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A review of the classification of Jurassic aspidoceratid ammonites – the Superfamily Aspidoceratoidea

Horacio PARENT[1], Günter SCHWEIGERT[2], Armin SCHERZINGER[3]

Key words: Superfamily Aspidoceratoidea, Aspidoceratidae, Epipeltoceratinae emended, Peltoceratidae, Gregoryceratinae nov. subfam.

Abstract. The aspidoceratid ammonites have been traditionally included in the superfamily Perisphinctoidea. However, the basis of this is unclear for they bear unique combinations of characters unknown in typical perisphinctoids: (1) the distinct laevaptychus, (2) stout shells with high growth rate of the whorl section area, (3) prominent ornamentation with tubercles, spines and strong growth lines running in parallel over strong ribs, (4) lack of constrictions, (5) short to very short bodychamber, and (6) sexual dimorphism characterized by miniaturized microconchs and small-sized macroconchs besides the larger ones, including changes of sex during ontogeny in many cases.
Considering the uniqueness of these characters we propose herein to raise the family Aspidoceratidae to the rank of a superfamily Aspidoceratoidea, ranging from the earliest Late Callovian to the Early Berriasian Jacobi Zone. The new superfamily includes two families, Aspidoceratidae (Aspidoceratinae, Euaspidoceratinae, Epipeltoceratinae and Hybonoticeratinae), and Peltoceratidae (Peltoceratinae and Gregoryceratinae nov. subfam.).
The highly differentiated features of the aspidoceratoids indicate that their life-histories were very different from those of the perisphinctoids; these ammonites show great promise for studies of developmental and evolutionary patterns and processes, and can be used for biostratigraphic-chronostratigraphic purposes and interprovincial correlations.

INTRODUCTION

The current systematics of the Jurassic Ammonitina is rather well-established, as recently reviewed by Howarth (2013, 2017) and Énay, Howarth (2019). The systematics of the Perisphinctoidea Steinmann, 1890 was essentially established by Schindewolf (1925), and through a vast number of papers, impossible to list all of them, many improvements based on new knowledge were gradually introduced, reflected in the major subsequent compilations, *e.g.*, by Spath (1927–1933), Roman (1938), Basse (1952), Arkell *et al.* (1957), and Donovan *et al.* (1981).

The aspidoceratids have stood traditionally as one of the families of the Perisphinctoidea, however, on an unclear basis, perhaps because of their often cited origin as offshoots from the Perisphinctidae (Basse, 1952; Arkell *et al.*, 1957; Donovan *et al.*, 1981), and/or because of the ontogeny of their septal suture line (Schindewolf, 1966). The general origin of aspidoceratids from the Grossouvriinae in the late Middle Callovian can be assumed with little doubt (see Énay, Howarth, 2019, and references therein), but they developed very distinctive shell morphologies, ornamentations, evolutionary trends, life-histories, and modifications of sexual dimorphism.

[1] Laboratorio de Paleontología, IFG, Facultad de Ingeniería, Universidad Nacional de Rosario, Pellegrini 250, 2000 Rosario, Argentina; parent@fceia.unr.edu.ar.
[2] Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany; guenter.schweigert@smns-bw.de.
[3] Maurenstraße 26, 78194 Immendingen-Hattingen, Germany; Armin.Scherzinger@t-online.de.

