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The ammonite genus *Diaziceras* Spath, 1921, from the Campanian of KwaZulu-Natal, South Africa, and Madagascar

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The ammonite genus *Diaziceras* Spath, 1921, and the type species, *D. tissotiaeforme* are revised and referred to the subfamily Lenticeratinae Hyatt, 1900, of the family Sphenodiscidae Hyatt, 1900. *Skoumalia* Summesberger, 1979, is interpreted as a junior synonym of *Diaziceras*. *Diaziceras guillantoni* Hourcq, 1949, and *D. spathi* Hourcq, 1949, are regarded as synonyms of *D. tissotiaeforme*, and all are referred to the Lower Campanian on the basis of records from Madagascar.

Keywords: ammonites, *Diaziceras*, Campanian, Cretaceous, KwaZulu, South Africa, Madagascar.

INTRODUCTION

L.F. Spath introduced the genus *Diaziceras* on the basis of a single specimen of the type species, *Diaziceras tissotiaeforme* Spath, 1921 (p. 245, pl. 19, figs 1a–k), collected by A. L. du Toit at Umkwelane Hill, south of Mtubatuba in what is now KwaZulu-Natal.

The holotype (Figs 1C–E, 2A,B, 3, 4F) remains the only specimen of the genus known from South Africa, the systematic position of which has been a matter of debate by subsequent authors. The age of the type specimen is also uncertain. The type locality corresponds to locality 10 of Kennedy & Klinger (1975, p. 282). Here, the basal shell-pebble bed of the St Lucia Formation rests unconformably on deeply weathered basalt of the Lebombo Volcanics . Concretions three metres above the base have yielded *Placenticeras kaffrarium* Etheridge, 1904, and *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine & Thévenin, 1907), indicating a Coniacian date for the base of the sequence (Coniacian II of Kennedy & Klinger (1975)). Taxa recorded from this locality by Spath (1921) also demonstrate the presence of Santonian: i.e.*Pseudoschloenbachia umbulazi* (Baily,1855), and Lower Campanian: i.e. *Submortoniceras woodsi* Spath, 1921. The *Parapachydiscus* sp. nov. aff. *colligatus* Binkhorst of Spath (1921, p. 226, pl. 22, fig. 1a,b) is the holotype of *Menuites* (*Menuites*) *spathi* (Venzo, 1936) (Kennedy & Klinger, 2006, p. 71, figs 52–68), indicating the presence of an even higher horizon, equivalent to Campanian III of Kennedy & Klinger (1975).

It is argued below, on the basis of records of *Diaziceras* from Madagascar that the type specimen is from the Lower Campanian. It is also argued that *Skoumalia* Summesberger, 1979, from the Santonian of Austria and southern France is a synonym of *Diaziceras*, and that the genus is closely allied to *Eulophoceras*, Hyatt, 1903, and a member of the Subfamily Lenticeratinae Hyatt, 1900.

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SYSTEMATIC PALAEONTOLOGY

Superfamily Acanthoceratoidea de Grossouvre, 1894
Family Sphenodiscidae Hyatt, 1900
(= Libycoceratinae Zaborski, 1982, p. 306)
Subfamily Lenticeratinae Hyatt, 1900
(= Eulophoceratinae Hyatt, 1903;
= Diaziceratinae Basse, 1947)

Genus *Diaziceras* Spath, 1921
(= *Skoumalia* Summesberger, 1979, p. 146)

Type species

Diaziceras tissotiaeforme Spath, 1921, p. 245, pl. 19, figs 1a–k, by original designation.

Diagnosis

Compressed to moderately inflated, involute. Whorl section compressed polygonal, with fastigiate venter and strong siphonal keel. Costal section markedly concave between umbilical and ventral tubercles, and on either side of strong siphonal keel. Weak to strong umbilical bullae give rise to pairs of low, broad, prosrsiradiate ribs which, together with additional intercalated ribs, all bear conical to bullate ventral tubercles. Suture moderately to deeply incised, with asymmetrically bifid to asymmetrically trifid E/A and bifid A.

Discussion

The holotype of the type species is a stout individual (Figs 1C–E, 2A,B). The holotype of *Diaziceras guillantoni* Hourcq, 1949, p. 22 (108), pl. 12(2), fig. 1; Fig. 9D herein) is compressed, with weaker ornament of the same basic pattern: umbilical bullae that give rise to pairs of ribs on the phragmocone, with additional intercalated ribs, All ribs bear ventral tubercles, but these are elongated and projected forwards, rather than being conical, as in *D. tissotiaeforme*. The venter is markedly concave on either side of the siphonal keel. E/A is asymmetrically trifid,



Figure 1. **A, B**, the holotype of *Diaziceras spathi* Hourcq, 1949, p. 107 (21), pl. 12 (2), fig. 2, from the 'region de Berere', Madagascar, an unregistered specimen in the collections of the École des Mines, Paris, now at the collections of the Université Claude Bernard, Lyon. No precise horizon was given. **C–E**, *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath 1921, p. 245, pl. 19, fig. 1a–k, from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. Figures are ×1.

and A bifid (Fig. 4B). The differences in ornament between *tissotiaeforme* and *guillantoni* reflect the common covariance between whorl inflation and strength ornament; they are clearly congeneric.

