
- 2017 Rugalindrites sp. Gründel: 33, pl. 15, fig. D

**Material.** Forty-eight mostly juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 93–97.

**Description.** A large specimen with damaged spire is 10 mm high. The shell is elongated fusiform. The last whorl is very high, cylindrical, tapering in abapical direction, embracing high on the previous whorl and covering most of it. The spire is relatively high for the genus and is acutely conical, consisting of several low whorls. A narrow but distinct horizontal ramp is formed early in ontogeny. The ramp is sharply demarcated from the whorl face by an edge. The shell is smooth. Growth lines are not visible, only on the ramp, remains of strengthened opisthocyrt growth lines are visible. The aperture is elongated, narrow and stretches over the entire height of the last whorl. Its adapical portion is narrow and acutely tapering. The abapical portion of the aperture is widened drop-shaped. The columellar portion of the


Plate 20. (1-9) Rugalindrites cylindracea (Cornuel, 1841). (1) SNSB-BSPG 2021 XV 93, Saal (collection Lang), lateral view, height 5 mm.
(2) SNSB-BSPG 2021 XV 94, Saal (collection Lang), apical view, width 5.5 mm. (3-4) Saal (collection Lang), lateral and apical views (specimen lost). (5) SNSB-BSPG 2021 XV 95, Saal (collection Lang), aperture, height 3.5 mm. (6-7) SNSB-BSPG 2021 XV 96, Saal (collection Lang); (6) lateral view, height 8.5 mm; (7) aperture, height 3.5 mm. (8-9) SNSB-BSPG 2021 XV 97, Saal (collection Lang);
(8) aperture, height 6 mm; (9) lateral view, height 9.5 mm. (10-12) Rugalindrites sp. 1, SNSB-BSPG 2021 XV 98, Saal (collection Lang);
(10) lateral view, height 5.5 mm; (11) apical view, width 2.5 mm; (12) detail of ornament, height ca. 1.3 mm.

aperture is covered by callus which also covers parts of the base. The abapical delimitation of the callus is formed by a somewhat oblique plait which also demarcates the columellar area from the abapical edge of the aperture. A further weak plait forms the outer edge of the callus of the aperture.

**Remarks.** Columellar plaits are mostly not mentioned for *Rugalindrites cylindracea* possibly due to insufficient preservation of the specimens and due to the fact that the plaits are rather weak. Even in the present material, plaits are rarely visible.

**Relationships.** Differences to *Rugalindrites* sp. 1 are discussed below. *Cylindrobullina humbertina* Buvignier sensu Cossmann (1895) has a weaker and oblique ramp and its bordering edge is less pronounced. Moreover, it lacks a columellar callus with plaits. *Tornatina boutillieri* Cossmann, 1895 has a lower spire and the last whorl is cylindrical with straight whorl face. *Acteonina davidsoni* Loriol, 1874 (in Lo-

riol and Pellat) has a lower spire, broader whorls, the last whorl is cylindrical and has a straight whorl face; columellar plaits have not been mentioned for this species.

#### Rugalindrites sp. 1

Plate 20: figs 10-12

Material. Two specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 98.

**Description.** The larger specimen is 6 mm high. The overall shape closely resembles that of *Rugalindrites cylindracea*. The spire is distinctly elevated and gradate. The spire whorls increase more rapidly in height than in width due to a downward shift of the suture. The whorls have a narrow ramp with a more rounded transition to the whorl face. The growth lines are almost straight and weakly pro-

socline. In the upper part of the whorls, they are strengthened and thread-like. The growth lines are distinctly prosocyrt on the convex base. At about mid-whorl of the last whorl, there is a broad band with a micro-ornament of numerous spiral threads (Plate 20: fig. 12). The aperture is not preserved.

