Cretaceous faunas from Zululand and Natal, South Africa. The ammonite Subfamily Desmoceratinae Zittel, 1895

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Three species of Desmoceratinae are described from KwaZulu-Natal/Eastern Cape Province. *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838) occurs in the Middle Albian to Middle Cenomanian of northern KwaZulu-Natal. *Desmophyllites diphylloides* (Forbes, 1846), and *Damesites sugata* (Forbes, 1846) occur in the Santonian to Lower Campanian Mzamba Formation of northern Eastern Cape Province. The latter also occurs in the Coniacian-Santonian part of the St Lucia Formation in northern KwaZulu-Natal.

Key words: Cretaceous, ammonite, Desmoceratinae, KwaZulu-Natal, Eastern Cape, South Africa.

CONTENTS

INTRODUCTION

The ammonite subfamily Desmoceratinae Zittel, 1895, is a small group of morphologically conservative ammonites with involute, little-ornamented shells, with collared constrictions, most prominent on the internal mould, in some. Eight genera are currently referred to the family (Wright, 1996) which ranges from Upper Aptian to upper Upper Maastrichtian. Three species, *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838), *Desmophyllites diphylloides* (Forbes, 1846), and *Damesites sugata* (Forbes, 1846), are described below.

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: 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 Natural History Collections Department, Iziko 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 parentheses 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

Superfamily **DESMOCERATOIDEA** Zittel, 1895
Family **DESMOCERATIDAE** Zittel, 1895
Subfamily **DESMOCERATINAE** Zittel, 1895

Genus and Subgenus ***Desmoceras*** Zittel, 1884
(=*Latidorsella* Jacob, 1907, p. 295; *Phyllodesmoceras* Spath, 1925, p. 100; *Lunatodorsella* Breistroffer, 1947, p. 76)

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Type species

Ammonites latidorsatus Michelin, 1838, p. 101, pl. 12, fig.9, by the subsequent designation of Böhm, 1895, p. 364.

Diagnosis

Involute, whorl section compressed to subquadrate to depressed reniform; straight to sinuous constrictions, most prominent on internal moulds with associated collar ribs most conspicuous on shell present or not, otherwise near-smooth but for dense growth lines and striae. Suture with bifid E/A, A/U2 and regularly declining auxiliaries; A, U2 and auxiliary lobes trifid.

Occurrence

Upper Aptian to Upper Cenomanian, southern England, southern France, northern Spain, southern Germany, Switzerland, Hungary, Serbia, Poland, Sardinia, Crimea, Mozambique, Angola, KwaZulu-Natal, South Africa, Madagascar, South India, Japan, Mexico and Venezuela.

Desmoceras* (*Desmoceras*) *latidorsatum (Michelin, 1838)