Skoumalia Summesberger, 1979, with type species *Skoumalia austriaca* Summesberger, 1979 (p. 141, text-figs 26–30; pl. 9, figs 37–41, text-figs 26–30), from the Upper Santonian of the Sandkalkbank of the Bibereckschichten of the Gosau Basin, Austria, has been regarded as a synonym of *Eulophoceras* Hyatt, 1903 (Kennedy (1987, p. 776; Kennedy *in* Kennedy *et al*. 1995, p. 425; Wright 1996, p. 204). Summesberger recognised two morphotypes in *Skoumalia austriaca*. His Form A, which included the holotype (Summesberger, 1979, pl. 9, figs 37, 38; text-figs. 26–28; Fig. 4A,C; 9A–C herein) has a compressed phragmocone with fastigiate venter, strong umbilical bullae that give rise to pairs of straight prorsiradiate ribs that, together with intercalated ribs, terminate in small ventral bullae. The ornament differs in no significant respects from that of *Diaziceras guillantoni* (compare Figs 9A–C and D). The suture of the holotype lacks the ventralward part of E/A (Fig. 4A) which is broad, asymmetric, with narrow deep median incision, a deep narrow A, and, bifid A/U2. The suture of a second specimen referred

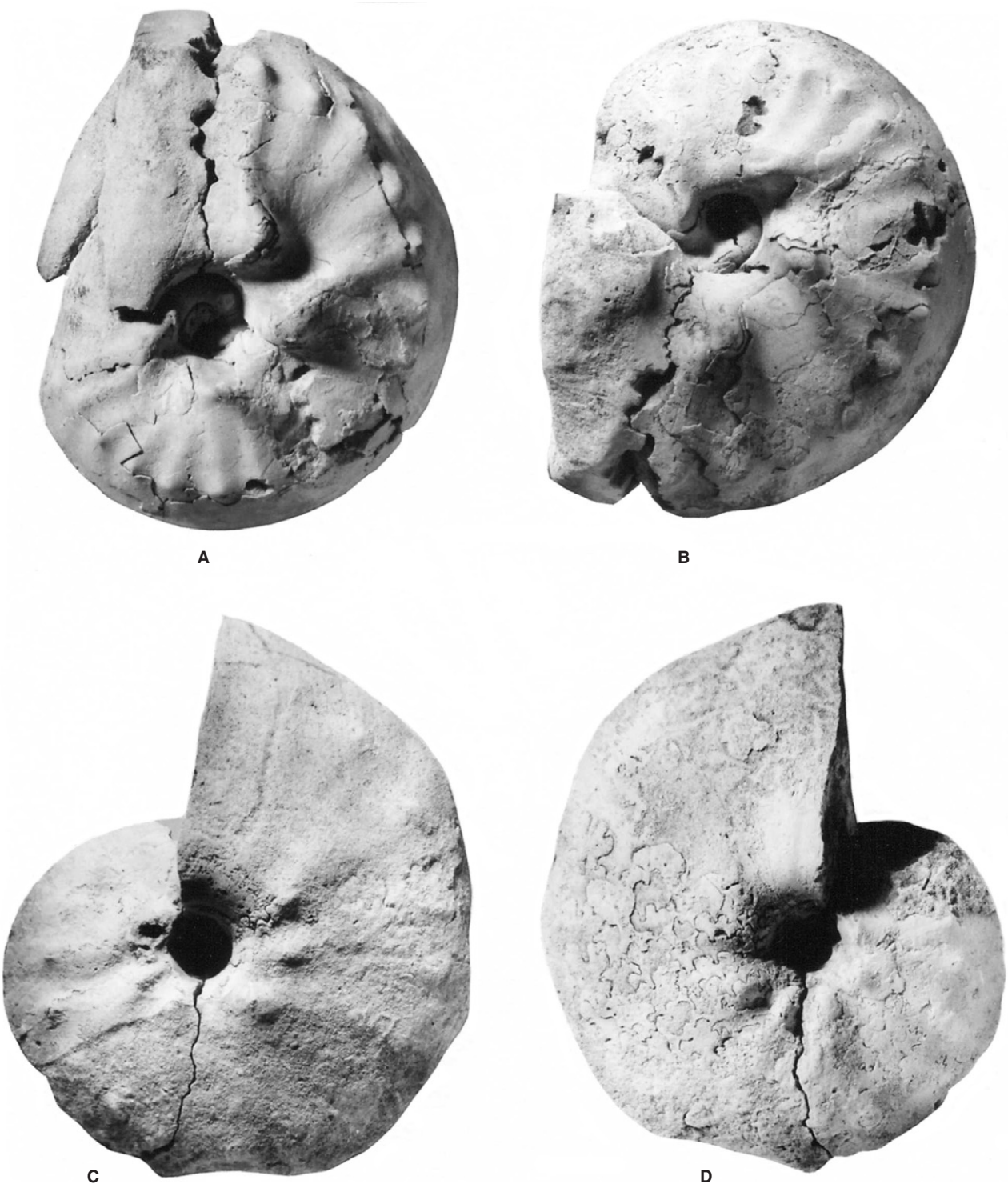


Figure 2. **A, B**, *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath (1921, p. 245, pl. 19, fig. 1a–k), from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. **C, D**, the holotype of *Diaziceras menabense* Hourcq, 1949,(p. 109 (23), pl. 13 (3)), fig. 3, from the 'région de Berere, sommet du Santonien', Madagascar, an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. Figures are ×1.

