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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

PENSOFT.

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;

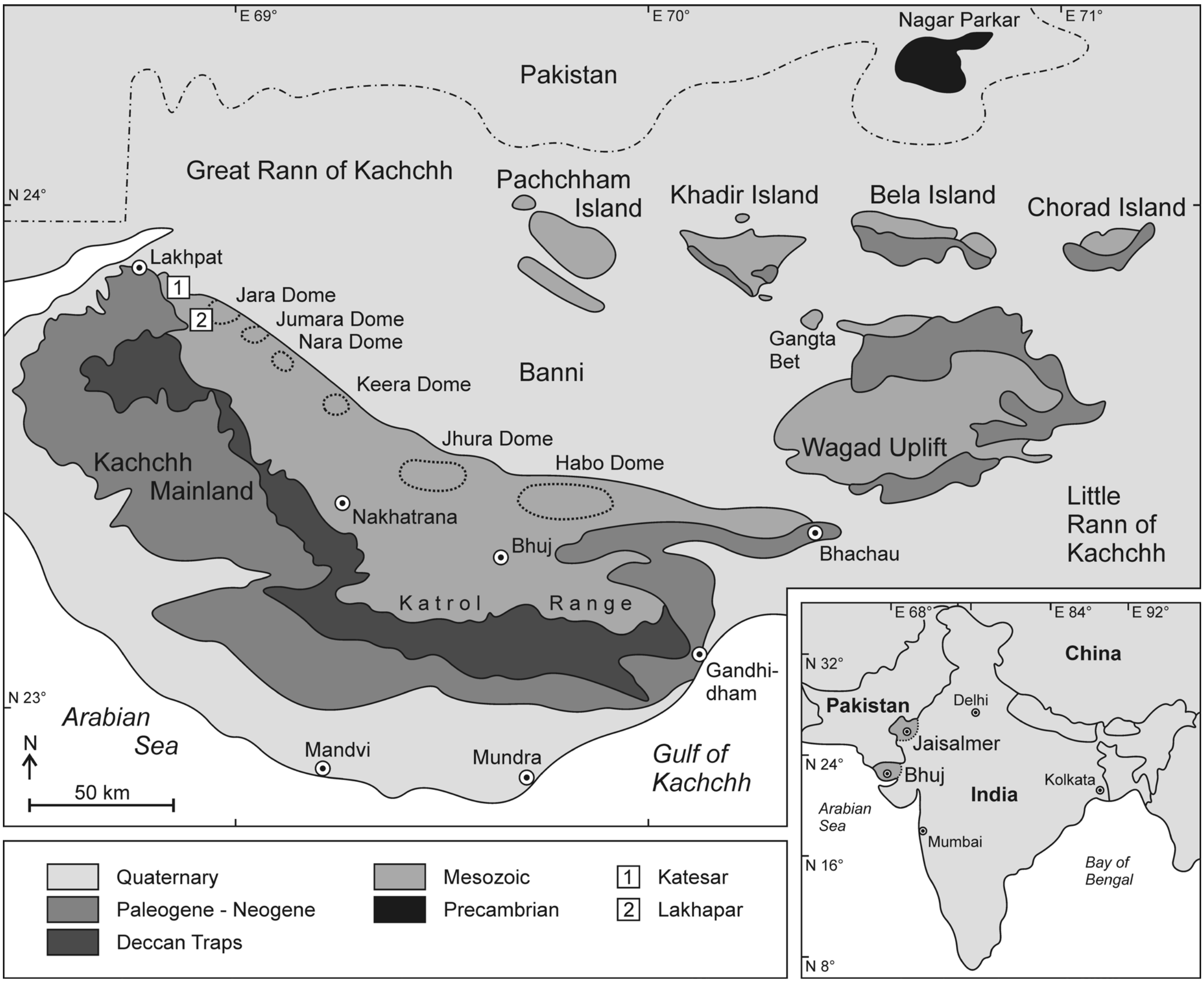
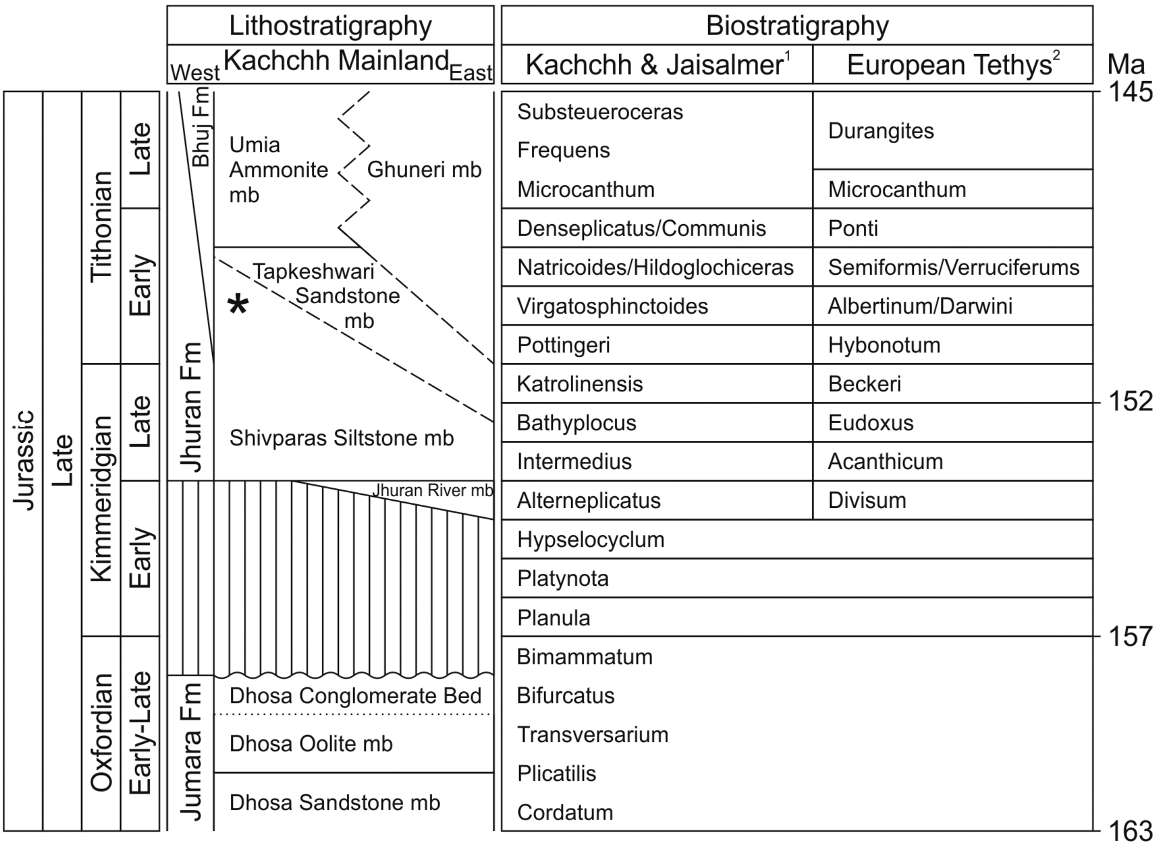


Figure 1. Geological map showing localities of *Hildoglochiceras* in the Jara Dome and Katesar section, Kachchh Mainland.

