

# Cretaceous faunas from Zululand and Natal, South Africa. The ammonite genera *Mojsisovicsia* Steinmann, 1881, *Dipoloceroides* Breistroffer, 1947, and *Falloticeras* Parona & Bonarelli, 1897

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*Mojsisovicsia ventanillensis* (Gabb, 1877), *Dipoloceroides delaruei* (d'Orbigny, 1841), *D. semicornutum* (Spath, 1931), *D. cornutum* (Pictet, 1847) and *Falloticeras proteus* (d'Orbigny, 1842) are described from the Middle Albian Mzinene Formation of northern KwaZulu-Natal. The interpretation of micromorph species associated with these taxa is reviewed, and *duerfeldi* of Steinmann, 1881, is interpreted as the microconch of *ventanillensis* as a working hypothesis. The status of *proteus* as either microconch or micromorph is unresolved

**Key words:** ammonites, Albian, micromorphs, KwaZulu-Natal, South Africa.

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## INTRODUCTION

The Middle Albian part of the Mzinene Formation of northern KwaZulu-Natal has yielded representatives of one species referred to the genus *Mojsisovicsia* Steinmann, 1881, three species referred to *Dipoloceroides* Breistroffer, 1947, and one referred to *Falloticeras* Parona & Bonarelli, 1897. In describing these taxa, and establishing their generic assignation, a wider problem arises, that of the relationship between 'normal-sized' and diminutive species of *Mojsisovicsiinae*. These have been regarded, in the case of the latter, as either the microconchs (m) of larger, macroconch (M) individuals, forming a dimorphic pair, or as dwarf, paedomorphic offshoots of 'normal-sized' species. The key taxa in this area were reviewed by Breistroffer (1947), Kennedy & Cooper (1977), Gebhard (1983), and Wright (1996).

The historical background to the problem was carefully reviewed by Gebhard, and is updated here.

1841 d'Orbigny described and illustrated his *Ammonites delaruei* from the condensed Middle Albian of south-

east France, based on a series of individuals up to 53 mm diameter (p. 296, pl. 87, figs 6-8) (Fig. 4A-E).

1842 d'Orbigny described, but did not figure his *Ammonites proteus* from the condensed Middle Albian of south-east France (p. 624) (Fig. 8F,G)

1877 Gabb described and illustrated his *Ammonites ventanillensis* from the Middle Albian of Parietambo, Peru (p. 273, pl. 39, figs 2, 2a-d; Fig. 1 herein).

1881 Steinmann described and illustrated his new genus *Mojsisovicsia* and the type species *Mojsisovicsia duerfeldi* from Parietambo, Peru (p. 144, pl. 6, fig. 2).

1882 Steinmann concluded that his species *duerfeldi* was a junior synonym of *ventanillensis*.

1897 Parona & Bonarelli introduced the genus *Falloticeras*, with *Ammonites proteus* d'Orbigny, 1842, as type species, and provided the first illustrations of the species (p. 89, pl. 12, fig. 1).

1921 Douglas accepted *Mojsisovicsia duerfeldi* as a junior

synonym of *Ammonites ventanillensis* (p. 270, pl. 15, fig. 8; pl. 17, fig. 4).

1942 Spath referred to both *Mojsisovicsia duerfeldi* and *M. ventanillensis*, but equivocated on their separate ness (p. 709).

1947 Breistroffer introduced the subgenus *Dipoloceras* (*Dipoloceroides*) with *Ammonites delaruei* as type species (p. 90 (74)), and noted: 'Enfin, il y a des liaisons certaines entre *D. (D.) delaruei* d'Orb. Sp. et *Falloticeras Proteus* d'ORB. sp. in Par. Et Bon., de même qu'entre *D. (D.) ventanillense* GABB sp. et *Mojsisovicsia Dürfeldi* STEINM. sp. Ce sous-genre et ses deux dérivés nains à cloisons simplifiées précèdent les *Dipoloceras* typiques.' (p. 90 (75)).

1957 Wright regarded *duerfeldi* of Steinmann as a junior synonym of *ventanillensis* of Gabb, and *Dipoloceroides* Breistroffer, 1947, as a junior synonym of *Mojsisovicsia* (sic) Steinmann, 1881.

1977 Kennedy & Cooper revised *Falloticeras*, and regard it as possibly a neotenous offshoot of *Mojsisovicsia*.

1979 Gebhard regarded *Falloticeras* as a junior synonym of *Mojsisovicsia* (p. 98).

1983 Gebhard revised and illustrated the type material of *Mojsisovicsia duerfeldi* and concluded that it was not a junior synonym of *ventanillensis*. *Falloticeras* was interpreted as a junior synonym of *Mojsisovicsia*. *Dipoloceroides* Breistroffer, 1947, was regarded as a valid taxon, and treated as a subgenus of *Dipoloceras* Hyatt, 1900. It was further suggested that *Mojsisovicsia* (= *Falloticeras*) and *Dipoloceras* (*Dipoloceroides*) are a dimorphic pair.

1996 Wright (p. 137) regarded *Mojsisovicsia* (sic) *duerfeldi* as a junior synonym of *Ammonites ventanillensis*, the former the microconch, the latter the macroconch. He also considered *Dipoloceroides* to be a junior synonym of *Mojsisovicsia* (sic). *Falloticeras* was retained as a separate genus.

We have re-examined the type material of the type species of *Falloticeras* and *Dipoloceroides* as well as topotype material of *Mojsisovicsia duerfeldi* and *Ammonites ventanillensis*, and reached the following conclusions.

1. *Mojsisovicsia duerfeldi* is characterized by an ornament of sinuous growth lines and constrictions, the aperture preceded by a constriction, the mouth border flared. Adults are up to 27 mm in diameter. It co-occurs with *Ammonites ventanillensis*, which has an initial smooth stage, then develops a keel, then ribs and tubercles, as clearly described by Douglas (1921, p. 271). Common early development is a necessary feature for *ventanillensis* and *duerfeldi* to be dimorphs, and this view is adopted here as a working hypothesis, following Wright (1996, p. 137). Recognition of dimorphism in larger *ventanillensis* at the ornamented stage, or in the diminutive *duerfeldi* would confirm that they are not a dimorphic pair, and that *duerfeldi* is a genuinely diminutive taxon, and a paedomorphic off shoot of *ventanillensis*.
2. *Ammonites delaruei* differs from *Ammonites ventanillensis* in having ribs from a much earlier stage, and thus lacks the distinctive unribbed but carinate stage

of the latter. *Dipoloceroides* and *Mojsisovicsia* (of which these are the type species) can be differentiated on this criterion, but whether this is a difference of species, subgenera, or genera, is debatable. Recognition of dimorphism in *Dipoloceroides delaruei* would help resolve this uncertainty.

3. *Falloticeras* differs from microconch *Mojsisovicsia* in having a ribbed early growth stage (Fig. 8), whereas microconch *Mojsisovicsia* lacks ribs throughout ontogeny. They can be separated on this basis.
4. The early developmental stages of *Dipoloceroides semicornutum* (Spath, 1931) and *Falloticeras proteus* are similar, suggesting a relationship between the two. *F. proteus* may be a paedomorphic offshoot of *D. semicornutum*, or the microconch, as suggested by Gebhard. The former of these alternatives can only be confirmed if dimorphism is demonstrated in either or both species.

These issues can only be fully addressed by a revision of the material from the classic Albian of Escragnolles in France (the type locality of *Falloticeras* and *Dipoloceroides*) and Parietambo in Peru. Accordingly, we adopt a conservative position with respect to the present material from northern KwaZulu-Natal, noting that the main record has what are interpreted as macroconchs of *Mojsisovicsia ventanillensis* co-occurring with the microconch/micromorph *Falloticeras proteus*.

## REPOSITORIES OF SPECIMENS

BMNH: The Natural History Museum, London.  
 MNHP: The Muséum National d'Histoire Naturelle, Paris.  
 OUM: Geological Collections, Oxford University Museum of Natural History, Oxford.  
 SAM: Natural History Collections Department, Iziko South African Museum, Cape Town.

## FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, The South African Museum, Cape Town, and the Department of Palaeontology, The Natural History Museum, London.

## CONVENTIONS

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in brackets are dimensions as a percentage of the diameter. The suture terminology is that of Korn *et al.* (2003): E = external lobe; A = adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann, 1970); U = umbilical lobe; I = internal lobe.