to form A by Summesberger (1979, text-fig. 28; Fig. 4C herein) has a broad asymmetric bifid E/A with a deep narrow incision. The suture is thus less deeply incised than in the holotype of *Diaziceras tissotiaeforme* (Fig. 4F), and lacks the complex folioles adjacent to E, which is obliquely trifid. The bifid E/A and lesser depth of incisions of *Skoumalia austriaca* as opposed to the trifid E/A and deep incisions in *Diaziceras tissotiaeforme* are the only clear distinguishing feature between the two. The sutures of other *Diaziceras*, e.g. *D. guillantoni* (Fig. 4B) are much less deeply incised than in the holotype of *D. tissotiaeforme*, and that of *D. menabense* (Fig. 4E) is bifid. *Skoumalia* is regarded here as a synonym of *Diaziceras*, rather than *Eulophoceras*. Summesberger recorded what he regarded as a second form, form B, of *Skoumalia austriaca*, that co-occurred with the lectotype (his form A). Form B of Summesberger (1979, p. 143, text-figs 29, 30; pl. 9, figs 39–41; text-figs 29, 30; 1980, p. 280, pl. 2, figs 5–6; pl. 3,

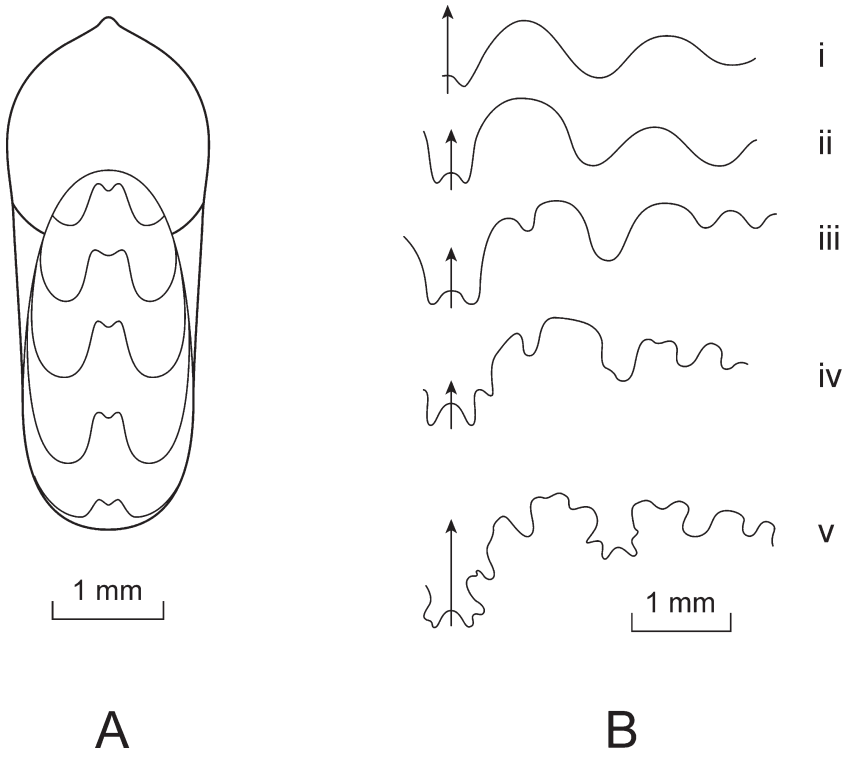


Figure 3. *Diaziceras tissotiaeforme* Spath, 1921, the holotype, by monotypy, SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath (1921, p. 245, pl. 19, fig. 1a–k), from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal. **A**, the inner whorls at a diameter of 3 mm; copy of Spath, (1921, pl. 1, fig.1d); **B**, development of the suture line at i, a diameter of 1.5 mm; ii at 2 mm; iii at 3 mm; iv at 5.5 mm; v at 8 mm. Copy of Spath, (1921, pl. 1, fig. 1g–1k). Scale bars are 1 mm.

figs 7–8; text-figs 5,6) is ornamented by delicate umbilical bullae on the phragmocone. The outer whorl bears delicate feebly flexuous growth lines and striae, with ten distant outer lateral bullae. Whereas form A has the ornament of *Diaziceras*, Form B (a juvenile from southwest France is shown in Fig. 9E–G for comparison) has delicate ribs and outer lateral bullae, recalling *Eulophoceras*, as discussed elsewhere (Kennedy & Klinger, 2012, in press).

Spath (1921, p. 242) was unequivocal in his view of the affinities of *Diaziceras*: 'Its suture-line stamps it as being near to the genera *Eulophoceras* Hyatt and *Spheniscoceras*' Spath also noted the similarity in ornament between *Diaziceras* and certain Tissotidae Hyatt, 1900, specifically *Metatissotia fourneli* (Bayle, 1878) (pl. 40, fig. 3), but dismissed the possibility of affinity, given the pseudoceratitic suture of the family. In contrast, Hourcq (1949, p. 116 (30)), placed *Diaziceras* and *Eulophoceras* in the family Tissotidae Hyatt, 1900. Basse (1947, p. 159 (63)) introduced a subfamily Diaziceratinae, which she placed in the Tissotidae. Wright (1957, p. L437) assigned the genus to the Lenticeratinae Hyatt, 1900 (= Eulophoceratinae Hyatt, 1903). In 1996 (p. 189) he preferred placement in the subfamily Barroisiceratinae Basse, 1947, of the family Collignoniceratidae Wright & Wright, 1951. An orphan genus indeed!

