INSTRUCTIONS TO AUTHORS

1. MATERIAL should be original and not published elsewhere, in whole or in part.

2. LAYOUT should be as follows:
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   Number of illustrations (figures, enumerated maps and tables, in this order)
   (b) Abstract of not more than 200 words, intelligible to the reader without reference to the text
   (c) Table of contents giving hierarchy of headings and subheadings
   (d) Introduction
   (e) Subject-matter of the paper, divided into sections to correspond with those given in table of contents
   (f) Summary, if paper is lengthy
   (g) Acknowledgements
   (b) References
   (i) Abbreviations, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2.5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

   Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

   Footnotes should be avoided unless they are short and essential.

   Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

   All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

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   ‘Smith (1969) describes . . .’
   ‘Smith (1969: 36, fig. 16) describes . . .’
   ‘As described (Smith 1969a, 1969b; Jones 1971)’
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(continued inside back cover)
LOWER CRETAEOUS
(MIDDLE ALBIAN)
AMMONITES FROM
DOMBE GRANDE, ANGOLA

By
MICHAEL R. COOPER

Cape Town        Kaapstad
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LOWER CRETACEOUS (MIDDLE ALBIAN) AMMONITES FROM DOMBE GRANDE, ANGOLA

By

MICHAEL R. COOPER
National Museum, Bulawayo

(With 31 figures)

[MS accepted 3 March 1982]

ABSTRACT

Two stratigraphically separated Middle Albian faunules, dominated by Douvilleiceras and Oxytropidoceras respectively, are described from the environs of Dombe Grande. The wide range of continuous variation within these assemblages has an important bearing on the taxonomy of these forms. The phylogeny of the Mojsisovicziinae is discussed, and the following new taxa are created: Mortoniceratoides gen. nov., Oxytropidoceras (Mirapelia) subgen. nov. and O. (Benavidesites) subgen. nov. Middle Albian biostratigraphy outside the Boreal Realm is discussed.

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INTRODUCTION

Choffat (in Choffat & De Loriol 1888) was the first to record ammonites from the lower part of the Albian succession of Angola, describing andFiguring an ‘Acanthoceras’ mamillare (Schlotheim) (= Douvilleiceras mammillatum aequinodum (Quenstedt)) (Choffat & De Loriol 1888: 71, pl. 3 (fig. 1)) from the Dombe Grande area. The specimen was said to have come from the ‘Couches à Pholadomya pleuromyaeforis’, but as these beds are almost certainly of Aptian age (Howarth 1965; Cooper 1976) this is an error. Howarth (1965) described a small collection of Douvilleiceras made in 1930–1 by Alexandre Borges from the Dombe Grande region, and recorded the species D. mammillatum var. ?aequinodum (Quenstedt) and D. orbignyi Hyatt, thereby suggesting the presence of upper Lower Albian (D. mammillatum Zone) strata. Cooper (1976) described the bio- and lithostratigraphy of the region. The present collections come from the immediate vicinity of Dombe Grande.
(Fig. 1), and well above the beds containing *Pholadomya pleuromyaeformis* Choffat.

Prefixes to catalogue numbers refer to material in the following institutions:

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Measurements are in millimetres, with dimensions, as a percentage of the diameter, in parentheses.

### REGIONAL GEOLOGY

The late Mesozoic succession in the Cuanza basin has been named the Cuanza Group (Cooper 1976). At Dombe Grande in the extreme south of the basin (12°54'S 13°13'E), the base of the Cuanza sequence is formed by the Dombe Formation, a unit of coarse clastics and lagoonal deposits with interbedded evaporites. The disconformably overlying transgressive deposits of the ‘Formação com Pholadomya’ (Neto 1960, 1961) attain a thickness of about 100 m and comprise a basal member of oolitic limestones, calcarenites and siltstones capped by calcareous siltstones rich in *Pholadomya pleuromyaeformis* and other bivalves (Fig. 2C–F). Also present at this level are the echinoids *Salenia dombeensis* De Loriol and *Pygurus africanus* De Loriol, and the molluscs *Neithia shawi* Pervinquière, *Retusa malheiroi* (Choffat), *Panopea gurgitis* (Brongniart), *Lithophaga praetonga* (d’Orbigny), *Nerita malheiroi* Choffat, ‘Natica’ feioi Choffat, *Actaeonella* (Trochactaeon) cordeiroi (Choffat), *Actaeon lenzi* Choffat, *Ampullina* (Pseudamura) bulbiformis (J. Sowerby), *Pinna robinaldina* d’Orbigny, *Cylindrites? delgadoi* Choffat, and *Tylostoma peschueli* Choffat.

Marine regression is reflected in the succeeding ‘Formação com Nerinea’ (Fig. 1, locality 2), a lithologically highly variable unit spanning some 400 m and comprising red and yellow lagoonal clastics yielding fossil wood, the gastropods *Nerinea capelloi* Choffat (Fig. 3G–H) and *Cerithium monteiroi* Choffat, and an indeterminate ammonite (*jide* Neto 1961).

The ‘Formação com Nerinea’ are overlain, perhaps disconformably, by limestones and marls at the base of the Cuio Formation, the lower beds of which have yielded the faunas described herein. The two assemblages, which were picked up mainly as surface scree, are stratigraphically separated at locality 4 (Fig. 1), with the *Oxytropidoceras* fauna occurring to the north-east and thus from the younger beds. Upward the sequence becomes increasingly unfossiliferous, and calcarenites and grits (Fig. 1, locality 1) span much of the
Fig. 2. A–B. *Puzosia bistricta* (White). SAM-PCA2649, ×1. C–F. Undetermined bivalves from the 'Couches a Pholadomya', Reinecke Collection, South African Museum, ×1.5.
Fig. 3. A–B. Oxypodoceras (Mirapelia) buarquianum (White), SAM-PCA5445, an individual transitional to douglasi morphotypes. C–D. Puzosia bistrica (White), SAM-PCA3474. E. Inoceramus gr. anglicus Woods, SAM-PCA3443, from the Douvilleiceras assemblage. F. Birostrina? cf. coptensis (Casey), SAM-PCA2664, from the Oxypodoceras assemblage. G–H. Nerinea capelloi Choffat. G. SAM-PCA5448, $\times 1.5$. H. SAM-PCA5450, $\times 1.5$. All $\times 1$ unless otherwise stated.
remainsd of the Middle Albian. These sediments are interpreted as reflecting marine regression. The Cuio Formation attains a thickness of some 200 m and is succeeded by bioclastic and oolitic limestones and calcarenites (Fig. 1, localities 3, 6) yielding a low Upper Albian fauna including Prohysteroceras wordiei Spath and Mortoniceras spp. This unit is to be correlated with the Catumbela Member of the Cabo Ledo Formation to the north, reflecting the early late Albian (Hysteroceras orbignyi Zone) transgression.

SYSTEMATICS

Subclass Ammonoidea Zittel, 1884

Family Douvilleiceratidae Parona & Bonarelli, 1897

Discussion

Since the lineage Procheloniceras → Cheloniceras → Eodouvilleiceras → Douvilleiceras represents a single phyletic lineage, the subfamily Cheloniceratinae should be included in the synonymy of the nominate subfamily.

Subfamily Douvilleiceratinae Parona & Bonarelli, 1897

Genus Douvilleiceras de Grossouvre, 1894

Type species Ammonites mammillatus Schlotheim, 1813; subsequent designation of I.C.Z.N., Opinion 422, 1956

Discussion

Casey (1962: 260) has given a detailed diagnosis and discussion of this genus, to which little may be added.