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.
¹Krishna et al. 2011; Pandey et al. 2012, 2014, 2016
²Cariou & Hantzpergue 1997; Wierzbowski 2008

Figure 2. Litho- and biostratigraphy of the Kachchh Mainland.

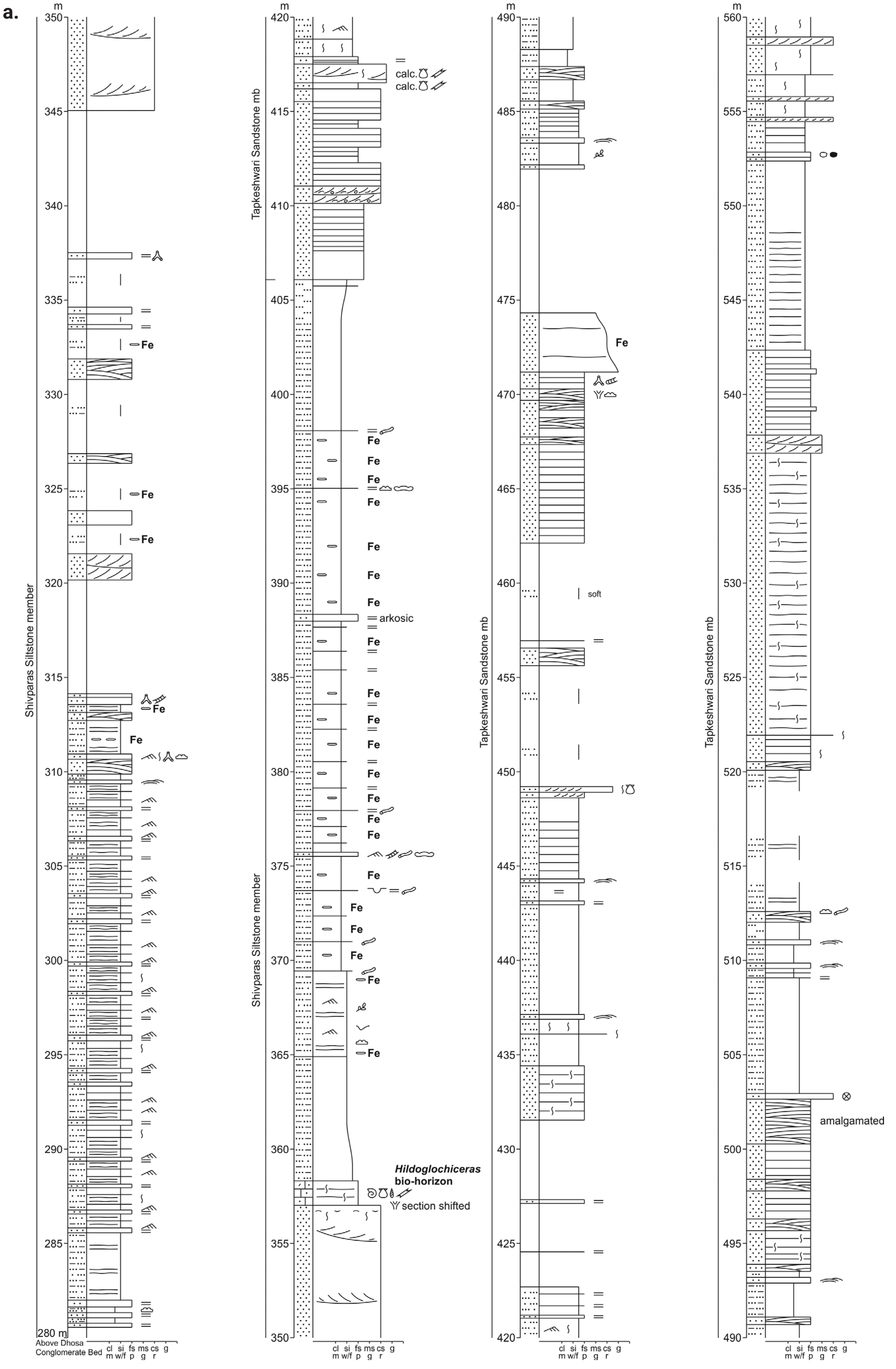


Figure 3. a, b. Lithology of the stratigraphic succession of the upper part of the Jhuran Formation in the western part of the Jara Dome (compare Fürsich et al. 2021).

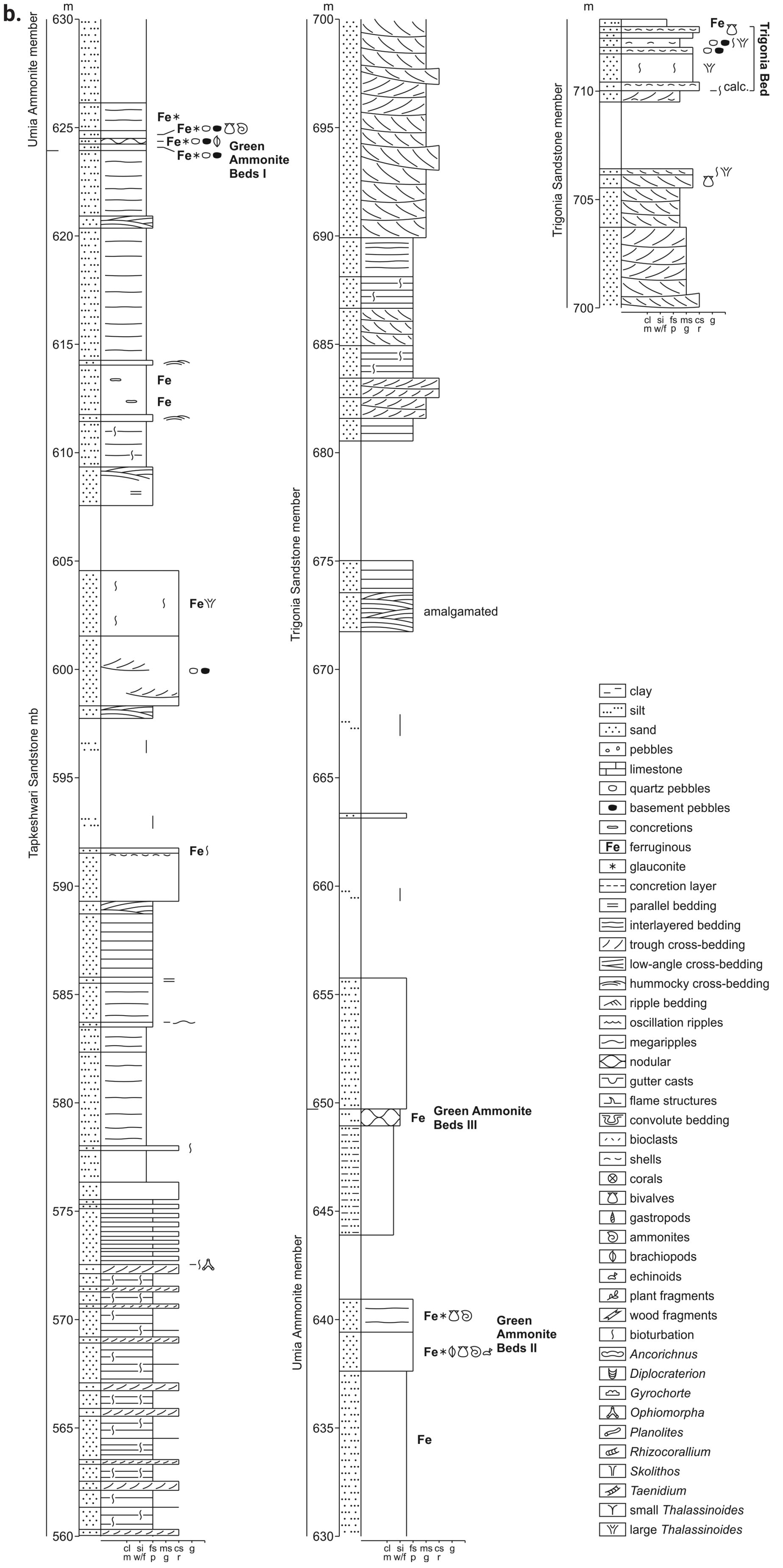


Figure 3. Continued.