We revert to the views of Spath. The sutures of *Diaziceras* and *Eulophoceras* share an asymmetrically trifid E/A. The weak ribs with no or feeble umbilical bullae, and strengthened rib terminations (but only rarely bullae) of *Eulophoceras* are a reflection of the compressed, oxycone whorl section. *Diaziceras tissotiaeforme* has inflated whorls and strong ribs and tubercles. The ribs and tubercles of compressed *Diaziceras guillantoni* Hourcq, 1949 (p. 108 (22), pl. 12 (2), fig. 1; text-fig. 15) are intermediate, differences that reflect covariance between ornament strength and whorl section.

Occurrence

Upper Santonian of the Gosau Basin, Austria, and Corbières in southern France. Lower Campanian of Madagascar (following Collignon, 1969, although originally referred to the top of the Santonian by Hourq, 1949). On the basis of the Madagascan occurrences, the type occurrence in KwaZulu-Natal is inferred to be in the Lower Campanian.

Diaziceras tissotiaeforme Spath, 1921

Figs 1C–E, 2–3, 4E,F, 5

1921 *Diaziceras tissotiaeforme* Spath, p. 245, pl. 19, figs 1a–k.
1949 *Diaziceras Spathi* Hourcq, p. 107 (21), pl. 12 (2), fig. 2.
1949 *Diaziceras menabense* Hourcq, p. 109 (23), pl. 13 (3), fig. 3; text-figs 16, 17.
1957 *Diaziceras tissotiaeforme* Spath; Wright, p. L437, text-fig. 552, 4a–c.
1969 *Diaziceras spathi* Hourcq; Collignon, p. 210, pl. 603, fig. 2258.
1996 *Diaziceras tissotiaeforme* Spath; Wright, p. 189, text-fig. 143, 2a–c.

Type

The holotype, by monotypy, is SAM-PCZ19040 (formerly 5478 in Spath 1921), the original of Spath 1921, p. 245, pl. 19, figs 1a–k, from the St Lucia Formation of Umkwelane Hill, northern KwaZulu-Natal, locality 10 of Kennedy & Klinger (1975, p. 282).

