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Diplesioceras Buckman, 1920 – an enigmatic Middle Jurassic ammonite genus revisited

Volker Dietze, Günter Schweigert & Robert B. Chandler

Abstract

New specimens of the rare ammonite genus *Diplesioceras* Buckman, 1920 from the Upper Bajocian of Normandy and from the Iberian Ranges of Spain provide additional information on the shell morphology and ontogeny of this previously monotypic genus. A new species of *Diplesioceras*, *D. fischeri*, is recorded by a single specimen probably originating from the Parkinsoni Zone. The new material clearly demonstrates the presence of a vertically undulating floored keel, a character previously only known from some Strigoceratidae Buckman, 1924. This observation let us to discuss whether *Diplesioceras* should be assigned to Strigoceratidae Buckman, 1924. Further characters such as ribbing style and conch ontogeny, intraspecific variation, biostratigraphic occurrence and palaeogeographic distribution were analyzed. Despite of a long stratigraphical gap to supposedly ancestral taxa, a systematic placement of *Diplesioceras* in Hammatoceratidae Buckman, 1887 appears to be more convenient; however, we cannot exclude an origination in Strigoceratidae either.

K e y w o r d s : Hammatoceratidae, Strigoceratidae, morphology, ontogeny, phylogeny, ammonite systematics, Lazarus taxon.

1. Introduction

Diplesioceras Buckman, 1920 is a very rare ammonite genus occurring in the Upper Bajocian of the Middle Jurassic. In previous literature, only a few fragmentary specimens and nuclei of *Diplesioceras* have been illustrated, all of them originating from the western Tethyan realm (Buckman 1920; Dietl 1974; Fernández-López 1985). The only record mentioned from outside of this distribution area is a very questionable and fragmentary specimen from Kenya (Galácz 1997). Since its introduction by Buckman, the higher systematic placement of *Diplesioceras* has been controversially discussed. Spath (1931), Roman (1938) and subsequently Haas (1942) identified some morphological resemblance of *Diplesioceras* – at that time only known by the tiny holotype – with the Cretaceous genus *Dipoloceras* as purely homoeomorphic. In the course of our studies of strigoceratids, a placement of *Diplesioceras* within this family was suspected but could not be confirmed due to the lack of adequately preserved new material (Schweigert et al. 2007). In the most recent attempt (Howarth 2013), *Diplesioceras* was still tentatively placed in «Incertae sedis» within Hildoceratoidea. The aim of this study is to present more complete material that adds significantly to our knowledge of the shell ontogeny of *Diplesioceras* and sheds some light upon the possible taxonomic relationships of this enigmatic genus.

2. The type locality and horizon of *Diplesioceras diplesium*

The genus *Diplesioceras* Buckman, 1920 is based on the monotypic *D. diplesium* Buckman, 1920 as type species. The type series consisted only of the holotype, a nucleus with a diameter of 16 mm (Fig. 1a). After Buckman (1920), it originated from the "Shell Bed" (= *Astarte*-bed; cf. Hudleston 1887) of the Inferior Oolite of Vetney Cross near Bridport (Dorset). This location is synonymous with Vitney Cross (Hudleston 1887 [profile no. 2 = Vitney Cross Quarry] or Vinney Cross (Parsons 1974 [= outcrop no. 14]; Senior 1977). Hudleston (1887) mentioned two small quarries at this locality, the stratigraphically more complete Limekiln Quarry [= probably Hudleston's profile no. 2 and outcrop no. 13 in Parsons 1974] and the Knight's Quarry. Knight's Quarry was lithostratigraphically studied in detail by Richardson (1928–1929). His "*Astarte-obliqua* Bed", which corresponds to the "Shell Bed" of Buckman (1920), has a thickness of almost 60 cm and was said to be very fossiliferous. Interestingly, Richardson (1928–1929) mentioned numerous heteromorphic ammonites from this bed. Hudleston (1887) divided the "*Astarte*-bed" into a lower part with the common bivalve *Astarte obliqua* (Lamarck, 1819) and an upper part with the brachiopod *Terebratula* (today: *Sphaeroidothyris*) *sphaeroidalis* Sowerby, 1823. At present, this bed is officially termed "*Astarte* Bed". In the area

