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Mosasauroid predation on an ammonite – *Pseudaspidoceras* – from the Early Turonian of south-eastern Morocco

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ABSTRACT:

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A juvenile specimen of the ammonite *Pseudaspidoceras* from the Early Turonian of the Goulmima area in the Province of Er-Rachida in south-eastern Morocco shows clear evidence of predation by a tooth-bearing vertebrate. Most of the body chamber is missing, as a result of post-burial compactional crushing. The adapertural part of the shell on the left flank of the surviving fragment of body chamber bears six circular punctuations; the right flank four. These are interpreted as the product of a single bite by a mosasauroid, probably a *Tethysaurus*.

The taxonomy of the Goulmima *Pseudaspidoceras* is discuused in an appendix.

Key words: Predation; Ammonite; Mosasauroidea; Cretaceous; Turonian; Morocco.

INTRODUCTION

The subject of predation on ammonites has a long history, but the identity of the predators involved usually remains problematic. Of early records, Frentzen (1936) described specimens of the Early Jurassic ammonite *Amaltheus* in saurian stomach contents, whilst chunks bitten from the adapical part of the body chamber of Jurassic haploceratid and oppellid ammonites and the Cretaceous perisphinctid *Endemoceras* were ascribed to decapod crustaceans by Roll (1935) and Thiermann (1964) respectively. Martill (1990) suggested that circular holes arranged in an arc on an example of *Kosmoceras* from the Middle Jurassic Oxford Clay of Cambridgeshire in eastern England were made by a semionotid fish with durophagous dentition. Damage to ammonite shells, in part the result of predation, and subsequent repair is reviewed by Hoffmann and Keupp (2015). In the late Cretaceous, it is the mosasaurs that have been identified as ammonite predators, beginning with the study of Kauffman and Kesling (1960), who described a 300mm diameter *Placenticeras* (first illustrated by Fenton and Fenton in 1958) from the Late Campanian Pierre Shale of South Dakota that had been bitten, in their interpretation no less than 16 times, by what they concluded to be a platycarpine mosasaur (we suggest that the mosasaur was playing with its prey, as do contemporary cetaceans). Kauffman (1990) took this view further, and wrote of coevolution of ammonites and mosasaurs, and claimed them as the ecologically dominant predators of Cretaceous marine seas, and indicated the existence in collections of around 30 more specimens with definite predation marks. The predation interpretation did not gain universal support. Thus Kase *et al.* (1998) and Seilacher (1998) concluded that the supposed mosasaur bite marks and punctuations were the crushed impressions of limpet pits.

By far the best documented account of the subject, which definitively defends the predator *vs* limpet view of the damage to *Placenticeras* shells is that of Tsujita and Westermann (2001). These authors studied over 200 perforated specimens from the Late Campanian Bearpaw Formation of southern Alberta, suggesting that approximately 10% of the *Placenticeras* shells from the area and interval had been so afflicted.

Evidence of mosasaur attack on externally shelled cephalopods outside of the northern part of the Western Interior of the United States and Canada is limited. Saul (1976) recorded possible mosasaur bite impressions on a specimen of *Anapachdiscus peninsularis* (Anderson and Hanna, 1935) from the Early Maastrichtian Rosario Formation of Baja California, Mexico. The specimen, 11.8 cm in maximum diameter, has a series of punctuations, interpreted as the result of two bites (Saul 1976); Kauffman (2004, p. 97) rejected this interpretation, and suggested that a large fish was responsible. He noted, however, a punctured shell of the ammonite *Pachydiscus suiciaensis* (Meek, 1861) described in Ludvigsen and Baird (1994) from the Late Campanian Lambert Formation of Vancouver Island, British Columbia, Canada. Kauffman (2004) defended the bites interpretation, and described evidence for mosasaur attack on nautiloids from the Campanian of San Diego County, California. A twice-bitten specimen referred to as *Argonautilus catarinae* Sundberg (presumably *Anglonautilus catarinae* Sundberg, 1984) was interpreted as sick or recently dead on the basis of the inferred direction of attack. An external mould at the same outcrop as this specimen was interpreted, on the basis of a latex cast, as being from a nautiloid bitten by both a large and a small mosasaur, "of the same species (i.e. a mother and her offspring)", interpreted as "possibly showing a mother teaching a juvenile to subdue its prey" (Kauffman 2004, p. 100).

Kauffman and Skwarko (2013) recorded over 100 specimens of *Placenticeras*, *Sphenodiscus* and, less commonly, *Baculites* that "show mosasaur and, rarely, giant fish predation marks". They also described a nautiloid (*Eutrephoceras*) with mosasaur bite marks from the Early Maastrichtian Pierre Shale south of Boulder in Jefferson County, Colorado.

Odunze and Mapes (2013) described and illustrated what they termed "nearly circular, oval and irregular holes in Cretaceous ammonoids" from the latest Campanian to Early Maastrichtian Nkoporo Formation of southern Nigeria (rather better illustrations of most of the specimens are to be found in Zaborski 1984, text-figs 17, 29, 32, 34). These structures on all but one of the specimens discussed by these authors are on internal moulds of phragmocones. The internal moulds are preserved in buff, well-cemented fine-grained material that was cemented at a relatively early point in the post-burial history of the shells, because they retain their original proportions, and do not show signs of crushing. The circular depressions are shallow, with a concave base, and are formed in the material that makes up the internal mould. Some are weathered free of enclosing shale matrix; others have a lining of compacted shale. The structures on phragmocones resemble those describes as lobe voids by Seilacher (1966); there are striking similarities between text-fig. 1d, e, in Odunze and Mapes (2013) and text-fig. 2a in Seilacher (1998). The single internal mould of a body chamber with pits (Odunze and Mapes 2013, text-fig. 2e; see Zaborski 1982, text-fig. 34a, b for a much better picture of this specimen) cannot, however be so explained. There are a number of possible processes that may have produced the shallow, circular depressions in this specimen, and possibly the others:

1. The depressions record the presence of low circular domes of thickened shell material laid down on the inner surface of the body chamber of the juvenile ammonites, and, as growth proceeded, were left on the wall of successive camerae. Following burial and cementation of the material infilling the camerae, the original aragonitic shell material dissolved, leaving depressions in the infilling of the camerae, into which subsequent compaction impressed shale matrix.

2. Rather that the result of thickenings in the shell, there were depressions in the shell of the ammonite that did not perforate the shell. These depressions corresponded to low domes on the interior of the shell, which gave rise to the shallow depressions as a result of the diagenetic sequence proposed above. Conceivably, these depressions could be the result of bites that did not perforate the shell, but convincing evidence is lacking.