## SYSTEMATIC PALAEONTOLOGY

Suborder **AMMONITINA** Hyatt, 1889

Superfamily **ACANTHOCERATOIDEA** de Grossouvre, 1894

Family **BRANOCERATIDAE** Spath, 1934

Subfamily **MOJSISOVICSINAE** Hyatt, 1900

## Genus *Mojsisovicsia* Steinmann, 1881

### Type species

*Mojsisovicsia duerfeldi* Steinmann, 1881, p. 144, pl. 6, fig. 2, by original designation = *Ammonites ventanillensis* Gabb, 1877, p. 273, pl. 39, figs 2, 2a-d.

### Diagnosis

Strongly dimorphic, macroconchs up to 100 mm diameter, microconchs 25–35 mm in diameter. Earliest growth stage of macroconch smooth but for growth lines, followed by the development of a keeled stage with growth lines only, then the abrupt appearance of flexuous primary ribs, flared on the outer flank, with a well developed inner ventrolateral bulla on some ribs, and transverse to oblique outer ventrolateral clavi on all ribs. Inner ventrolateral bullae efface on the adapertural part of the adult body chamber. Microconchs with rounded whorl section, ornamented by growth lines and occasional constrictions; adult aperture preceded by broad shallow constriction with flared aperture, produced into a blunt ventral lappet.

### Occurrence

Middle Albian, Peru, northern KwaZulu-Natal.

### *Mojsisovicsia ventanillensis* (Gabb, 1877)

#### Figs 1–3

1877 *Ammonites ventanillensis* Gabb, p. 273, pl. 39, figs 2, 2a-d.

1881 *Mojsisovicsia Dürfeldi* Steinmann, p. 144, pl. 6, fig. 2.

1903 *Mojsisovicsia durfeldi* Steinmann; Hyatt, p. 25, pl. 1, figs 1–3.

1908 *Schloenbachia* juv. *Ventanillensis* Gabb (?*Mojsisovicsia Dürfeldi* Steinmann); Lisson, p. 15, pl. 15, figs 1–3.

1908 *Schloenbachia ventanillensis* Gabb; Lisson, p. 16a–c, pl. 16a, figs 16, 1–4.

1911 ?*Mojsisovicsia Dürfeldi* Steinmann; Lisson, p. 168.

1921 *Schloenbachia ventanillensis* (Gabb); Douglas, p. 270, pl. 15, fig. 8; pl. 17, fig. 4.

1922 *Mojsisovicsia dürfeldi* (Steinmann); Spath, p. 97.

1924 *Mortoniceras Ventanillensis* Gabb juv.; Lisson, pp. 71, 146.

1938 *Mojsisovicsia Dürfeldi* Stein.; Roman, p. 37, figs 352, 352a, 352b.

1942 *Mojsisovicsia dürfeldi* Steinmann; Spath, p. 708.

1942 *Mojsisovicsia ventanillensis* (Gabb); Spath, p. 708.

1947 *Mojsisovicsia Dürfeldi* Steinmann; Breistroffer, p. 90 (75).

1957 *Mojsisovicsia* (sic) *ventanillensis* (Gabb); Wright, p. L 404, text-fig. 522, 4a,b.

1977 *Mojsisovicsia* aff. *ventanillensis* (Gabb); Kennedy & Cooper, p. 800.

1977 *Mojsisovicsia* sp. juv. Kennedy & Cooper, pl. 105, figs 4, 12.

1977 *Mojsisovicsia ventanillensis* (Gabb); Kennedy & Cooper, pl. 105, figs 11, 13, 18.

1977 *Falloticeras* sp. Kennedy & Cooper, pl. 105, fig. 14.

1982 *Mojsisovicsia* cf. *ventanillensis* (Gabb); Cooper, text-fig. 20.

1983 *Mojsisovicsia dürfeldi* Steinmann; Gebhard, p. 114, text-figs 1a, 3.3, 3.4.

1996 *Mojsisovicsia* [sic] *ventanillensis* (Gabb); Wright, p. 137, text-fig. 105, 1a–g.

?2002 *Mojsisovicsia* cf. *ventanillensis* (Gabb, 1869); Robert, p. 180, pl. 32, figs 1–3.

### Types

The lectotype, here designated is the original of Gabb, 1877, p. 273, pl. 39, fig. 2, 2a, 2b, from the 'limestones of the Cerro del Ventanillo, between Pachanchaca and Jauja, Height 5000 metres'. The paralectotype is the original of Gabb, 1877 p. 273, fig. 2a,b, from the 'coal mine of Paraiatambo, 5 leagues from Morococho.' The original illustrations are reproduced here as Fig. 1. A second, unfigured paralectotype is from the 'neighbourhood of Fingo, Prov. of Huari, Dept. of Huaraz, from a schist containing coal'. The specimens were collected by Dr Antonio Raimondi (1826–1890), who considered them to be of Jurassic age. We have not seen these specimens, which we presume survive in the Raimondi Museum in Lima.

### Material

SAM-PCZ022404 (ex H207/1/1), SAM-PCZ022405–409 (ex H201/1/4–8), BMNH C78865, C78867, all from the Middle Albian fauna of bed 1 of the Mzinene Formation at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E.

### Dimensions

	D	Wb	Wh	Wb:Wh	U
C78867	20.9 (100)	9.4 (45.0)	9.6 (45.9)	0.98	6.2 (29.7)
At c	34.8 (100)	15.6 (44.8)	16.4 (47.1)	0.95	10.0 (28.7)
C78865	36.8 (100)	16.7 (45.4)	16.9 (45.9)	0.98	10.5 (28.5)
At c	60.3 (100)	28.3 (46.9)	29.0 (48.1)	0.98	16.8 (27.9)

All the available specimens are macroconchs. BMNH C78872 (Fig. 3D–F), a wholly septate internal mould lacking the innermost whorls, preserves parts of two successive growth stages. Coiling is moderately evolute, with 45.2% of the previous whorl covered at the largest preserved diameter. The umbilicus comprises 27.8% of the diameter, and is shallow, with a low, convex umbilical wall that inclines outwards and merges with the broadly rounded umbilical shoulder. There is no flank ornament to a diameter of 27.5 mm, and the flanks are very feebly convex, subparallel, the ventrolateral shoulder relatively narrowly rounded, the venter broad, and very feebly convex. There is a well-developed siphonal ridge that strengthens progressively as size increases. Ribs appear abruptly at a diameter of 27.5 mm, and there are nine in the 90° sector between 27.5 and 34.8 mm diameter. They arise at the umbilical seam or on the umbilical wall, and strengthen across the umbilical shoulder without developing a bulla. They are narrow, straight and prorsiradiate on the flanks, across which they strengthen progressively. They sweep forwards over the ventrolateral shoulders and venter, and terminate against a progressively strengthening siphonal keel. The adapical two ribs bear a weak outer ventrolateral clavus; these strengthen progressively on the succeeding ribs. Inner ventrolateral bullae are present on two ribs, with three intervening ribs that lack such bullae. SAM-PCZ022404 (ex

H207/1/1) (Fig. 3G) shows an identical ontogenetic change from smooth to ribbed stages.

BMNH C78865 (Fig. 3A–C, J–L) is a near-complete adult individual broken into three pieces. The smooth stage described in the previous specimen extends to an estimated diameter of 21 mm, at which size feeble, irregularly spaced flank ribs appear (Fig. 3A–C). Regular ornament appears at a diameter of 25 mm. There are 14 ribs on the adapertural half whorl at a diameter of 36.8 mm. They arise at the umbilical seam, or on the umbilical wall, and are narrower than the interspaces, straight and prorsiradiate on the flanks, across which they strengthen progressively, sweeping forwards and strengthening further on the ventrolateral shoulder and venter, where they decline, forming an obtuse chevron with a progressively strengthening keel at the apex. Every third or fourth rib bears a strong inner ventrolateral bulla, and all ribs bear an oblique outer ventrolateral clavus, strong on the ribs with an inner ventrolateral bulla and weak on those without. The second fragment (Fig. 3K,L) extends to the end of the phragmocone at an estimated diameter of 70 mm. The adapertural half of the outer whorl bears 13 primary ribs. These are prorsiradiate, narrow, high and strong, convex on the umbilical wall, shoulder and inner flank, and feebly concave on the ventrolateral shoulders. Strong to weak umbilical bullae are present on the adapical 3 or 4 ribs. The remaining ribs lack any trace of a bulla. All ribs bear strong oblique outer ventrolateral clavi, from which the ribs project forwards and decline, forming a chevron with the very strong, high siphonal keel at the apex. A 120° sector of body chamber is present, extending to a maximum preserved diameter of 98 mm (Fig. 3J). Parts of seven ribs are preserved. They are very narrow, and widely spaced. They arise on the umbilical wall and shoulder and are initially weak, strengthening progressively across the flanks, where they are markedly prorsiradiate and flexuous, concave on the umbilical wall, convex across the inner and middle flanks, and concave on the outermost flank and ventrolateral shoulder, where they strengthen into strong, near-transverse outer ventrolateral bullae. A broad smooth zone separates the bullae from the very high, strong siphonal keel.