**Relationships.** *Rugalindrites cylindracea* (Cornuel, 1841) has a more convex whorl face, a higher spire, the edge that borders the ramp is more pronounced, it lacks spiral ornament and strengthened growth lines. *Cylindrobullina peroni* Cossmann, 1895, *Tornatina boutillieri* Cossmann, 1895, *Cylindrites nitidens* Loriol, 1889 (in Loriol and Koby 1889–1892), and *Actaeonina cylindracea* d'Orbigny sensu Loriol and Pellat (1874) are larger (some of them considerably larger), the edge that borders the ramp is more pronounced, and lack any visible ornament. *Cylindrobullina* cf. *disjuncta* Terquem and Jourdy sensu Nalivkin and Akimov (1917) has a stouter shell, is larger, and lacks ornament.

#### Genus Ptychocylindrites Cossmann, 1895

**Type species.** *Bulla condati* Guirand & Ogérien, 1865; Kimmeridgian; Switzerland.

# Ptychocylindrites condati (Guirand & Ogérien, 1865)

Plate 21: figs 1, 2

- \* 1865 Bulla condati sp. nov. Guirand and Ogérien: 388, figs 38, 39.
- 1886–1888 Cylindrites condati Guirand and Ogérien Loriol in Loriol and Bourgeat: 51, pl. 3, figs 4, 5.
- non 1893 *Cylindrites condati* Guirand and Ogérien Greppin: 26, pl. 3, fig. 9.
- 1895 Ptychocylindrites condati Guir. et Ogér. Cossmann: 89, pl. 4, figs 28–32.
- 1895 Ptychocylindrites condati (Guir. et Og). Cossmann: 72, pl. 3, figs 4–6.
- 1917 Ptychocylindrites caudati Cossmann Nalivkin and Akimov: 41, pl. 3, fig. 27.
- 1997 Cylindrites (Ptychocylindrites) condati (Guirand & Ogérien, 1865) – Hägele: 120, fig. p. 121 upper right.
- 2012 Ptychocylindrites condati (Guirand & Ogérien, 1865) Gründel and Nützel: 37, fig. 3 d–f.

**Material.** One specimen from the Nattheim area (collection Sauerborn).

**Description.** The specimen is 13 mm high. The shell is slender, fusiforme and convolute with weakly convex flanks. The apex is blunt. The last whorl covers all previous ones in lateral view. Some of the earlier whorls can be seen in apical view. The adapical portion of the last whorl is bulging and possibly knobby (uncertain due to poor preservation). This portion of the shell is narrower than the portion below it and is demarcated by a shallow furrow. No ornament is visible. The damaged aperture stretches from the adapical furrow to the base. It is very narrow and somewhat broadened at its abapical termination. The columella has two strong plaits.

**Remarks.** Seemingly, only the type species *Ptychocy-lindrites condati* can be assigned to the genus *Ptychocy-lindrites* with certainty. It ranges from the Oxfordian to the Kimmeridgian according to the literature. It seems unclear whether this species was long-lived or several species have been identified as this taxon. *Cylindrites condati* sensu Greppin (1893) does not belong to this species. If Greppin's (1893) illustration is accurate, then this specimen represents a much slenderer, probably undescribed species. *Tornatellina corallina* sensu Quenstedt (1881–1884) differs significantly from *Ptychocylindrites condati*. It is slenderer and lacks a bulging adapical portion of the last whorl.

#### Genus Volvocylindrites Cossmann, 1895

**Type species.** Bulla marcousana Guirand & Ogérien, 1865; Kimmeridgian; Switzerland.

# Volvocylindrites marcousana (Guirand & Ogérien, 1865)

Plate 21: figs 3-5

- \*1865 Bulla marcousana sp. nov. Guirand and Ogérien: 388, figs 40, 41.
- 1872 Volvula marcousana Guirand et Ogérien Loriol in Loriol, Royer and Tombeck: 72, pl. 5, fig. 8.
- 1886–1888 Volvula marcousana Guirand et Ogérien Loriol in Loriol and Bourgeat: 53, pl. 3, figs 6–9.
- 1893 Volvula marcousana Guirand et Ogérien Loriol in Loriol and Lambert: 13, pl. 1, fig. 4.
- 1895 Volvocylindrites marcousanus Guir. et Ogér. Cossmann: 87, pl. 4, fig. 14.
- 1927 Cylindrites extensus nov. sp. Maire: 122, pl. 6, figs 55-57.
- 2012 Volvocylindrites marcousana (Guirand and Ogérien) Gründel and Nützel: 37, fig. 3g–h.