All of the convincing well-documented examples of mosasaur-bitten ammonite shells are thus from North America, the overwhelming majority from the Late Campanian of the northern part of the Western Interior of the United States and Alberta in Canada.

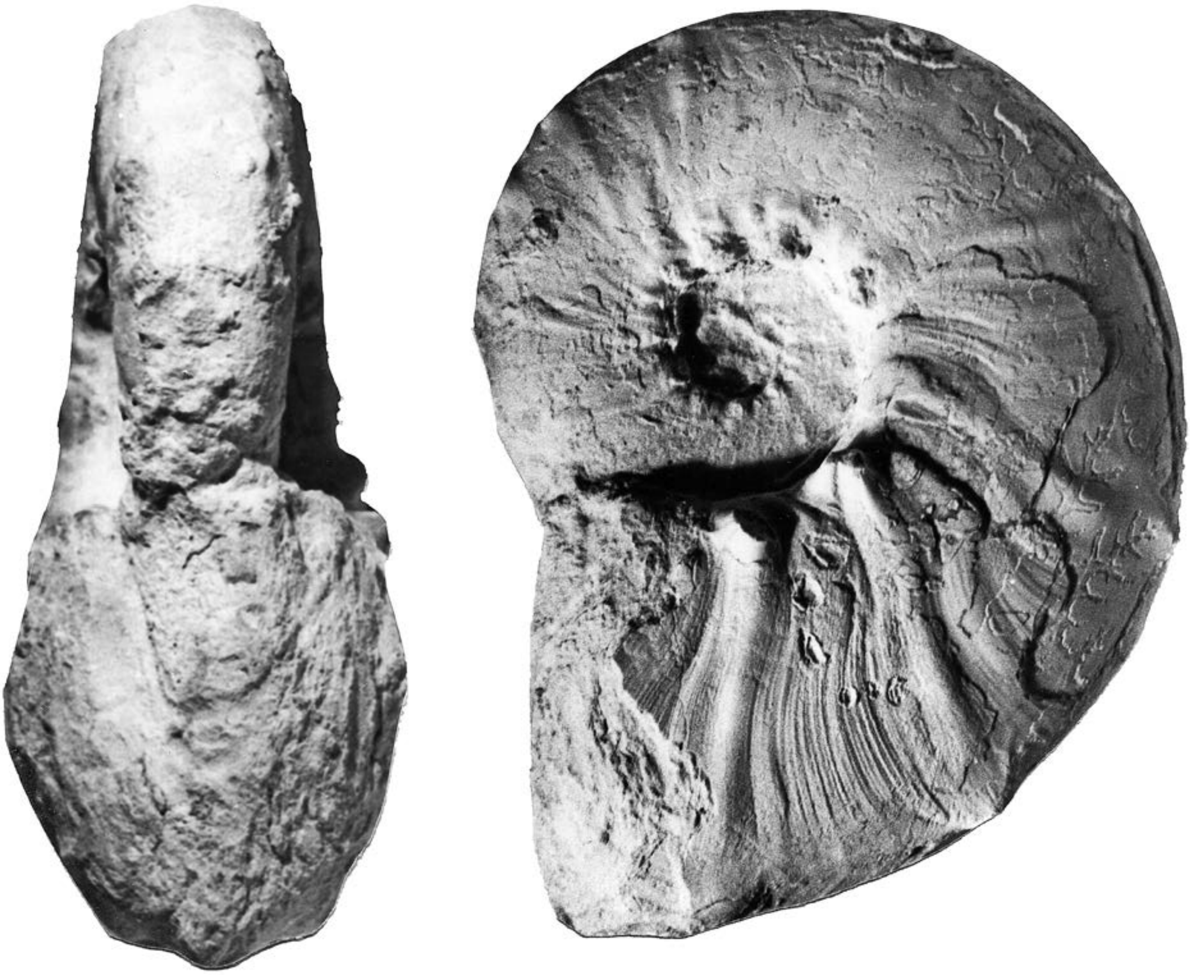
The only older record is "One possible *Globidens* bite mark (with blunt, shell-crushing teeth) is known from an Upper Cenomanian *Metoicoceras* from Texas" (Kauffman 1990, p. 188). Without illustration or description it is impossible to evaluate this record (an examination of more than 30 *Metoicoceras* and *Placenticeras* with aragonitic shell preserved from the Late Cenomanian Britton Formation of north-central Texas housed in the collections of the Oxford University Museum of Natural History revealed only one undoubtedly damaged shell, OUM KT1631, a *Metoicoceras* with an irregular break to the entire periphery of the body chamber, succeeded by an approximately 30° sector of regenerated shell without puncture marks of the type regarded as characteristic of mosasaur attack.)

We describe below, what we consider to be a convincing example of attack by a mosasauroid on a juvenile *Pseudasidoceras* from the Early Turonian of Goulmima in south-eastern Morocco, the earliest, and only convincing example from outside North America.

THE PREY

The predated ammonite, OUM KX17236 (Text-figs 1–3) comes from the Akrabou Formation (Ettachifi and Androu 2004) in the Goulmima area of Er-Rachida Province in south-eastern Morocco (see Kennedy *et al.* 2008, text-figs 1and 2 for a locality map and lithostrati-

Text-fig. 1. *Pseudaspidoceras madagascariensis* (Basse, 1954). OUM KX17236, from the Early Turonian of Goulmima in south-eastern Morocco. The left flank, showing the arc of six punctures in the shell at the adapical end of the body chamber. See Text-fig. 4A–C for interpretative drawings