The suture (Fig. 2) is moderately incised, with a very broad, asymmetrically bifid E/A with a small median element, and small U2.

## Discussion

Gabb's original figures (Fig. 1) illustrate two individuals that differ in no significant respects from the present specimens: the juvenile, smooth but for the prominent siphonal keel, and the adult fragment with comparable flexuous ribs, inner and outer ventrolateral tubercles. The costal whorl breadth to height ratio, measured from his figure, is 0.87, and if accurate suggests a slightly more compressed individual, but not significantly so. Lisson (1908) provides photographic illustrations of specimens that match well with the present material.

Douglas (1921, p. 270, pl. 15, fig. 8; pl. 17, fig. 4) described and figured material from what he regarded as the same stratigraphic unit as that described by Gabb and Lisson, the associated faunas indicating a lower Middle Albian horizon. His material matches well with the present specimens

## Occurrence

Middle Albian of Saco, Peru, and northern KwaZulu-Natal.

## Genus *Dipoloceroides* Breistroffer, 1947

### Type species

*Ammonites delaruei* d'Orbigny, 1841, p. 296, pl. 87, figs 6–8, by the original designation of Breistroffer, 1947, p. 90 (74).

### Diagnosis

Moderately evolute, compressed to depressed, with persistent siphonal keel; inner whorls with ribs on outer flank and ventrolateral shoulders, thereafter extending to the umbilical seam, some or all ribs flared on outer flank with a lateral bulla and outer ventrolateral tubercle, the latter either transverse or forming part of a ventral chevron. In forms with differentiated ribbing, the minor ribs lack a lateral flared bulla. Lateral bullae lost on adapertural part of adult body chamber.

## Occurrence

Middle Albian, southern England, France, Switzerland, Poland, Pakistan, and northern KwaZulu-Natal.

## *Dipoloceroides delaruei* (d'Orbigny, 1841)

### Fig. 4

- 1841 *Ammonites Delaruei* d'Orbigny, p. 296, pl. 87, figs 6–8.
- 1850 *Ammonites Delaruei* d'Orbigny; d'Orbigny, p. 124.
- 1897 *Schloenbachia delaruei* d'Orbigny, 1841; Parona & Bonarelli, p. 88, pl. 2, figs 9, 10.
- 1920 *Oxytrypidoceras delaruei* (d'Orbigny); Stieler, p. 350.
- 1930 *Mojsisovicsia aff. delaruei* (d'Orbigny); Spath, p. 61, pl. 9, figs 13, 16.
- 1930 *Mortoniceras delaruei* d'Orb.; Passendorfer p. 657.
- 1931 *Dipoloceras delaruei* (d'Orbigny); Spath, p. 355, text-fig. 116 (copy of d'Orbigny).
- 1931 *Dipoloceras delaruei compressa* Spath, p. 355, text-fig. 115a; table on p. 355.
- 1947 *Dipoloceras (Dipoloceroides) Delaruei* (d'Orbigny); Breistroffer, p. 90 (74).
- 1963 *Mojsisovicsia delaruei* (d'Orbigny); Milbourne, table 1.
- 1971 *Dipoloceras delaruei* (d'Orbigny); Owen, table 3.
- 1979 *Dipoloceras (Mojsisovicsia) delaruei* (d'Orbigny); Gebhard, p. 99, pl. 7, figs 4, 5; text-figs 65, 66.
- 1983 *Dipoloceras (Dipoloceroides) delaruei* (d'Orbigny); Gebhard, p. 112.
- 1990 *Dipoloceras (Dipoloceroides) delaruei* (d'Orbigny); Marcinowski & Wiedmann, p. 84, pl. 8, fig. 6.
- 2006 *Mojsisovicsia delaruei* (d'Orbigny, 1841); Kennedy & Juignet in Gauthier, p. 109, pl. 41, figs 6, 7.

### Type

The neotype, designated by Kennedy & Juignet in Gauthier, 2006, p. 109, is MNHP-B46122, ex d'Orbigny Collection 5671-1, illustrated here as Fig. 4C–E, from the condensed Albian of Escragnolles, Alpes-Maritimes, France.

### Material

SAM-PCZ022410 (ex EM 175), presumably from the Pongola River, near localities Z16 to 20 of Haughton (1936, p. 290–291, fig. 3).

## Dimensions

	D	Wb	Wh	Wb: Wh	U
MNHPB46122	53.0 (100)	27.3 (51.5)	22.3 (42.1)	1.22	18.0 (34.0)
PCZ022410 (ex EM175)	77.0 (100)	34.0 (44.2)	34.7 (45.1)	0.97	21.4 (27.8)

## Description

The neotype of *Dipoloceroides delaruei* (Fig. 4C–E) is a phosphatized individual 53 mm in diameter, retaining part of the body chamber. Coiling is moderately evolute, the umbilicus comprising 34% of the diameter, deep, with a broadly rounded umbilical wall and shoulder. The whorl section is depressed, oval in intercostal section and polygonal in costal section, with the greatest breadth at mid-flank. There are 29–30 ribs per whorl (not ‘par demi-tour’ as in Kennedy & Juignet in Gauthier, 2006, p. 109), all primaries that arise at the umbilical seam, strengthening and sweeping back across the umbilical wall and shoulder. They are high and sharp on the flanks, narrower than the interspaces, prorsiradiate and straight on the umbilical shoulder, then flexing back and feebly convex on the inner flank and feebly concave on the outer flank. On the adapical parts of the outer whorl, some ribs are strengthened into a mid-lateral flare and sharp bulla, with up to three non-bullate ribs between. All ribs terminate in coarse, blunt transverse ventral clavi, separated by a smooth zone from a high, sharp siphonal keel.

PCZ022410 (exEM175) (Fig. 4F,G) is a beautifully preserved specimen that retains traces of the original aragonitic shell material. It has suffered non-lethal damage in life, and shows pathological modification of the ornament beyond a diameter of 70 mm. On the normal part of the shell, coiling is relatively evolute, with an umbilicus of moderate depth that comprises 27% of the diameter. The umbilical wall is feebly convex, the umbilical shoulder broadly rounded. The whorls are as broad as high, and trapezoidal in costal section, the flanks convergent, the venter flattened, with a strong, high, entire siphonal keel. At the smallest diameter visible there are 27 ribs per whorl, and 27–28 at 78 mm diameter, beyond which the pathological ornament appears. The ribs are prorsiradiate, strong, sharp, high, and crowded. They arise at the umbilical seam, sweep forwards across the umbilical wall, strengthen markedly and are feebly convex on the umbilical shoulder. They are straight and prorsiradiate on the inner flank, where they are produced into a high, narrow incipiently bullate flare. They flex backwards from the flare, broaden, decline in elevation, and terminate in a strong, blunt ventrolateral tubercle. On the venter, these tubercles give rise to a low, blunt, coarse rib, transverse on the outer part of the venter, but projected forwards and declining in strength, ultimately sweeping forwards as mere growth striae on the siphonal keel. Beyond 77 mm diameter the ribs change markedly, becoming convex, crowded, and narrow, without a flared section on the inner flank. At the largest preserved diameter, the keel is replaced by an irregular mass of shell material, indicating substantial non-lethal damage to the mantle in this region.

## Discussion

The present specimen is much larger than the neotype and topotype material before us, one of the largest of which is the basis of var. *compressa* of Spath, BMNH C37612a, 65 mm in diameter, with ornament very close to that of the present specimen at the same diameter.

*Dipoloceroides delaruei* differs from *Dipoloceras semicornutum*, described below (Fig. 5) in that the latter has a very depressed whorl section in middle and later growth, far fewer ribs – 14 to 15 per whorl, the stronger with massive flared ventrolateral horns that give rise to a wedge-shaped ventral rib. The weaker ribs, two between successive stronger ribs on the penultimate whorl and adapical part of the outer whorl, one beyond this, bear a weak outer ventrolateral tubercle only.

*Mojsisovicsia ventanillensis* (Gabb, 1877) (p. 273, pl. 39, figs 2, 2a–d) (Figs 1–3) is discussed fully above. It has an early developmental stage that extends to a diameter of up to 27.5 mm where the shell lacks ornament other than growth lines and a strong siphonal keel, thereafter the ribs are weaker on the inner flank, more widely spaced and more markedly flexuous, the tubercles are an inner ventrolateral rather than lateral flared rib/bulla on some ribs and an oblique to near-transverse outer ventrolateral clavus on all ribs.