**Material.** Thirty-nine mostly juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 99, 100.

**Description.** The largest specimen is 12 mm high. The shell is slender cylindrical and convolute with tapering anterior portion. The last whorl completely covers all previous ones. No ornament is visible on the whorl face except of few spiral furrows on the abapical end of the shell in some specimens (not preserved in most specimens). The aperture stretches over the entire shell height. It is narrow and only somewhat widened anteriorly. It has a columellar callus with one or possibly two plaits.

**Remarks.** Volvocylindrites marcousana ranges from the (upper) Oxfordian to the upper Kimmeridgian according to the literature. Spiral furrows are not mentioned in published descriptions. According to the literature this species has one or two plaits on the columella. *Cylindrites* 



Plate 21. (1–2) Ptychocylindrites condati (Guirand & Ogérien, 1865), Nattheim (collection Sauerborn); (1) apical view, width 5 mm; (2) lateral view, height 12 mm. (3–5) Volvocylindrites marcousana (Guirand & Ogérien, 1865). (3) SNSB-BSPG 2021 XV 99, Saal (collection Lang), lateral view, height 5.5 mm. (4–5) SNSB-BSPG 2021 XV 100, Saal (collection Lang); (4) lateral view, height 8.8 mm; (5) aperture, height 3.2 mm. (6–7) Sulcoactaeon sp. 1, SNSB-BSPG 2021 XV 101, Saal (collection Lang), lateral views, height 3.7 mm.

extensus Maire, 1927 from the upper Rauracien (= middle Oxfordian) is similar but very slender. Similar slender forms have been illustrated by Loriol in Loriol and Bourgeat (1886–1888: pl. 3, figs 6–7) as Volvula marcousana from the upper Kimmeridgian of Valfin. These slender forms are interpreted herein as variations of *V. marcousana*.

#### Familie Aplustridae Gray, 1847

#### Genus Sulcoactaeon Cossmann, 1895

**Type species.** Actaeon striatosulcatus Zittel & Goubert, 1861; Oxfordian; France.

#### Sulcoactaeon sp. 1

Plate 21: figs 6, 7

?1997 – Sulcoactaeon leblanci (Loriol, 1875) – Hägele: 118, p. 118 below, 2<sup>nd</sup> fig. from left.

Material. One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 101.

Description. The shell is 4.2 mm high. It is slender oval. The last whorl is higher than the distinctly elevated and gradate spire. The whorl height increases rapidly by a downward shift of the suture. The sutures are accentuated by the presence of a narrow ramp. The whorl face is weakly convex. The spire whorls have a suprasutural spiral furrow. The transition from whorl face to the strongly convex base is evenly rounded. The base is entirely covered by spiral furrows (ca. 15). The furrows are widely distant to each other on the adapical portion of the base and become increasingly more narrowly spaced towards the abapical portion of the base. The aperture is elongated oval and acute posteriorly. The outer lip is convex. The inner lip consists of the parietal and columellar lips that meet at an obtuse angle. The columella terminates abruptly at the anterior margin of the aperture.

**Relationships.** Sulcoactaeon leblanci (Loriol) sensu Hägele (1997) is probably conspecific. However, its spire whorls are lower, it has a subsutural spiral cord, and the last whorl is broader and has a more convex outline.