The genus Trinitoceras was erected (Scott 1940: 1016) for very large douvilleiceratids in which the . . . douvilleiceratid sculpture is evident up to or beyond a diameter of 200 mm. Costae are multituberculate as in Douvilleiceras, but the umbilical tubercles are greatly exaggerated in size, forming large bullae on the umbilical margin at the ends of alternate costae. On later whorls costae lose all trace of tuberculation but retain, irregularly, their alternate primary and secondary arrangement. On the latest whorls shown, the ribs are nearly equal, except that the occasional secondary (marked only by the fact that it does not reach the umbilicus) is intercalated between the primaries. The whorl section, degree of evolution, and the umbilical area do not differ greatly from like features of well-known species of Douvilleiceras.

It is clear from the above description that the genus Trinitoceras is based upon the gigantic shells that accompany virtually all Douvilleiceras populations; thus D. leightonense Casey, D. cheloniceratiforme Tavani, D. restitutum Anderson, and D. charshangense Mirzoyev are all typical Trinitoceras. However, the fact that Trinitoceras and Douvilleiceras everywhere occur together as well as the fact that they are indistinguishable in their early ontogenetic stages and
attain maturity at vastly different diameters, suggests to the writer that the
differences are those between sexual dimorphs. *Trinitoceras* is here considered
to be based upon *Douvilleiceras* macroconchs, and Casey (1962) is followed in
regarding it a synonym of *Douvilleiceras*.

Up to now almost fifty trivial names have been applied to *Douvilleiceras*;
these include *D. mammillatum* (Schlotheim) and its varieties *paucicostatum*
Parona & Bonarelli, *praecox* Casey, *baylei* Spath and *aequinodum* (Quenstedt),
*D. inaequinodum* (Quenstedt), *D. pseudinaequinodum* Collignon, *D. orbignyi*
Hyatt, *D. clementinum* (d’Orbigny). *D. solitae* (d’Orbigny), *D. tarapacaense*
Etayo-Serna, *D. abozaglio* Etayo-Serna, *D. ivenosi* (Coquand), *D. spiniferum*
(Whiteaves), *D. rex* (Scott), *D. reesidei* (Scott), *D. grandense* (Scott),
*D. adkinsi* (Scott), *D? dunlapii* (Scott), *D. quitmanense* Scott, *D. spathi* Scott,
*D. cuchillense* Scott, *D. muralense* Stoyanow, *D. aurarium* Anderson, *D. re-
titutum* Anderson, *D. offcinatum* (White), *D. euzebioi* (Maury), *D. ser-
Tavani, *D. albiense* (Tavani), *D. variabile* Tavani, *D. cheloniceratiforme* Ta-
vanii, *D. scabrosus* Casey, *D. alternans* Casey, *D. pustulosum* Casey, *D. leigh-
tonense* Casey and its variety *pringlei* Casey, *D. magnodosum* Casey,
*D. subleightonense* Mirzoyev, and *D. charshangense* Mirzoyev.

The extreme range of morphological variation exhibited by most assem-
blages is emphasized by the splitting of the British collections into fourteen taxa
(Casey 1962), those from Texas into eleven species (Scott 1940), and the
Somali collections into eight species (Tavani 1942, 1949), and this seems to
suggest genetic polymorphism. Thus Casey (1962: 263) has noted that all the
mostly endemic species of *Douvilleiceras* recorded from southern England ‘ . . .
come from a limited range of strata and they constitute a closely interconnected
plexus that in former days would have been interpreted (perhaps correctly) as
one very large, highly variable species’. Unfortunately Casey’s revision, coming
at a time when it was the practice to base species on very narrowly defined
limits, suffers from oversplitting, since recent studies of ammonite populations
(Kennedy & Cobban 1976) suggests that such variation is not extraordinary. In
addition, Mirzoyev (1967: 54) has also commented that ‘ . . . all species of
*Douvilleiceras* are closely interrelated and could have been treated as a single
very extensive and varied species; but investigators concerned with this group
of ammonites have made efforts to discover differences, based entirely on the
frequency, degree of development and modifications of the conch sculpture in
the course of its development’.

Casey (1962), in his revision of the British species of *Douvilleiceras*, laid
much emphasis on the width of the ventral sulcus, number of notches per rib,
and the ontogenetic stage at which ornament change occurred as taxonomic
criteria. However, many writers have noted that the number of notches
increases with diameter, while Collignon (1963), Mirzoyev (1967), and
McLearn (1972) have all reported specimens with different numbers of notches
on opposing flanks. Consequently, this criterion is considered to be of very
limited taxonomic significance, if at all. Both the width of the ventral sulcus and the ontogenetic stage at which morphological changes occur are relative characters that are unlikely to stand up to population analysis, especially when it is considered that many of the taxa so defined are contemporaneous, occurring together in the same bed. As such, the writer believes *Douvilleiceras* to display genetic polymorphism and thus high intraspecific variability.

Stratigraphically *Douvilleiceras* ranges from the top of the *Leymeriella tardefurcata* Zone (*Leymeriella regularis* Subzone) into the lower part of the Middle Albian (*Lyelliceras lyelli* Subzone of the *Hoplites dentatus* Zone). During this period it attained a cosmopolitan distribution and is currently reported from North America (British Columbia, California, Arizona, Texas, New Mexico), South America (Peru, Columbia, Brazil), Africa (Gabon, Angola, Zululand, Mozambique, Somalia), Madagascar, Asia (eastern Carpathians, northern Caucasus, western and central Kopet Dag, Bol’shoy Balkhan, Tuarkyr, Mangyshlak, Badkhiz Islands, southern Gissar Range, Afghanistan), Europe (southern England, France, Switzerland, Germany, Poland, Bulgaria), and Japan.

*Douvilleiceras mammillatum aequinodum* (Quenstedt, 1849)

Figs 4A–B, 6C–G, 7D, G–I, 8A–B, 9A–C, E, 10C–D, F–H, 12A–B, 17A

*Ammonites monile aequinodus* Quenstedt, 1849: 137, pl. 10 (fig. 2).

? *Ammonites offarctinus* White, 1887: 219, pl. 23 (fig. 4 only).

*Acanthoceras mammillare* (Schlotheim) Choffat (*in* Choffat & De Loriol). 1888: 71, pl. 3 (fig. 1).

*Douvilleiceras monile var. aequinodum* (Quenstedt) Breistroffer, 1947: 65.

? *Douvilleiceras cheloniceratiforme* Tavani, 1949: 38, pl. 8 (fig. 6).


? *Douvilleiceras restitutum* Anderson. 1938: 175, pl. 54 (fig. 2).

*Douvilleiceras mammillatum var. aequinodum* (Quenstedt) Casey, 1962: 271, pl. 40 (fig. 5), pl. 41 (figs 5–7), pl. 42 (fig. 10), figs 94a–c, 95a–b. 102d, 103a–b. Howarth, 1965: 343, pl. 1 (figs 1–4).


? *Douvilleiceras spiniferum* (Whiteaves) McLearn, 1972: 62, pl. 28 (fig. 1 only).

*Douvilleiceras* cf. *mammillatum* (Schlotheim) Young. 1974: 184, pl. 4 (figs 1, 3, 6).

**Material**


**Description**

This taxon is the most abundant component of the *Douvilleiceras* fauna, although many of the specimens are fragmentary and most are more or less eroded, having been picked up as surface scree. This erosion gives a number of
Fig. 4. A–B. *Douvilleiceras mammillatum aequinodum* (Quenstedt), SAM–PCA3434. C–D, F. *Douvilleiceras inaequinodum* (Quenstedt). C–D. SAM–PCA3435, a juvenile showing very fine intercalated ribs. F. SAM–PCA5451, a badly eroded fragment showing three intercalated ribs between main ribs. E. *Nerinea capelloi* Choffat, SAM–PCA5449, ×1.5. G. *Douvilleiceras variabile* Tavani, SAM–PCA3448. All ×1 unless otherwise stated.
Fig. 5. A–B. *Oxytropidoceras (Oxytropidoceras) rossyanum* (d'Orbigny). The original of D'Orbigny's (1841) photograph, NHMP. C–D. *Douvilleiceras mammillatum mammillatum* (Schlotheim). The neotype, BM-C12491. Both × 1. Photos: W. J. Kennedy.
specimens the appearance of having had very much narrower ribs than, in fact, they probably had.

