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The Arestoceratinae van Hoepen, 1942: A resurrected subfamily of late Albian brancoceratid ammonites, with description of a new genus

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ABSTRACT

The subfamily Arestoceratinae van Hoepen (1942), long relegated to the synonymy of Mortoniceratinae (Wright, 1957, 1981, 1996), is resurrected for a phyletically-distinct group of strongly-compressed, generally bituberculate, late Albian brancoceratid ammonites in which there is a strong tendency for the umbilical seam to egress and the narrow subtabulate keeled venter to become fastigiate in later growth. Upper Albian biostratigraphy is discussed and a new zonation proposed with the introduction of the *Goodhallites goodhalli* Zone (=*binum* + *choffati* subzones) to emphasize the importance of arestoceratines to upper Albian biostratigraphy. The group is highly provincialized, and the new genus *Lobitoceras* is introduced for a member from the upper Albian of Angola. Sexual dimorphism is addressed, and the problem of recognizing dimorphic pairs is discussed. In addition the new genus *Moutaiceras* is created for a mortoniceratine from the uppermost Albian of Angola incorrectly-assigned to *Arestoceras*.

1. Introduction

The subfamily Mortoniceratinae (*sensu* Wright, 1957, 1981, 1996) is a group of late Albian ammonites with near-cosmopolitan distribution. Due to complex evolutionary relationships most workers have opted for a "lumping" approach to their classification (cf. Wright, 1957, 1981, 1996), often without careful analysis of the taxa involved. However taxonomic lumping involves unification on the basis of shared primitive characters (Linnean taxonomy), thereby obfuscating the finer branches of the evolutionary tree. It creates "categories of convenience" (Mayr, 1963) and, all too often, is used to dispose of taxonomic inconveniences. Here the writer is guided by the Darwinian dictum that, in order to be natural,"… *the arrangements of the groups in each class …. must be strictly genealogical*" (Darwin, 1859, p. 378). This guidance, a profound truism, has been overlooked by most ammonitologists who continue to group like with like (Linnean taxonomy). Stated simply a natural classification (Darwinian taxonomy) is one which seeks to identify the branches of the evolutionary tree and to accurately replicate these in an appropriate classification; it is a phylogenetic taxonomy. Classifications not strictly rooted in genealogy are no more than convenient fiction (van Deemter, 2010).

With respect to the validity of arestoceratine genera the taxonomic literature is replete with subjective comments on rank, such as "… the differences do not warrant generic separation", "…. the differences are regarded as specific only", and "… generic separation seems unnecessary". This recognition/rejection of genera is highly subjective since they are "…. merely artificial combinations made for convenience" (Darwin, 1859: 437), and because "…. generic limits are not defined by any rules …. for practical reasons, the lumping of several distinct species-groups into a single genus is currently in vogue (Fry et al., 2004, p. 456). Such is the fickle ground on which Linnean genera are constructed; it represents "… the tyranny of taxonomy" (Cooper, 2015b, p.159). In phylogenetic taxonomy however rank is not discretionary; it is pre-determined by evolutionary position. Hence the validity of genera does not rely on authoritative proclamation, but on unraveling the evolutionary history of the group. With this in mind the content and validity of the subfamily Arestoceratinae is revisited.

2. Material and methods

The current analysis is based upon re-examination and redescription of type material housed in the South African Museum, Cape Town (SAM) and the Natural History Museum, London (BMNH). Unfortunately a significant number of types are missing from the van Hoepen collection in the SAM, presumed to be

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lost. The biochores used here are those defined by benthic infaunas (trigoniid bivalves, cf. Cooper, 2015a) but, obviously, these boundaries would be blurred by the nektonic habit of ammonites and the capacity for their buoyant shells to be driven by currents and wind far from their natural habitat.

Abbreviations for measurements in millimetres are as follows: D = shell diameter, Dmax = maximum shell diameter, H = height of whorl, Wi = intercostal width of whorl, U = umbilical diameter. Measurements as a percentage of shell diameters are given in parentheses.

The repositories of material are as follows:

AMNH – American Museum of Natural History, Washington.
BMNH – Natural History Museum, London.
DNSM – Durban Natural Science Museum, Durban
OUM – Oxford University Museum, Oxford.
MHNP – Museum d'Histoire Naturelle, Paris
SAM – South African Museum, Cape Town.
TMM – Texas Memorial Museum, Austin.
UT – University of Texas, Austin.

3. Biostratigraphy

In order to facilitate comparison among arestoceratines, the following upper Albian ammonite zonal scheme is used:

Stoliczkaiella dispar Zone
Durnovarites perinflatus Zone
Subschloenbachia rostrata Zone
Pervinquieria inflata Zone
Goodhallites goodhalli Zone
Rusoceras pricei Zone
Dipoloceras cristatum Zone