## Occurrence

The geographic range of the species extends from southern England to the Pas-de-Calais, Aube, and Alpes-Maritimes in France, the Samana Range in the Kohat District of the North-West Frontier Province, Pakistan, and northern KwaZulu-Natal. The species is well dated as Lower Middle Albian (*Hoplites spathi* Subzone of the *Hoplites dentatus* Zone) in southern England (Owen, 1971, table on p. 155).

### *Dipoloceroides semicornutum* (Spath, 1931)

Fig. 5

1931 *Dipoloceras semicornutum* Spath, p. 349, text-fig. 115c.  
1947 *Dipoloceras (Dipoloceroides) semicornutum* Spath; Breistroffer, p. 90 (74).  
1977 *Mojsisovicsia* sp. juv. Kennedy & Cooper, pl. 105, figs 1, 2; text-fig. 2a.  
1979 *Dipoloceras (Mojsisovicsia) semicornutum* Spath; Gebhard, p. 100, pl. 7, fig. 6; text-figs 67, 68.  
1983 *Dipoloceras (Dipoloceroides) semicornutum* Spath; Gebhard, p. 116, text-figs 1d, 2, 5a,b, 3.

## Type

The holotype is BMNH 3760a, the original of Spath, 1931, text-fig. 115c, from the condensed Albian of Escragnolles, Alpes-Maritimes, France (ex Astier Collection). It was referred to by Gebhardt (1983, p. 117) as C12493. It is re-illustrated here as Fig. 5B–D.

## Material

SAM-PCZ022411 (ex H201/1) from Bed 1, at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E.

## Dimensions

	D	Wb	Wh	Wb: Wh	U
BNHC37610a	50.9 (100)	36.6 (71.9)	22.3 (43.8)	1.64	(26.5)

## Description

The holotype was previously known only from a line drawing of the venter. It is a phosphatised internal mould with a maximum preserved diameter of 50.9 mm. The adapertural 180° sector of the outer whorl is body chamber. Coiling is evolute, the umbilical seam notched to accommodate the inner ventrolateral horns of the previous whorl. The umbilicus comprises 26.5% of the diameter and is deep, with a high convex wall. The intercostal whorl section is depressed oval; the costal section is very depressed, with the greatest breadth at the prominent inner ventrolateral horns. There are 14–15 ribs on the right flank of the outer whorl. Very strong, narrow primary ribs arise at the umbilical seam, and are straight, strong, high, and prorsiradiate on the flanks. They develop into a massive flare on the ventrolateral shoulder that is produced into a large inner ventrolateral horn and a much smaller outer ventrolateral tubercle, which gives rise to a wedge-shaped ventral rib that declines and effaces before reaching the coarse, prominent siphonal keel. Two weak primary ribs, each bearing a weak outer ventrolateral tubercle, separate the massive flared primaries at the adapical end of the outer whorl, to be replaced by a single weak intercalated rib as size increases. These weak intercalated ribs decline and efface at the adapertural end of the outer whorl. Sixteen ribs are preserved on the left flank of the outer whorl. The ornament corresponds to that on the right flank on the adapical 120° sector of the outer whorl; beyond this, the major ribs lack the inner ventrolateral horn (possibly but not necessarily a pathological condition, the result of damage to the shell in life); it only reappears on the penultimate rib, where symmetry is restored.

SAM-PCZ022411 (Fig. 5A) is a cameral fragment only, but it shows the utterly distinctive whorl section of *Dipoloceroides semicornutum*. The maximum preserved whorl height is 16 mm. The intercostal whorl section is depressed reniform, with intercostal whorl breadth to height ratio of 1.6, and a strong siphonal keel. The costal whorl section is even more depressed, with a whorl breadth to height ratio 2.3, the rib enormously flared on the ventrolateral shoulder and expanded into an inner ventrolateral horn, with a much smaller outer ventrolateral tubercle, exactly as in the holotype.

## Discussion

The massively expanded, flared ventrolateral rib and inner ventrolateral horn and very feeble minor ribs immediately distinguish the species from *Dipoloceroides delaruei* (compare Figs 4C–E and 5B–D). It differs from *Mojsisovicsia ventanillensis* in the same respects, and in being ribbed at a size where juveniles of the latter are not. There are close similarities to *Dipoloceroides cornutum* (Pictet, 1847) (p. 93, pl. 8, fig. 6), a cast of the holotype of which is illustrated here as Fig. 6C–E, I, and described below. The major ribs of *cornutum* also develop into a massive ventrolateral flare.

But this is directed adapically, with parallel edges, and broad, evenly rounded termination, and there is no outer ventrolateral tubercle. The weaker ribs between the flared ribs have thickened ends on the venter, but no clearly differentiated tubercle.

## Occurrence

Condensed Middle Albian of southeastern France, Middle Albian of northern KwaZulu-Natal.

*Dipoloceroides cornutum* (Pictet, 1847)

Fig. 6

1847 *Ammonites cornutus* Pictet, p. 93, pl. 8, fig. 6.  
 1850 *Ammonites cornutus* Pictet; d'Orbigny, p. 124.  
 1860 *Ammonites cornutus* Pictet & Campiche, p. 310.  
 1875a *Ammonites cornutus* Pictet; Neumayr, p. 21.  
 1875b *Ammonites cornutus* Pictet; Neumayr, p. 888.  
 1920 *Inflaticeras cornutum* (Pictet); Stieler, p. 399.  
 1921 *Dipoloceras cornutum* (Pictet); Spath, p. 278.  
 1921 *Dipoloceras cornutum* (Pictet); Douglas, p. 270.  
 1922 *Inflaticeras cornutum* (Pictet); Stieler, p. 309,  
     text-figs 2, 3, 9.  
 1923 *Dipoloceras cornutum* (Pictet); Spath, p. 75.  
 1926 *Dipoloceras cornutum* (Pictet); Spath, p. 421.  
 1931 *Dipoloceras cornutum* (Pictet); Spath, p. 358 (pars),  
     pl. 35, figs 1–4; text-figs 117a–c, 118d,e,f only; *non*  
     var. *corbulata*, *non.* var. *multispinosa* (with additional  
     synonymy).  
 1941 *Dipoloceras cornutum* Pictet sp.; Van Hoepen, p. 58,  
     text-fig. 3.  
 1947 *D. (D.) cornutum* (Pictet); Breistroffer, p. 90 (74).

## Type

The lectotype, designated by Spath, 1931, p. 360, is the original of Pictet, 1847, pl. 8, fig. 6, no. 18904 in the collections of the Muséum d'Histoire Naturelle, Geneva, from the condensed Albian of la Perte du Rhône, Ain, France. A cast (kindly supplied by Dr Christian Meister) is illustrated here as Fig. 6C–E, I.

## Material

SAM-PCZ19170 (*ex* D2355), the original of Van Hoepen, 1941, p. 58, text-fig. 3, from the Middle Albian Mzinene Formation, according to Van Hoepen's catalogue entry on the banks of the Munywana, below the causeway on the Somkele-Mkuze road; this seems to be in the general region of Kennedy & Klinger's (1975) localities 68–70.

## Dimensions

	D	Wb	Wh	Wb: Wh	U
Lectotype ic	25.9 (100)	12.5(48.3)	10.7 (41.3)	1.17	8.5 (32.8)

## Description

The lectotype is an internal mould 25.9 mm in maximum preserved diameter, the adapical 90° is body chamber. Coiling is moderately evolute, the umbilicus comprising 32.8% of the diameter, deep, with a feebly convex, outward-inclined umbilical wall, and broadly rounded umbilical shoulder. The intercostal whorl section is depressed oval,

with a whorl breadth to height ratio of 1.17. There is a strong continuous siphonal keel. The inner to mid-flank region of the penultimate whorl is smooth; delicate prorsiradiate ribs appear on the outer flank. On the adapical 90° sector of the outer whorl ten delicate primary ribs arise on the umbilical wall, sweep forwards, strengthen, and are convex across the umbilical shoulder, straight and prorsiradiate on the flanks, strengthening further on the outermost flanks and ventrolateral shoulder, where they are feebly convex. The ribs sweep forwards on the venter, forming an obtuse chevron, but efface before they reach the keel. There are three major ribs on the adapical sector of the outer whorl. They are narrow and prorsiradiate on the inner to middle flank, strengthening into a massive spatulate ventrolateral horn. This is directed upwards and backwards, with adapertural and adapical edges parallel, and a broadly and evenly rounded termination. The horns are slightly offset on either side of the venter, the best-preserved pair, at the adapertural end of the specimen, are unequally developed (Fig. 6I), the one smaller than the other. A smooth zone separates the horns from the siphonal keel. The major ribs are separated by two, three and, adaperturally, a single minor rib. These are narrower than the interspaces, very feebly convex across the umbilical shoulder, prorsiradiate on the inner flank, sweeping forwards and concave on the ventrolateral shoulder, to form an obtuse chevron on the venter. They efface before reaching the siphonal keel; some are incipiently bullate.