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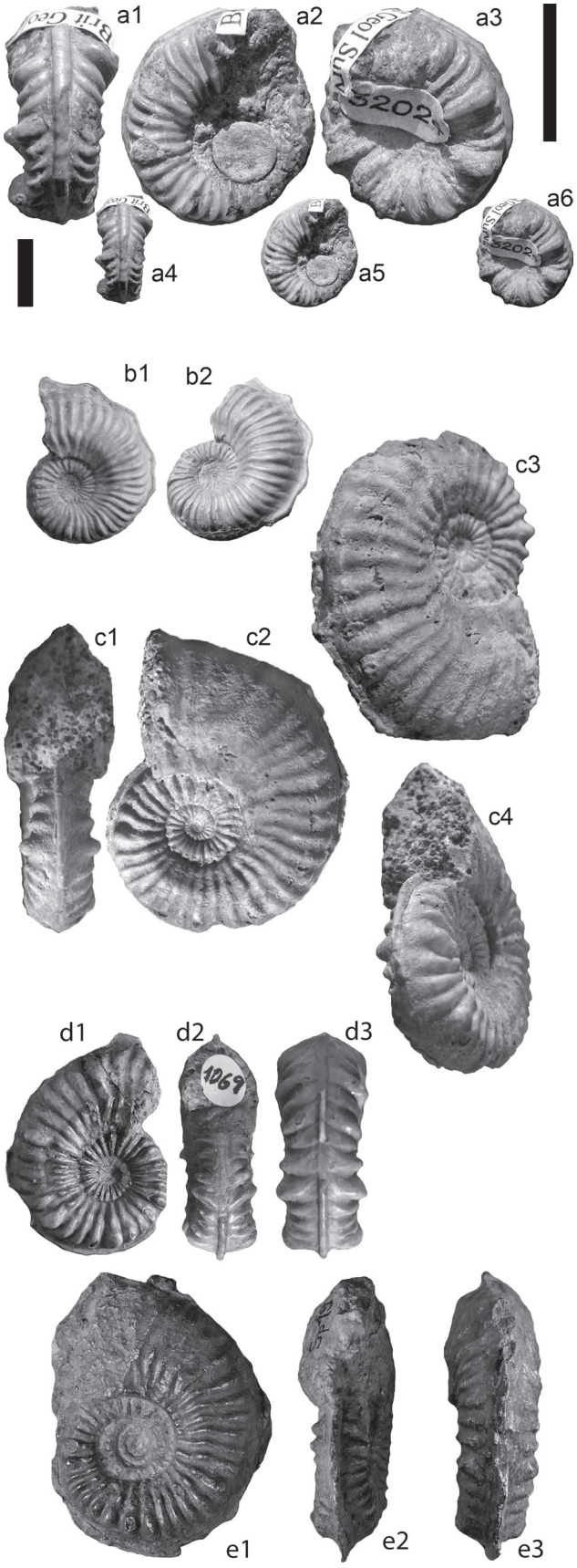

of the type locality of *D. diplesium*, within a few square kilometres between Bridport, Shipton Gorge and Uploders, the *Astarte* Bed belongs to the upper Garantiana Zone (Parsons 1974), at least in its lower part. The road cutting "Loders Cross" located near outcrop no. 1 in Parsons (1974) was exposed during the construction of the motorway A 35 in the 1980s and became well-known among amateur collectors for its abundant white-shelled specimens of *Prorsisphinctes*. In that outcrop, the lower part of the *Astarte* Bed (with *Prorsisphinctes*) belonged to the Garantiana Zone (Tetragona Subzone), whereas the upper part already contained ammonites of the Parkinsoni Zone (Acris Subzone). Similar observations were made in 2010 during an excavation in the *Astarte* Bed near Uploders (close to the outcrops no. 16 and 17 of Parsons 1974).