### Discussion

With this final part or the study of the Late Jurassic gastropods from Saal and the Nattheim area, a total of five new families, 15 new genera, and all in all 156 species haven been reported (problematic species of Nerineoidea not included) (Gründel et al. 2015, 2017, 2019, herein) (Table 1). Of these species, 125 have been reported from Saal and 54 from the Nattheim area (Nattheim, Gerstetten, Gussenstadt, Blaubeuren, Bosler, all in Swabian Alb, about 140 km West of Saal). Only 23 species occur, both, at Saal and in the Nattheim area. A total of 100 nominate gastropod species have been identified, and among those 45 new species have been erected in this monographic series (Gründel et al. 2015, 2017, 2019, herein). The remainig 56 species were reported in open nomenclature, mainly due to insufficient preservation. The clade proportions are as follows: Table 1. Species list of gastropods from the Saal quarry and theNattheim area with abundances (number of specimens) and sub-lass attribution (Pat = Patellogastropoda, Vet = Vetigastropoda, Ner= Neritimorpha, Cae = Caenogastropoda, Het = Heterobranchia).

		Saal	Nattheim area
Pat	Hennocquia saalensis Gründel et al., 2017	3	
Vet	Emarginula (Tauschia) sp. 1	1	
Vet	Rimulopsis broesamleni Gründel et al., 2017	7	1
Vet	Rimulopsis perforata Gründel et al., 2017	3	
Vet	Pleurotomaria agassizii Münster in Goldfuss, 1844		5
Vet	Bathrotomaria reticulata (Sowerby, 1821)		2
Vet	Leptomaria goldfussi (Sieberer, 1907)	2	3
Vet	Leptomaria tuberosa Gründel et al., 2017	3	
Vet	Pyrgotrochus sp. 1		2
Vet	Placostoma suevica (Quenstedt, 1881–1884)	6	1
Vet	Valfinia qinquecincta (Zieten, 1830–1833)	12	2
Vet	Scissurella? sp. 1	1	
Vet	Falsotectus parvus Gründel et al., 2017	/6	
vet	Faisotectus sp. nov. I	9	
vet	Discotectus crassiplicatus (Etalion, 1859)	9	
Vet	Wernersoutus angulatenlieatus (Münster in Coldfuss	9	11
vei	1844)	5	11
vet	Ambercyclus longinquus (Quensteat, 1881–1884) sensu Brösamlen (1909)		I
Vet	Eucycloscala? filifer (Brösamlen, 1909)		4
Vet	Eucycloscala? anchura (Münster in Goldfuss, 1844)		1
Vet	Marloffsteinia? funatoides (Quenstedt, 1881–1884)		3
Vet	Eucycloscalidae? gen. inc. sp. 1	1	_
Vet	Chilodonta quadratofoveata Gründel et al., 2017	3	1
Vet	Chilodonta haegelei Gründel et al., 2017	1	
Vet	Odontoturbo suevicus Brosamlen, 1909	-	2
vet	Unkospira ranellata (Quenstedt, 1852)	I	25
vet	Dracespira? gussenstationsis (Quenstedt, 1881–1884)		5 11
Vet	Proconulus aequilineatus (Munster III Goldiuss, 1844)	2	11
Vet	Amphitrachus muanatari Gründal at al. 2017	1	
Vet	Amphitrochus? gerberi Gründel et al. 2017	1	
Vet	Nododelphinula magnotuberosa Gründel et al. 2017	2	
Vet	Heliacanthus? sp. 1	1	
Vet	Nododelphinulidae? gen. et sp. inc. 1	1	
Vet	Torusataphrus inornatus (Ouenstedt, 1858)	1	3
Vet	Cochleochilus? longinguoides (Quenstedt, 1881–84)		1
Vet	Metriomphalus parvotuberosus Gründel et al., 2017	8	
Vet	Metriomphalus sp. 1	8	
Vet	Planiturbo funatus (Goldfuss, 1844)		1
Vet	Planiturbo procerus Gründel et al., 2017	6	
Vet	Planiturbo validotuberosus Gründel et al., 2017	7	
Vet	Caryomphalus funatoplicosus (Quenstedt, 1858)		6
Vet	Caryomphalus concavus Gründel et al., 2017	11	
Vet	Metriomphalidae n. gen.? sp. 1	4	1
Vet	Metriomphalidae? gen. et sp. inc.		2
Vet	Asperilla longispina (Rolle, 1861)		5
Vet	Metriacanthus crenocarina (Rolle, 1861)		1
Vet	Tegulacanthus tegulatus (Münster in Goldfuss, 1844)	1	22
Vet	Sclarotrarda coronilla (Brösamlen, 1909)	6	2
Vet	"Scalaria" tenuis Brösamlen, 1909		1
Vet	gen. inc., sp. inc.	9	
Ner	Dauterria rotundata Gründel et al., 2015	110	
Ner	Dauterria variocostata Gründel et al., 2015	100	
Ner	Pileopsella biconvexa Grundel et al., 2015	6	
Ner	Neridomus an 1	112	
iver	menuomus sp. i	2	