The shell is moderately evolute (umbilicus 32.5–39% of the diameter), with rather inflated whorls, and a subreniform depressed whorl section. In all the better preserved material the ventral sulcus is, or appears to have been, rather narrow. The number of notches to each rib varies with ontogeny, with about 5 at 30 mm diameter increasing to 8–9 at about 60 mm diameter. Up to about 40 mm diameter the ribs tend to be simple, distant and rursiradiate, commonly with 10–14 ribs per half whorl. However, several of the more densicostate juveniles have 16 ribs per half whorl. Beyond this diameter intercalation and bifurcation becomes increasingly common, generally with 16–20 rather uniform ribs per half whorl. One individual, SAM–PCA3417, retains simple ribbing to 62 mm diameter, whereas SAM–PCA3431 has very fine, nontuberculate intercalatories between main ribs at about 40 mm diameter, only to loose them with further growth. The tuberculation of this subspecies is very reduced, typically with the lateral tubercle subdued and bullate. In SAM–PCA3472, however, main ribs bear a prominent lateral tubercle and, up to 35 mm diameter, alternate with fine nontuberculate intercalatories. Beyond this diameter all the ribbing becomes uniform and the lateral tubercule is much reduced and bullate. In SAM–PCA3435, the early whorls are strongly tuberculate and distantly ribbed but, at 47 mm diameter, there is a sudden and dramatic reversion to normal *aequinodum*-type ornament. SAM–PCA3430 connects typical *aequinodum*-type morphologies to the large macroconch fragments (SAM–PCA3408, 3410–3411, 3414, 3425, 3433, 3465, 3483, 3500) in the collection.

**Measurements**

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**Discussion**

Quenstedt (1849) described two species of *Douvilleiceras*, *D. aequinodum* and *D. inaequinodum*. Since the latter species is typically lower Middle Albian (Casey 1962), it may be reasonable to assume this is also the level of *D. aequinodum*. Such a supposition tends to be supported by their coexistence in the *eodentatus* Nodule Bed (Bed e of Destombes et al. 1977) (Fig. 12A–D, G–H) at Bully, Pays de Bray, France, and also in Angola. Since the Angolan *D. mammillatum* material is dominated by *aequinodum* morphotypes, with no undoubted individuals of *D. mammillatum* s.s. (Fig. 5C–D), it seems reasonable to assume that a genuine shift in population structure has occurred when
Fig. 6. A. Douvilleiceras inaequidum (Quenstedt). SAM-PCA3535, a juvenile. B. Oxytropidoceras (Mirapelia) buarquianum (White), SAM-PCA3765, a typical juvenile. C-G. Douvilleiceras mammillatum inaequidum (Quenstedt). C. SAM-PCA3427. D-E. SAM-PCA2639. F-G. SAM-PCA3431. All × 1.
compared with the typical mammillatum Zone assemblages of D. mammillatum (cf. Casey 1962). It is for this reason, and because D. aequinodum can arguably be regarded as typically Middle Albian, that the writer has used Quenstedt’s name at subspecific level. As noted by Casey (1962) aequinodum morphotypes are also abundant in the mammillatum Zone of England, but at this level coexist with, and are connected by transitions to, D. mammillatum s.s., D. mammillatum var. praecox Casey, and D. monile (J. Sowerby). Since there is, in the writer’s opinion, but a single biological taxon involved in the latter list, the various nominal forms are merely morphotypes within a single polytypic species. Disregarding the nomenclatural problems, it is clear that the Angolan population of D. mammillatum is substantially different from that at Copt Point, Folkestone, and thus warrants subspecific distinction.

Both Douvilleiceras restitutum Anderson and D. cheloniceratiforme are based upon macroconchs whose inner whorls suggest they may belong here. Similarly, the hypotype of D. spiniferum (Whiteaves) figured by McLearn (1972, pl. 28 (fig. 1)) also shows few features to distinguish it from typical aequinodum morphotypes. In addition, one of White’s (1887, pl. 23 (fig. 4)) syntypes of D. offarcinatum shows a rib density that suggests possible reference to Quenstedt’s taxon.

**Douvilleiceras variabile** Tavani, 1949


*Ammonites mammillaris* Schlotheim, d’Orbigny, 1841: 249, pl. 72 (fig. 5 only).

*Douvilleiceras variabile* Tavani, 1949: 37, pl. 10 (figs 1–2).

? *Douvilleiceras pseudinaequinodum* Collignon, 1963: 120, pl. 288 (fig. 1249).

*Douvilleiceras monile* (J. Sowerby) Collignon, 1963: 118, pl. 287 (fig. 1248).

*Douvilleiceras aff. baylei* Spath, Collignon, 1963: 118, pl. 287 (fig. 1247).

*Douvilleiceras subleightonense* Mirzoyev, 1967: 59, pl. 8 (figs 1–5).

? *Douvilleiceras* sp. B, McLearn, 1972: 67, pl. 13 (fig. 1), pl. 16 (fig. 1).

**Material**

Four specimens, SAM–PCA3422, 3447–3448 and 3496, all preserved as internal moulds.

**Description**

In shell form, this species is very similar to the last but with substantially different ornament. In the Angolan material, ornament comprises well-developed main ribs ornamented with a distinct umbilical tubercle, a pronounced mid-lateral tubercle and bullate ventral tubercles that weaken beyond about 45 mm diameter and are lost at about 60 mm diameter. At about this stage a small tubercle also appears between the umbilical and mid-lateral tubercle, and the ventral tubercles bear three notches. There are, therefore, eight notches per rib. Between these long ribs are invariably one, sometimes two intercalatories that do not connect with the umbilicus and lack mid-lateral tubercles. These ribs tend to be somewhat finer than the main ribs and give rise to the typical ‘variable’ ornament of this species.
Fig. 8. A-B. *Douvilleiceras mammillatum aequinodum* (Quenstedt), SAM-PCA 3429. C-D. *Douvilleiceras variabile* Tavani, SAM-PCA3447. Note the alternating long and short ribs and prominent lateral tubercle typical of this species. Both $\times 1$. 
**Measurements**

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<td>51</td>
<td>19</td>
<td>22</td>
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**Discussion**

*Douvilleiceras variabile* Tavani seems to be based upon the inner whorls of a macroconch, showing the irregular ornament of the early growth stages, with 1–2 weak ribs between main ribs, and the more regular ornament of the macroconch on the adoral half of the last whorl. Tavani’s (1949) species is undoubtedly very close to *D. mammillatum* (Schlotheim), and D’Orbigny’s (1841, pl. 72 (fig. 5)) *Ammonites mammillaris* seems to be a typical example of this species. Indeed, even in the present collection, several individuals seem to combine the characters of *D. variabile* and *D. mammillatum aequinodum* (Fig. 15E). This tends to suggest that *D. variabile* is merely another morphotype within a polytypic *D. mammillatum*. While this is the writer’s belief, opposition to the gross ‘lumping’ that such synonymies would involve from one of the referee’s of this paper has led to the adoption of a somewhat more cautious approach. *Douvilleiceras variabile* is here maintained as a distinct species because the writer does not believe in sympatric subspecies.