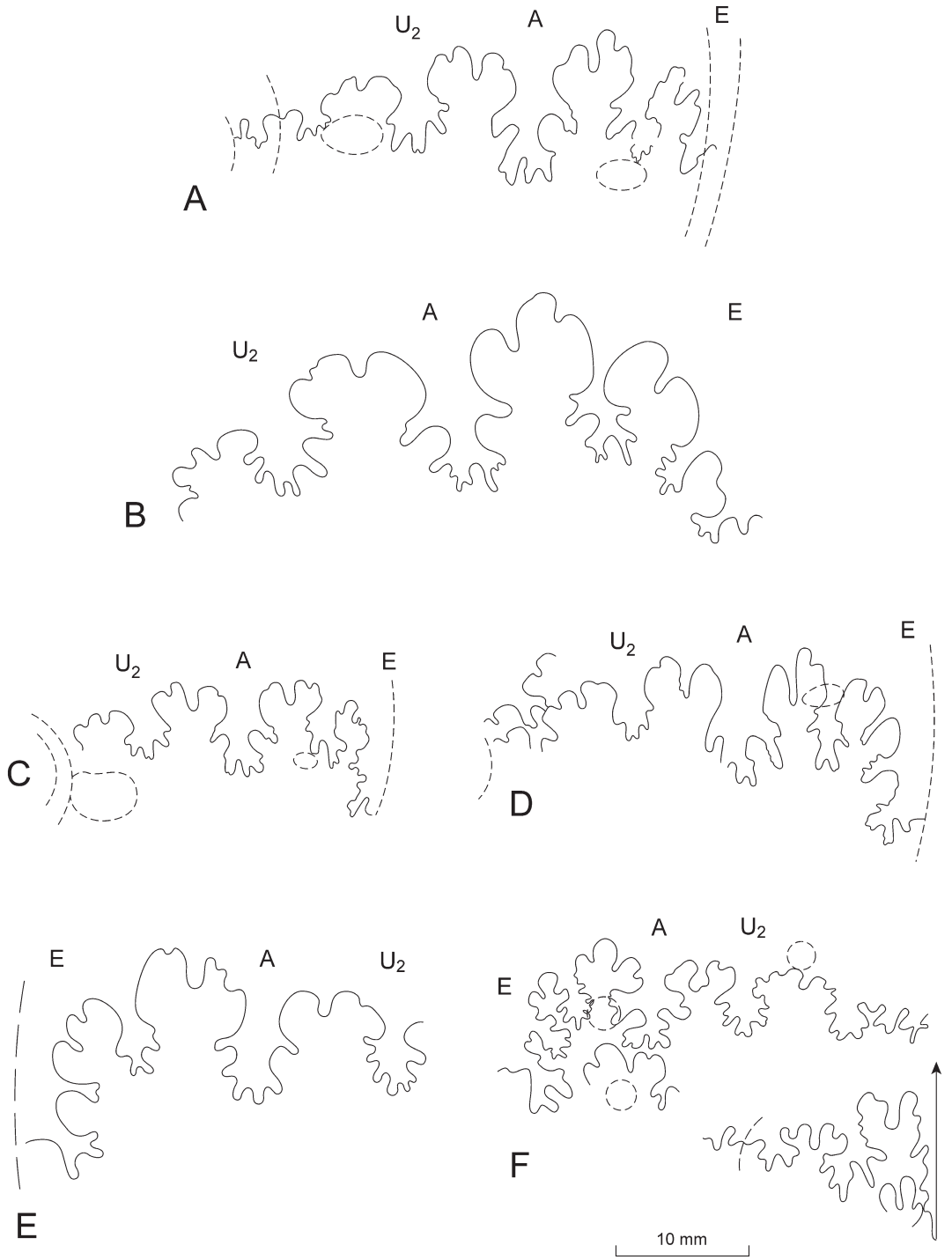


Figure 4. Suture lines. **A**, *Skoumalia austriaca* Summesberger, 1979, form A (copy of Summesberger 1979, text-fig. 27). **B**, the holotype of *Diaziceras guillantoni* Hourcq, 1949, p. 108 (22), pl. 12 (2), fig. 1. **C**, *Skoumalia austriaca* Summesberger, 1979, form A, (copy of Summesberger 1979, text-fig. 28. **D**, *Skoumalia austriaca* Summesberger, 1979, form B (copy of Summesberger 1979, text-fig. 30). **E**, the holotype of *Diaziceras menabense* Hourcq, 1949, p. 109 (23), pl. 13 (3), fig. 3. **F**, the holotype of *Diaziceras tissotiaeforme* Spath, 1921, copy of Spath (1921, pl. 19, fig. 1e, f.). Scale bar is 10 mm.

Dimensions of the holotype

	D	Wb	Wh	Wb:Wh	U
PCZ19040,c	80.6 (100)	47.7 (59)	42.1 (52)	1.13	13.6 (16)
PCZ19040,ic	80.6 (100)	38.6 (47)	42.1 (52)	0.92	13.6 (16)

Description

The holotype is a well-preserved undeformed individual retaining traces of the original aragonitic shell. It is septate to a diameter of 81.4 mm, the last few septa crowded, suggesting the specimen may be the phragmocone of an adult. A short, worn section of body chamber survives, and extends the specimen to a maximum preserved diameter of 84.5 mm. Coiling is very involute, with a small, very deep conical umbilicus that comprises 16.9% of the diameter, the umbilical wall flattened and outwardly-inclined. The umbilical shoulder is broadly rounded. The intercostal whorl section is compressed polygonal, with the greatest breadth just outside the umbilical shoulder and a whorl breadth to height ratio of 0.92. The inner flanks are broadly rounded, the outer flanks flattened and



Figure 5. *Diaziceras tissotiaeforme* Spath, 1921, the original of *Diaziceras spathi* Hourcq, 1941, *sensu* Collignon, (1969, pl. 603, fig. 2258), from the 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*. Sous-Zone à *Besairiella besairiei* (base). Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is ×1.

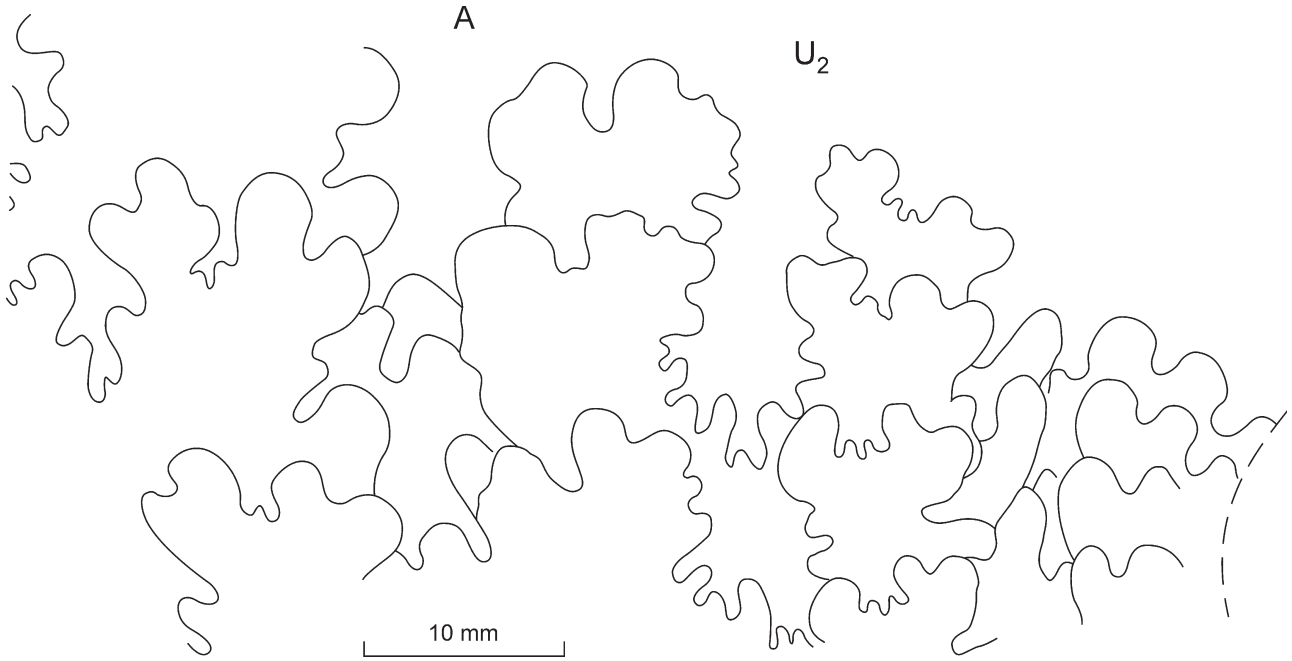


Figure 6. External suture of *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 614, fig. 2261). Scale bar is 10 mm.