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). Énay (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. *propinquum* (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 3rd 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 1st, 2nd, and 3rd order T-R cycles in Kachchh. He interpreted a major 1st order regressive trend during Kimmeridgian and Tithonian times, with 2nd and 3rd 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 Sª 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. Énay (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 *Hildoglochiceras* 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 20th 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-Ateequzzaman 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 Pooniya 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 NJT13a-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 2nd 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 quinqueloba* 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 *Himalayites*, 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 Krishna 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 #:

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

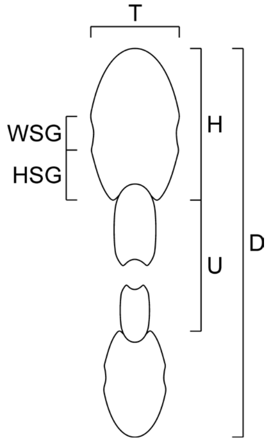


Figure 5. Diagram of dimensions of ammonites, measured with a digital caliper.

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	H	H/D	T	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

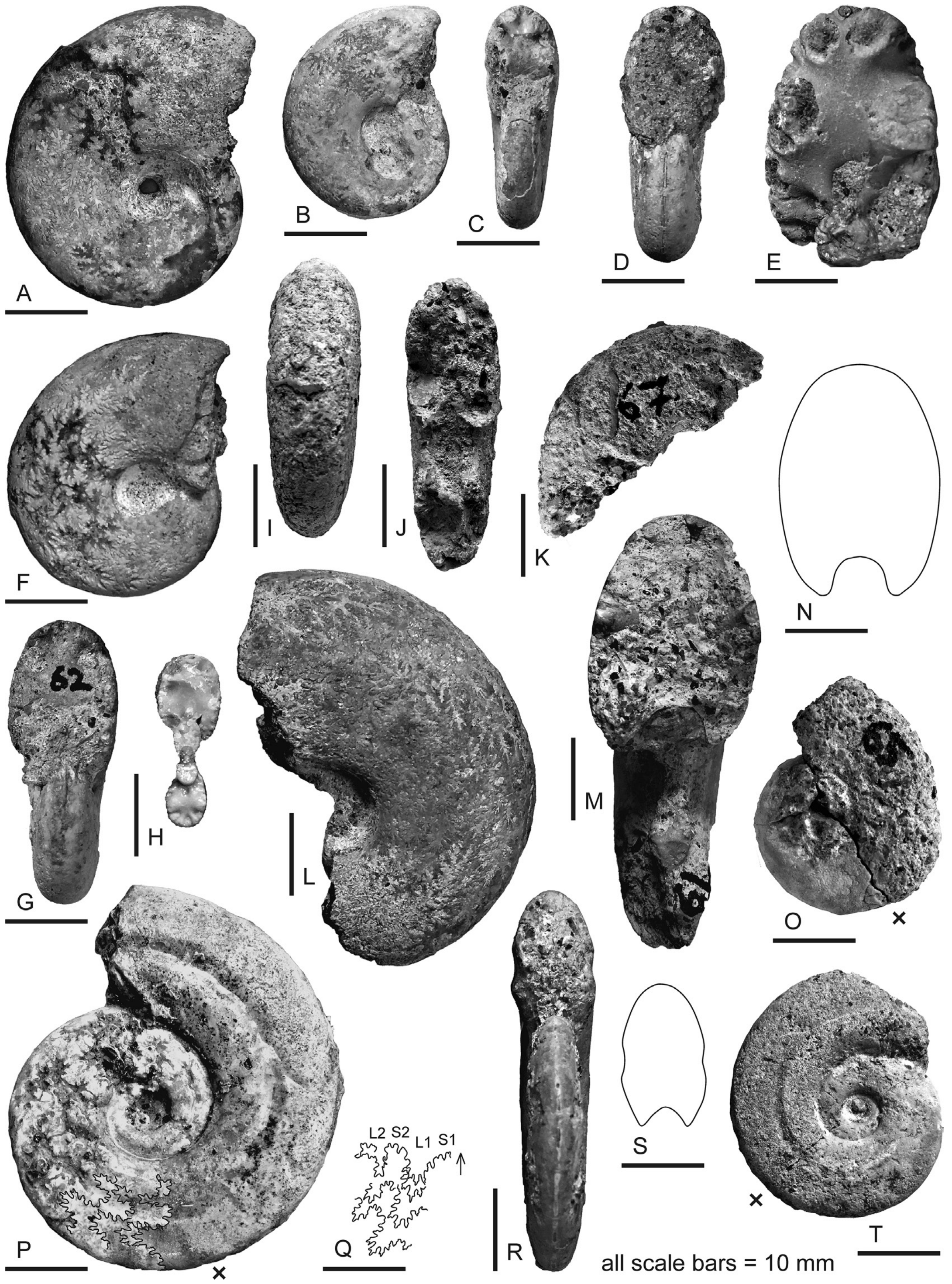


Figure 6. A–G, L–N. *Haploceras staszycii* (Zeuschner, 1846). **A.** KSKV2019Jara/63, left side view of phragmocone, note well preserved suture lines; **B, C.** KSKV2019Jara/64; **B.** Left side view of phragmocone; **C.** Apertural view showing broken aperture along a septum; **D.** KSKV2019Jara/66, 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 genus. His *Haploceras deplanatum* does not belong to this genus, and his *Haploceras propinquum* 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 Énay (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. propinquum*) 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 propinquum* 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 3rd-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 3rd-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	H	H/D	T	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.