		Saal	Nattheirr area
Ner	Parvulatopsis quinquecostatus Gründel et al., 2015	33	
Ner	Wallowiella (Plicaropsis) cancellata (Stahl, 1824)	28	19
Ner	Wallowiella (Plicaropsis) compacta Gründel et al., 2015	2	
Ner	Cassianopsis quenstedti (Brösamlen, 1909)	7	1
Ner	Cassianopsis ratua Gründel et al., 2015	2	
Ner	Lavomiollo cohoctori Cründel et al., 2015	5 10	1
Ver	Havamiella decussata (Münster in Goldfuss 1844)	12	3
Ver	Havamiella seminlicata (Brösamlen 1909)	2	2
Ner	Bipartopsis robustus Gründel et al., 2015	8	
Cae	Rugosacyclus rugosus (Brösamlen, 1909)		1
Cae	Pseudomelania sp. 1	8	
Cae	Pseudomelania? sp. 2	7	
Cae	Saalensia birugata Gründel et al., 2015	42	1
Cae	Petersia sp. 1	1	
Cae	Costazygia sp. 1	3	
ae	Erratopleura sp. 1	1	
Cae	Ampullina sp. 1	7	
Cae	Pictavia silicea (Quenstedt, 1858)	1	
;ae	Pictavia lactera Gründel et al., 2019	2	
cae	Pictavia? sp. 1	1	
cae	Gymnocerithium convexoconcavum Grundel et al., 2019	10	F
Jae Doo	Metacerithium nodospirum (Quenstedt, 1881–1884)	15	5
ae	Tweaterna sp. 1	6	
ae ae	Ditretus sp. of rostellaria (Buyignier 1852)	3	
ae	Coninoda strekwera Gründel et al. 2019	10	
ae	Coninoda? sp. 1	5	
Cae	Maoraxis sp. 1	1	
ae	Cryptoptyxis rarenodosa Gründel et al., 2019	21	
ae	Nudivagus sp. 1	5	
ae	Nudivagus? sp. 2		1
ae	Uchauxia ex gr. limaeforme (Roemer, 1836)	44	
ae	Provolibathra? sp., cf. septemplicata (Roemer, 1836)	69	
ae	Cryptaulax? parvum Gründel et al., 2019	3	
ae	Cryptaulax? triangulare Gründel et al., 2019	3	
Cae	Tyrnoviella sp. 1	1	
Cae	Exelissa sp. 1	2	
Cae	Shurovites robustus Gründel et al., 2019	5	
Jae	Snurovites sp. 1	1	
Jae	Tropacerithium cumaritum Grundel et al., 2019	9 15	
Jae Cae	Rievtonella saalensis Gründel et al. 2019	10 10	
Сае	Juvenile cerithioid	1	
Cae	Palaeorissoina sp. 1	1	
Cae	Boreomica costaspiralis Gründel et al., 2019	10	
Cae	Boreomica sp.	1	
Cae	Boreomica sp. 2	1	
Cae	Buvignieria sp. nov. 1	2	
Cae	Buvignieria racitana Gründel et al., 2019	106	
Cae	Buvignieria convexa Gründel et al., 2019	14	
Cae	Palaeorissoinidae? gen. inc., sp. 1	1	
Cae	Falsobuvigna peregrina Gründel et al., 2019	24	
Cae	Columbellaria corallina (Quenstedt, 1852)	7	
Cae	Columbellaria sp. 1	1	-
Jae De	Columbellaria globosa (Brosamlen, 1909)	1	1
Cae	Suomoldae gen. Inc., Sp. 1 Diarthoma sp. 1	I	2
Jae	Diamaterius sp. 1	л	2
Jae	Diempterus sp. 1 Diempterus? fusiformis (Münster in Coldfuss, 1944)	4 5	6
Jae Het	Cossmannea desvoidvi (d'Orbiany 1851)	J	2
-let	Aptyxiella planata (Quenstedt, 1858)		2
Het	Aptyxiella guenstedti Geiger. 1901		1
			•