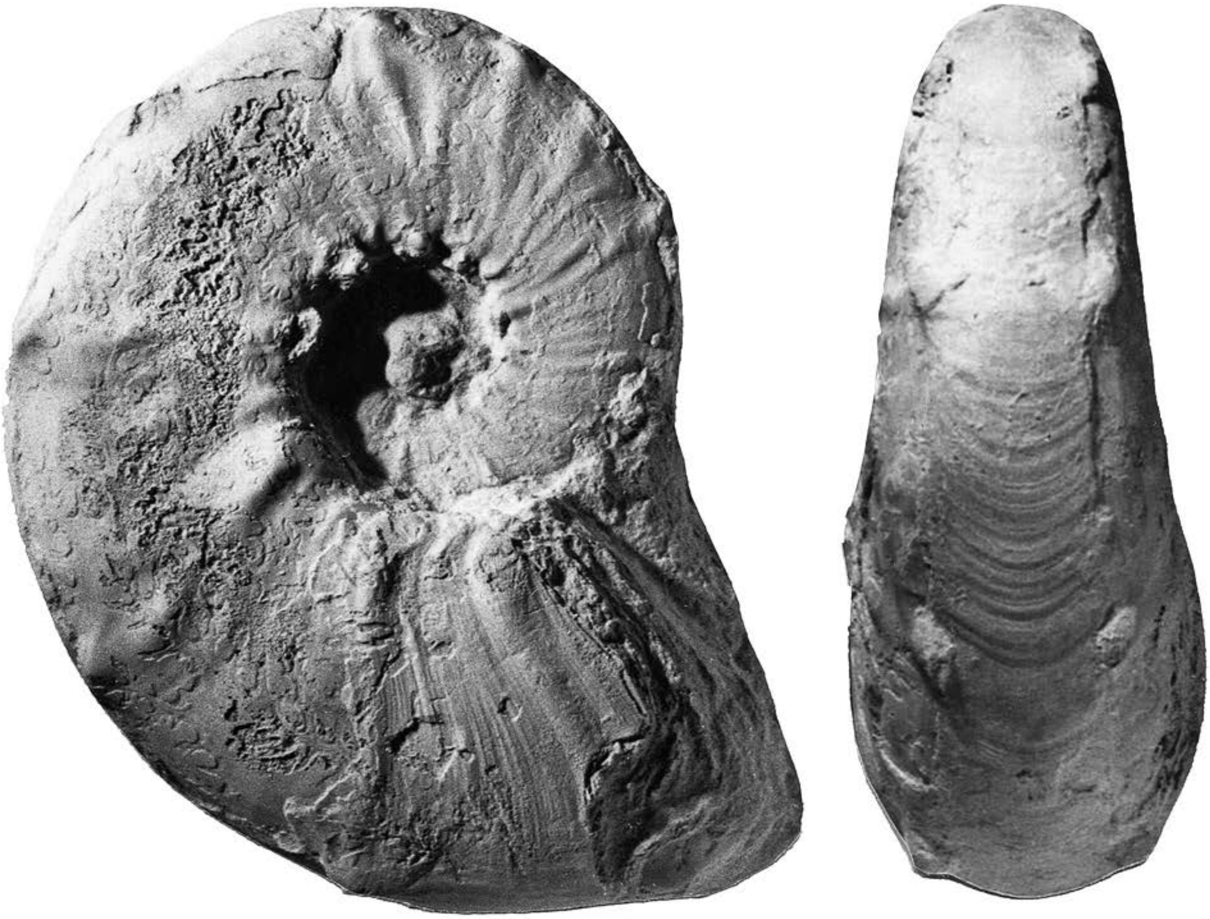


Text-fig. 2. *Pseudaspidoceras madagascariensis* (Basse, 1954). OUM KX17236, from the Early Turonian of Goulmima in south-eastern Morocco. Left flank and venter. Figures are × 1

graphic section), where Early Turonian ammonites of the *Mammites nodosoides* Zone are abundant. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
OUM KX17236	135.2 (100)	50.2 (37.2)	62.6 (46.3)	0.8	37.4 (27.7)

The specimen is septate to a diameter of at least 120 mm, and appears to retain a short sector of body chamber. It retains extensive areas of calcite-replaced shell. Coiling is evolute, the umbilicus comprising 27.7% of the diameter, of moderate depth, with a flattened wall and quite narrowly rounded umbilical shoulder. The whorl section is compressed, with an intercostal whorl breadth to height ratio of 0.8, the greatest breadth around mid-flank. The flanks are subparallel, very feebly convex, the ventrolateral shoulders broadly rounded, the venter very feebly convex. Fourteen blunt, subspinose tubercles perch on the umbilical shoulder of the outer whorl, and project into the umbilicus. They increase rapidly in strength around the outer whorl. The tubercles give rise to a single broad, blunt primary rib, straight and prorsiradiate on the innermost flank, then flexing forwards and feebly concave across the remainder of the flanks. The primary ribs branch once or twice on the mid-flank, the secondary ribs weaker than the primaries. The latter develop a feeble inner ventrolateral bulla, linked by a broad rib to a stronger rounded-conical outer ventrolateral tubercle. Ribs and interspaces are covered in an ornament of dense lirae and growth lines, groups of which that are closest



Text-fig. 3. *Pseudaspidoceras madagascariensis* (Basse, 1954). OUM KX17236, from the Early Turonian of Goulmima in south-eastern Morocco. Right flank and apertural view. Figures are × 1

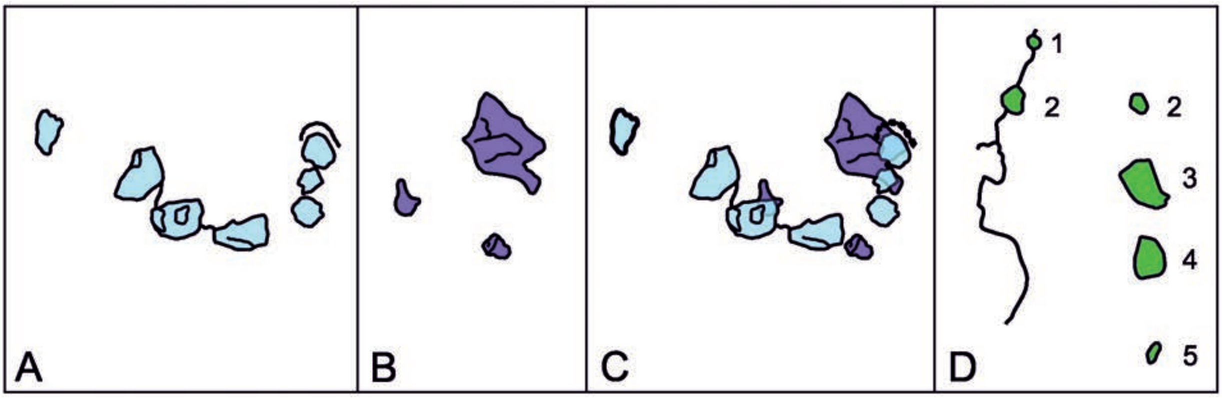
to the primary ribs flex back across the ventrolateral shoulder and link to the outer ventrolateral tubercles. The lirae , sometimes borne on a feeble riblet, loop across the venter and link the outer ventrolateral tubercles in a broad convexity. Oher lirae in the interspaces sweep back across the ventrolateral shoulder then flex forwards and cross the venter in a broad convexity. The overall ribbing pattern is irregular.

The suture, only partially exposed in OUM KX17236, is deeply incised, with broad rounded folioles on the visible parts of E/A and A/U2.

Of described *Pseudaspidoceras* species, the specimen has a comparable style of ribbing and tuberculation to the types of *Pseudaspidoceras* [*Ampakabites*] *auriculatum* Collignon, 1965 (pp. 29, 31, pl. 387, fig. 1662, pl. 388, fig. 1664; Text-figs 4, 5 herein). As demonstrated below, this is a junior synonym of *Pseudaspidoceras* [*Donjuaniceras* (?)] *madagascariensis* Basse, 1954.