*Douvilleiceras subleightonense* Mirzoyev is a gigantic macroconch attaining some 600 mm diameter, whose inner whorls show the irregular ribbing typical of this species, and it may reasonably be included here. The *Douvilleiceras* sp. B of McLearn (1972, pl. 13 (fig. 1), pl. 26 (fig. 1)) is another macroconch that may belong here. Yet another macroconch whose inner whorls are reminiscent of this species is *D. pseudinaequinodum* Collignon. *Douvilleiceras ibernosi* (Coquand) (Pictet & Renevier, 1854, pl. 2 (fig. 1)) is somewhat similar to *D. variabile*, but lacks the pronounced lateral tubercle.

*Douvilleiceras inaequinostrum* (Quenstedt, 1849)


*Ammonites mammillaris* Schlotheim, d’Orbigny, 1841: 249, pl. 73 (figs 1–3 only).

*Ammonites monile inaequinostrum* Quenstedt, 1849: 138, pl. 10 (fig. 1).

*Douvilleiceras inaequinostrum* (Quenstedt) Parona & Bonarelli, 1897: 95, pl. 4 (fig. 6), pl. 13 (fig. 6). Collignon, 1950: 46, fig. 2; 1963: 114, pl. 285 (fig. 1245). Casey, 1962: 282, fig. 95c.


*Douvilleiceras mammillatum* var. *baylei* Spath. 1923: 70, pl. 5 (fig. 4).

*Douvilleiceras* aff. *iaequinostrum* (Quenstedt) Spath, 1923: 73, pl. 4 (fig. 5).


*Douvilleiceras alternans* Casey, 1962: 282, pl. 42 (fig. 1), fig. 1021.

? *Douvilleiceras magnadousum* Casey, 1962: 284, pl. 42 (fig. 4), fig. 102k.

? *Douvilleiceras charshangense* Mirzoyev, 1967: 54, pl. 7 (figs 1–5).


*Douvilleiceras* cf. *orbignyi* Hyatt, Young, 1974: 188, pl. 5 (figs 9–10).
Fig. 10 A-B. Oxytropidoceras (Mirapelia) buarquianum (White). SAM-PCA2656, a douglasi morphotype which very closely approaches *O. mirapelianum* (d'Orbigny). × 0.75. C-D, F-H. *Douvilleiceras mammillatum aequinodum* (Quenstedt). C. SAM-PCA3494. D. SAM-PCA3503. F. SAM-PCA3527. G. SAM-PCA3499. H. SAM-PCA3518. E. *Douvilleiceras inaequinodum* (Quenstedt), SAM-PCA3504. All × 1 unless otherwise stated.
Fig. 11. A. *Douvilleiceras inaequidum* (Quenstedt), SAM–PCA3458, a specimen showing the increased number of intercalatories in maturity. B. *Oxytropidoceras (Mirapelia) sergipense* (White). Front view of SAM–PCA5444. C–D. *Douvilleiceras variabile* Tavani, SAM–PCA3422. E. *Plagiostoma* sp., SAM–PCA5490, from the *Oxytropidoceras* assemblage. All × 1.
Material

Eighteen specimens, SAM–PCA3435–3438, 3444, 3451, 3453, 3456–3458, 3466, 3492, 3495, 3498, 3504, 3512, 3525, and 3535, all preserved as limestone steinkerns.

Description

This is a rather common species in the Angolan fauna. The shell is generally moderately evolute, inflated, with a subreniform, depressed whorl section. The umbilicus is rather wide, with steep umbilical walls and well-rounded shoulders. Ornament comprises sparse, distant, slightly rursiradiate ribs, which are narrower than the interspaces and alternate weak and strong. The strong main ribs are ornamented with small umbilical tubercles, a prominent lateral tubercle, and exaggerated ventral bulges, each with three spiral notches. In juveniles, only two spiral notches are present on the ventral bulges. With ontogeny, a small tubercle appears between the umbilical and mid-lateral tubercle and another between the latter and the ventrolateral bulges. Thus, there may be up to eight crenulations per rib in adults. The fine intercalated ribs, usually one and rarely two, between main ribs generally lack discernible ornament (on the weathered internal moulds), but in some individuals develop a small but distinct mid-lateral tubercle. In the early growth stages (Figs 4C–D, 12G–H) the intercalated ribs may be absent or so fine that there is difficulty in distinguishing this species from *D. mammillatum* s.s. There are probably about 7–8 main ribs per half whorl. The ventral sulcus is moderately broad and rather deep.

Discussion

Casey (1962) considered *D. inaequinodum* to be a typical Middle Albian species, distinguished from the earlier *D. orbignyi* Hyatt and *D. alternans* Casey in having two, not one, fine intercalatories between main ribs. However, material from the *Isohoplites eodentatus* nodule bed at Bully, Pays de Bray, France (Fig. 12C–D), shows that at least some individuals of *D. inaequinodum* have but a single fine intercalated rib between main ribs. In view of this, and because Casey (1962) has noted transitions between *D. alternans* and *D. orbignyi*, the latter two species are included in the synonymy of *D. inaequinodum*. Until the population structures of the *mammillatum* Zone assemblages are better known, it is perhaps prudent to retain *orbignyi* as a subspecies for these forms, as *D. inaequinodum orbignyi* Hyatt.

Family *Anisoceratidae* Hyatt, 1900
Genus *Protanisoceras* Spath, 1923

Type species *Hamites rautlinianus* d’Orbigny, 1842; by original designation *Protanisoceras* sp.

Fig. 13B

Material

A single fragment, SAM–PCA3461, preserved as a limestone steinkern from the *Douvilleiceras* assemblage.
Fig. 13. A. *Douvilleiceras variabile* Tavani, SAM-PCA3472. B. *Protanisoceras* sp., SAM-PCA3461. C-D. *Venezoliceras acostae* (d’Orbigny), syntypes in the D’Orbigny Collection, NHMP. E-F. *Mortoniceratoides rigidus* (Spath), the holotype, BM-C34879. All ×1.
Fig. 14. A–C. *Puzosia bistricta* (White), the lectotype, designated herein, USNMNH 12102, from Porto dos Barcos, Mariom, Sergipe, Brazil. D–E. *Oxytropidoceras* (*Mirapelia*) *mirapelianum* (d’Orbigny), NHMP-5758, in the D’Orbigny Collection, from Clar, France. F–G. *Oxytropidoceras* (*Oxytropidoceras*) *carbonarium* (Gabb), the holotype of *O. cantianum* Spath, BM-C12501, from the *D. cristatum* Zone at Folkestone.
Fig. 15. A–B. *Oxytropidoceras (Mirapelia) buarquanum* (White), the lectotype, designated herein (after White 1887). C–D. *Puzosia bistricta* (White), copy of White’s (1887) original illustration. E. *Douvilleiceras cf. variabile* Tavani. SAM–PCA3435. Note the abrupt change from a *variabile* to an *aequinodum*-type ornament. All ×1.
Description

The short curved fragment gives the impression of having had a compressed, elliptical whorl section. Ornament comprises rather broad, low, russiradiate ribs, wider than the interspaces, each bearing a distinct ventrolateral tubercle. There are about three ribs in a distance equal to the whorl height.

Discussion

The available specimen is too fragmentary to warrant comparison with the many described species of *Protanisoceras*, but does provide the first record of this genus from Angola.

Family **Desmoceratidae** Zittel, 1895
Subfamily **Puzosiinae** Spath, 1922
Genus **Puzosia** Bayle, 1878

Type species *Ammonites majoriana* d’Orbigny, 1842
(= replacement name for *A. planulatus* J. de C. Sowerby non Schlotheim 1820 nec Schuebler 1830);
by subsequent designation

**Puzosia bistricta** (White, 1887)

*Ammonites bistrictus* White, 1887: 216, pl. 23 (figs 5–8).
*Ammonites hopkinsi* Forbes, White, 1887: 213, pl. 21 (figs 1–3), pl. 22 (fig. 5).
*Puzosia welwitschia* Choffat (in Choffat & de Loriol), 1888: 68, pl. 2 (fig. 4).