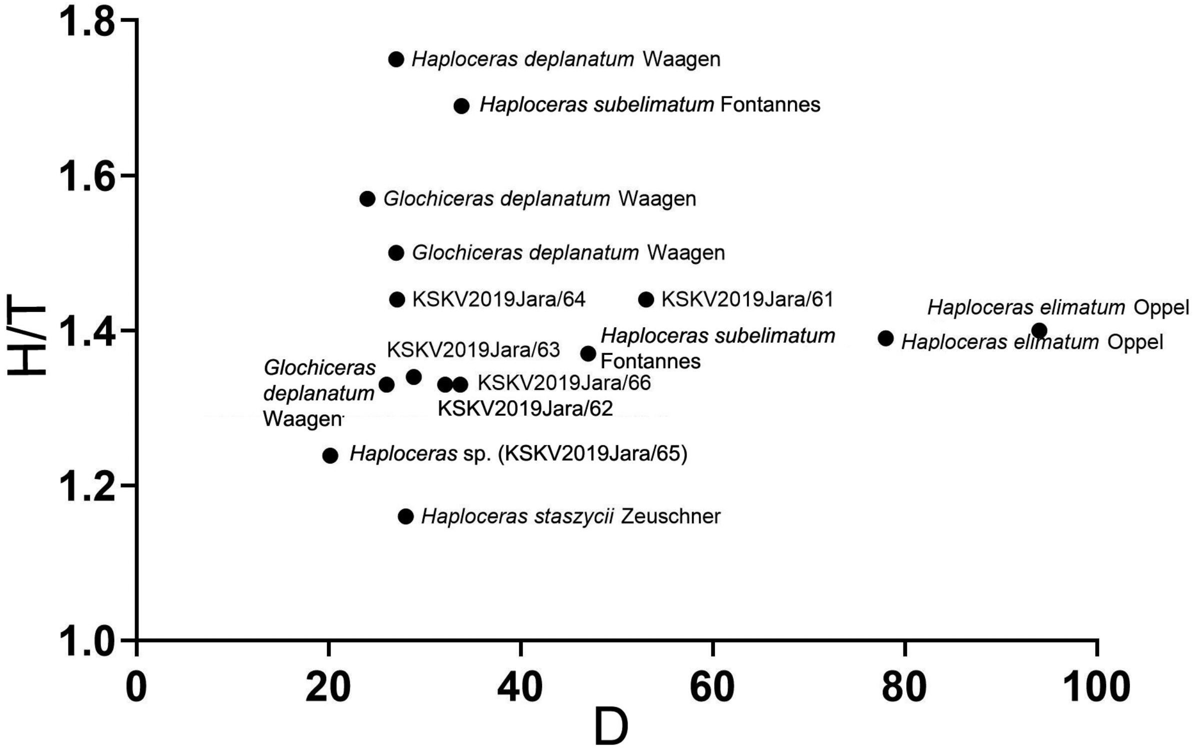


Figure 7. Scatter plot showing D:H/T ratios of some related species of *Haploceras*.

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,

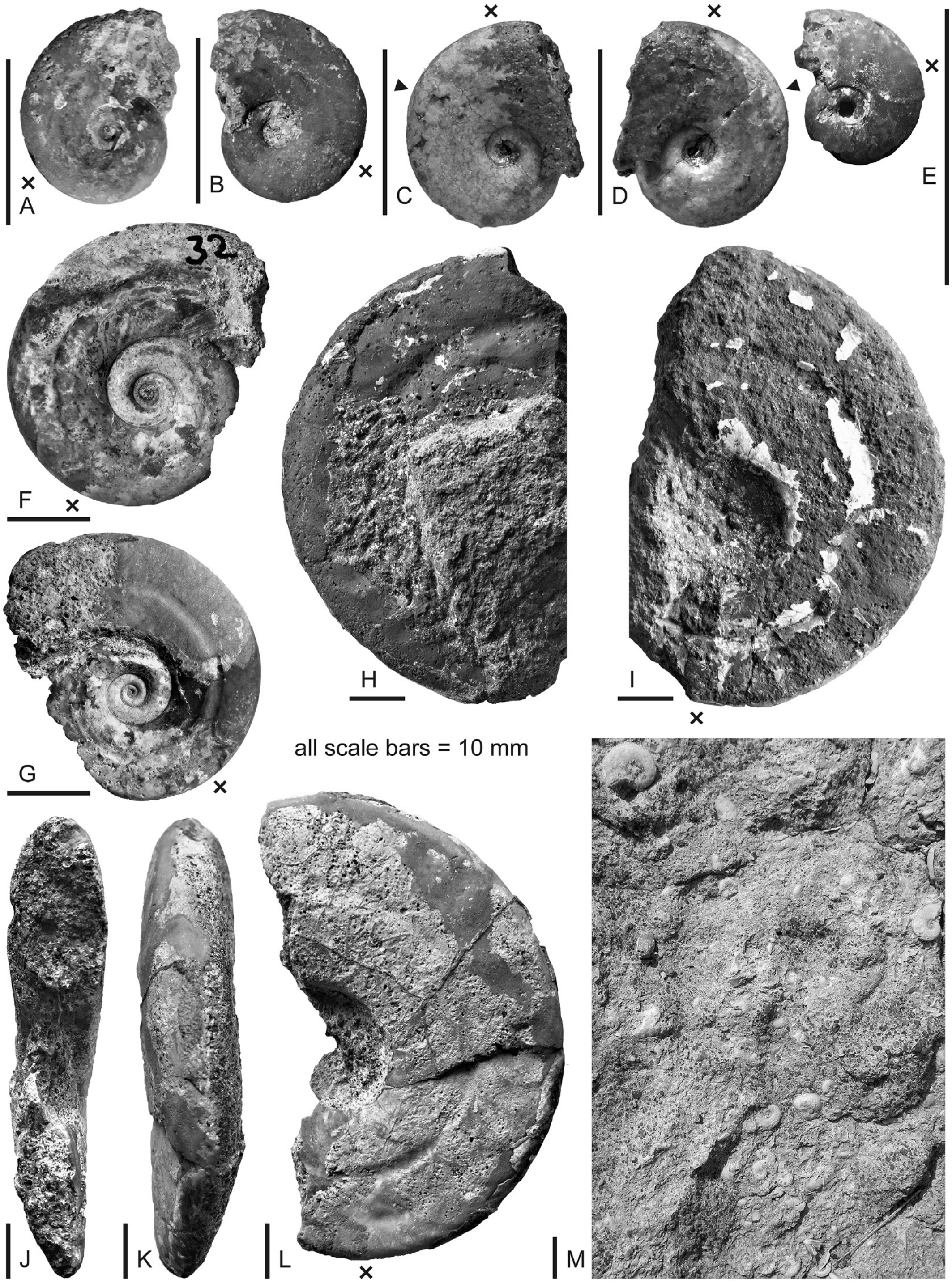


Figure 8. A–E, H–L. *Hildoglochiceras kobelli* (Oppel, 1863b) (M); **A, B.** KSKV2019Jara/42. **A.** Left side view showing phragmocone and part of body chamber; **B.** Right side view showing phragmocone and part of body chamber, note on both sides spiral grooves are developed even at a diameter less 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 on the body chamber closely spaced crescentic ribs. Note remains of the shell at umbilical shoulder and along 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 view, both showing phragmocone and a part of body chamber, presence of a wide spiral groove. Note traces of ribs both near the end of phragmocone and in the beginning of the body chamber; **M.** Close up view of upper surface of the lower most part of the *Hildoglochiceras* bed which is coarse grained micritic sandstone showing juvenile *Hildoglochiceras* and haploceratids.