Figs 1–5

1838 *Ammonites latidorsatus* Michelin, p. 101, pl. 12, fig. 9.
1907 *Tetragonites Timotheanus* (?Mayor, sp.) Stoliczka sp.; Crick, p. 172, pl. 13, fig. 5.
1907 *Desmoceras* sp. (cf. *latidorsatum* Michelin sp); Crick, p. 211, pl. 14, fig. 1.
1907 *Desmoceras inane,* Stoliczka, sp. Crick, p. 212, pl. 14, figs 2, 3.
1923 '*Tetragonites timotheanus*'; Spath, p. 41, footnote 5.
1967 *Tetragonites* aff. *T. subtimotheanus* Wiedmann; Murphy, pp. 63, 65.
1968 *Desmoceras* (*Desmoceras*) *latidorsatum* (Mich.); Wiedmann & Dieni, p.131, pl. 12, figs 2, 6–13, text-fig. 81 (with synonymy).
1990 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838); Marcinowski & Wiedmann, p. 62, pl. 7, figs 2, 3 (with synonymy).
1996 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838): Kennedy *in* Gale *et al*., p. 551, text-figs. 11h–j; 13d,o; 17l (*pars*).
1997 *Desmoceras latidorsatum* (Michelin): Delamette, Charrolais, Decrouez & Caron, pl. 13, fig. 8; pl. 18, fig. 1.
1997 *Desmoceras latidorsatum* (Michelin, 1838); Arkadiev & Bogdanova, p. 120, pl. 45, figs 2–6.
2000 *Desmoceras latidorsatum* (Michelin, 1838); Arkadiev, Atabekian, Baraboshkin & Bogdanova, p. 107, pl. 9, figs 3–5.
2000 *Desmoceras latidorsatum* Michelin; Monod, Busnardo & Guerrero-Suastegui, p. 386, fig. 5f.
2003 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838); Kawabe & Haggart, p. 315, figs 3–5.
2006 *Desmoceras latidorsatum* (Michelin, 1838); Joly *in* Gauthier, p. 97, text-fig. 53, pl. 33, figs 1, 2.
2007 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838); Kennedy & Latil, p. 458, pl. 2, fig. 1; pl. 6, figs 2, 3; text-fig. 4.
2007 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838); Szives, p. 98, pl. 3, fig. 25; pl. 14, fig. 10; pl. 19, figs 3, 4; pl. 26, figs 1, 2; pl. 28, fig. 6.
2009 *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838); Kennedy & Bilotte, p. 46, pl. 2, figs 6, 7, 19–28; pl. 8, figs 21–23; text-fig. 4.
2011 *Desmoceras latidorsatum* (Michelin, 1838); Kennedy *in* Gale *et al.,* p. 75.

Type

The holotype by monotypy, and now lost, is the original of Michelin, 1838, p. 101, pl. 12, fig. 9, from the Albian Gault Clay of Aube, France. Joly *in* Gauthier (2006, p. 97, pl. 3, fig. 1) has designated a specimen in the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris, no. B46095, *ex* d'Orbigny Collection 5773-B1, as neotype. It is from the condensed Albian of Escragnolles, Var, France, and is reillustrated here as Fig. 1.

Material

OUM KX4808, from the Middle Albian Mzinene Formation at locality 53 of Kennedy & Klinger (1975, p. 288), derelict dam site on Indabana 13162, 2.2 km south of the farm Izwehelia, north of Hluhluwe, 27°52′24″S, 32°19′02″E. SAM PCZ022449 (ex A686), PCZ022449a (ex A599), PCZ022450 (ex A785), PCZ022451 (ex A1057),PCZ022452 (ex A1079), PCZ022453a–d (ex D991a–d), D922, PCZ022454 (ex D994), PCZ022455a–b (ex D997a, b), PCZ022456a–b (ex D1388a, b), PCZ022457 (ex D2491), PCZ022458 (exSM (27)), OUM KX4636–4644, from the Lower to Middle Cenomanian Mzinene Formation at locality 62 of Kennedy & Klinger (1975, p. 289), hill slopes at and extending west from the western end of the Skoenberg, 27°52′17″S, 32°20′26″E, northern KwaZulu-Natal. OUM KX11481 and 11482, from bed 2 of the Upper Albian Mzinene Formation at locality 61 of Kennedy & Klinger (1975, p. 289, text-fig. 6), hill slopes and gullies west of the western 'horn' of the Skoenberg, 27°52′19″S, 32°20′19″E, northern KwaZulu-Natal. OUM KX5026, from the Upper Albian Mzinene Formation at locality 65 of Kennedy & Klinger (1975, p. 289), dam site excavations 1300 m southwest of the farm Izwehelia, 27°51′38″S, 32°19′30″E, northern KwaZulu-Natal.

Crick (1907) recorded a series of specimens from the 'deposit at the north end of False Bay' that come from the Skoenberg in the environs of locality 62 that we refer to *Desmoceras* (*D.*) *latidorstum*:

BMNH C18223, the original of *Desmoceras* sp. (cf. *latidorsatum* Michelin sp.) of Crick, 1907, p. 211, pl. 14, fig. 1.