Based on the descriptions of the lithological section by Hudleston (1887) and Richardson (1928–1929) which include information on the associated perisphinctids and *Spiroceras*, we conclude that the holotype of *D. diplesium* most likely originates from the upper part of the Garantiana Zone (Tetragona Subzone) and not from the Acris Subzone of the Parkinsoni Zone. The information that *Diplesioceras* was a Bathonian genus (Dacqué 1934) is definitely erroneous; moreover, the latter misspelled the genus as "*Diplesiceras*".

3. Morphological observations in published *Diplesioceras* specimens

The three-dimensionally preserved holotype of *D. diplesium* (Fig. 1a) is a phragmocone with a diameter of only 16 mm preserved with its calcitic replacement shell. The coarse rectiradiate primary ribs do not diverge and curve ventrally towards the aperture but do not touch the keel. Every 3rd, 4th or 5th rib is remarkably prominent and ventrolaterally flared. The floored keel is smooth and broadly rounded.

Fig. 1. a, c–e – *Diplesioceras diplesium* Buckman, 1920. **a**: Holotype, British Geological Survey, coll. no. 32024, Inferior Oolite, Astarte Bed, Garantiana Zone (Tetragona Subzone), Vetney Cross near Bridport, Dorset, UK. **c**: SNSB-BSPG 2014 XXXIV 69269 (ex coll. H. Keupp), Oolithe de Bayeux Formation, ? Garantiana Zone, Évrecy, Normandy, France. **d**: Specimen in private collection of Dieter Berger, Wiesloch, Germany (plaster cast: SMNS 70656), Oolithe de Bayeux Formation, ? Garantiana Zone, Sainte-Honorine-des-Pertes, Normandy, France. **e**: SMNS 70657 (plaster cast), Garantiana Zone, Aldea del Pinar, near Salas de los Infantes, Burgos province, Spain (repository of original specimen unknown). **b** – *Diplesioceras fischeri* n. sp., holotype, SMNS 70658, Oolithe de Bayeux Formation, ? Parkinsoni Zone, Port-en-Bessin, Normandy, France. Scale bars equal 1 cm (Fig. 1a1–a3 in double size).

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The fragmentary specimen from N Spain reported by Dietl (1974: pl. 3, fig. 3) and another small fragment illustrated by Fernández-López (1985: pl. 17, fig. 7) correspond well with the tiny holotype and do not provide further morphological information except for a juvenile suture line in the first one. The suture line at this early stage is very similarly developed in a wide range of Middle Jurassic hildoceratoid ammonoids and provided no hints for the systematic placement.

4. New records of *Diplesioceras diplesium* from Normandy and Spain

New and more complete specimens from the Upper Bajocian of Normandy and from northern Spain add to our knowledge of the morphological characters and ontogeny of *Diplesioceras*.

The first one is a *D. diplesium* (Fig. 1c) from the Oolithe de Bayeux Formation of Évrecy. It is a phragmocone with a diameter of *c.* 45 mm. The ventrally rounded keel exhibits a very weak vertical undulation. It seems that the onset of this undulating stage appears later than in the specimen of *Diplesioceras fischeri* n. sp. from Porten-Bessin described below. On the last preserved whorl, another short section of the keel is preserved; however, the undulation is still less prominent than in *D. fischeri* n. sp. The specimen from Évrecy shows an advanced ontogenetic stage, but its body chamber is broken off and thus we do not know the adult stage. After about one third of the outer whorl the ventrolateral nodes disappear, the ribs become weaker and shallower, especially on the inner flank. In some parts of the flank the shell is missing and the suture lines are discernible. The suture shows only few elements on the flank, a very deep and prominent lateral lobe and a single umbilical lobe. Despite of the relatively small size of the ammonite this suture line is very complex ("fissilobate") already at this early ontogenetic stage.