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 one-third 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 *Hildoglochiceras 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 *Hildoglochiceras* Spath from Indo-Malagasy faunal province (in mm).

species	notation	D	H	H/D	T	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).	B	35	13	37	8.7	25	11.9	34	1.5
Hildoglochiceras sp. aff. *kobelliforme* (Bonarelli) (Enay 2009: 84, pl. 1, fig. 6a, b).	C	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)	H	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)	M	55	22	40	14	25	19	35	1.57
Hildoglochiceras kobelli Oppel (Collignon 1960: pl. 143, fig. 549)	N	42	17	40	11	26	12	29	1.54
Haploceras (*Hecticoceras*) *spira* Zwierzycki (1914: 49, pl. 5, figs l1–13; Spath 1928: 160).	O	33	13.2	40	8.91	27	10.56	32	1.48
Oppelia plana Waagen (1875: 56, pl. 11, fig. 3)	P	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

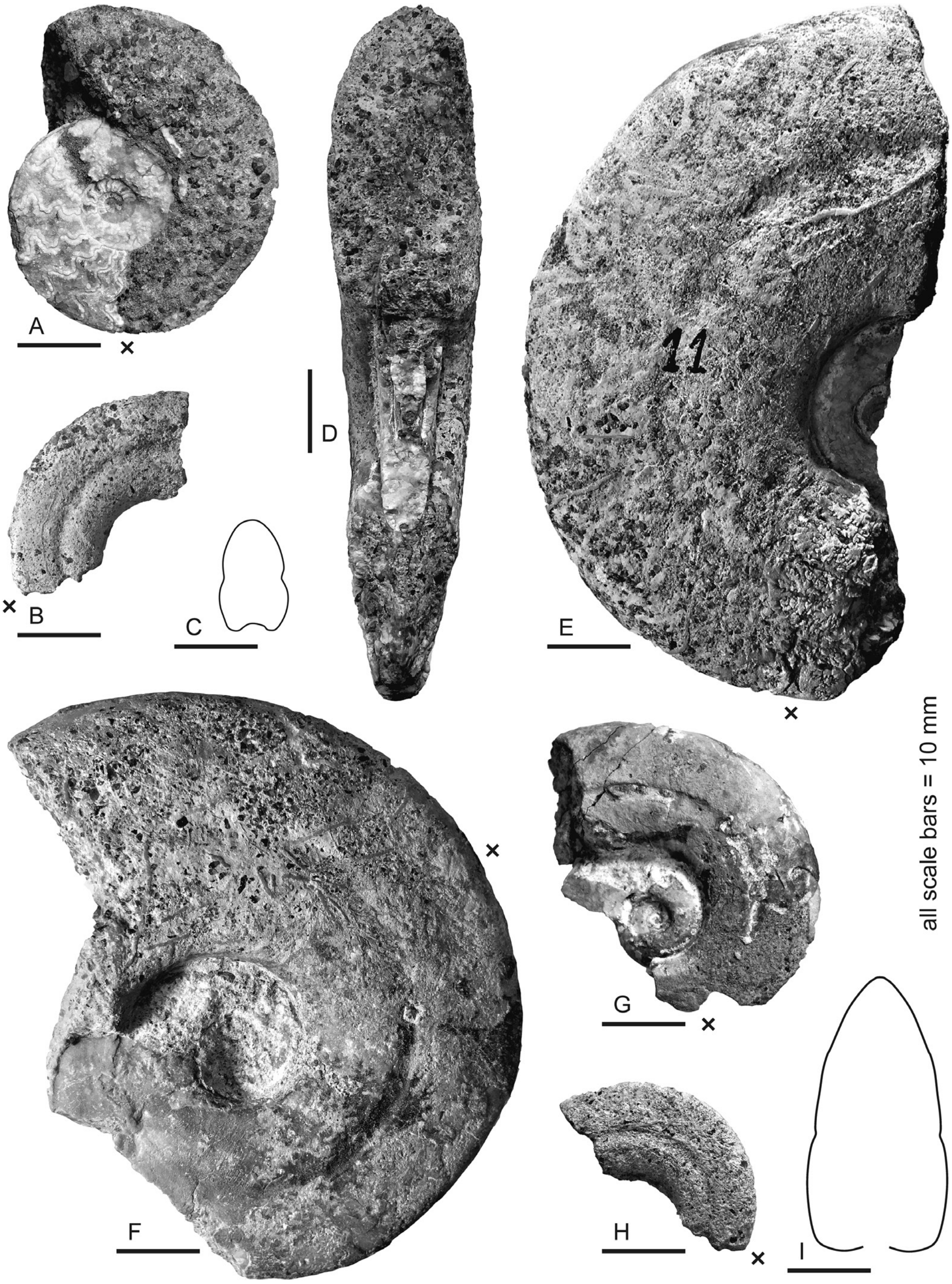


Figure 9. A–C, G, H. *Hildoglochiceras kobelliforme* (Bonarelli, 1894) (m); **A.** KSKV2019Jara/3, inner cast, right side view of abraded, moderately evolute (U ≈ H) adult specimen with clear final uncoiling. Specimen without remains of epigenized shell and showing recrystallized phragmocone with last 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: 1.35–2.0) 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	H	H/D	T	T/D	U	U/D	H/T	WSG	HSG	#	Type
KSKV2019Jara/1	45.6	16.2	35.5	10.3	22.5	15.7	34.5	1.57	2.39	6.24	0	1(m)
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)
KSKV2019Jara/2	31.6	12	37.9	7.8	25.3	10.6	33.5	1.5	1.93	4.17	0	1(m)
KSKV2019Jara/2A	-	9.2	-	5.6	-	-	-	1.64	0.6	3.6	0	1(m)
KSKV2019Jara/3	37.7	14.7	38.9	8.1	21.4	11.8	31.2	1.8	5.60	2.62	0	1(m)
KSKV2019Jara/4	-	11.49	-	6.44	-	-	-	1.78	1.46	4.48	0	1(m)
KSKV2019Jara/4A	-	12.22	-	6.8	-	-	-	1.79	1.99	4.77	0	1(m)
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)
KSKV2019Jara/6	-	13.1	-	8.09	-	-	-	1.61	2.21	5.24	0	1(m)
KSKV2019Jara/6A	-	11.8	-	6.8	-	-	-	1.74	1.93	4.64	0	1(m)
KSKV2019Jara/7	-	13.6	-	8.1	-	-	-	1.67	1.35	4.8	0	1(m)
KSKV2019Jara/8	-	7.04	-	4.65	-	-	-	1.51	0.69	2.90	0	1(m)
KSKV2019Jara/8A	20.5	8.7	42.4	5.03	24.5	5.83	28.4	1.72	0.69	3.95	0	1(m)
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)
KSKV2019Jara/9A	32.8	13.5	41.1	7.38	22.5	8.3	25.3	1.82	1.7	5.75	0	1(m)
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)
KSKV2019Jara/10A	51.41	25.2	49.0	12.72	24.7	10.13	19.7	1.98	2.6	10.3	0	2(M)
KSKV2019Jara/11	83.0	38.6	46.1	18.7	22.5	21	25.3	1.8	4.02	17.59	0	2(M)
KSKV2019Jara/11A	-	34.3	-	16.8	-	-	-	2.0	3.75	15.4	0	2(M)
KSKV2019Jara/12	-	29.5	-	15.04	-	-	-	1.96	3.1	12.09	0	2(M)
KSKV2019Jara/13	42.6	21	49.2	10.5	24.6	9.7	22.7	2	1.77	8.8	0	2(M)
KSKV2019Jara/14	-	16	-	8.4	-	-	-	1.9	1.86	7.5	0	2(M)
KSKV2019Jara/14A	-	14.3	-	7.3	-	-	-	1.95	1.5	6.0	0	2(M)