Material

Thirty specimens, SAM–PCA2623, 2625–2626, 2636, 2638, 2649, 2652, 2660–2661, 3412, 3415–3416, 3419–3421, 3424, 3426, 3429, 3432, 3434, 3449, 3452, 3474–3475, 3635, 3749, 3751, 3753, 3757, all preserved as limestone steinkerns and mostly from the beds with *Douvilleiceras*.

Description

Shell moderately large, compressed, with a moderately narrow umbilicus (21–27% of the diameter). The umbilical walls are steep, with evenly rounded shoulders, and the flanks slightly convex, almost flat. Maximum width is just below mid-flank and the whorl section (Fig. 16) is elliptical. There are generally about 7–8 straight, prorsiradiate constrictions per whorl, which flex forward just before crossing the venter. Characteristically, the whorls show an increase in inflation immediately after a constriction. The constrictions are broad and shallow, typically with a peculiar wedge-shaped rib intercalated across the
venter in the middle growth stages. Because of the nature of preservation, the true characters of the ribbing are difficult to assess. They first appear on the outer parts of the flanks at about 60–80 mm diameter, and coarsen and become more prominent across the venter with age. On SAM–PCA2623 there are twenty fine ribs between successive constrictions whereas on SAM–PCA2649 there are only seven.

Discussion

*Puzosia welwitschia* Choffat is clearly conspecific with the *Ammonites hopkinsi* figured by White (1887), which was later renamed *Puzosia garajauana* by Maury (1930). They almost certainly merely represent the middle and adult growth stages, respectively, of *P. bistricta* (White) (Fig. 14A–C). *Puzosia rosarica* Maury occurs with *P. bistricta* and is based upon juvenile material which probably does not warrant specific separation. There are few species of *Puzosia* with which this highly distinctive Middle Albian species may be confused.

Family **Brancoceratidae** Spath, 1933

Subfamily **Mojsisovicziinae** Hyatt, 1903

Genus **Oxytropidoceras** Stieler, 1920

Type species *Ammonites roissyanus* d'Orbigny, 1841; by original designation

Discussion

The most comprehensive treatment of this genus is that of Young (1966). He included *Androiaavites* Collignon (1936) in the synonymy of *Adkinsites* and provided the following emended diagnosis of *Manuaniceras*: ‘Ammonites with
few whorls, which are much higher than wide; there are many flat ribs at some stage in the ontogeny, and ribs may be single or bifurcating at one or more positions at the umbilicus or on the flank’ (p. 95).

Unfortunately, however, flat-topped ribs are not a feature of Manuaniceras manuanense (Spath) (Fig. 31B) and hence cannot be used in the formulation of a diagnosis of this taxon. As Young (1966) rightly pointed out, Manuaniceras is a direct descendant of the Oxytropidoceras roissyanum group, which mainly differs in showing rib bifurcation at various levels on the flank. The differences are slight and the writer finds little use for the genus/subgenus Manuaniceras which is here included in the synonymy of Oxytropidoceras s.s.

As noted by Young (1966), and is clear both from the stratigraphic record and described species of Oxytropidoceras, the history of this taxon is one of parallel evolution between two species groups. The O. mirapelianum (d’Orbigny) (Fig. 14D–E herein) plexus comprises O. mirapelianum (d’Orbigny), O. evansi (Spath), O. douglasi Knetchel, O. buarquianum (White), O. sergipense (White), O. packardi Anderson, O. boulei Collignon, O. pauciuberculatum (Collignon), and O. colcanapi Collignon. These are all coarsely ribbed species without bifurcation or intercalation of the simple ribs. To this group the writer would assign the strongly derived species of O. salasi Young, O. stenzeli Young, and O. pandalense Young in which the adult whorls become dencostate, with occasional bifurcation and intercalation, and thus homoeomorph ‘Manuaniceras’. The other species group is that of O. roissyanum (d’Orbigny) in which the ribs are fine, with frequent bifurcation at or above the umbilical edge, and which includes all the described ‘Manuaniceras’ species of Young (1966). Since these two plexi appear almost simultaneously at the base of the Middle Albian (Owen 1971) and evolved in parallel until their final extinction in the early late Albian, the writer believes they merit sub-generic distinction. The writer proposes, therefore, the new subgenus Oxytropidoceras (Mirapelia) to include all those coarse-ribbed species assigned to the mirapelianum plexus above, with Ammonites mirapelianus d’Orbigny as type species. Oxytropidoceras (Mirapelia) sergipense (White) provides the root-stock from which the typical coarse-ribbed species of Venezoliceras (of which Tarfayites Collignon (1966) is a synonym), such as V. venezolanum (Stieler), V. acostae (d’Orbigny) (Fig. 13C–D), V. heueri Young, V. obscurum Young, V. texanum Young, V? chihuahuaense (Böse), V. kiowanum (Twenhofel), V. umsinnenense (Van Hoepen), V. bituberculatum (Collignon), V. madagascariense (Collignon), V. robustum (Renz) and V. clavicostratum (Renz), are derived. However, as noted by Young (1966) and Renz (1968), there is a second group of Venezoliceras, typified by Venezoliceras harrisoni Benavides-Cáceres, in which the early and middle growth stages show dense, bifurcating, nontuberculate ribbing, with a flank tubercle developed only at relatively large diameters. This group, which also includes V. acutocarinatum (Shumard), V. multicostratum (Renz), V. intermedium (Renz), and V. karsteni (Stieler), seems to have its ancestry in ‘Manuaniceras’ and, as such, its similar-
Fig. 17. A. *Douvilleiceras mammillatum aequumodum* (Quenstedt), SAM-PCA3423, a macroconch fragment, $\times 0.67$. B-C. *Puzosia bstricta* (White), SAM-PCA5447, $\times 1$. 
Fig. 18. A–B. *Oxytropidoceras (Mirapelia) sergipense* (White), SAM–PCA5444. C–D. *Puzosia bistricta* (White), SAM–PCA3420. Both ×1.
ity to the *V. acostae* group is due to convergence. Consequently, the writer proposes the new subgenus *Oxytropicoceras (Benavidesites)*, with type species *Venezoliceras harrisoni* Benavides-Cáceres (1956: 460, pl. 53 (fig. 6)), for this homoeomorphic development.

The origins of *Adkinsites* are obscure; Young (1966) would derive this taxon from *Dipoloceras*, but this view is unacceptable to the writer. They could represent derivatives of the more densely ribbed *O. (Mirapelia)* species or of paucicostate *Oxytropicoceras* s.s., or of both. This taxon is not present in the Angolan material and hence the writer defers judgement. Because of its obscure, and perhaps polyphyletic origins, Young (1966) is followed in treating *Adkinsites* as a genus, of which *Androiavites* Collignon (1936) is a synonym.

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Fig. 20. *Mojsisoviczia cf. ventanillensis* (Gabb). A reconstruction based upon BM-C78865, from the Middle Albion of Zululand. × 1.
Mortoniceratinae, subfamily Oxytropidoceratinae, is closely related to M. rigidum with the Mojsisovicziinae and it seems likely that M. rigidum is closely allied to, and perhaps descended from Adkinsites. Since the origins of Mortoniceratinae are generally thought to lie in Dipoloceras (Wright in Arkell et al., 1957), the similarities are due to convergence. It is proposed, therefore, to make M. rigidum Spath the type species for the new genus Mortoniceras. It differs from Adkinsites in having a subquadrate whorl section, low ventral keel, and with a symmetrically bifid first lateral saddle.