The exact finding level of this specimen within the highly condensed Oolithe de Bayeux Formation is unknown and cannot be reconstructed by lithological means alone (see Pavia et al. 2013); however, typical ammonites of the upper Garantiana Zone are well recorded from Évrecy in an identical rock matrix.

A further specimen of *D. diplesium* (Fig. 1d) was collected from the Oolithe de Bayeux Formation at Sainte-Honorine-des-Pertes, Normandy. It is a phragmocone of *c.* 31 mm diameter preserved with its calcitic replacement shell. The ribbing is relatively coarse, exclusively consisting of rectiradiate to slightly falcoid primaries. Numerous flared ribs occur at irregular distances. The flares are clearly formed by parabolic nodes. In the falcoid stage present in the last half whorl, the kinking points of the ribs bear small nodes as well. On the venter, the ribs become proverse and widen up before they abruptly end along the unsculptured floored keel. The keel is thick and ventrally rounded; parts of it were lost, however, in the latest part of the phragmocone there is an undulation.

The section at Sainte-Honorine-des-Pertes is the historical type section of d'Orbigny's Bajocian stage. A detailed analysis of the Oolithe de Bayeux section has shown that there is strong condensation and re-elaboration (Pavia 1994). The preservation of ammonites allows to assign the *D. diplesium* of Fig. 1d to Pavia's taphorecord 5/2 which corresponds to the late Garantiana to early Parkinsoni zones. We assume from the striking morphological similarity with other specimens that this specimen most likely originates from the late Garantiana Zone as well.

From the same area in the Burgos province of Spain where Dietl (1974) and Fernández-López (1985) previously had recorded very fragmentary specimens of *Diplesioceras diplesium*, two more complete specimens were collected decades ago by a German amateur fossil collector. Unfortunately, the whereabouts of these specimens are unknown, because the specimens were later purchased to an anonymous person; however, there exists a nice plaster cast (Fig. 1e) of the bigger one of the two specimens. The latter is a completely septate phragmocone of 40 mm diameter lacking the body chamber. The sharp undulating keel is partially preserved. The inner whorls of the specimen are poorly preserved and roughly prepared and thus cannot be studied. Flared ribs occur irregularly, some of which even directly follow one another, without any intercalated normal ribs. The latest flared rib occurs at a diameter of c. 30 mm. The last half of the outer whorl shows prorsiradiate falcoid primaries that arise from a steeply dipping umbilical edge. In the lower third of the flank, the kink of the falcoid ribs is pronounced by weak parabolic nodes.

Further records of *Diplesioceras* from the Garantiana Zone have been mentioned in faunal lists of various localities of the Sierra de Albarracín of eastern Spain (Meléndez et al. 2002); however, none of this material has been illustrated.

5. Description of a new species of *Diplesioceras* from Normandy

Genus *Diplesioceras* Buckman, 1920

Type species: *Diplesioceras diplesium* Buckman, 1920, by monotypy.

Additional taxa included: *Diplesioceras fischeri* n. sp., herein.

Diplesioceras fischeri n. sp.
Fig. 1b

1998 *Phlycticeras aenigmaticum*. – Schweigert & Dietze, p. 5 only.

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Table 1. Measurements [mm] of *Diplesioceras* spp. D = diameter; Wh = whorl height; Ww = whorl width; Uw = umbilical width; R = secondary ribs per whorl.

Specimen	D	Wh	Ww	Uw	R
D. diplesium, holotype	16	7.5	9	?	?
D. diplesium, SMNS 70656	31	11	14.5	9.5	28
D. diplesium, SMNS 70657	40	17.5	12.7	11.3	32
D. diplesium, SNSB-BSPG 2014 XXXIV 69269	45	20.8	13	13	32
D. fischeri, SMNS 70658	24	12.5	(7)	7	37

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E t y m o l o g y : Named after the finder, Wolfgang Fischer (Schriesheim).

H o l o t y p e : SMNS 70658, a macroconch, illustrated on Fig. 1b.