SAM-PCZ 19170 (ex D2335) (Fig. 6A,B) is 18.5 mm in diameter. Coiling is moderately evolute, the small, deep umbilicus comprising 24.3% of the diameter, the umbilical wall feebly convex, the umbilical shoulder relatively broadly rounded. The intercostal whorl section is depressed oval, the costal section polygonal. Primary ribs arise at the umbilical seam, flex back and are convex on the umbilical shoulder, rursiradiate and feebly flexuous across the flanks, convex on the inner flank, concave on the outer flank, projected forwards on the ventrolateral shoulder, where they terminate in feeble oblique elongated ventrolateral bullae, separated by a smooth zone from a blunt siphonal keel. The specimen bears periodic massive, blunt, outward-directed ventrolateral horns, borne on a single rib. There are two on the adapertural half of the outer whorl.

## Discussion

*Ammonites cornutus* has generally been referred to *Dipoloceras* by previous authors. It is however, significantly older than the type species, which is the marker fossil for the base of the Upper Albian, whereas *cornutum*, where well dated (Owen, 1971, p. 155) is upper Middle Albian. The presence of massive ventrolateral horns, not seen in *Dipoloceras*, links it to *Dipoloceroides semicornutum*, and this in turn links to the type species, *Dipoloceroides delaruei*. We illustrate here well-preserved individuals from the English Gault Clay (Fig. 6F–H, J–L), which further confirm the identity of the KwaZulu specimen.

Spath (1931) introduced two varieties of this species, which we exclude from *cornutum*. The specimens described in Spath's text on *Dipoloceras cornutum* var. *corbulata* Spath, 1931 (p. 362) were never figured. One of the specimens referred to by Spath, BMNH C793a, is illustrated here

(Fig. 7E). It is a large individual, over 80 mm in diameter, characterized by the development of flared ribs and strong spiral ridges; its affinities lie with lower Upper Albian forms of the type referred to as *Cechenoceras* by Van Hoepen (1941). The smaller specimen figured (Spath, 1931, pl. 36, fig. 8) but not mentioned by Spath in his text, is BMNH 48835 (Fig. 7B,C), which more closely resembles his variety *multispinosa*. The type of this form is BMNH C34884, the original of Spath, 1931, p. 363, pl. 38, fig. 9 (Fig. 7A,D). Spath noted transitions to *Dipoloceras cristatum* (1931, p. 308, pl. 32, fig. 3), and the affinities of *multispinosa* lie with *Dipoloceras* rather than *Dipoloceroides cornutum* in our view.

## Occurrence

Where well-dated, this is an upper Middle Albian species. The geographic distribution is Southern England, northwest and southeast France, and northern KwaZulu-Natal.

## Genus *Falloticeras* Parona & Bonarelli, 1897

### Type species

*Ammonites proteus* d'Orbigny, 1842, p. 624, by the original designation of Parona & Bonarelli, 1897, p. 89.

### *Falloticeras proteus* (d'Orbigny, 1842)

Fig. 8

- 1842 *Ammonites Proteus* d'Orbigny, p. 624.
- 1850 *Ammonites Proteus* d'Orbigny; d'Orbigny, p. 124.
- 1860 *Ammonites proteus* d'Orbigny; Pictet & Campiche, p. 306.
- 1897 *Falloticeras proteus* d'Orb.; Parona & Bonarelli, p. 89, pl. 12, fig. 1.
- 1922 *Falloticeras* Spath, p. 97.
- 1931 *Falloticeras* Spath, pp. 346, 352.
- 1938 *Falloticeras Proteus* d'Orb.; Roman, p. 370, pl. 37, fig. 353, 353a, 353b.
- 1942 *Falloticeras* Spath, p. 708.
- 1947 *Falloticeras Proteus* d'Orb. sp.; Breistroffer, p. 30.
- 1949 *Falloticeras proteus* d'Orbigny; Collignon, p. 122.
- 1957 *Falloticeras proteus* (d'Orbigny); Wright, p. L304.
- 1959 *Falloticeras* cf. *proteus* (d'Orbigny); Casey, p. 207.
- 1963 *Falloticeras proteus* (d'Orbigny); Milbourne, table 1.
- 1971 *Falloticeras proteum* (d'Orbigny); Owen, p. 155.
- 1977 *Falloticeras proteus* (d'Orbigny); Kennedy & Cooper, p. 800, pl. 104, figs 1–19; pl. 105, figs 3, 6, 7, 10, 15; text-figs 1–3.
- 1983 *Mojsisovicsia proteus* (d'Orbigny); Gebhard, p. 116, figs 1b,c, 2.1, 2.2.
- 1996 *Falloticeras proteus* (d'Orbigny); Wright, p. 137, fig. 105, 2a–c.
- 2006 *Falloticeras proteus* (d'Orbigny, 1842); Kennedy & Juignet in Gauthier, p. 176, pl. 41, figs 3, 4.

### Type

The lectotype, by the subsequent designation of Kennedy & Cooper (1977, p. 800) is BMNH C68140 (ex Astier Collection), from the condensed Albian in the environs of Escragnolles, Alpes-Maritimes, France, re-illustrated here as Figure 8F,G, T–V. There are numerous paralectotypes, listed by Kennedy & Juignet (2006, p. 176).

## Material

SAM-PCZ022431 (ex H207/1/21), SAM-PCZ17089, BMNH C78867, C78868, C78870, C78871, C78873, all from the Middle Albian fauna of bed 1 of the Mzinene Formation at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E.

## Dimensions

	D	Wb	Wh	Wb: Wh	U
C78871	12.6(100)	5.8 (46.0)	5.3(42.1)	1.09	3.8 (30.2)
C78870	16.7(100)	7.7 (46.1)	6.6(39.5)	1.17	5.2 (31.1)
C78873	23.4(100)	10.5(44.9)	9.6 (41.0)	1.1	7.8 (33.3)

## Description

BMNH C78871 (Fig. 8B,C) is an internal mould of a juvenile phragmocone 12.6 mm in diameter. Coiling is moderately involute, with a convex, outward-inclined wall and broadly rounded umbilical shoulder. The whorl section is depressed oval, with a whorl breadth to height ratio of 1.1. The flanks, ventrolateral shoulders, and venter are broadly convex. There is a distinct keel from the smallest diameter visible. The umbilical seam of the outer whorl is notched to accommodate the estimated 10 umbilical bullae per whorl of the penultimate whorl. There are no such bullae on the outer whorl of this specimen.

BMNH C78870 is 16.7 mm in diameter, and broken into two pieces. The adapertural 90° whorl sector of his specimen is body chamber. As in the previous specimen, there are coarse umbilical bullae, 10–12 on the penultimate whorl, but disappearing at the beginning of the outer whorl. The siphonal keel effaces at the adapertural end of the body chamber.

BMNH C78867 (Fig. 8J,K,O) is the phragmocone of a more compressed individual, 20.4 mm in diameter, the shallow umbilicus comprising 34% of the diameter. The siphonal keel is strong throughout. There are well-developed umbilical bullae on the adapical 90° sector of the penultimate whorl, and all of the antepenultimate whorl. SAM-PCZ022431 (ex H207/1/21) (Fig. 8A, L–N) is a similarly compressed individual, with well-developed ribs on the adapical part of the outer whorl.

BMNH 78873 (Fig. 8H,I,P,Q) is 23.4 mm in diameter, retains well-preserved aragonitic shell, and is part body chamber. Coiling is moderately involute, the umbilicus of moderate depth, comprising 33% of the diameter. The umbilical wall is broadly convex and outward-inclined, the umbilical shoulder broadly rounded. The whorl section is only slightly compressed, with a whorl breadth to height ratio of 1.1, the flanks feebly convex, the ventrolateral shoulders and venter broadly rounded. There are 12 coarse umbilical bullae on the 90° adapertural sector of the penultimate whorl, and the adapical 270° sector of the outer whorl. The surface of the shell is ornamented by delicate growth lines and striae, convex across the umbilical wall and shoulder, prorsiradiate across the flanks, concave on the ventrolateral shoulders,

and projected forwards to produce an obtuse ventral chevron, with the blunt siphonal keel at the apex. The keel declines and effaces on the adapertural 90° sector of the outer whorl.

BMNH C78868 (Fig. 8D,E,R,S) is a beautifully preserved internal mould of a 180° sector of body chamber. The whorl breadth to height ratio is 1.05 at the adapical end of the body chamber. The external mould of the antepenultimate whorl reveals the presence of crenulations in the umbilical seam, indicating the presence of strong umbilical bullae on the inner whorls, as in the previous specimens. The ventral keel is very subdued at the adapical end of the body chamber, and effaces progressively, leaving only a blunt mid-ventral angulation at the greatest preserved diameter.