Figure 7. *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 604, fig. 2261), from 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*. Sous-Zone à *Hourcquiella hourcqui*. Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is ×1.

convergent, the venter obtusely fastigiate, with a strong siphonal keel. The greatest breadth is at the massive umbilical bullae in costal section, with a whorl breadth to height ratio of 1.13. The whorl section is concave between umbilical bullae and ventrolateral tubercles, and between ventrolateral tubercles and keeled venter. There are five massive umbilical bullae, perched on the umbilical shoulder. The bullae give rise to pairs of low, broad, convex prorsiradiate ribs that sweep across the flanks and link to small conical ventral tubercles. One or more short ribs intercalate between the successive pairs of bullate primaries, to give a total of 12 ribs on the adapertural half of the outer whorl, and an estimated 24 per whorl.

The mature suture (Fig. 4F) has a broad, deeply incised asymmetrically trifid E/A, A with deep incisions and a small, bifid U2. The early sutural development is shown in Fig. 3.

Discussion

Diaziceras menabense Hourcq, 1949 (p. 23 (109), text-figs 16,17; pl. 13 (3), fig. 3) is a synonym of *D. tissotiaeforme* in our view. The holotype (Figs 2C,D, 4E) is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. It is from Berere, Madagascar, and was referred to the top of the Santonian by Hourcq. A worn and battered internal mould with a 60° sector of body chamber preserved, the dimensions are a follows:

Dic: 98.0 (100) Wb: 37.5 (38.3) Wh: 54.0 (55.1) Wb:Wh:0.69 U:10.7 (10.9)

Coiling is very involute, the small deep umbilicus comprising 10.9% of the diameter, with a flattened, outward-inclined wall and a broadly rounded umbilical shoulder. The intercostal whorl section is compressed lanceolate, with the greatest breadth just outside the umbilical shoulder. Nine to 10 conical umbilical tubercles perch on the umbilical shoulder; strong on the phragmocone, they weaken markedly on the body chamber. On the phragmocone, the bullae give rise to pairs of low broad prorsiradiate ribs that terminate in conical outer lateral tubercles. Beyond the tubercles the flanks are concave and converge to the acute venter. The tubercles and flank ribs persist onto the body chamber, but the venter becomes less acute. The suture (Fig. 4E) has a broad, little-incised incipiently obliquely trifid E/A, a narrow A, and little-incised bifid U2. The ornament is slightly weaker, and the whorl section compressed when compared to that of the holotype of *tissotiaeforme* while the