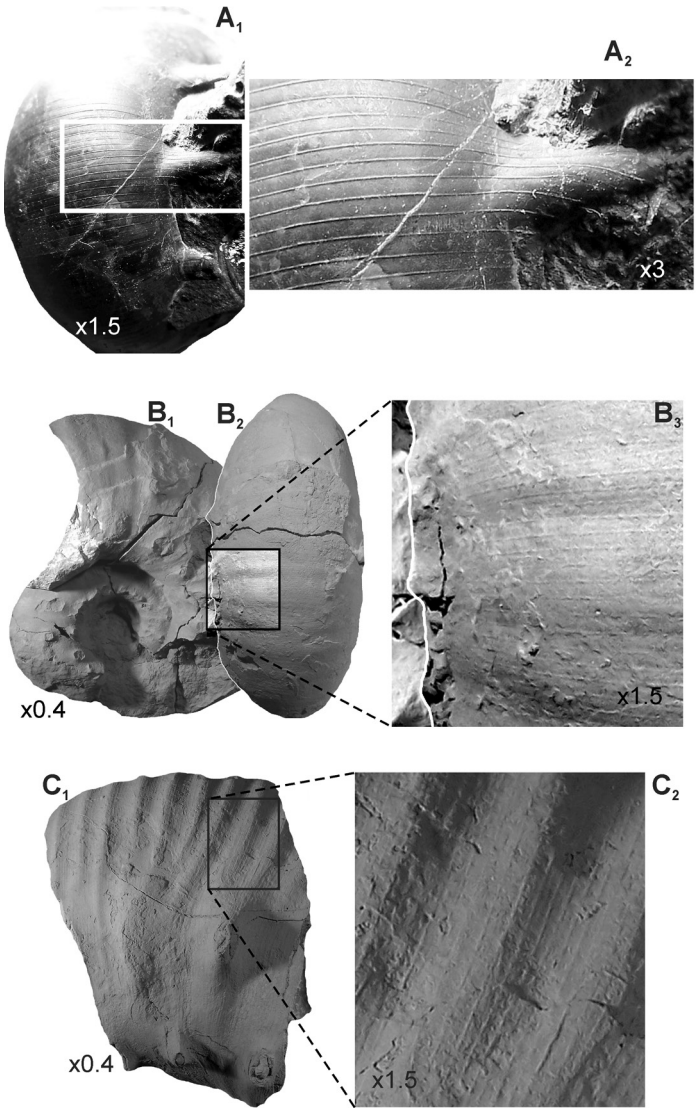

Fig. 1. Some ornamental details typical of aspidoceratoids

A – *Aspidoceras euomphalum* Steuer, 1897, Arroyo Cieneguita (Mendoza Province, Argentina), Internispinosum Zone (Andean upper Middle Tithonian). Juvenile macroconch phragmocone (Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano": MCNAM-24456/2), ventral views showing the growth lines evenly distributed, extended through the ventrolateral spines. The juvenile stages of the species bear no ribs, only growth lines. This specimen was formerly figured in Parent *et al.* (2011: fig. 36C) showing the structure of the spines; **B** – *Aspidoceras euomphalum* Steuer, 1897, Cerro Lotena (Neuquén Province, Argentina), Internispinosum Zone (Andean upper Middle Tithonian). Adult macroconch phragmocone (Laboratorio de Paleontología, Universidad Nacional de Rosario: LPB-1221), lateral (B_1) and ventral (B_2) views; B_3: gross growth lines evenly distributed, running in parallel over wide, blunt ribs; **C** – *Toulisphinctes* cf. *rafaeli* (Oppel, 1863), Cerro Lotena, upper Proximus Zone (Andean Middle Tithonian). Fragmentary adult macroconch phragmocone (Laboratorio de Paleontología, Universidad Nacional de Rosario: LPB-1222); lateral views showing gross growth lines evenly distributed, running in parallel over gross ribs

In this paper we analyze the distinctive features of the aspidoceratids, concluding that this group of ammonites must be grouped as a separate superfamily.

CHARACTERISTICS OF THE ASPIDOCERATIDS

Throughout their evolution, the aspidoceratids have developed different combinations of unique characters unknown from any of the representatives of the other families included in the Perisphinctoidea, and many of them are unique even among the remaining Middle and Late Jurassic Ammonitina.

The most significant characters which make the aspidoceratids a group highly differentiated from typical perisphinctoids are:

1. Their very thick, strongly calcified, porous aptychus (lower mandible), the laevaptychus. This type of aptychus differs strongly from all the remaining types (see reviews by Lehmann, 1987; Parent *et al.*, 2014; Parent, Westermann, 2016).
2. Most macroconchs (females) are more or less globose or stout, with different morphologies (from platycones to sphaerocones, see Arkell *et al.*, 1957; Énay, Howarth, 2019), all of which show a high growth rate of the whorl section area.
3. Shells are in most cases heavily armoured; the sculpture includes floored and non-floored spines and/or tubercles (bullate or spiny) (Checa, Martin-Ramos, 1989; Ifrim *et al.*, 2018), and ribs often connecting the spines/tubercles. Shells are usually covered by strong growth lines running in parallel over gross ribs (Fig. 1).
4. Aspidoceratids lack any constrictions, which are otherwise characteristic and persistent for perisphinctoids.
5. The adult bodychamber is short to very short, with lengths <180°, sometimes only close to 90°, both in microconchs (males) and especially in the macroconchs (females). In true perisphinctoids, the macroconchs have usually bodychamber lengths ≥270–360°.
6. Sexual dimorphism is characterized by miniaturized microconchs and the abundant occurrence of small-sized macroconchs (mesoconchs of Chandler, 2019) as well as occasional sexual change during ontogeny (see Parent *et al.*, 2008; Scherzinger *et al.*, 2018). In some aspidoceratid genera (*e.g.*, *Orthaspidoceras*) corresponding microconchs have not been recorded; possibly the males became further reduced and lost their shell completely (Schweigert, 1997: 15, 16).

Other characteristics which are very conspicuous in aspidoceratids and not common in other perisphinctoids:

a. A microphagous feeding style preying on small-sized planktonic organisms such as saccocomid crinoids (Keupp *et al.*, 2016). This is known from their crop- or stomach contents preserved in specimens from lithographic limestones (Schweigert, Dietl, 1999), making them the baleen whales among Late Jurassic ammonites.
b. Aspidoceratids have successfully adapted to a wide range of biotopes and ecological settings, as reflected in their worldwide palaeogeographic distribution except for the Boreal/Polar regions.
c. Phyletic lineages tended to be long-lived, and many species occur morphologically almost unchanged in distant parts of the world, *e.g.*, the Late Callovian *Peltoceras retrospinatum* Gérard & Contaut, 1936 (Hillebrandt, Gröschke, 1995) and the Early Tithonian *Pseudhimalayites subpretiosus* (Uhlig, 1878; see Parent *et al.*, 2011) in the Andes and in the western Tethys.
d. The septal suture line (whose subadult design and frilling are highly dependant upon the whorl section, Pictet, 1854: 669; Spath, 1919), has a wide and tabulated first saddle with a shallow mid-incision, the saddle usually covering radially one third to one half of the height of the flank of the shell (*e.g.*, Basse, 1952: fig. 52: 22, 23; Schindewolf, 1966).