KSKV2019Jara/15	12.4	5.4	43.5	4	32.2	3	24.1	1.35	0.31	2.34	0	3(M)
KSKV2019Jara/16	15	6.2	41	4.1	27.3	3.5	23	1.5	0.41	2.46	0	3(M)
KSKV2019Jara/19	32.1	14.5	45	9.2	28.6	8.5	26.4	1.57	1.53	6.25	0	4(M)
KSKV2019Jara/19A	-	17.3	-	10.1	-	-	-	1.71	1.53	7.48	0	4(M)
KSKV2019Jara/20	-	20.2	-	12.37	-	-	-	1.63	3.34	7.22	0	4(M)
KSKV2019Jara/20A	-	23.7	-	13.9	-	-	-	1.70	5.58	8.54	0	4(M)
KSKV2019Jara/21	18.4	8	43	5.4	29.3	5.5	29.8	1.4	0.6	2.64	0	1(m)
KSKV2019Jara/22	25.3	11.5	45.4	6.6	26	4.6	18	1.74	0.4	5.3	0	2(M)
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)
KSKV2019Jara/23	-	14.1	-	7.3	-	-	-	1.93	1.48	4.9	0	2(M)
KSKV2019Jara/24	-	10.5	-	5.53	-	-	-	1.89	0.75	4.06	0	2(M)
KSKV2019Jara/25	18.3	8.7	47.5	4.5	24.5	4.4	24	1.9	0.61	3.0	0	2(M)
KSKV2019Jara/25A	-	6.3	-	3.4	-	-	-	1.8	0.34	2.53	0	2(M)
KSKV2019Jara/26	33.6	11.8	35.1	8.6	25.5	13.5	40	1.37	1.71	4.73	0	1(m)
KSKV2019Jara/26A	24.02	10.18	42.3	7.0	29.1	7.76	32	1.4	1.16	4.67	0	1(m)
KSKV2019Jara/26B	17.4	7.3	41.9	5.4	31.0	5.1	29.3	1.3	0.5	3.0	2	1(m)
KSKV2019Jara/27	-	13.55	-	7.29	-	-	-	1.85	0.96	5.65	0	2(M)
KSKV2019Jara/28	24.52	11.40	46.4	6.56	26.7	6.01	24.5	1.73	0.96	4.1	0	2(M)
KSKV2019Jara/29	-	15	-	8.4	-	-	-	1.78	1.31	6.42	0	2(M)
KSKV2019Jara/30	-	14.57	-	8.51	-	-	-	1.71	2.18	5.49	0	2(M)
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)
KSKV2019Jara/32	34.3	13.3	38.7	8.78	25.5	10.94	31.8	1.51	2.92	5.20	0	1(m)
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)
KSKV2019Jara/34	-	32.8	-	16.6	-	-	-	1.97	4.1	13.6	0	2(M)
KSKV2019Jara/35	-	26.9	-	14.1	-	-	-	1.89	2.95	8.6	0	2(M)
KSKV2019Jara/36	-	27.8	-	13.9	-	-	-	2.0	2.6	11.9	0	2(M)
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)
KSKV2019Jara/37A	-	15.3	-	7.7	-	-	-	1.98	1.7	6.22	0	2(M)
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)
KSKV2019Jara/39	11.38	5.78	50.7	3.42	30	2.73	23.9	1.69	0.34	2.97	2	3(M)
KSKV2019Jara/40	06.06	2.82	46.5	2.22	36.6	1.35	22.2	1.27	-	-	-	3(M)
KSKV2019Jara/40A	04.6	2.2	47.8	2.06	43.9	-	-	1.08	-	-	-	3(M)
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)
KSKV2019Jara/42	12.0	5.7	47.5	3.46	28.8	2.64	22	1.64	0.18	2.26	0	3(M)
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)
KSKV2019Jara/44	11.6	5.6	48.27	3.19	27.5	2.2	18.9	1.75	0.3	0.9	0	3(M)
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)
KSKV2019Jara/46	-	9.16	-	4.99	-	-	-	1.83	1.14	3.6	0	1(m)
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	0	1(m)
KSKV2019Jara/49	-	10.35	-	7.3	-	-	-	1.41	1.7	4.77	0	1(m)
KSKV2019Jara/50	-	8.87	-	5.20	-	-	-	1.70	0.35	3.35	0	1(m)
KSKV2019Jara/51	-	9.27	-	5.43	-	-	-	1.70	0.98	3.4	0	1(m)
KSKV2019Jara/52	-	9.45	-	5.21	-	-	-	1.81	0.6	3.65	0	2(M)
KSKV2019Jara/53	-	10.28	-	4.99	-	-	-	2.06	0.67	4.13	0	2(M)

Specimen no.	D	H	H/D	T	T/D	U	U/D	H/T	WSG	HSG	#	Type
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)