THE EVIDENCE OF PREDATION

The shell is preserved as radial arrays of calcite crystals, after the original aragonite, on the outer part of the phragmocone and the remnant of the body chamber (Text-figs 1–3), the margin of which is irregularly broken, probably as a result of post-burial compaction. The external surface of the shell is well preserved, with growth lines clearly visible. On the left side of the body chamber, adjacent to the last septum, the shell is punctured by a group of 6 holes which have a V-shaped arrangement (Text-figs 1, 2, 4A), the base of the V being directed obliquely towards the venter. The holes are oval to irregularly triangular and have a maximum diameter of 2 to 7 mm. The margins are sharply defined and vertical, and several display partly detached fragments of shell which are slightly inset beneath the outer surface. Other small shell fragments are present within the central regions of the holes. The



Text-fig. 4. A–C – Drawings of bites on the left side (A) the right side (B) and both sides superimposed (C) of the Goulemima *Pseudaspidoceras*. D – damage pattern on a *Nautilus* shell generated using a "restrained bite" by a metal facsimile of a mosasaur skull, redrawn from text-fig. 3D of Kase *et al*. 1998. Similarities include the irregular size and shape of the holes, which are angular, and the fractures in the shell between some of the holes. The presence of shell fragments within the holes is taken as evidence that these were held in place by periostracum. Numbers refer to the position of the teeth on the skull, with 1 most anterior

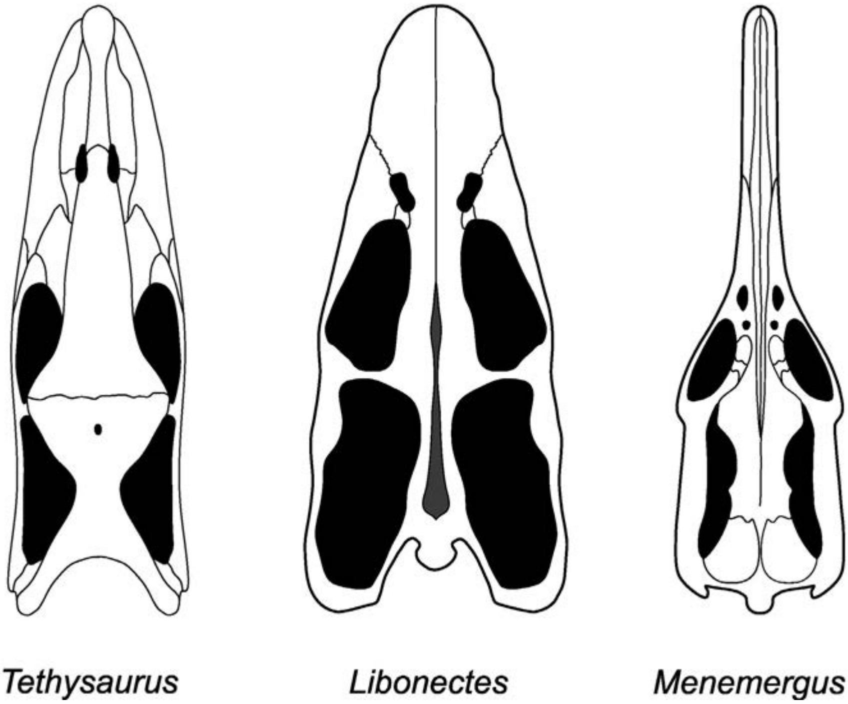
right side of the base of the body chamber (Text-figs 3, 4B) is perforated by three holes, which correspond well with those on the left side when superimposed, but they are more irregular in size and shape (Text-fig. 4C).

The irregular shape and size of the holes, and the presence of fractures which extend between them are closely comparable to those made in the shell of a *Nautilus* using a metal replica of a mosasaur skull (*Prognathodon*; Kase *et al*. 1998) with a "partial or restrained bite" (p. 949; see Text-fig. 4D herein). In contrast, deep bites resulted in fragmentation of the shell into variably sized angular pieces. The presence of fragments of shell within the bites provides evidence that periostracum was present on the outside of the shell at the time that the bite was made.

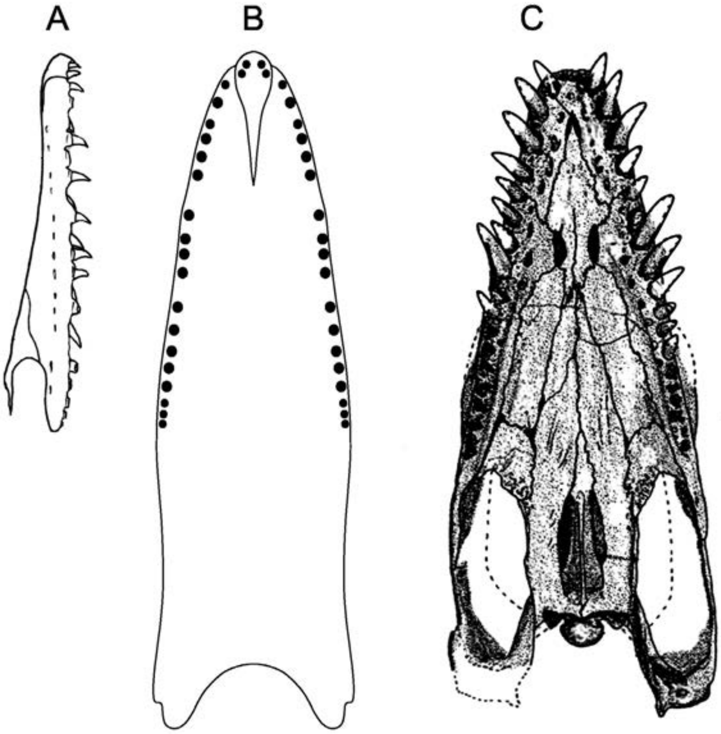
THE PREDATOR

The vertebrate assemblage of the Turonian Akrabou Formation of the Goulmima region is known entirely from exposures near the hamlets of Tadirhoust and Asfla, where commercial fossil extraction yields an incredible abundance of ammonites as well as significant remains of vertebrates, often as fully articulated skeletons preserved in three-dimensions. The vertebrate assemblage is dominated by osteichthyans, including pycnodonts, araripeichthyids, ichthyodectids, osmeroidids, enchodontids, and pachyrhizodontids. Elasmobranchs are much rarer but include the platyrhinid (thornback) ray *Tingitanius tenuimandibulus* Claeson, Underwood and Ward, 2013, the ptychotrigonids *Microprystis* sp., and *Ptychotrigon* sp., an as yet undescribed sclerorhynchid saw shark (Ward and Underwood, personal communication 2014) and the small lamniform *Squalicorax* sp. (Ward, personal communication, 2016).