## Discussion

The KwaZulu specimens match well with the lectotype: compare Figs 8P–S and 8T–V, leaving no doubt as to the affinities of the present material.

## Occurrence

Lower Middle Albian of southeast France, southern England, and northern KwaZulu-Natal. Gebhard (1983, p. 116) records the species from Austria, but the specimen was not illustrated.

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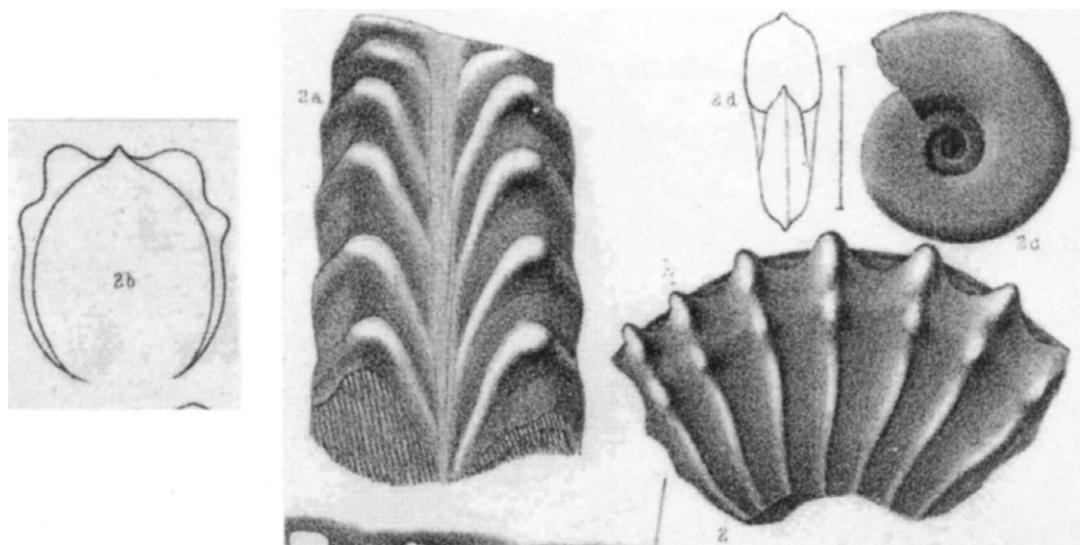
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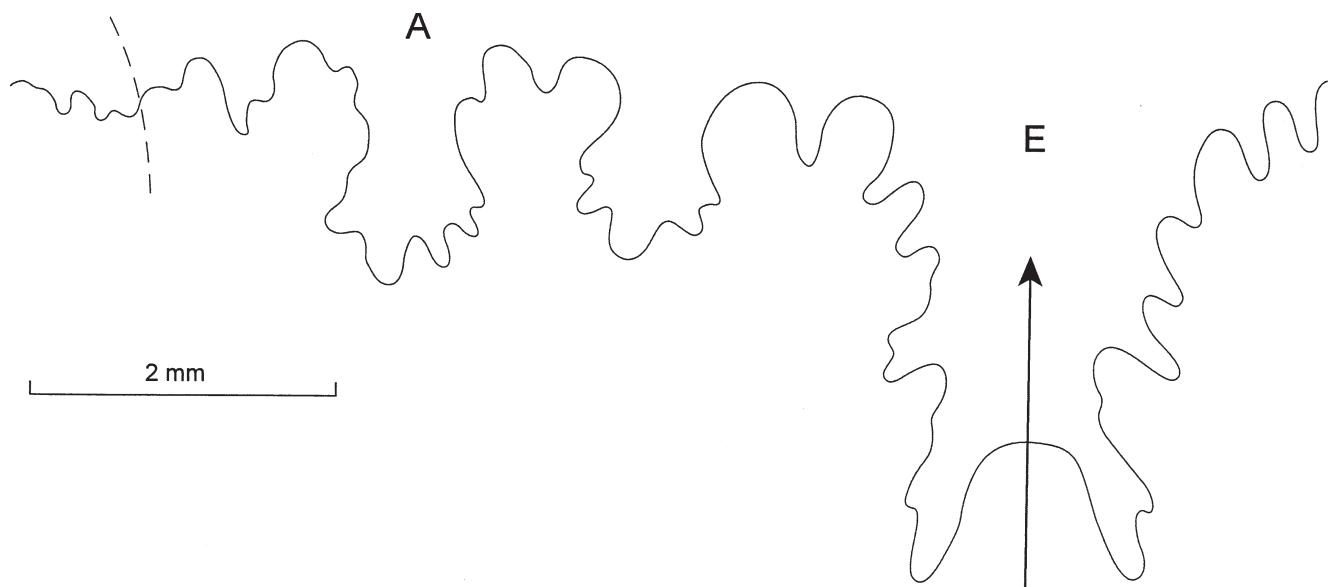
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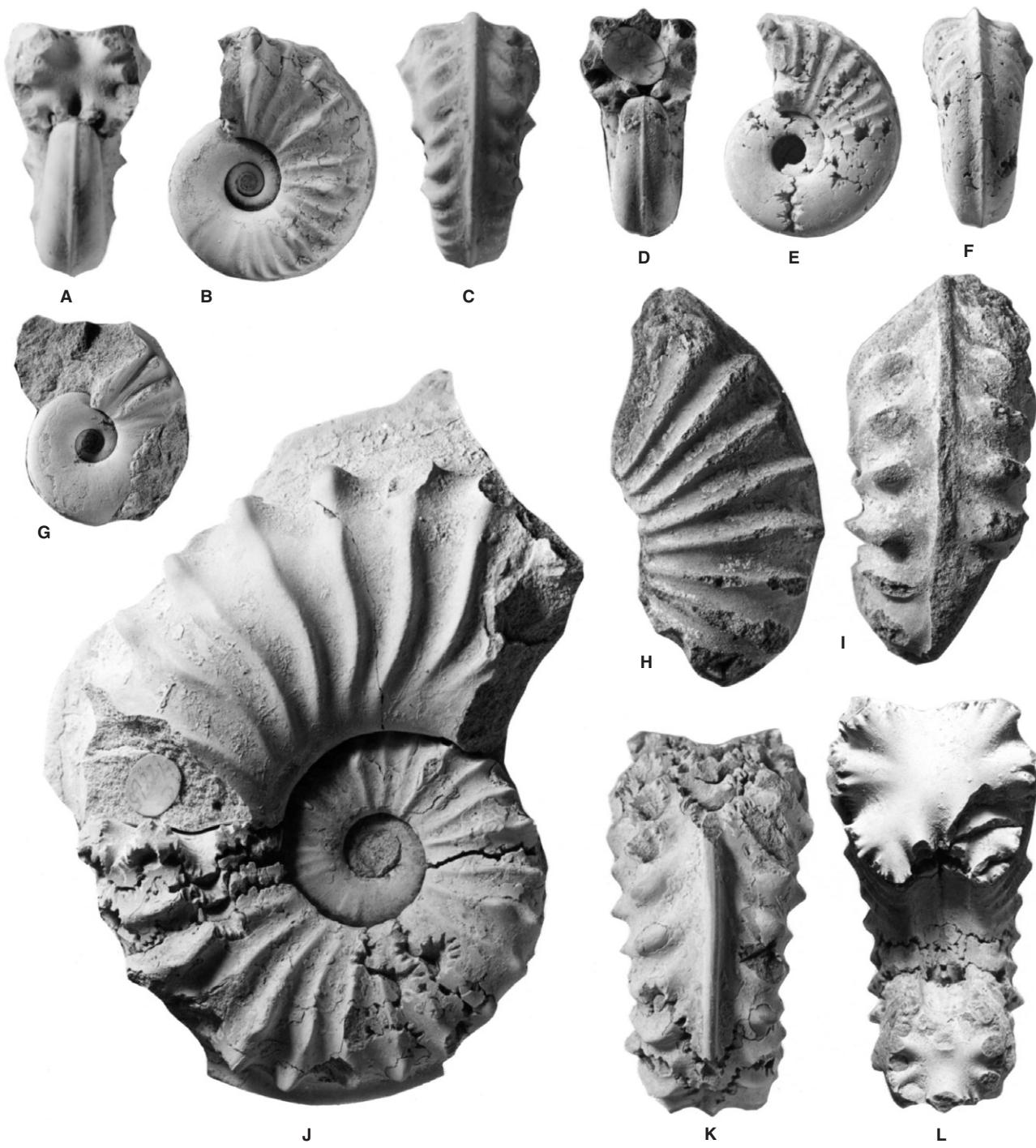
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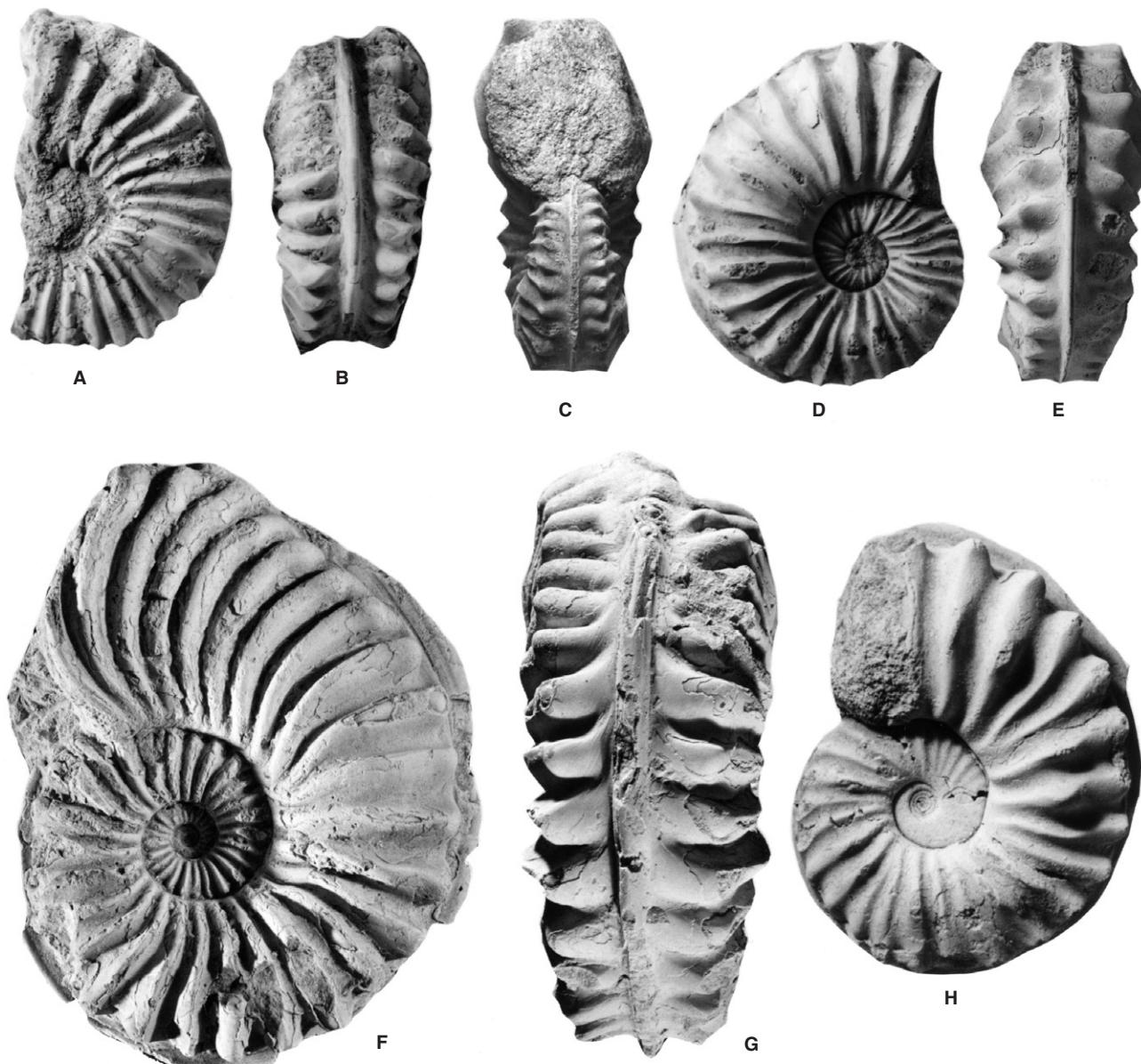
**Fig. 1.** The original figures of *Ammonites ventanillensis* Gabb, 1877, pl. 39, figs 2, 2a–d.