As discussed by Kennedy & Cooper (1977), Mojsisoviczia and Falloticotheca are closely allied and, on the basis of the available evidence, Falloticotheca may reasonably be considered a neotonous offshoot of Mojsisoviczia. From their first appearance (Fig. 20), the ribs of Mojsisoviczia are coarse and simple and the origins of this taxon seem to lie in O. (Mirapelia) sergipense (White) or a closely allied form.

Dipoloceras is believed by Spath (1931) to have descended from Oxytropidoceras, and is included in the Mojsisovicziinae by Wright (in Arkell et al. 1957). However, the inflated whorls, low ventral keel and strong spiral ornament suggest a closer relationship with the Mortoniceratinae, to which subfamily Dipolocerae is here referred. The suggested phylogeny within the Mojsisovicziinae, as here interpreted, is shown as Figure 21.

Oxytropidoceras (Mirapelia) buarquianum (White, 1887)


Ammonites buarquianus White, 1887: 222, pl. 24 (figs 3–4 only), pl. 25 (figs 7–8).
Schloenbachia cf. roissiana (d’Orbigny) Douville, 1906: 147, pl. 4 (fig. 3).
Schloenbachia aff. belknapi (Marcou) Douville, 1906: 148, pl. 2 (fig. 4).
Schloenbachia cf. belknapi Böse (non Marcou) Douglas, 1921: 269, pl. 17 (figs 1–2).
Schloenbachia cf. chihuahuaensis Böse, Douglas, 1921: 269, pl. 17 (fig. 3).
?
Oxytropidoceras colcanapi Collignon. 1936: 182, pl. 18 (fig. 7), fig. 12k.
?
Oxytropidoceras sp. juv., Spath, 1930: 61, pl. 9 (fig. 18).
Oxytropidoceras packardi Anderson, 1938: 198, pl. 50 (fig. 1).
Oxytropidoceras douglasi Knetchel, 1947: 106, pl. 24 (figs 1–4), pl. 25 (figs 1–2), pl. 26, pl. 27 (figs 2–3). pl. 28 (fig. 1). Young, 1966: 88, pl. 10 (figs 1–5), pl. 36 (figs 3–4), pl. 37 (figs 4–5).
?
Oxytropidoceras involutum Beurlen, 1952: 162, fig. 3.
?
Oxytropidoceras (Manuaniaceras) involutum Beurlen, 1970: 465, pl. 5 (fig. 4).
Oxytropidoceras sp. A. Beurlen, 1970: 464, pl. 5 (fig. 3).
LOWER CRETACEOUS AMMONITES FROM ANGOLA

Fig. 21. A suggested phylogeny of the Mojsisoviciinae.

Material


Description

The Angolan population is polytypic, with morphotypes agreeing exactly with *O. buarquianum* (White), *O. packardi* Anderson, *O. douglasi* Knetchel, *O. salasi* Young, and two specimens very closely approaching *O. mirapelianum* (d'Orbigny). The relationship between these morphotypes is shown in Figure 26. Because of this wide range of intraspecific variation, no single description will fully cover all morphotypes and hence they are described separately.

Two specimens, SAM–PCA2656–2657, very closely approach *O. mirapelianum* (d'Orbigny) and, with a typological approach, would be referred to that species. The Angolan examples (Fig. 10A–B) are, however, insensibly con-
Fig. 22. A. *Douvilleiceras variabile* Tavani, D’Orbigny’s (1841, pl. 72 (fig. 5)) protograph, × 0.5. B–C. *Mojsisoviczia delaruei* (d’Orbigny), NHMP-5761, one of D’Orbigny’s syntypes from Clar, France. D–E. *Oxytropidoceras (Mirapelia) buarquianum* (White), SAM–PCA2641, a rather densely ribbed *douglasi* morphotype, thus transitional to *salasi* variants. All × 1 unless otherwise stated.
Fig. 24. Oxytropidoceras (Mirapelia) buarquianum (White). SAM-PCA3418, a douglasi morphotype. × 1.
Fig. 25. *Oxytropidoceras (Mirapelia) buarquianum* (White). A–B. SAM–PCA2693, the typical variant. C. SAM–PCA2674, a *douglasi* morphotype. D. SAM–PCA2665, a rather eroded, finely ribbed variant. All × 1.
Fig. 26. Interrelationships between the Oxytropidoceras (Mirapelia) buarquianum morphotypes and closely allied species. Figures given are the number of morphotypes in the present collection followed, in parentheses, by the percentage which they constitute.

Connected to O. douglasi morphotypes and differ from D’Orbigny’s (1841) species (Fig. 14D–E) in being slightly less inflated and in having the ribs somewhat thicker at the umbilical margin.

The O. douglasi morphotypes are the most abundant in the present collection and show the following features: shell compressed, evolute (umbilicus 24–28% of the diameter), with a compressed, lanceolate whorl section and a prominent, sharp, high, siphonal keel. The umbilicus is rather wide and shallow, with fairly steep umbilical walls and evenly rounded shoulders at moderate diameters. The umbilical walls become increasingly inclined with growth and, in maturity, the umbilical shoulder is gently rounded and indistinct. At this stage, the outer whorl covers about 15 per cent of the ribbing of the preceding whorl. Maximum width is slightly below mid-flank in most individuals. Ornament comprises simple, generally flexuous ribs, which arise at the umbilical seam but only become prominent on the flanks. All ribs are slightly prorsiradiate, steepest adorally and convex adapically, and broaden towards the ventrolateral shoulders where they swell but do not form tubercles.
There are 13–20 ribs per half whorl. A somewhat eroded suture-line is shown as Figure 27.

*O. buarquianum* morphotypes are insensibly connected to *O. douglasi* morphotypes (Fig. 3A–B). Typically (Fig. 25A–B), this morphotype is strongly compressed, with 22–32 broad, low, weak ribs per whorl, and an indistinct umbilical wall. It is perhaps worth noting that it is a ‘law’ of polytypic ammonite species that the compressed variants are weakly ornamented, and that strength of ornament increases with inflation.

Two examples, SAM–PCA 3603–3604, show the rather dense, straight ribs of *O. salasi* Young, becoming projected near the venter (Fig. 19D–E), and are connected by intermediates to *O. douglasi*. These *O. salasi* variants show a low umbilical wall, broad convex flanks and a lanceolate whorl section, and were clearly rather evolute. Although the siphonal keel is not preserved, it certainly stood well above the venter. The dense, narrow, simple ribs are distinctly prorsiradiate and only very slightly flexuous, with at least twenty-two ribs per half whorl. The ribs swell slightly at the ventrolateral shoulders and curve strongly forward to meet the siphonal keel.

**Discussion**

The Angolan material shows an insensible transition between *O. buarquianum* (White) and *O. douglasi* Knetchel and they are synonyms. It is unfortunate that White’s (1887) species has priority because the *O. douglasi* morphotypes predominate. There is little to separate *O. packardi* Anderson from the *O. douglasi* morphotypes and it should also fall into synonymy. Several of the Angolan morphotypes are extremely close to *O. mirapelianum*, which is a broadly contemporaneous European species. However, until the population
structure of D'Orbigny's (1841) species is better understood, they are maintained as specifically distinct.

As already noted, there are *O. salasi* morphotypes within the Angolan material, which are connected by transitions to *O. douglasii* morphotypes, but they constitute only 4 per cent of the present material. Because of this, and because Young (1966) had over 300 specimens of *O. salasi* from the Key Valley Marl, the Texas form is maintained as a distinct species. Occasional *O. salasi* morphotypes within the Angolan population merely indicate that *O. salasi* is descended from an *O. buarquianum* ancestor by a major change in population structure. *Oxytropidoceras stenzeli* Young (1966: 93, pl. 22 (fig. 1), pl. 26 (fig. 1), pl. 34 (fig. 1), pl. 35 (fig. 4), figs 7h, 18c) is a Middle to low Upper Albian species that may not bear separation from *O. salasi*.