Several tetrapods have also been reported from the Akrabou Formation, including marine turtles, long necked plesiosaurs (Plesiosauria) and pliosaurs, but by far the most abundant are specimens of the marine reptile *Tethysaurus nopcsai* Bardet, Pereda Suberbiola and Jalil, 2003, a mosasauroid known from many hundreds of specimensfrom juvenile to adult (Text-figs 5A, 6A, B).The turtles are as yet undescribed, but represent at least one taxon reaching a size of approximately 600 mm diameter across the carapace, and perhaps a little larger (DMM personal observations). At least two longirostrine polycotylid plesiosaur (Sauropterygia, Polycotylidae) are described. *Thililua longicollis* Bardet, Pereda Suberbiola and Jalil, 2003, was a large animal, reaching lengths of perhaps 8 metres, while *Menemergus anguirostris* Buchy *et al*., 2005 (Text-fig. 5C) was a smaller animal with stiff neck and smooth teeth. The long-necked elasmosaur *Libonectes atlasense* Buchy, 2005 (Text-fig. 5B) was also a large animal, but with a comparatively small skull. Its mandibular symphysis is short, with an arcuate outline to the anterior margin when seen in dorsal or ventral view. A fourth, undescribed sauropterygian, probably belonging to the Pliosauroidea is known from fragmentary jaw remains,with massive caniniform teeth set in a long, parallel-sided rostrum (the possibility exists that this is simply a very large polycotylid). Missing from the assemblage are ichthyosaurs, marine crocodilians, and pterosaurs, but this is probably due to the extinction of Thalattosuchia and Ichthyosauria at some time



Text-fig. 5. General skull morphology of tooth-bearing marine reptiles from the Akrabou Formation of the Goulmima area. A – the mosasauroid *Tethysaurus nopcsai* Bardet, Pereda Suberbiola and Jalil, 2003. B – the elasmosaurid plesiosaur *Libonectes atlasense* Buchy, 2005; C – the polycotylid plesiosaur *Menemergus anguirostris* Buchy, Metayer and Frey, 2005 (redrawn from original sources)

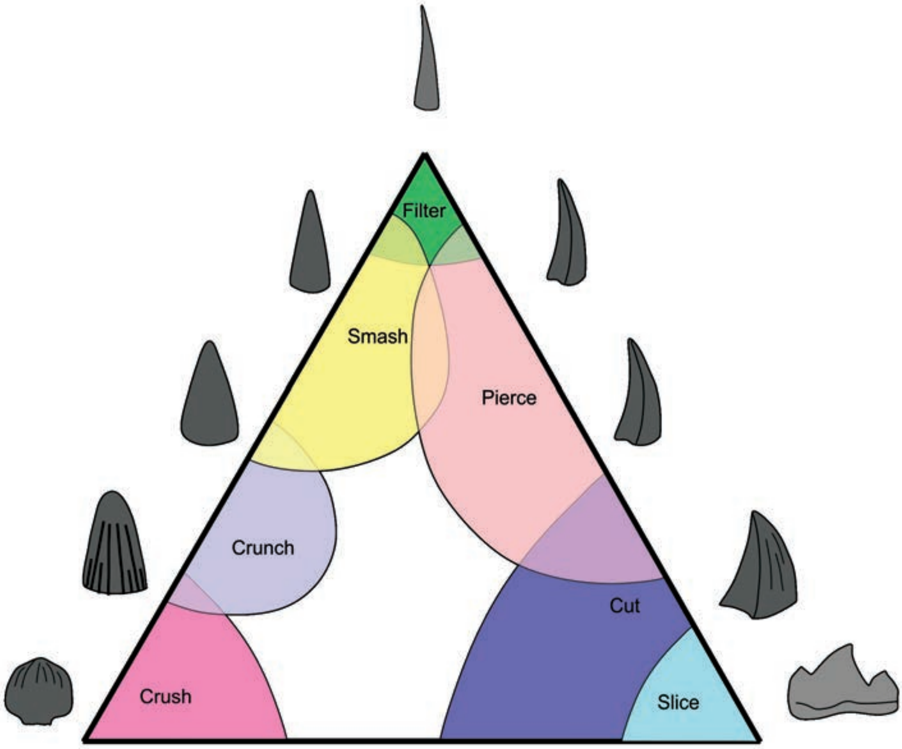


Text-fig. 6. Dental arrangement for *Tethysaurus* (A, B) and *Libonectes* (C). A – right maxillary and premaxillary dentition of *Tethysaurus nopcsai* from Bardet *et al.* (2003). B – schematic restoration of dental arrangement in *Tethysaurus* based on A. C – dental arrangement in the elasmosaurid *Libonectes* (Based on Carpenter 1997) during the Cenomanian marine transgresson. On the other hand, the lack of pterosaurs may relate to their ecology, as at least three families (Azdarchidae, Nyctosauridae and Pteranodontidae) persisted well into the Late Cretaceous (Witton 2013), but these were all edentulous.

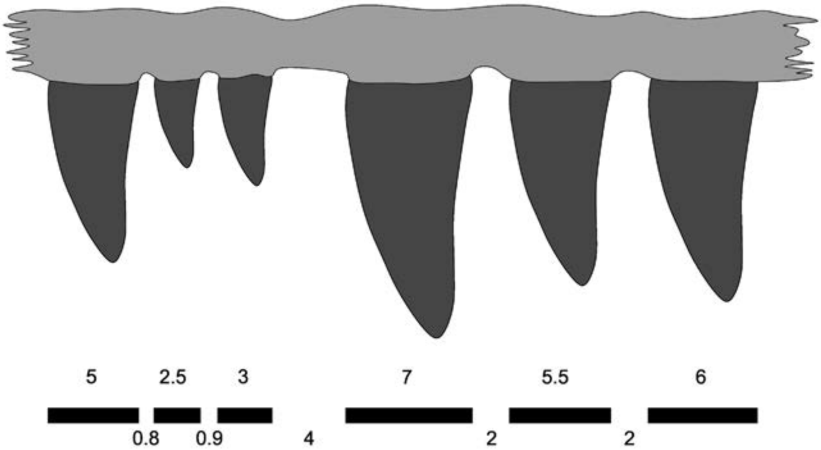
These vertebrates, from the fish to the large pliosaurs, were carnivores or piscivores or both, with the possible exception of the turtles which may have also fed on invertebrates, and the benthic sharks, pcynodonts and the edentulous *Araripichthys*, some of which may also have fed exclusively on invertebrates. Only fishes have been reported with preserved stomach contents (e.g. Cavin 1999), but these include only the remains of arthropods and other, smaller fishes. Ammonite remains have not been found in fish guts, but this could always be a consequence of the acid digestion technique used to prepare the specimen.