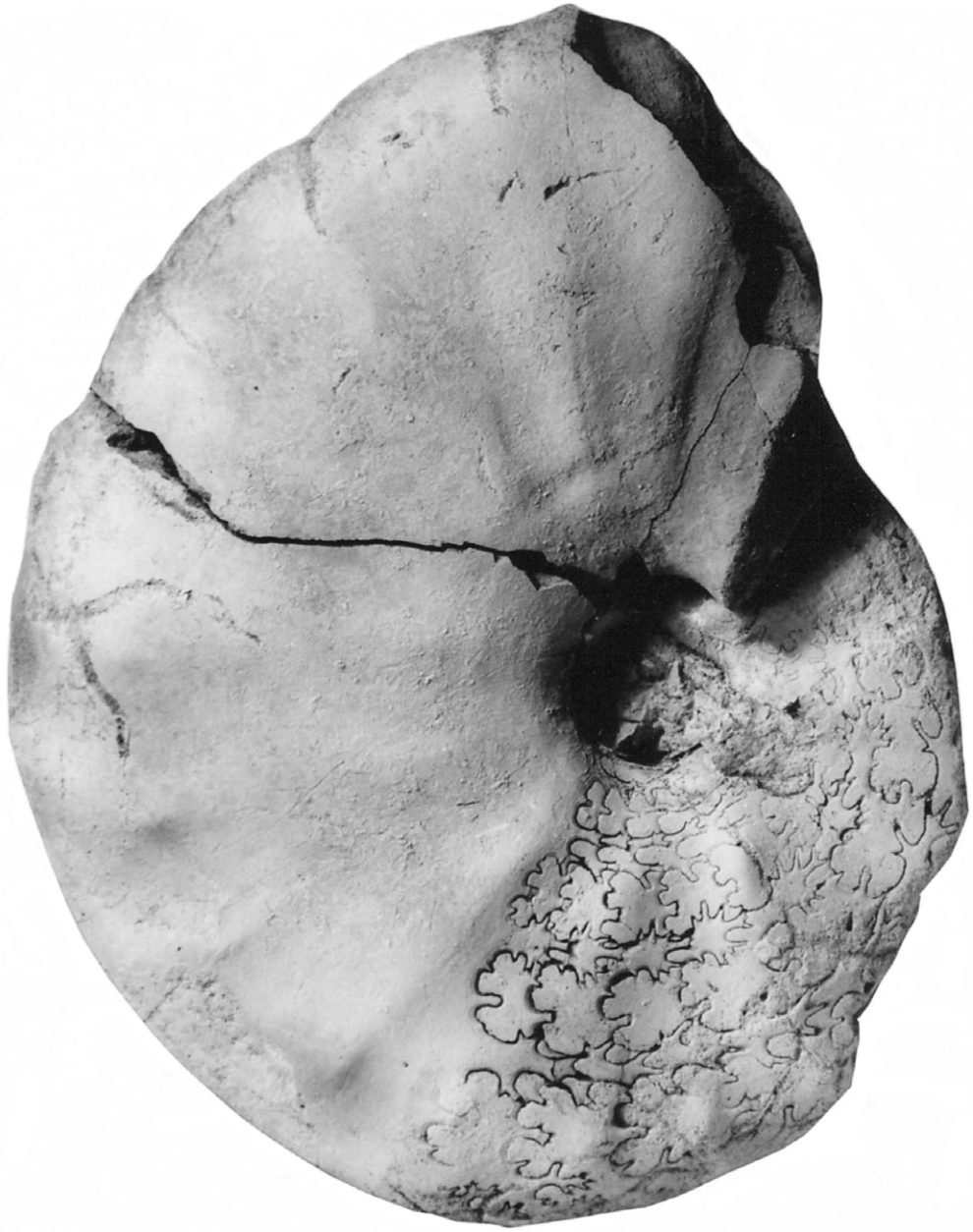


Figure 8. *Diaziceras guillantoni* Hourcq, 1949, the original of Collignon, (1969, pl. 604, fig. 2261), with the previously unfigured body chamber fragment included, from the 'base du Campanien Inférieur. Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*. Sous-Zone à *Hourcquiella hourcqui*. Gisement 195 de la Coupe de Berere II-B (Belo-sur-Tsiribihina)', Madagascar. The figure is ×1.

suture is much less deeply incised, lacking the long complx folioles on E/A adjacent to A, and barely trifid.

Diaziceras spathi Hourcq, 1949 (p. 107 (21), pl. 12 (2), fig. 2) is a further synonym. The holotype, by monotypy (Fig. 1A,B), is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. It from Berere, Madagascar. A worn, wholly septate internal mould, the dimensions are as follows:

D ic: 88.5 (100); Wb: 42.0 (0.47); Wh:47.5 (0.54) Wb:Wh0.89 U:15.5 (17.5)

Coiling is involute, the deep umbilicus comprising 17.5% of the diameter, with a flattened, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The whorl section is stoutly lanceolate in intercostal section, with the greatest breadth just outside the umbilical shoulder. The greatest breadth is at the umbilical bullae in costal section. These number eight per whorl, and are perched on the umbilical shoulder. They give rise to pairs of low, broad blunt straight prorsiradiate ribs that terminate in conical outer lateral tubercles, 19–20 per whorl. The flanks are concave in costal section between these tubercles and the obtuse venter. The specimen has a slightly more compressed whorl section than the holotype of *D. tissotiaeforme,* but is otherwise identical in our view (compare Figs 1A,B and 1C–E).

Diaziceras guillantoni Hourcq, 1949 (p. 108 (22), pl. 12 (2), fig. 1; text-fig. 15), is a distinct compressed form (Fig. 9D). The holotype by monotypy is an unregistered specimen in the collections of the École des Mines, Paris, now housed at the Université Claude Bernard, Lyon. It is from Berere, Madagascar, and was referred to the top of the Santonian by Hourcq. A worn internal mould with a 180° sector of body chamber preserved, and a near-complete