Collignon (1936) recorded *O. mirapelianum*, *O. colcanapi* Collignon, *O. boulet* Collignon, and *O. bravoense* Collignon (non Böse) from the same level and locality (Berambo) in the Middle Albian of Madagascar. His *O. colcanapi* is certainly very close to *O. buarquianum*, although the true affinities of the Madagascan material must await reassessment at the population level.

The species of *Oxytropidoceras* figured by Reyment (1955) from Nigeria are all poorly preserved juveniles with the simple, flexuous ribbing of *O. (Mirapelia)*. Additional and better preserved material is required for a satisfactory identification.

*Oxytropidoceras chihuahuaense* (Böse) (1910: 73, pl. 5 (figs 3–4). pl. 7 (figs 3–4), pl. 8 (figs 1–2)) was assigned by Young (1966) to *Venezoliceras*, but the absence of a flank tubercle clearly places it in *O. (Mirapelia)*. The lectotype is the original of the specimen figured by Böse (1910, pl. 7 (figs 3–4), pl. 8 (fig. 1)), which shows rather rigid, slightly prorsiradiate single ribs that broaden ventrally and terminate in weak ventrolateral swellings. These features are within the range of variation of the Angolan material, but since Böse's species is, in Texas at least (Young 1966), dated as upper Middle Albian–lower Upper Albian, it is maintained as distinct.

*Oxytropidoceras involatum* Beurlen is based upon immature material that is very close to typical examples of this species. It is likely to prove a synonym of *O. buarquianum*.

*Oxytropidoceras (Mirapelia) sergipense* (White, 1887)

Figs 11B, 18A–B, 23E, H, 28

Ammonites sergipensis White, 1887: 221, pl. 24 (figs 1–2).


? Oxytropidoceras buarquianum (White) Maury. 1936: 250. pl. 9 (fig. 1 only).

Oxytropidoceras mauryae Beurlen, 1952: 162, fig. 3.


Oxytropidoceras (Venezoliceras) sergipense (White) Renz, 1968: 630.

Oxytropidoceras (Androiaevites) mauryae Beurlen, 1970: 468, pl. 6 (fig. 1).

Non Mortoniceras sergipensis (White) Beurlen, 1970: 468, pl. 6 (figs 2–4). fig. 19.
Fig. 28. *Oxytropicoceras (Mirapelia) sergipense* (White). A–B. White’s (1887) original illustration. C–D. The original of White’s illustration, herein selected as lectotype, in the Natural History Museum, Rio de Janeiro. Photo: P. Bengtson. Both × 1.
Material

Six specimens in the South African Museum, SAM–PCA3755, 3765, and 5444, together with three unnumbered examples. All are preserved as limestone steinkerns.

Description

The shell is rather inflated and moderately evolute, with the outer whorl covering about 25 per cent of the preceding whorl. The umbilicus is moderately wide (32–35% of the diameter) and fairly shallow, with steep umbilical walls and evenly rounded shoulders. Intercostally the whorl section is oval, compressed, whereas costally it is subquadrate (Fig. 23E, H). Ribs begin at the umbilical seam and, across the flank, are slightly flexuous and prorsiradiate, terminating in prominent ventrolateral tubercles that are projected forward on the venter. There are thirty ribs on the outer whorl. The flanks are convex and converge slightly towards the venter, with maximum width about one-third of the way up the flanks. The keel is not preserved but must have stood high above the venter.

Discussion

The confusion surrounding the generic status of White’s (1887) species is evident from the synonymy. It is, indeed, very close to Venezoliceras, as noted by Renz (1968), but lacks the development of flank tubercles. On the other hand, it is also very similar to the more inflated Oxytropidoceras douglasi morphotypes with which it coexists, differing only in the very pronounced development of ventrolateral tubercles. In gross morphology and stratigraphic position, therefore, O. (M.) sergipense is intermediate between O. (Mirapelia) and Venezoliceras. Phylogenetically, it is perhaps worth noting that Young (1966) assigned this species to Dipoloceras, while Spath (1932) referred such typical O. (Mirapelia) species as O. evansi (Spath), and even O. miripelium (d’Orbigny) itself, to Dipoloceras. As such, it seems likely that the origins of Dipoloceras also lie in O. (Mirapelia) of the sergipense group.

Oxytropidoceras (Androiaevites) mauryae Beurlen shows the same prominent ventrolateral tubercles and simple ribbing as O. (M.) sergipense and is here regarded as conspecific. The specimen figured by Beurlen (1970) is an Upper Albian Mortoniceras (Angolaites) with distinct umbilical and doubled ventrolateral tubercles.

Oxytropidoceras (Mirapelia) sergipense (White) is very close to certain species of Mojisoviczia (Figs 20. 22B–C), from which it is readily distinguished by its greater compression and the absence of a lateral tubercle. In this respect the figured but undescribed material of Mojisoviczia aff. delaruei (d’Orbigny) (Spath 1930: 61, pl. 9 (figs 13, 16)) closely resembles the present species, since a lateral tubercle is not evident in the illustrations. It seems reasonable to assume that the ancestry of Mojisoviczia lies in O. (Mirapelia) of the sergipense group.
Fig. 29. *Oxytropidoceras (Oxytropidoceras) boeae* Knechtel, SAM-PCA5452, × 1.
Oxytropidoceras (Oxytropidoceras) boesei Knechtel, 1947

Figs 29–31A

Oxytropidoceras (Manuaniceras) boesei Knechtel, 1947: 109, pl. 27 (fig. 1).

? Manuaniceras uddeni Young, 1966: 95, pl. 12 (figs 1, 4–5), pl. 13 (fig. 1), pl. 16 (figs 1, 3), figs 10b, 12b.

Material

Three specimens, SAM–PCA5452–5453 and an unnumbered example in the South African Museum, preserved as limestone steinkerns.

Description

The Angolan material comprises several rather eroded internal moulds of body chamber fragments that, because of scaphitoid-uncoiling of the body chamber, appear to be more evolute (umbilicus 33% of the diameter) than the earlier growth stages actually were. The shell is strongly compressed, with a lanceolate whorl section (Fig. 30) and broad, convex flanks. Maximum width is about one-third of the way up the flanks. Although the siphonal keel is not preserved, it certainly stood well above the venter.

Ornament comprises dense, flexuous flank ribs that arise at, or close to, the umbilical seam and pass forward across the flanks. The ribs are narrower than the interspaces with a steep, concave, adoral surface and a sloping, convex, adapical face. They frequently bifurcate close to the umbilical seam, but only rarely at, or above, mid-flank. There are 8–9 ribs along the venter in a distance equal to the whorl height. There is no sign of bullae on any part of the flanks.

Fig. 30. Oxytropidoceras (Oxytropidoceras) boesei Knechtel. Whorl sections. A. SAM–PCA5452. B. SAM–PCA5453. × 1.
Discussion

Oxytropidoceras (Manuaniceras) boesei Knetchel was based upon fragmentary material, without proper description, which shows no features to distinguish it from the Angolan material. The Texas species, Manuaniceras uddeni Young, which coexists with O. (M.) buarquianum, is very close to the present material. It is said to differ in the presence of a few very weak bullae at the umbilical shoulder, and sometimes also at the point of bifurcation or intercalation of a rib. Since the presence of such bullae is likely to be markedly affected by state of preservation, M. uddeni is probably a synonym of O. boesei.

Oxytropidoceras roissyanum (d’Orbigny) (Fig. 5A–B) is difficult to compare with the present species because the known material of both species represents vastly different growth stages. So far as can be judged, O. roissyanum is much more inflated, with stronger, more robust ribs, about as wide as the interspaces, and does not show bifurcation above the umbilical shoulder. Oxytropidoceras applanatus Collignon (1936: 183, pl. 16. (fig. 5)) is doubtfully distinct from O. roissyanum.