T y p e l o c a l i t y : Port-en-Bessin, Normandy, NW France.

T y p e h o r i z o n : Oolithe de Bayeux Formation, upper Bajocian, probably Parkinsoni Zone (for discussion of the age see below).

M a t e r i a l s t u d i e d : Only holotype.

M e a s u r e m e n t s : See Table 1.

D i a g n o s i s : Fine-ribbed species of *Diplesioceras* with an accelerated ontogeny.

D e s c r i p t i o n : The holotype is a laterally prepared specimen preserved with its calcitic replacement shell. At the end of the preserved part, the inner mould is discernible and clearly indicates that the specimen is a fully septate phragmocone, and hence, the body chamber is completely missing. The specimen has a diameter of 24 mm and an estimated maximum whorl width of 7 mm. The floored, ventrally well-rounded keel shows a prominent vertical undulation. Its lateral margins are slightly concave. Up to a diameter of *c.* 15 mm, the relatively broad whorl section and ribbing style resemble those of *D. diplesium*, but its ribs are finer than in the latter. Every fourth rib thickens ventrolaterally and ends in a node; these flared ribs are weaker than in *D. diplesium*. On the last half of the outer whorl, there is a marked habitual change. The whorl section becomes higher, the flares disappear, and the simple ribs touch laterally the vertically undulating keel. The rectiradiate ribbing in the juvenile stage is replaced by a slighty falcoid ribbing. The kinking point is less marked than in *D. diplesium*. In the latest part of the outer whorl, a few secondary ribs are intercalated.

D i s c u s s i o n : In *Diplesioceras fischeri* n. sp. the change from the juvenile stage with flared ribs to the next stage with a discoidal whorl section occurs very early in ontogeny. Since at least the entire body chamber was lost prior to burial, we cannot reconstruct the final size of this specimen, but we assume that the maximum conch size was smaller than in *D. diplesium*. Of course, more material is needed to confirm this assumption. Superficially, *Diplesioceras fischeri* n. sp. resembles the holotype of *Phlycticeras aenigmaticum* (Fernández-López, 1985), with which it was originally confused (Schweigert & Dietze 1998). The latter differs from *D. fischeri* n. sp. in the whorl section, the absence of flared ribs, a strictly falcoid ribbing style throughout ontogeny, and a sharpened keel.

At Port-en-Bessin, most parts of the ferruginous Oolithe de Bayeux Formation belong to the Upper Bajocian Parkinsoni Zone. Only at its basalmost part, ammonites of the Niortense Zone sporadically occur (pers. comm. G. Pavia 2022). Hence, this *Diplesioceras* specimen must originate either from the Niortense Zone or, much more likely, from the Parkinsoni Zone. Since the stage with flared ribs is significantly shorter than in all *Diplesioceras diplesium* specimens of the Garantiana Zone, we suspect that the unique specimen represents a younger chronospecies of the Parkinsoni Zone.

6. Comments on possible sexual dimorphism in *Diplesioceras*

Fernández-López (1985) considered *Diplesioceras* being the microconchiate counterpart of his newly introduced oxyconic genus *Melendezia* Fernández-López, 1985. Subsequently, however, *Melendezia* was interpreted as a younger subjective synonym of *Phlycticeras* Hyatt, 1900 (Schweigert & Dietze 1998; Schweigert et al. 2000). Indeed, unequivocal *Phlycticeras* from the Garantiana Zone and slightly younger chronospecies of this lineage differ significantly from *Diplesioceras* in a strictly oxyconic whorl section with a sharp and narrow keel, complete absence of tubercles and, if the shell is well preserved, in the presence of a spiral strigation. Among the ammonites studied and illustrated by Fernández-López (1985), a relatively evolute specimen included by him in *Melendezia* (Fernández-López 1985, pl. 17, fig. 10) might well represent a microconchiate *Diplesioceras*, since it shares both the whorl section and subadult ribbing style of our new material presented here. The preserved body chamber with a length of about one whorl suggests it was nearly adult, although the aperture is not preserved. The corresponding microconchs of *Phlycticeras* spp. are represented by the small-sized *Oecoptychius* Neumayr, 1878 (Schweigert & Dietze 1998, 1999), which differs from this putative *Diplesioceras* microconch both in its ornamentation and eccentric coiling, a much smaller size and, most important, by the complete absence of a keel.