The writer prefers to reserve subzones for particular sedimentary basins, whereas faunal assemblages traceable over a substantial number of geographically-widespread sedimentary basins are accorded zonal recognition. The *Dipoloceras cristatum* Zone is now accepted as defining the base of the upper Albian (Owen, 2012). According to revised identifications provided by Dr Owen, *Hysteroceras choffati* Spath (= *crassicostatum* van Hoepen) already occurs at this level. Here the *Rusoceras pricei* Zone (Amédro, 2009) is restricted to the *H. orbignyi* Subzone of Owen (2012) and Gallois et al., 2012). It is defined by the first appearance of *Hysteroceras varicosum* (J. de C. Sowerby) and large mortoniceratines (*Rusoceras*, *Deiradoceras*, *Mimeloceras*). The *Goodhallites goodhalli* Zone (= *binum* + *choffati* subzones of Gallois et al., 2012) is introduced to emphasize the importance of arestoceratine ammonites to upper Albian biostratigraphy and palaeobiogeography, the most widespread member of which is *G. goodhalli* (J. de C. Sowerby). Arestoceratines first appear in the *binum* Subzone (= *varicosum* Zone of Spath, 1942, p. 707, table 3) and range upwards into the *rostrata* Zone of Texas (Kennedy et al., 1998), and thus characterize the middle part of the upper Albian. Following Owen (1988) it might be appropriate to unite the *price* and *goodhalli* zones as the *Hysteroceras varicosum* Superzone. Owen's (2012) re-definition of the *P. inflata* Zone is followed here. *Subschloenbachia rostrata* has been reported from as far afield as the Crimea (Marcinowski & Naidin, 1975), Germany (Owen, 1989), England (Spath, 1932), Texas (Kennedy et al., 1998; Kennedy, 2004), Angola (Meister et al., 2011) and Madagascar (Collignon, 1963), and the *perinflatus* Zone has a similar but even wider distribution with typical associations also in Hungary (Scholz, 1979) and Zululand (DNSM collections). Both these subzones, with distributions as wide as or wider than the *cristatum* Zone, are here elevated to zonal rank. Treatment of the *perinflatus* Zone as a subzone of the *dispar* Zone is inappropriate since *S. dispar* (d'Orbigny) is a younger species that does not occur at this stratigraphical level which, instead, is characterized by *Stoliczkaiella* of the *notha* (Spath) group.

In view of the importance of van Hoepen's work to brancoceratid classification it should be emphasized that he made every effort to stratigraphically locate his material; "… In the field the exact locality and the precise bed in which the specimen occurred were recorded. During five expeditions the stratigraphy of the area concerned of the Zululand Cretaceous was studied carefully and the mutual relationships of localities without direct connection with each other were established without any doubt" (van Hoepen, 1946c, p.267). Unfortunately exposures in Zululand are mostly poor, and much material is picked up loose from surface colluvium and erosional gullies. The bed-by-bed collecting and rigorous stratigraphical control available in cliff exposures is not possible, except for very limited intervals, and some degree of faunal mixing is implicit. On the flip side the classic Folkestone succession is significantly condensed (Gallois et al., 2012), with a number of stratigraphical breaks (phosphatic nodule beds), whereas the upper Albian of Zululand is an expanded sequence with only one minor discontinuity. Van Hoepen's Bed 11 contains *Dipoloceras cristatum* (Brongniart) and his highest level, at Beacon 624, has yielded a *P. inflata* Zone faunule.

Dealing with stratigraphically-mixed samples, whether depositionally condensed or accidentally mixed, it is not possible to know if recorded differences are due to material from slightly different stratigraphical levels, i.e. evolutionary, or due to intraspecific, ontogenetic and/or sexual variation. Clearly all of these are likely to be factors. Unfortunately many of the sites collected by van Hoepen have since been flooded by the construction of a dam, and the area is now part of the Phinda wildlife reserve in which lions are free to roam, thus making resampling very difficult.

4. Sexual dimorphism

The side-by-side presence of small (*Cainoceras*, *Poikiloceras*, *Lethargoceras*) and large arestoceratines (*Arestoceras*, *Aidoceras*, *Letheceras*, *Pagoceras*, *Tetagmenoceras*) in the upper Albian strata of Zululand invites interpretation as sexual dimorphs. However arestoceratine populations in other parts of the world do not display similar morphological variation or dimorphism, and the diversity of the group seems to have been largely an Ethiopian radiation. Moreover matching macroconchs 200–300 mm in diameter with microconchs <100 mm in diameter, with different although grossly-similar morphology, is pure guesswork since similarity of early whorls is as much an indication of ancestry as it is of dimorphism. Indeed full knowledge of the ontogenetic change of arestoceratines and mortoniceratines, in particular the characters of the adult body chamber, is critical to satisfactory identification.

Wright (1996) suggested mortoniceratine macroconchs may have had simple apertures whereas microconchs had a rostrum of some sort. However no known arestoceratines have a simple peristome; there is either at straight diagonal horn or a gently-curved rostrum that follows the spiral curvature of the venter. Henderson & Kennedy (2002) figure an undoubted macroconch of *G. goodhalli* with a rostrum of the latter type, but some small species, e.g. *Poikiloceras bonum* (van Hoepen) (see below in Fig. 4K), also have a rostrum of this type. No small arestoceratines, e.g. *Cainoceras*, are known to have a diagonal rostrum, and material in the SAM suggests that both macroconchs and microconchs of *Prohysteroceras wordiei* Spath have a straight diagonal horn. It would appear therefore that the character of the rostrum in arestoceratines is not sexually induced.