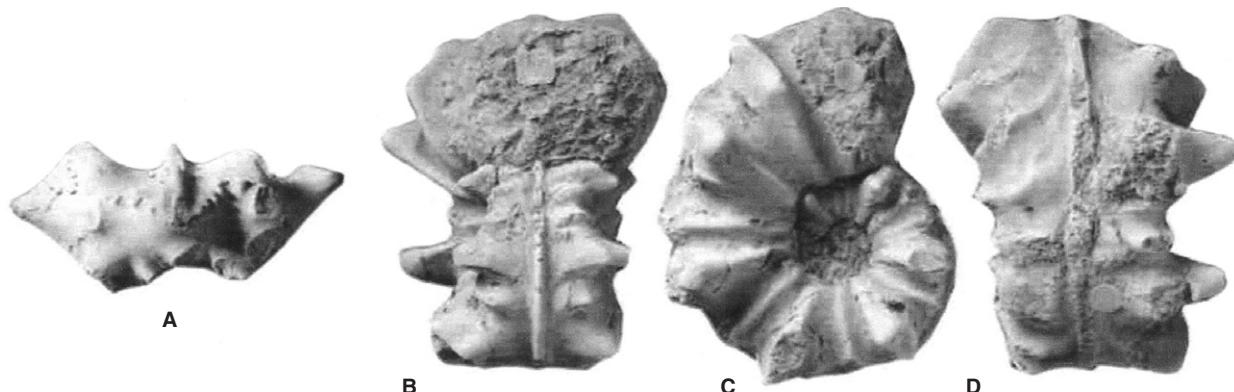
**Fig. 2.** External suture of *Mojsisovicsia ventanillensis* (Gabb, 1877), BMNH C78872, from the Middle Albian fauna of bed 1 of the Mzinene Formation at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E.



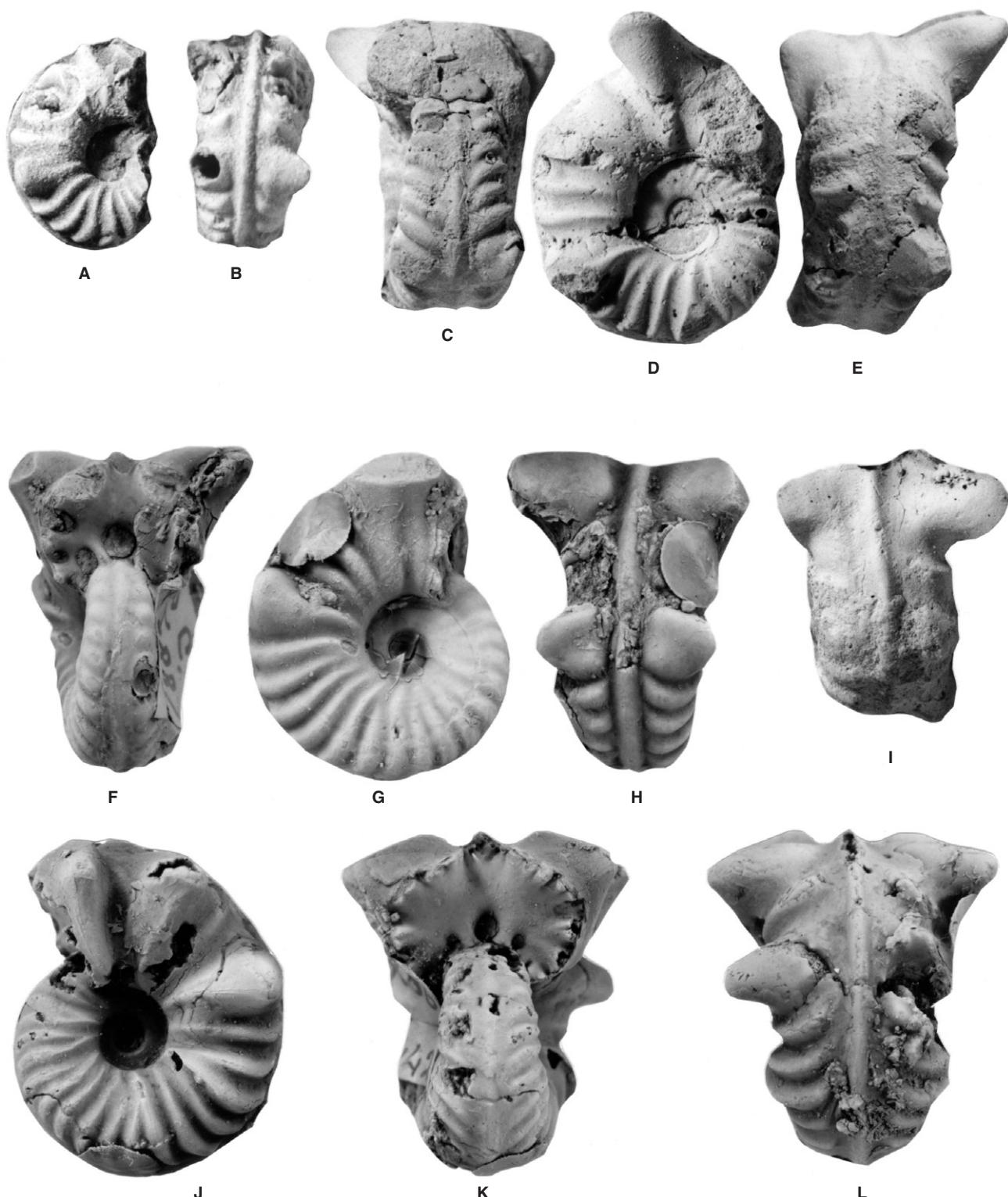
**Fig. 3.** *Mojsisovicsia ventanillensis* (Gabb, 1877). **A–C, J–L**, BMH C78865; **D–F**, BMNH C78872; **G**, SAM-PCZ022404; **H, I**, BMNH C78876. All specimens are from the Middle Albian fauna of bed 1 of the Mzinene Formation at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E. All figures are  $\times 1$ .