Fernández-López (1997, fig. 4B) illustrated a tiny globose ammonite from the Parkinsoni Zone of Ricla

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(Zaragoza, Spain) as "*Diplesioceras* sp. nov." and interpreted the latter as the corresponding microconch of *Melendezia enigmatica* [recte: *aenigmatica*] Fernández-López, 1985. In our view, a generic assignment of this very strongly corroded internal mould is impossible due to its poor state of preservation.

The small and densely ribbed specimen illustrated by Fernández-López (1985, pl. 17, fig. 8) as "*Diplesioceras* sp. nov. 1" is not a microconchiate *Diplesioceras* either, but more likely a representative of *Toxamblyites* with a relatively broad section but lacking a keel. A fragmentary specimen which is well comparable in lateral view to the latter has been recorded from the Bajocian of Kenya (Galácz 1997). The fine and truly biplicate ribbing of these specimens contradicts a determination as *Diplesioceras*.

In respect of their rather involute coiling and despite of their relatively small sizes, all herein newly recorded specimens of *Diplesioceras* are considered as juvenile macroconchs.

7. Discussion of the systematic relationships of *Diplesioceras*

The systematic placement of *Diplesioceras* was controversially discussed from the first mention until today. Originally, Buckman (1920: 25) had placed it in Oppeliidae Douvillé, 1890. Subsequently, Spath (1931) and later Arkell (in Arkell et al. 1957) tentatively included it in Sonniniidae Buckman, 1892. The latter saw some morphological similarities with *Poecilomorphus* Buckman, 1889, *Sonninia* Bayle, 1878 or *Zurcheria* Douvillé, 1885. Arkell's opinion, however, was strictly rejected by Donovan et al. (1981). These authors found little similarities with sonniniids and pointed to the relatively long stratigraphical gap between the latest sonniniids and the sudden appearance of *Diplesioceras*. Consequently, they kept the higher systematic placement as open. Fernández-López (1985) added *Diplesioceras* after the representatives of the subfamily Bradfordiinae Callomon in Donovan et al., 1981, thus suggesting a placement within Haploceratidae Zittel, 1884. More recently, Howarth (2013) concurred with Callomon et al.'s opinion and placed it again in "incertae sedis" within Hildoceratoidea. This was the state of the art until our new study.

The herein documented specimens add significantly to the knowledge of the morphological characters of *Diplesioceras*. The shell surface is absolutely smooth, lacking any remains of spiral strigation. Coarse, rectiradiate primaries occur from the earliest visible stage onwards. In the juvenile stage, parabolic nodes occur in a ventrolateral position and form flared ribs. In a slightly later ontogenetic stage, the conch becomes discoidal and below mid-flank some ribs are thickened. The floored keel is broadly rounded and undulates vertically. Last preserved (?adult) stage shows a weakening of ribbing. These additional characters must be safely taken into account when discussing the systematic affiliation of *Diplesioceras*.

An assignment of *Diplesioceras* to Oppeliidae as suggested by Buckman (1920) and later repeated by Dacqué (1934) can be easily excluded because of the floored keel, which is not developed in typical oppeliid genera (*Oppelia* Waagen, 1869, *Oxycerites* Rollier, 1909, *Oecotraustes* Waagen, 1869, etc.). This important character also excludes the subfamily Bradfordiinae. Fernández-López (1985) suspected an origination of *Diplesioceras* from latest representatives of *Poecilomorphus* Buckman, 1889, which itself is said to have evolved from *Toxamblyites* Buckman, 1924 (Sturani 1971; Donovan et al. 1981). Striking differences in the ribbing style and the keel in *Diplesioceras* and *Poecilomorphus*, however, do not point to a closer phyletic relationship but only to a superficial homoeomorphy (in the juvenile stage) between these two genera.