			Saal	Nattheim area
Het	Ceritellopsis gramanni Huckriede,	1967	25	
Het	Ceritellopsis plicatula Huckriede, 1	1967	5	
Het	Ceritella convexa Gründel et al., 20	)22	26	
Het	Ceritella sp. 1		9	
Het	Nerinea donosa Gründel et al., 202	22	10	
Het	Endoplocus acutus Gründel et al.,	2022	17	
Het	Endoplocus inflatus Gründel et al.,	2022	10	
Het	Ptygmatis pseudomelaniformis Gr	ündel et al., 2022	37	
Het	Ptygmatis mandelslohi (Bronn, 18	36)	4	
Het	Ptygmatis tornata (Quenstedt, 185	52)	37	3
Het	Ptygmatis nodosa (Voltz, 1836)		142	
Het	Ptygmatis? polyspira (Quenstedt,	1884		1
Het	<i>Ptygmatis? ursicina</i> Thurmann in <sup>-</sup> 1861	Thurmann & Étallon,	19	
Het	Bactroptyxis teres (Münster in Gol	dfuss, 1844)		2
Het	Bactroptyxis? tricincta (Münster, 1	844)	1	
Het	Bactroptyxis? tricincta (Münster, 1 Quenstedt 1881–1884	844) sensu	3	1
Het	Bactroptyxis cf. fasciata (Voltz, 18	36)	1	
Het	Bactroptyxis? subcochlearis (Müns	ster in Goldfuss, 1844)	5	2
Het	Polyptyxisella clio (d'Orbigny, 1852	2)	2	
Het	Cryptoplocus depressus (Voltz, 18	36)	3	10
Het	Cryptoplocus subpyramidalis (Mün	ster, 1844 in Goldfuss)	3	
Het	Nerinella subscalaris (Münster, 18	44 in Goldfuss)		19
Het	Nerinella sp. 1		4	7
Het	Nerinella ornata (d'Orbigny, 1852)		1	2
Het	Nerinella sp. 2		2	
Het	Nerinella sequana (Bronn ex Thirri	a, 1836)	1	
Het	Nerinella biplicata (Quenstedt, 185	58)	4	
Het	Nerinella? sp. 3		1	
Het	Eunerinea sp. 1			3
Het	Eunerinea sp. 2		1	
Het	Itieroptygmatis cylindrata Gründel	et al., 2022	57	
Het	Itieroptygmatis sp. 1		2	
Het	Rugalindrites cylindracea (Cornuel	, 1841)	48	
Het	Rugalindrites sp. 1		2	
Het	t Ptychocylindrites condati (Guirand & Ogérien, 1865)			1
Het	et Volvocylindrites marcousana (Guirand & Ogérien, 1865)			
Het	Sulcoactaeon sp. 1		1 1663	224
F	Patellogastropda	1 species		
١	/etigastropoda	50 species		
, N	Ioritimorpho	1E openico		

Vetigastropoda	50 species
Neritimorpha	15 species
Caenogastropoda	50 species
Heterobranchia	40 species.