Oxytropidoceras manuanense (Spath) (1921: 281, pl. 25 (fig. 1)) (Fig. 31B) resembles the present species in lacking flattened ribs, but differs in that nearly all ribs bifurcate at some level on the flanks and in the effacement of ribbing in maturity.

Oxytropidoceras cantianum Spath (Fig. 14F–G) is an Upper Albian (Dipoloceras cristatum Zone) species that is based upon a juvenile showing strongly branching ribs. It closely approaches the example figured by Young (1966, pl. 7 (figs 4, 6)) as ‘probably M. carbonarium (Gabb)’, and Owen (1971) seems to be right in regarding it a synonym of O. carbonarium.

Oxytropidoceras aroeirium Maury (1936: 251, pl. 26, (fig. 7)) is, to judge from the description, very close to the present species. Unfortunately, the writer has not seen the illustrations of this species and thus further comment is unjustified.

AGE OF THE PRESENT FAUNA

Douvilleiceras mammillatum (Schlotheim) has long been considered diagnostic of the uppermost biostratigraphic zone in the Lower Albian, to which it gives its name. Thus, the rich Douvilleiceras faunas from the rest of the world are almost invariably assigned to the zone of D. mammillatum and considered to be of late early Albian age. Despite the fact that Douvilleiceras has long been known to persist into the Middle Albian (Casey 1962; Owen 1971; Destombes et al. 1977), including D. mammillatum itself (Fig. 12E–F), this has never been a problem in the boreal realm where the incoming of Hoplites forms an easily recognizable and diagnostic base to the Middle Albian. Outside the hoplitinid faunal province, however, no such aid is available and the problem of
Fig. 31. A. *Oxytropidoceras (Oxytropidoceras) boesei* Knechtel. SAM-PCA5453. B. *Oxytropidoceras (Oxytropidoceras) manuanense* (Spath). SAM-2726, a paratype.
the Lower-Middle Albian boundary is far more complex. These problems led Young (1966) to suggest that *Lyelliceras* may date a younger level in South America than it does in Europe. Contrary to Young's (1966) opinion, however, the writer feels that *Lyelliceras* is critical to the problem of the Lower-Middle Albian boundary, in view of its widespread geographic distribution and common association with hoplitinids in the boreal realm.

In the Anglo-Paris basin, the type region for the Albian Stage, Owen (1971) recognized the following subdivisions of the Middle Albian:

- **Euhoplites laetus** Zone
  - Anahoplites daviesi Subzone
  - Euhoplites nitidus Subzone

- **Euhoplites loricatus** Zone
  - Euhoplites meandrinus Subzone
  - Mojisovicia subdelaruei Subzone
  - Dimorphoplites niobe Subzone
  - Anahoplites intermedius Subzone

- **Hoplitus dentatus** Zone
  - Hoplitus spathii Subzone
  - *Lyelliceras lyelli* Subzone
  - Isohoplites eodentatus Subzone

In the Anglo-Paris basin, *Douvilleiceras inaequinodum* (Quenstedt) does not range above the *eodentatus* Subzone, while *Oxytropidoceras* (*Mirapelvia* mirapeliana) (d'Orbigny) is a constituent of the *Hoplitus spathii* Subzone (Owen 1971). Moreover in Peru, Benavides-Cáceres (1956) records *Oxytropidoceras* 'douglasi' in association with *Lyelliceras lyelli* (d'Orbigny). There can also be little doubt that the Angolan *Oxytropidoceras* fauna is strictly contemporaneous with those from the Texan zone of *O. salasi*, and it is certainly also represented in Brazil (White 1887; Maury 1936; Beurlen 1970). As such, the *Lyelliceras lyelli* Subzone is represented in the south-central Atlantic region by *Oxytropidoceras buarquianum* (White) and/or *Lyelliceras lyelli* (d'Orbigny), and their associated species. The underlying beds in Angola, dominated by *Douvilleiceras mammillatum aequinodum* (Quenstedt) and *D. inaequinodum* (Quenstedt), are thus certainly to be correlated with the *Isohoplites eodentatus* Subzone of the Anglo-Paris basin. It is perhaps worthy of note that *O. mirapelianum* (d'Orbigny) is a replacement name for *Ammonites cristatus* Quenstedt (*non* DeLuc) and, as such, Quenstedt (1849) was dealing with a faunal horizon closely comparable, and probably strictly contemporaneous, with those at Dombe Grande.

As such, the Dombe Grande faunas are here regarded as of basal Middle Albian age, to be correlated with the *Isohoplites eodentatus* and *Lyelliceras lyelli* Subzones of the European succession. The absence of lyelliceratids and brancoceratids is enigmatic. Since *Oxytropidoceras* species are relatively long-lived, the *Oxytropidoceras* (*M.*) *buarquianum* faunule may prove to range somewhat higher. The fact that many of the *Douvilleiceras* assemblages from around the world could now prove to be of basal Middle Albian age suggests
that the late early Albian eustatic transgression (Cooper 1977) might actually have peaked during the earliest Middle Albian.

SUMMARY

Two Middle Albian faunules rich in numbers, but poor in species, are described from the vicinity of Dombe Grande, Angola. The lower faunule, which is correlated with the Isochelites eodentatus Subzone of the European sequence has yielded *Douvileiceras mammillatum aequinodum* (Quenstedt), *D. inaequiondum* (Quenstedt), *D. variabile* Tavani and *Puzosia bistricta* (White). The upper faunule has yielded *Oxytropidoceras* (Oxytropidoceras) *boesei* Knechtel, O. (M.) *buarquianum* (White), O. (M.) *sergipense* (White), *Puzosia bistricta* (White), *Protanisoceras* sp. and a *Hamites* sp., and is to be correlated with the *Lielliceras lyelli* Subzone of the Anglo-Paris basin. Mojsisovichziind phylogeny is discussed, and the following new taxa introduced: *Mortoniceratoides* gen. nov., *Oxytropidoceras* (Mirapelia) subgen. nov. and O. (Benavidesites) subgen. nov., while *Manuaniceras* is included in the synonymy of *Oxytropidoceras* s.s.

ACKNOWLEDGEMENTS

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REFERENCES


6. **SYSTEMATIC** papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author’s name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author’s name and year. The author’s name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

```
Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14-15A

*Nucula* (Leda) *bicuspidata* Gould, 1845: 37.

*Leda pleifer*a A. Adams, 1856: 50.

*Leda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillieri* Philippi, 1861: 87.


Note: punctuation in the above example:
- comma separates author’s name and year
- semicolon separates more than one reference by the same author
- full stop separates references by different authors
- figures of plates are enclosed in parentheses to distinguish them from text-figures
- dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King’s Beach


Note: standard form of writing South African Museum registration numbers and date.

7. **SPECIAL HOUSE RULES**

**Capital initial letters**

(a) The Figures, Maps and Tables of the paper when referred to in the text:

- e.g. ‘... the Figure depicting *C. namacolus* ...’; ‘... in *C. namacolus* (Fig. 10) ...’

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names:

- e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives:

- e.g. Therocelphalia, but therocelphalian

**Punctuation** should be loose, omitting all not strictly necessary

**Reference to the author** should be expressed in the third person

**Roman numerals** should be converted to Arabic, except when forming part of the title of a book or article, such as

‘Revision of the Crustacea. Part VIII. The Amphipoda.’

**Specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

**Name of new genus or species** is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.
MICHAEL R. COOPER

LOWER CRETACEOUS (MIDDLE ALBIAN) AMMONITES FROM DOMBE GRANDE, ANGOLA