In first view, the vertically undulating keel of *Diplesioceras* points to an assignment to Strigoceratidae, where an undulating keel occurred independently within two phyletic lineages. In Phlycticeratinae (*Phlycticeras*, *Oxydiscites*), the keel is very sharp and finely serrate, unlike that in *Diplesioceras*. In Strigoceratinae, the keel is smooth and rounded, closer to that of *Diplesioceras*. Within Strigoceratinae, only the genus *Granulochetoceras* Geyer, 1960 exhibits a floored undulating keel (Schweigert et al. 2007). Its earliest known representative, *G. oppeliisculptum* Schweigert et al., 2007, from the Garantiana Zone of Spain, is still closely reminiscent to a strigoceratid ancestor. In *Diplesioceras diplesium* occurring at the same time and even in the same area as *G. oppeliisculptum*, there is no spiral striation discernible despite of the perfect preservation of the shell. Additionally, Strigoceratinae (as well as Phlycticeratinae) never show a coarse ribbing already in the nucleus as in *Diplesioceras*. Thickened ribs at mid-flank occur in some Phlycticeratinae, but never in Strigoceratinae, and parabolic nodes as on the flared ribs of *Diplesioceras* are unknown yet in both subfamilies. If we have correctly interpreted the specimen illustrated by Fernández-López (1985, pl. 17, fig. 10) as a microconchiate *Diplesioceras*, this morphology is untypical of a member of Strigoceratinae, where the microconchs are much smaller and always show an eccentric coiling. Hence, this analysis of characters does not confirm an affiliation to Strigoceratidae (Strigoceratinae and Phlycticeratinae) except for the presence of an undulating keel.

Alternatively, a placement of *Diplesioceras* within Sonniniidae Buckman, 1892 must be considered. Both the blunt ribbing and the undulating keel are unknown in sonniniids, whereas the presence of spines does not contradict

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such a placement. However, there is a significant stratigraphical gap between the last occurrence of sonniniids in the Humphriesianum Zone and the appearance of *Diplesioceras* in the Garantiana Zone.

Finally, we may suspect a placement of *Diplesioceras* in Hammatoceratidae. This is corroborated by the broad section of the nucleus, the rounded floored keel and the blunt ribbing style. Most important, the development of parabolic nodes on the ribs is a rather common character of hammatoceratids. But if *Diplesioceras* was a hammatoceratid, what are the ancestral forms? The youngest known hammatoceratids, sometimes included in Sonniniidae, are represented by *Fissilobiceras* Buckman, 1919, a genus which ranges up to the Humphriesianum Zone (Dietze et al. 2011). Morphologically, the poorly sculptured *Fissilobiceras* is no adequate candidate for an ancestral form leading to *Diplesioceras*. In contrast, hammatoceratids of the *Eudmetoceras* / *Euaptetoceras* group are morphologically much closer, especially in respect of their blunt ribbing style developed very early in ontogeny and their gradual ontogenetic change towards a discoidal whorl section (see e.g. Linares 2002, Kovács 2009). In any case, the undulation of the keel must be interpreted as a derived character. A placement of *Diplesioceras* within Hammatoceratidae, however, is questioned by the fact that both *Eudmetoceras* Buckman, 1920 and *Euaptetoceras* Buckman, 1922 are unknown from strata younger than the early Bajocian Discites Zone. There is a wide stratigraphical gap between the last occurrence of unequivocal hammatoceratids and the sudden appearance of *Diplesioceras* in the late Bajocian. Following its interpretation as a hammatoceratid, *Diplesioceras* must be considered as a "Lazarus taxon", the ancestors of which had survived in a still unknown area for millions of years. Similar arguments may be put forward for an alternative placement in Sonniniidae. As a conclusion, the systematic placement of *Diplesioceras* remains enigmatic.

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