THE SUPERFAMILY ASPIDOCERATOIDEA

All or many of the above mentioned features are not known to be combined in any other group of the Perisphinctoidea. On this basis, it is herein proposed to raise the family Aspidoceratidae Zittel, 1895 to the rank of a superfamily, with the following arrangement:

Superfamily Aspidoceratoidea Zittel, 1895

Family Aspidoceratidae Zittel, 1895

Subfamily Aspidoceratinae Zittel, 1895

Subfamily Euaspidoceratinae Spath, 1931

Subfamily Epipeltoceratinae Donovan *et al.*, 1981

Subfamily Hybonoceratinae Olóriz, 1978

Family Peltoceratidae Spath, 1924

Subfamily Peltoceratinae Spath, 1924

Subfamily Gregoryceratinae nov. Diagnosis. Smooth or ribbed flanks in the inner whorls; outer whorls with strongly angular and rursiradiate ribbing; subtrapezoidal whorl section with flattened venter and concave flanks in the adult stage. Genera included: *Gregoryceras* Spath, 1924, *Pseudogregoryceras* Jeannet, 1951.

Remarks. The Aspidoceratoidea includes two main lineages, whose earliest representatives belong to *Euaspidoceras* Spath, 1931 (Aspidoceratidae) and *Peltoceras* Waagen, 1871 (Peltoceratidae), respectively. The total stratigraphic range of this superfamily is rather well established. The earliest known forms appear during the earliest Late Callovian (Bonnot *et al.*, 2005). The latest representatives are globose *Physodoceras* (see Wierzbowski, Remane, 1992: pl. 2: 7) and evolute "*Aspidoceras*" *taverai* Checa (1985: pl. 19: 3, 4) of the Early Berriasian Jacobi Zone.

For the distribution of genera within each family see Énay, Howarth, 2019. *Euaspidoceras* seems to have been the root of the other main lineages of the Aspidoceratinae (*Clambites* Rollier, 1922, *Physodoceras* Hyatt, 1900, and *Aspidoceras* Zittel, 1868) in the Bimammatum Zone (see *e.g.*, Schweigert, 1997; Schweigert, Callomon, 1997; Énay, Howarth, 2019), whose earliest representatives are known from the Submediterranean Province and the western Tethys.

Epipeltoceratinae is emended from its original definition to (1) include the genera *Clambites*, *Epipeltoceras* Spath, 1924, and *Amoebopeltoceras* Schweigert, 1995, and (2) to exclude the genera *Klematosphinctes* Buckman, 1922 and *Mirosphinctes* Schindewolf, 1926, the latter two represent microconchs of *Euaspidoceras* (Euaspidoceratinae). The continued use of the Epipeltoceratinae is preferred instead of introducing a new subfamily based on *Clambites*, a genus which is morphologically still close to its euaspidoceratin rootstock, whereas the corresponding microconchs are highly diagnostic.

Gregoryceratinae nov. subfam. is characterized by total reduction of microconchs; they are only represented as fossils by meso- and macroconchs. Stratigraphic range (Schweigert, Ebel, 1999; Bert, 2004; Énay, Howarth, 2019): Cordatum Zone (Lower Oxfordian) to Bimammatum Zone (base of the Kimmeridgian *sensu* Wierzbowski *et al.*, 2016).

DISCUSSION AND CONCLUSION

Engeser, Keupp (2002: 88) suggested the Aspidoceratidae could be separated from the Perisphinctoidea, based on a supposed condition of "well defined monophyletic unit".

The highly differentiated features of the aspidoceratoids indicate that their life-histories were very different from those of the perisphinctoids. This could be discussed at length, but there is room here just for a short set of speculations. A direct consequence of the high growth rates of the whorl section area seems to be the fact that the adult macro-

and microconchs have comparatively lower numbers of whorls than most, if not all the perisphinctoids, *i.e.* either they grew up rapidly, or (less probably, see Hewitt *et al.*, 1993; Bucher *et al.*, 1996) their life-span was shorter. Sexual change as well as accelerated sexual maturation resulting in small-sized females, so-called "mesoconchs" (Chandler, 2019), has been demonstrated for some Late Jurassic aspidoceratids (Parent *et al.*, 2008; Scherzinger *et al.*, 2018). The great variety of morphologies known in aspidoceratoids seems to indicate that their genetic programs were able to evolve fast morphologic changes, enabling adaptations to a wide spectrum of environmental conditions.

The group of the aspidoceratid ammonites should be arranged into the rank of superfamily since they are significantly different from all other perisphinctoids. The members of the Aspidoceratoidea show great potential for studies of the developmental and evolutionary patterns and processes in ammonites, and can be used for biostratigraphic-chronostratigraphic purposes and interprovincial correlations.

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