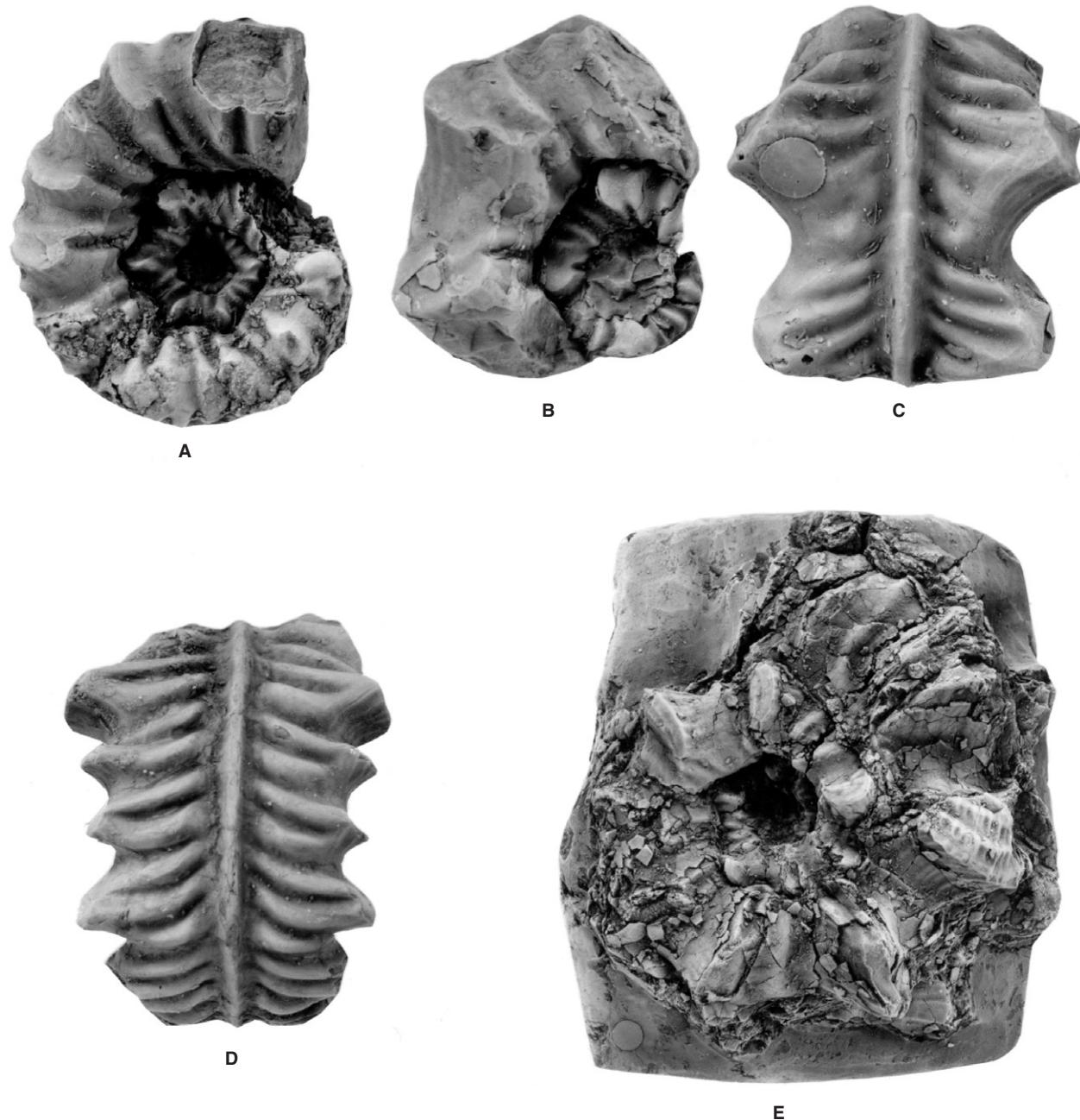
**Fig. 4.** *Dipoloceroides delaruei* (d'Orbigny, 1841). **A, B**, MNHP 5761–2 (d'Orbigny Collection); **C–E**, the neotype, MNHP B46122 (d'Orbigny Collection 5761–1); **H**, BMNH 37611a, all from the condensed Middle Albian of Escragnolles, Alpes-Maritimes, France. **F, G**, SAM-PCZ022410 (ex EM 175) presumably from Haughton's (1936) localities on the Pongola River. Figures A–G are  $\times 1$ ; Fig. H is  $\times 2$ .



**Fig. 5.** *Dipoloceroides semicornutum* (Spath, 1931). **A**, SAM-PCZ022431. **B–D**, The holotype BMNH 37610a, the original of Spath, 1931, text-fig. 115c, from the condensed Albian of Escragnolles, Alpes-Maritimes, France. All figures are  $\times 1$ .



**Fig. 6.** *Dipoloceroides cornutum* (Pictet, 1847). **A, B**, SAM-PCZ19170 (ex D2355), the original of Van Hoepen, 1941, text-fig. 3, from the Middle Albian Mzinene Formation, according to van Hoepen's catalogue entry on the banks of the Munywana, below the causeway on the Somkele-Mkuze Road; this seems to be in the general region of Kennedy & Klinger's (1975,) localities 68–70. **C–E, I**, a cast of the lectotype, the original of Pictet, 1847, pl. 8, fig. 6, no. 18904 in the collections of the Muséum d'Histoire Naturelle, Geneva, from the condensed Albian of la Perte du Rhône, Ain, France. **F–H**, BMNH C348887, the original of Spath, 1931, pl. 35, fig. 3; **J–L**, BMNH C34886, the original of Spath, 1931, pl. 35, fig. 2, both from the Middle Albian Lower Gault Clay of Folkestone, Kent. All figures are  $\times 2$ .



**Fig. 7.** **A, D**, the original of *Dipoloceras cornutum* var. *multispinatum* of Spath, 1931, pl. 36, fig. 9, BMNH C34884. **B, C**, the original of *Dipoloceras cornutum* var. *corbulata* of Spath, 1931, pl. 36, fig. 8, BMNH 48835. Both specimens are from the Middle Albian Gault Clay of Folkestone, Kent. **E**, the original of *Dipoloceras cornutum* var. *corbulata* of Spath, 1931, p. 362, BMNH C793a, from the Middle or Upper Albian Gault Clay of Folkestone, Kent. Figures A–D are  $\times 2$ ; Fig. E is  $\times 1$ .



**Fig. 8.** *Falloticeras proteus* (d'Orbigny, 1842). **A, L–N**, SAM-PCZ022431b, (ex H207/1/21); **B, C**, BMNH C78871; **D, E, R, S**, BMNH C78868; **H, I**, BMNH C78873; **J, K, O**, BMNH C78867, all from the Middle Albian fauna of bed 1 of the Mzinene Formation at locality 51 of Kennedy & Klinger (1975, p. 288, text-fig. 4), stream bed and bank exposures in the Mzinene River north of Hluhluwe, northern KwaZulu-Natal, coordinates 27°53'43"S, 32°19'22"E; **F, G, T–V**, the lectotype, BMNH C68140 (ex Astier Collection), from the condensed Albian in the environs of Escragnolles, Alpes-Maritimes, France. Figures A, D–K are  $\times 1$ , Figures B, C, L–V are  $\times 2$ .