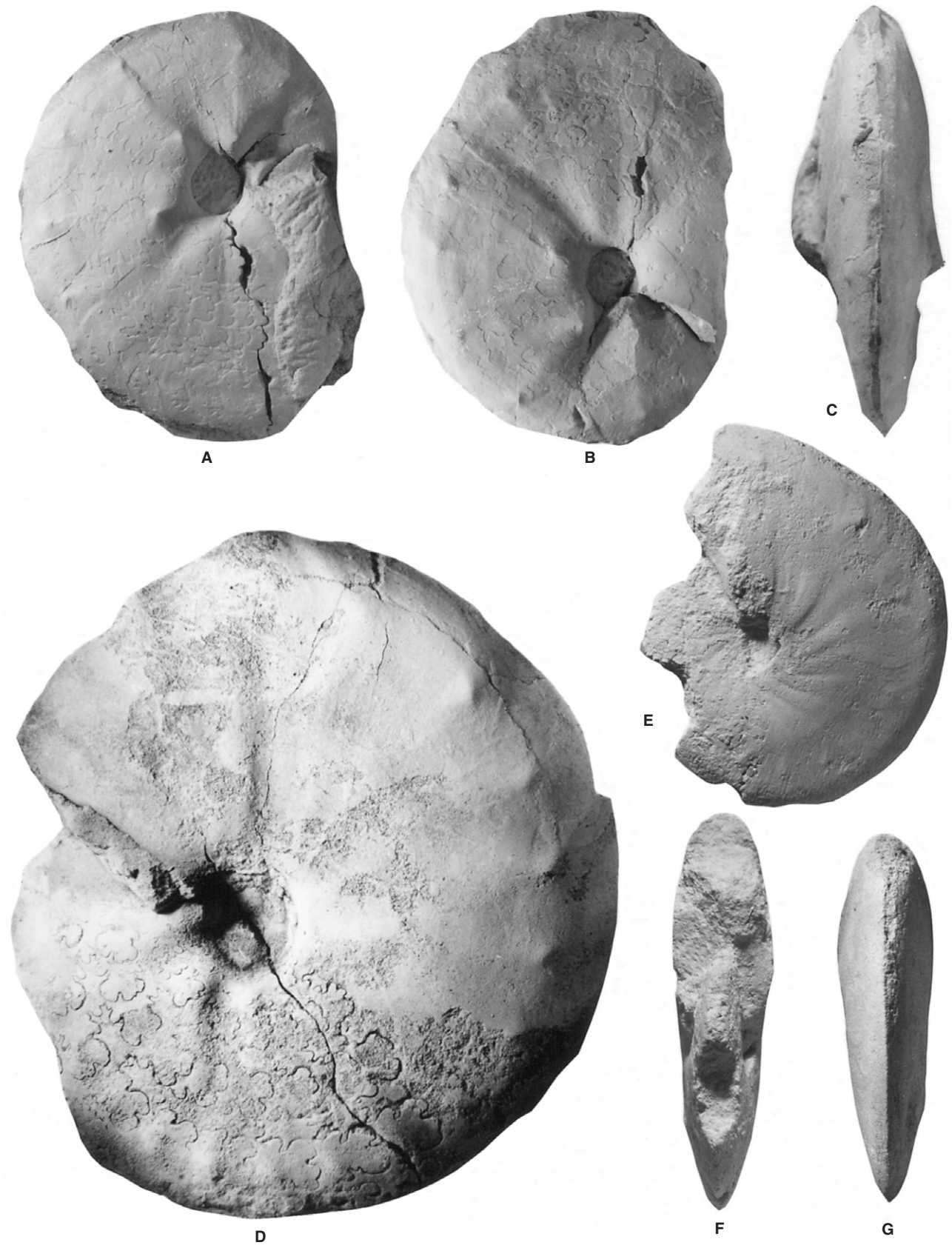


Figure 9. **A–C**, the holotype of *Skoumalia austriaca* Summesberger, 1979, SK,N.1977/14, the original of Summesberger, (1979, pl. 9, figs 37, 38) from the Upper Santonian Sandkalkbank of the Bibereckschichten of the Gosau Basin, Upper Austria. **D**, the holotype of *Diaziceras guillantoni* Hourcq, 1949, the original of Hourcq, (1949, pl. 12 (2), fig. 1), from the 'Région de Berere, sommet du Santonien.' **E–G**, *Skoumalia austriaca* Summesberger, 1979, form B of Summesberger, (1980), A363, from the Upper Santonian of Autoroute cutting S2, west of Saintes, Charente-Maritime, France in the collections of the Université Claude Bernard. All figures are ×1.

adult, the dimensions of which are as follows:

D: 132.0 (100) Wb: 40.5 (30.7) Wh: 70.0 (53.0) Wb:Wh0.58 U:18.0 (13.6)

Coiling is involute, the umbilicus small and deep, comprising 13.6% of the diameter, with an outward-inclined wall and broadly rounded umbilical shoulder. The whorl section is compressed lanceolate, with a whorl breadth to height ratio of 0.58. Four massive bullae perch on the umbilical shoulder of the adapical half of the outer whorl. They give rise to pairs of low, broad, straight prorsiradiate ribs with occasional intercalated ribs arising around mid-flank, to give a total of ten ribs per half whorl on the outer flank, where the ribs strengthen into conical to feebly bullate tubercles. The umbilical bullae efface progressively on the body chamber and the flank ribs weaken. The outer lateral tubercles become markedly bullate and prorsiradiate before weakening at the greatest preserved diameter. The suture (Fig. 4B) has a very broad, obliquely trifid E/A, with deep incisions and plump folioles; A is asymmetrically bifid; U2 is broad, bifid with only minor incisions. It is interpreted as a microconch. The macroconch is represented by the original of Collignon (1969, pl. 604, fig. 2261, see Figs 6–8 herein) from the Lower Campanian *Hourcquiella bererensis* Subzone of Collignon's 'Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi*' of Berere (Belo-sur-Tsiribihina), Madagascar. The umbilical bullae are weak and very elongate, the ribs straight and prorsiradiate, arising from the bullae in pairs and intercalating, with an oblique prorsiradiate ventrolateral bulla on the phragmocone. Ribs and tubercles weaken and efface on the body chamber, which occupies a 180° sector and may be incomplete (Fig. 8). The sutures (Fig. 6) are crowded and interfere. The saddles are broad and plump, with A narrower.

Diaziceras austriaca (Summesberger, 1979), is discussed above, and figured here as Figs 4A,C, 9A–C, E–G. It combines a compressed whorl section with massive umbilical tubercles and weak flank ribs in form A of Summesberger, the suture (Figs 4A,C) is a little less deeply incised than that of *D. tissotiaeforme*, and has E/A obliquely asymmetrically bifid, rather than trifid.

The holotype of *Diaziceras tissotiaeforme* is interpreted as a microconch. Collignon (1969, pl. 603, fig. 2258) figured (as *D. spathi*) a worn and battered individual 150 mm in diameter with a 180° sector of body chamber preserved that is interpreted as a near-complete macroconch (Fig. 5). It has seven massive bullae perched on the umbilical shoulder that give rise to pairs of ribs on the phragmocone, the ribs on the body chamber simple, to give a total of 17 ribs on the outer whorl that terminate in strong ventrolateral tubercles. It is from the base of the Campanian, the base of the *Besairiella besairiei* Subzone of Collignon's Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi* of Berere (Belo-sur-Tsiribihina), Madagascar.

Occurrence

The type occurrence at Umkwelane Hill in KwaZulu-Natal is imprecisely dated, but inferred to be Lower Campanian on the basis of the record of Collignon (1969) from Madagascar.

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ABBREVIATIONS

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

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