Several of the fishes can be excluded as candidates for the bite marks on the ammonite on account of their tooth morphology and their dental arrangement. While *Squalocorax* is a large predatory shark in Late Cretaceous strata of Morocco, the form identified in the Akrabou Formation is extremely rare and known from very small teeth. The elongate, serrated blade-like teeth generate a distinctive semi-circular bite, incompatible with the morphology found on the *Pseudaspidoceras*. Other predatory fish, such as *Goulmimichthys* and *Osmeroides* also have small, though sharp teeth, but these are numerous and arranged tightly packed on the jaws. Consequently, these forms would also be incapable of generating a bite like that found on the ammonite. Large examples of *Enchodus* would have widely spaced teeth capable of delivering a powerful bite, but large examples of this fish are not yet reported from the locality. One large and common fish that might be capable of a powerful bite able to puncture an ammonite test is *Ichthyodectes bardacki* Cavin, 1997. In this taxon the well-spaced, short, conical teeth, fused to the jaw bones, would probably have been capable of delivering a powerful bite, but they are very small on jaws that are directed sharply upwards. Furthermore, the skull is laterally compressed and would deliver a narrow, rather than wide bite.

It is thus more likely the bite was generated by one of the marine reptiles. Turtles are excluded on account of their edentulous jaws, although some turtles do develop pseudo-tooth like structures on the horny covering of the beak that may be able to inflict tooth-like bite marks. No reports of fossil turtle bites are documented, but recent turtles tend to leave crenulated, continuous arc-like bite marks.



Text-fig. 7. Tooth morphology of marine reptiles plotted with predator guilds. Based on Massare (1987), but with the addition of a filter feeding guild as an extension of increasing slenderness of conical crowns (e.g. teeth of cryptoclided plesiosaurs), and slicing as an extension of lateral compression of carinate teeth (e.g. laterally compressed, recurved teeth of water monitors, and including laterally compressed multicusped and serrated teeth)



Text-fig. 8. Size and spacing, in millimetres, of the dental puncture marks on the left side of the Goulmima *Pseudaspidoceras*, with supposed tooth sizes superimposed over the punctures. A simple crown attributed to the piercing guild of Massare (1987) has been used

Pliosaurs, generally regarded as macro-predators, and perhaps hyper-carnivores (Massare 1987) are an important component in the Akrabou Formation, but their elongate mandibular symphysis, narrow rostrum and large caniniform teeth would leave a paralled-sided bite rather than an arc. Only two of the marine reptiles possessed a muzzle morphology capable of generating an arcuate bite pattern: the mosasauroid *Tethysaurus* and the elasmosaur *Libonectes*, and of these two, the muzzle of *Libonectes* is the broader, and perhaps more comparable with the arc of dental piercings on the *Pseudaspidoceras*. The teeth of both *Tethysaurus* and *Libonectes* are uniform and well-spaced and conform closely to an isodont arrangement. However, the premaxillary teeth of *Tethysaurus* appear to be somewhat smaller than those of the maxilla and dentary. In *Libonectes* the teeth are of similar size in the premaxilla, maxilla and dentary, although there is an increase in size for the second and third teeth of the maxilla followed by a slight and continuous reduction in size posteriorly. The teeth of *Libonectes* are thecodont, comprising simple straight cones (Carpenter 1997), conforming to the smash and pierce guilds of Massare (1987) (Text-fig. 7). Those of *Tethysaurus* are acrodont, short, robust, but slightly curved rather than straight crowns. Their robust morphology suggests that they too would be capable of biting through an ammonite test.

The bite marks on the*Pseudaspidoceras* form an arcuate pattern of small holes (max diameter 6 mm, minimum diameter 2.7 mm, spacing from 4 mm to 7 mm) and are irregularly spaced (Text-fig. 8). That the marks are on both sides of the shell and in corresponding position (text-fig. 4C) demonstrate that this fairly small sized individual was capable of opening its mouth to a minimum of 50 mm (the whorl width of the shell at the bite mark) and some more to accommodate the teeth. By calculating the width of the tooth from the diameter of the bite mark, the largest tooth that would have had to clear the shell to enable a bite would have been approximately 14 mm high (Text-fig. 8). As teeth are on both the upper and lower jaws for all of the Akrabou Formation reptiles, then a maw of approximately 80 mm was required to bite the ammonite. This suggests that the more elongate jaws with smaller teeth of a *Tethysaurus* were responsible for the bite. While the bite could possibly have been inflicted by a juvenile *Libonectes*, it is doubtful if a juvenile *Libonectes* would be able to open its jaws sufficiently wide to bite the ammonite as it lacks the intermandibular joint found in mosasaroids. Furthermore, no juvenile sauropterygians have been recorded from the Akrabou Formation, suggesting that young of these fully marine reptiles lived elsewhere. The different size ranges and spacing of the puncture marks (Text-figs 1, 2, 8) may be explained as either a result of small teeth of the premaxilla and larger teeth of the anterior maxilla puncturing the shell. Conversely, some of the teeth may have been only partially erupted, and thus left smaller punctures.

DISCUSSION

We conclude that:

1. The juvenile *Pseudaspidoceras* from the Early Turonian of Goulmima was bitten by the mosasauroid *Tethysaurus*. The bite was not demonstrably lethal, nor was it demonstrably attempted predation.

2. There is a 20 million year gap in evidence of mosasauroid attack/predation on ammonites between the Goulmima occurrence and the numerous records from

the Late Campanian of the northern part of the United States Western Interior and Alberta in Canada.

3. The Goulmima occurrence is the only convincing record of mosasauroid attack on an ammonite outside North America, and of the latter, the overwhelming majority are restricted to the Late Campanian of the northern interior. The only adequately documented putative occurrence outside of the interior, in the Early Maastrichtian Rosario Formation of Baja California, Mexico, may not in fact be by a mosasaur, although there is evidence of mosasauroid attack on two Campanian nautiloids from San Diego County in California.

4. Given the above, we see no evidence to support the view that there was coevolution between ammonites and mosasaurs, nor that mosasaurs were "The ecologically dominant predators of Cretaceous marine seas" as proposed by Kauffman (1990).

5. The is clear evidence from the careful study by Tsujita and Westermann (2001) that over a limited geographical area and time interval in what is now southern Alberta, there was extensive predation on the ammonite *Placenticeras* during the Late Campanian, given that 10% of specimens recovered show evidence of mosasaur attack and predation. The reason for this occurrence remains to be established. The simplest explanation may be that there was little else to eat.