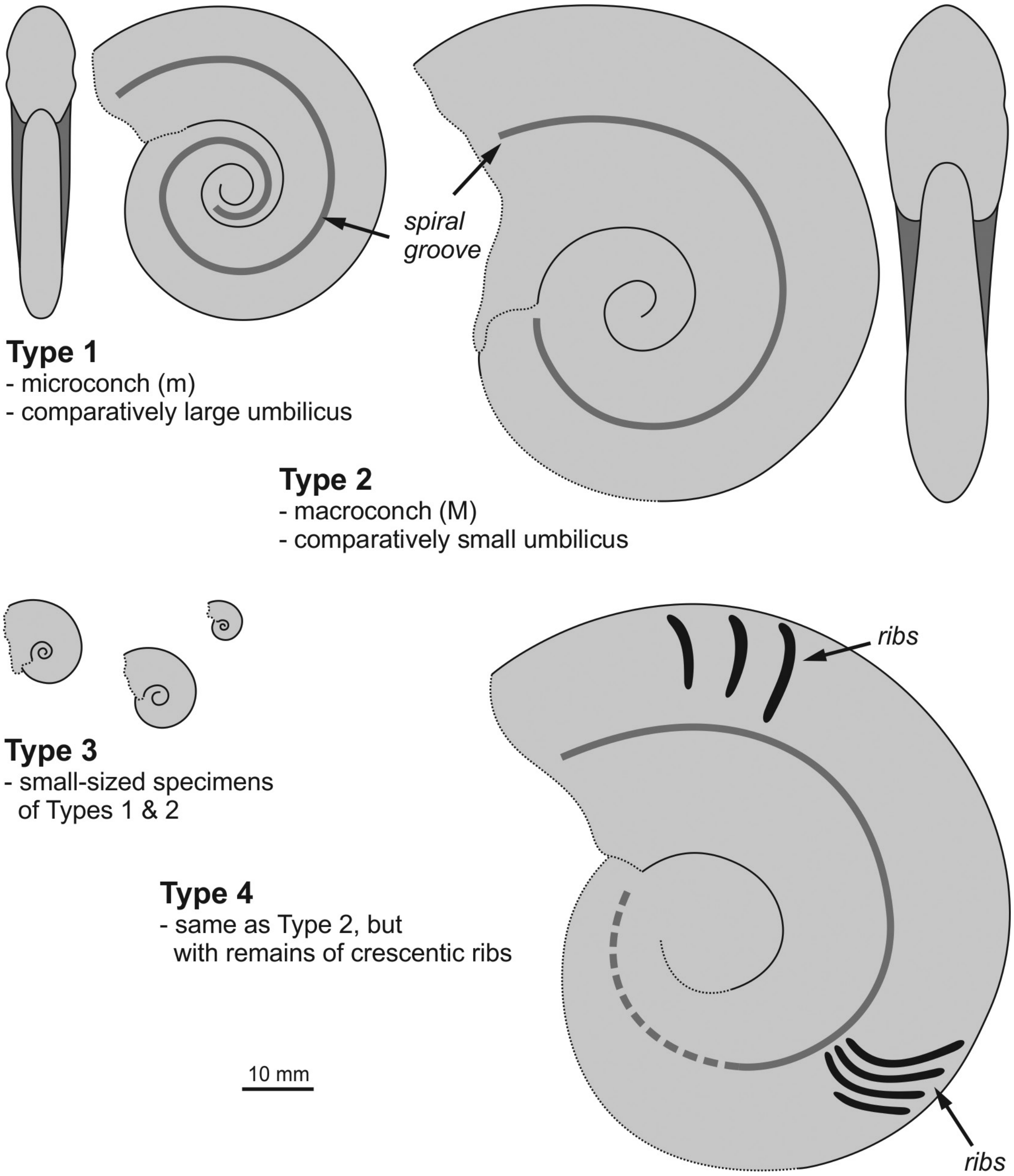


Figure 10. Sketch diagrams of four types (Type 1 to 4) of specimens assigned to *Hildoglochiceras kobelliforme* (Bonarelli) (m) and *kobelli* (Oppel) (M). Type 1 – with large umbilicus, compressed whorl section and acute venter (m). Type 2 – with small umbilicus and compressed whorl-section with acute 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 l l –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 Énay (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 propinquum* 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	H	T	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

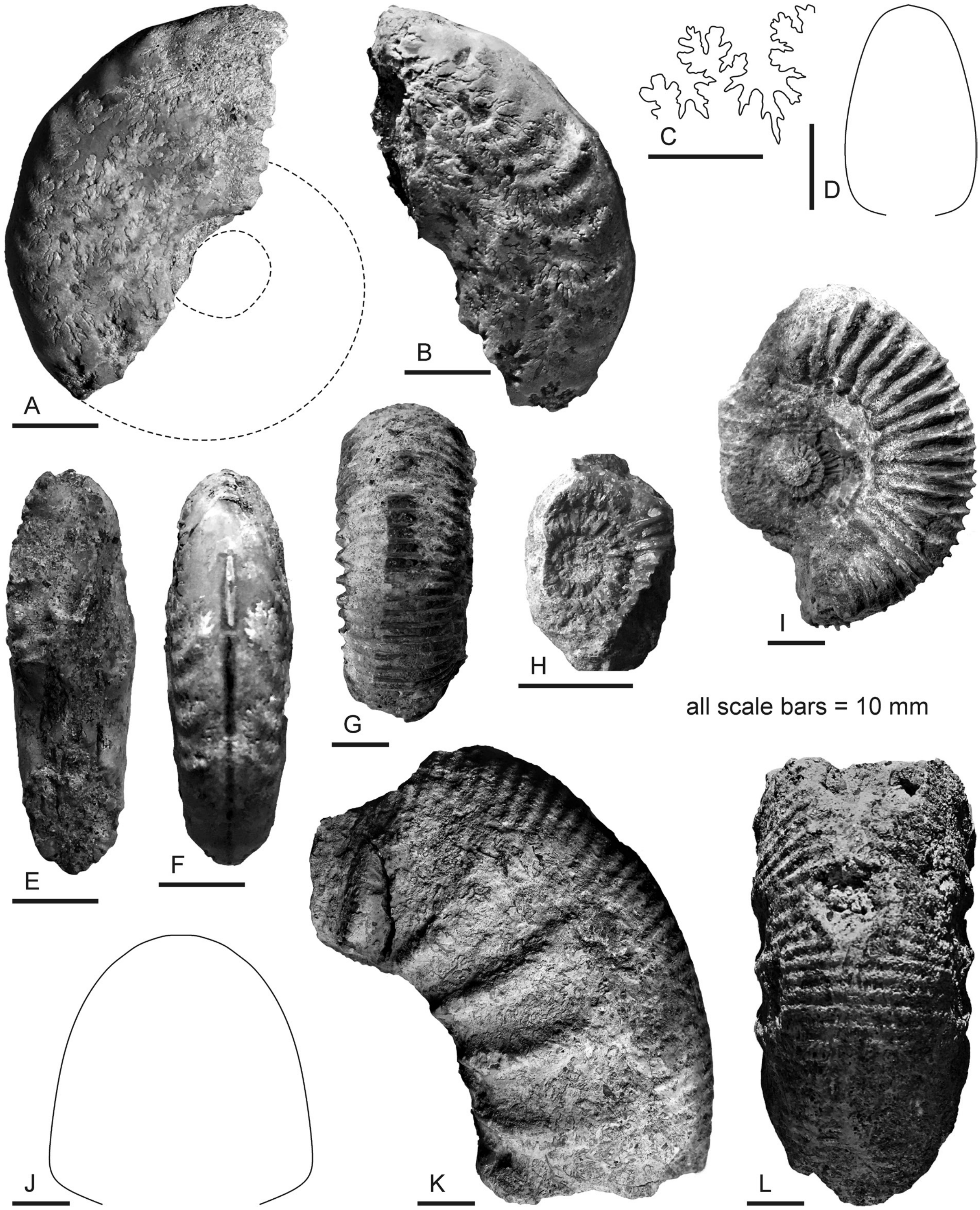


Figure 11. A–F. Taramelliceratinae gen. and sp. ind. KSKV2019Jara/17. **A.** Internal cast, left side view of a fragment of phragmocone showing remnants of blunt secondaries along the periphery; **B.** Right side view showing moderately coarse ornamentation across the flank, with a shallow and discontinuous 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, prorsiradiate, 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 ε to ζ_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_3 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