Vetigastropoda and Neritimorpha are rather diverse when compared with Early to Late Jurassic soft-bottom communities from shales of South Germany that were studied in the last years (e.g., Schröder 1995; Gründel et al. 2011; Schulbert and Nützel 2013; Gründel and Nützel 2015; Nützel and Gründel 2015). Especially the high neritimorph diversity is remarkable when compared with other faunas and is probably due to their hard substrate, shallow water preference. The generic diversity of Pleurotomariida (Vetigastropoda) is also still relatively high, given that this group is today restricted to deeper water settings. Pleurotomariida occur in shallow water settings until the Late Cretaceous (Kiel and Bandel 2004). Middle

and Late Jurassic faunas reported from clays (soft bottom) of Poland and Russia are, however, dominated for the most part by small caenogastropods and heterobranchs, whereas Vetigastropoda and Neritimorpha are mostly rare (Guzhov 2004; Kaim 2004). It is likely that the strong lithification of the calcareous rocks in Saal produces a bias against small caenogastropod and heterobranch species when compared with faunas from shales that can be easily disaggregated so that such species can be retrieved (liberation effect sensu Roden et al. 2020). Moreover, neritimorphs and vetigastropods commonly have calcitic outer shell layers which facilitate preservation. However, abundance and diversity of Vetigastropoda and Neritimorpha preserves an original signal. The abundance and diversity of nerineoids (Heterobranchia) in the calcareous rocks of South Germany is typical of Late Jurassic shallow water carbonates.

The sample sizes (number of specimens) from Saal and the Nattheim area differ considerably and few species are shared. Diversity indices and rarefaction analysis suggest the same high diversity at both sites (Tables 1, 2). Diversity indices suggest a very high gastropod diversity which can be expected for a tropical reef associated fauna. The gastropod diversity of both studied Late Jurassic sites even exceeds that of the reef associated Late Triassic gastropod fauna of the St. Cassian Formation (N Italy) as is indicated by rarefaction at sample size of 200 individuals (around 40 expected species in the St. Cassian samples from Stuores Meadows and Alpe di Specie (Hausmann and Nützel 2015), and ca. 50 at Saal and Nattheim).

The gastropod fauna from the Saal quarry has yielded particularly much new information – all new species are based on specimens from Saal with only two of the new species also being present in the Nattheim area. The considerable sampling effort including the sample technique applied by one of us (FL, see Methods section above) resulted in the recovery of large numbers of mostly small and well-preserved specimens.

With 125 gastropod species from a single outcrop, the diversity at the Saal quarry is the highest from the Kimmeridgian worldwide that we are aware of. Moreover, a new collection from Saal currently under study will yield even more gastropod species so that likely more than 150 gastropod species are present in the Saal quarry. In addition, numerous other macro-invertebrates have been recovered from the Saal quarry; the following species (or genus) numbers were reported by Lang et al. (2017):

Table 2. Diversity of the gastropod fauna from Saal and from the Nattheim area (Nattheim, Gerstetten, Gussenstadt, Blaubeuren, Bosler, all in Swabian Alb); number of indiduals, species richness, Simpson- and Shannon index, rarefaction at 200 specimens: expected species richness; both gastropod faunas have the same diversity although few species are shared.

	Individuals	Species	Simpson	Shannon	Rarefaction at 200 spcms.
Saal	1663	125	0.96	3.864	50 exp. Species
Nattheim	224	54	0.95	3.417	52 exp. Species

bivalves: 33 (up to 50 according to Werner oral communication 2022) ammonites: 6 brachiopods: 13 serpulids: 8 echinids: 7 corals: 27 (genera) arthropods: 19 and others (e.g. sponges)

In total, up to 300 species of macro-invertebrate species have been reported from this quarry, which is a very high point diversity. Gastropods are by far the most diverse group from Saal, which is a modern aspect of this fauna (see also Roden et al. 2020, who found another example for early gastropod dominance in the Late Triassic St. Cassian Formation).

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