APPENDIX

As noted above, we regard *madagascariensis* of Basse, 1954, as the prior species name for *Pseudaspidoceras* from the Early Turonian of Goulmima. The arguments are set out below.

Superfamily Acanthoceratoidea de Grossouvre, 1894
Family Acanthoceratidae de Grossouvre, 1894
Subfamily Euomphaloceratinae Cooper, 1978
Genus *Pseudaspidoceras* Hyatt, 1903
(= *Ampakabite*s Collignon, 1964)
Pseudaspidoceras madagascariensis
(Basse, 1954)
(Text-figs 1–3, 9–13)

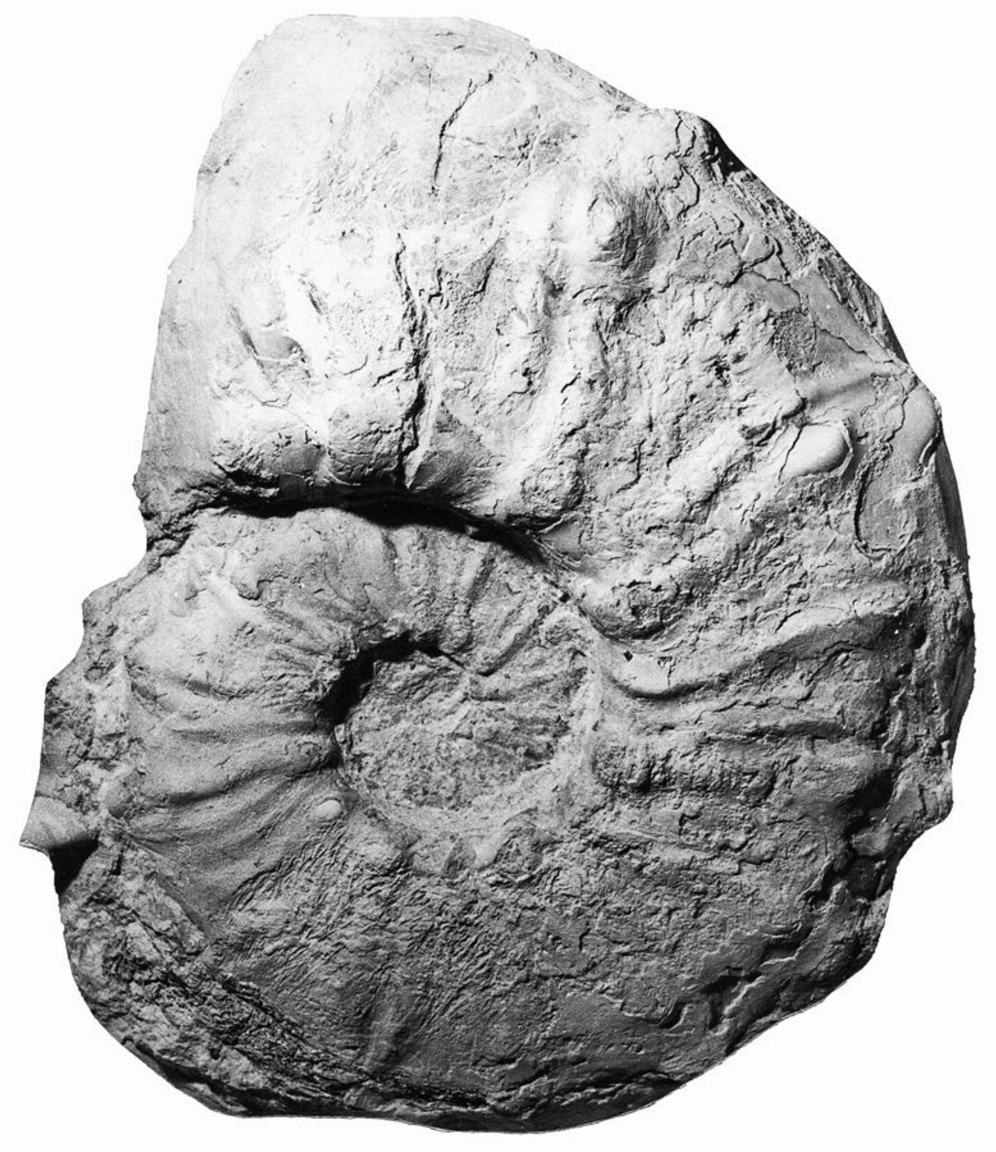
Text-fig. 9. *Pseudaspidoceras madagascariensis* (Basse, 1954). The holotype, copy of Basse (1954, pl. 4, fig. 2), "receuille dans le sud-ouest de Madagascar par COLCANAN en 1907, vraisemblement au sud de L'Onilahy, dans le Crétacé moyen (?)" . The figures are reduced by 0.46; the original is 250 mm in diameter

1954. *Donjuaniceras* (?) *madagascariensis* Basse, p. 201, pl. 4, fig. 2; text-fig. 2-3-1 on p. 202.
1965. *Kamerunoceras* (*Ampakabites*) *auriculatus* Collignon, pp. 29, 31, pl. 388, fig. 1662; pl. 389, fig. 1664.
1987. *Kamerunoceras* (*Ampakabites*) *auriculatum* Collignon; Kennedy, Wright and Hancock, p. 38, text-figs 5a–c, 6d.
1996. *Pseudaspidoceras auriculatum* (Collignon); Wright, p. 169, text-fig. 128, 1d, e.

TYPE: The holotype is the original of Basse 1954, p. 201, pl. 4, fig. 2; text-fig. 2-3-1 on p. 202.

DESCRIPTION: The original figures of the holotype are reproduced here as Text-fig. 9. It was described as follows: “Ammonite subdiscoïde, de dimensions: diamètre, 250 mm, ombilic, 75 mm (rapport 0.30), épaisseur maximum du tour, 90 mm (rapport 0.36).

Text-fig.10. *Pseudaspidoceras madagascariensis* (Basse, 1954). OUM KX172367, from the Early Turonian of Goulmima in south-eastern Morocco. Figures are × 1



Text-fig. 11. *Pseudaspidoceras madagascariensis* (Basse, 1954). OUM KX17238, from the Early Turonian of Goulmima in south-eastern Morocco. Reduced × 0.66, the original is 230 mm in diameter

Forme à croissance rapide, comme celle du Liban, avec une involution tout à fait comparable; toutefois la section du tour offre une involution tout à fait comparable; toutefois la section du tour offer une tendance nette à devenir ogivale dans la region ventral.