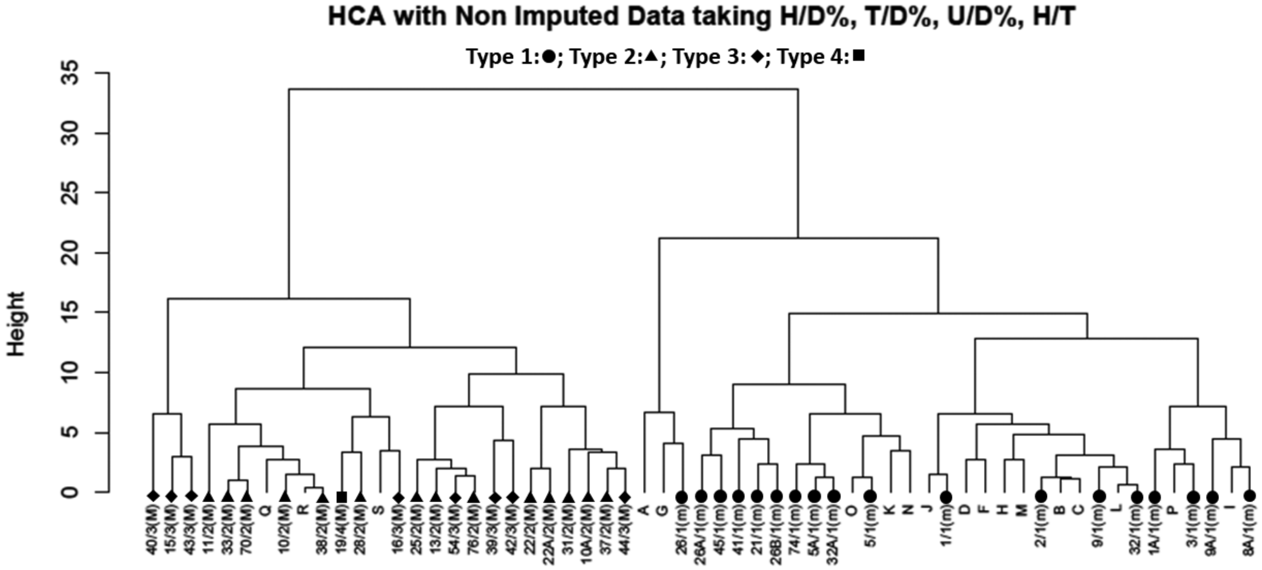


Figure 12. Hierarchical Clustering Analysis (HCA) for the non-imputed (N = 59) dataset using '*hclust*' command in R v3.5.1. Euclidean distances among the specimens were calculated using the '*dist*' command in R. In both cases the normalized data (H/D%, T/D%, U/D% and H/T) were used for Euclidean distance 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.

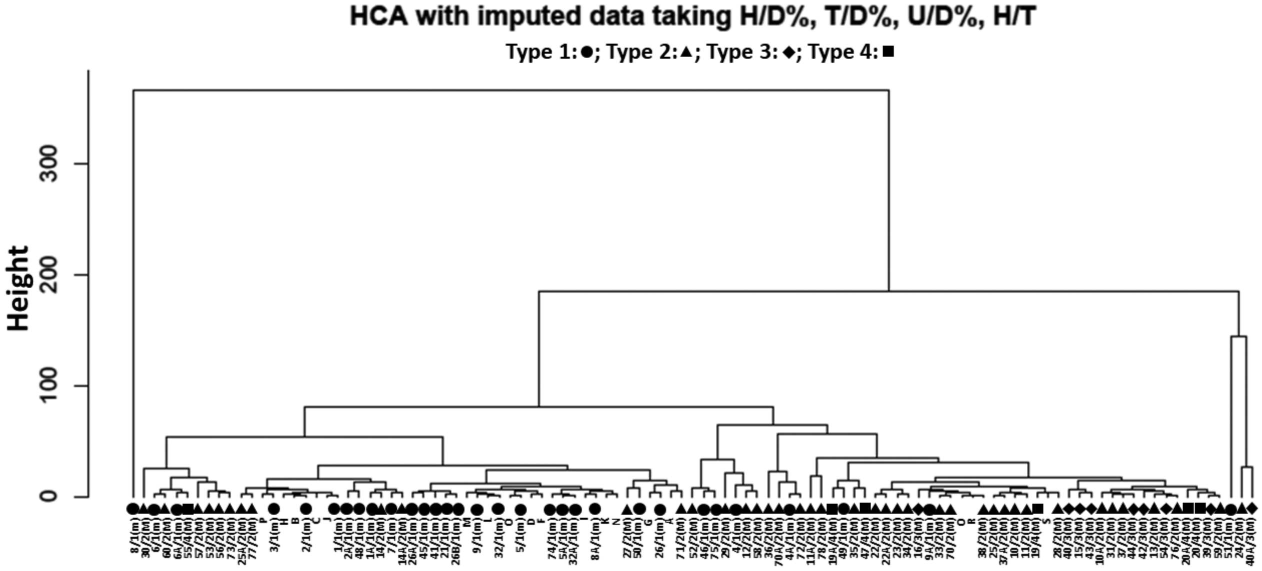


Figure 13. Hierarchical Clustering Analysis (HCA) for the imputed (N = 105) dataset using '*hclust*' command in R v3.5.1. Euclidean distances among the specimens were calculated using the '*dist*' command in R. In both cases the normalized data (H/D%, T/D%, U/D% and H/T) were used for Euclidean distance 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.

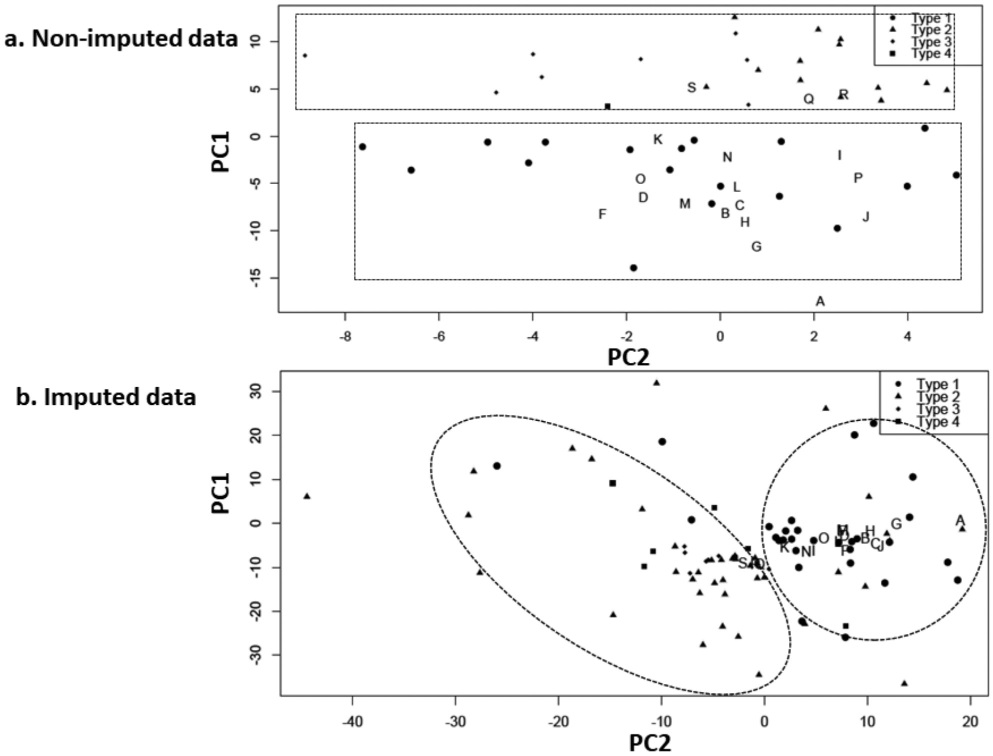


Figure 14. Principal Component Analysis (PCA). Based on their morphological similarities all specimens at the author's disposal were manually grouped into four types, Type 1 to Type 4; **a.** PCA for non-imputed dataset (N = 59) using '*prcomp*' command in R employing the normalized data; **b**. PCA 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^2) 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 '*lr.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 chi-square 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 dependent 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^2	Adjusted R^2	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, **For T = 0.462**, 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			
Model 2 vs. Model 6	42.082	8.75E-11			
Model 2 vs. Model 7	137.835	1.17E-30			
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			

P value: Probability value
AIC: Akaike information criterion
R2: Regression coefficient

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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