Le test, qui devait être mince, est conserve à l'état cristallin sur l'une des faces; il présente une costulation flexueuse très fine et très belle, legèrement fasciculée aux voisinage de tubercles marginaux (une douzaine sur le dernière tour) pincés obliquement, surtout proéminents sur la dernière moitié de la tour externe. Au bord de l'ombilic, les côtes confluent en tubercles courbes peu distincts. Notons l' analogie frappant de l'ornamentation avec celle de *Donjuaniceras longispina*, mais cette dernière forme ne present pas le rétrécissement ventral, si net sur le spécimen malgache. En effet, une carène médio-ventrale, d'abord nette, s'estompe progressivement tandis que la région ventral tout entire s'elève en s'arrondissant et en rétrécissant. La loge d'habitation, probablement de grand fragilité, n'est-pas conservée.

La suture est nettement visible sur l'un des côtes; comme on le voir d'après les fig. 2 et 3, elle present des analogies avec celles de l'ammonite libanaise."

We have failed to trace this specimen.

Text-fig. 12. *Pseudaspidoceras madagascariensis* (Basse, 1954). The holotype of *Kamerunoceras* (*Ampakabites*) *auriculatus* Collignon, 1965, from Ampakabo (Betioky) in southwestern Madgascar, the original of Collignon (1965, pl. 358, fig. 1662). Figures are × 1

OUM KX17237 (Text-fig. 10) is slightly distorted. It has a maximum preserved diameter of 190 mm; the umbilicus comprises 26.3% of the diameter, and the whorl breadth: height ratio is 0.78. Eighteen to nineteen weak bullae of variable strength perch on the umbilical shoulder. The bullae give rise to weak, narrow, feebly flexuous primary ribs, and additional riblets and lirae arise at the umbilical shoulder, branching on the flanks to produce a dense irregular ornament between successive primaries. These bear very feeble inner ventrolateral bullae, from which a primary rib sweeps forwards to link to an outer ventrolateral clavus. Both umbilical bullae and ventrolateral tubercles increase in relative strength around the outer whorl, the strengthening of the outer ventrolateral is the most marked. Strengthened riblets and lirae pass over the venter in a broad convexity.

The suture, only partially exposed, is deeply incised, with broad rounded folioles on the visible parts of E/A and A/U2.

This specimen differs in no significant respects from the holotype of *madagascariensis.*

OUM KX17238 (Text-fig. 11) is interpreted as a coarser ornamented variant of the species, 230 mm in diameter, and retains a short sector of body chamber and extensive areas of calcite-replaced shell. There are indications of the former presence of a 180–200° sector of body chamber. The umbilicus comprises 31% of the diameter; the intercostal whorl breadth to height ratio is 0.81 approximately at the adapical end of the outer whorl. Fifteen tubercles perch on the umbilical shoulder of the outer whorl. They increase rapidly in strength, and at the largest preserved diameter, are massive and rounded. They give

Text-fig. 13. *Pseudaspidoceras madagascariensis* (Basse, 1954). The original of *Kamerunoceras* (*Ampakabites*) *auriculatus* Collignon, 1965, from Ampakabo (Betioky) in south-eastern Madgascar, the original of Collignon (1965, pl. 359, fig. 1664). Figures are × 1

rise to blunt, broad primary ribs, either singly or in pairs; a few bifurcate, to give in excess of 30 ribs of variable srrength on the outer flank. The primary ribs bear strong inner ventrolateral bullae and strong rounded- clavate outer ventrolateral tubercles, the secondary, and occasional intercalated ribs, bear weaker inner ventrolateral bullae. There are traces of lirae like those developed on the previous specimen. Two further specimens, with comparable ornament are housed in the collections of the Natural History Musem, London: CA5566 and 5570, 150 and 122 mm in diameter respectively.

DISCUSSION: The Moroccan specimens are interpreted as weak (Text-fig. 10) to moderately (Text-figs 1–3) to strongly ornamented (Text-fig. 11) variants of a single species. The first corresponds to the holotype of *Pseudaspidoceras madagascariensis*. The second and third differ in no significant respects from the type material of *Kamerunoceras* (*Ampakabites*) *auriculatus* Collignon, 1965 (pp. 29, 31, pl. 388, fig. 1662; pl. 389, fig. 1664) refigured here as Text-figs 12–13, which we accordingly regard as a junior synonym of the *madasgascariensis*.

It can be argued that this conclusion is compatible with the Madagascan records. Basse stated that the holotype of *madagascariensis* was "receuille dans le sud-ouest de Madagascar par COLCANAN en 1907, vraisemblement au sud de L'Onilahy, dans le Crétacé moyen (?)" (note that Colcan is an error for Colcanap).

Kamerunoceras (Ampakabites) auriculatus is from the "Turonien Moyen. Zone á *Pseudaspidoceras conciliatum*. Gisement 409, Ampakabo (Betioky)". This is also south of the Onilahy River in south-western Madagascar, so that the type material of the two species come from the same area. The fauna from Collignon's *Pseudaspidoceras conciliatum* Zone appears to be Lower, rather than Middle Turonian, as indicated by the zonal fauna listed from Anontzy (also in south-western Madagascar) by Besairie and Collignon (1972, p. 408), where *P. auriculatum* is associated with *Mammites nodosoides*, index species of the eponymous upper Lower Turonian Zone. Collignon (1965, p. 29, pl. 388, fig. 1663) described his *Schindewolfites isovokyensis* from the *Pseudaspidoceras conciliatum* Zone of Aontsy (Betioky), basing it in a specimen in the Colcanap collection; Aontsy (Betioky) is south of the Onilahy river, and this might even be the source of the holotype of *madagascariensis*, also collected by Captain Colcanap. Given the occurrence of individuals corresponding to *auriculatus* and *madagascariensis* at Goulmima in Morocco it seems likely that the type material of these two species also came from the same horizon, if not locality, in south-western Madagascar.

Kennedy, Wright and Hancock (1985) concluded that *auriculatus* of Collignon was a junior synonym of *flexuosum* of Powell (1963, p. 318, pl. 32, figs 1, 9, 10; text-fig. 2a–c, f, g). The material from Goulmima suggests otherwise. OUM KX17236 and 17238 differ from specimens of comparable size referred to *flexuosum*, including the holotype (Powell 1963, pl. 32, figs 1, 9; text-fig. 2c) in having a compressed, rather than depressed whorl section, more numerous umbilical bullae per whorl, together with coarser and more numerous flank ribs. The feebly ornamented body chamber of *flexuosum* figured by Kennedy *et al.* (1987, text-fig. 7a–c) has very distant and strong umbilical bullae, only two in a 60° sector, and is quite distinct from OUM KX17237 (Text-fig. 5) and the holotype of *madagascariensis* (Text-fig. 12).

OCCURRENCE: Upper Lower Turonian, southwestern Madagascar, and Goulmima, central Morocco.

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