The following specimens referred to *Desmoceras inane* Stoliczka sp. by Crick (p. 213); his specimen (a) is BMNH C18234; (b) is BMNH C18235; (c) is BMNH C18236 (1907, pl. 14, fig. 2); (d) is BMNH C18237 (1907, pl. 14, fig. 3).

BMNH C18143, the original of *Tetragonites Timotheanus* Stoliczka sp. (?Mayor sp.) of Crick, p. 172, pl. 13, fig. 5.

Description and discussion

Desmoceras (*D.*) *latidorsatum* is chiefly known from small nuclei. A number of species/subspecies have been named, as reviewed in detail by Wiedmann & Dieni (1968, p. 132). The range of variation of these nuclei varies between assemblages, and the following forms are recognized on the basis of whorl proportions and the presence/absence of constrictions:

forma complanata Jacob, 1907 (p. 38, pl. 14 (4), fig. 10; pl. 15 (5), fig. 2);

forma media Jacob, 1907 (p. 37, pl. 16 (4), fig. 14);

forma inflata Breistroffer, 1933, p. 193 (as *nomen novum* for var α Kossmat, 1897 as emended by Jacob, 1907, p. 35, pl. 14 (4), fig. 13;

forma perinflatum Cooper & Kennedy, 1979 (p. 237, figs 37–38, 39d–f).

Howarth (1985, p. 82) recognized as *Desmoceras* (*Desmoceras*) *latidorsatum lemoinei* Collignon, 1928, a compressed and constricted subspecies from the Lower Cenomanian of Angola. To what extent this variation in juveniles is reflected in adults is unclear, as so few have been described and illustrated. Stoliczka (1865, p. 148) mentioned individuals from the Upper Albian or Cenomanian Utatur Group of South India that are up to 180 mm in diameter, and figured an example 150 mm in diameter, with most of the body chamber preserved, a whorl breadth to height ratio of 1.05, and 10 increasingly conspicuous sinuous constrictions with associated adapical collar rib. A large (131-mm diameter) Indian specimen is illustrated here as Fig 5. Renz (1972, p. 717, pl. 10, fig. 1) figured an individual 100 mm in diameter with comparable constrictions on the internal mould that are barely expressed on the surface of the shell, and a larger, 143 mm internal mould with strong sinuous constrictions, both specimens with a whorl breadth to height ratio of 0.96. They are from the Upper Albian of Venezuela. Kennedy & Latil (2007, fig. 4) figured a crushed internal mould 201 mm in diameter with a 180° sector of body chamber preserved, with five sinuous constrictions and associated collar ribs on the body chamber, from the Upper Albian of southwest France. These specimens are interpreted as the macroconch of the species. We have been unable to recognize the microconch with confidence: are the smaller constricted juveniles microconchs, and unconstricted individuals of the same size juvenile macroconchs?

A Middle Albian representative of the species (OUM KX4808; Fig. 4D–E) has the following dimensions:

	D	Wb	Wh	Wb:Wh	U
OUMKX4808	52.6 (100)	21.8 (41.4)	25.7 (48.9)	0.85	10.2 (19.4)

Coiling is involute, with over 70% of the previous whorl covered, the umbilicus small, comprising 19.4% of the diameter, shallow, the umbilical wall flattened and outward-inclined, the umbilical shoulder narrowly rounded. The whorl section is compressed, the whorl breadth to height ratio 0.85, the flanks very feebly convex, subparallel, the ventrolateral shoulders broadly rounded, the venter flattened and very feebly convex. The specimen retains corroded shell, the surface poorly preserved, with traces of falcoid growth lines and riblets that are convex on the inner flank, concave on the outer flank, and cross the venter in a shallow convexity. At one point a riblet strengthens over the venter and precedes the feeblest of constrictions. This individual corresponds most closely to *forma complanata*.

A series of small individuals from the upper Upper Albian have the following dimensions:

	D	Wb	Wh	Wb:Wh	U
PCZ022459	31.4 (100)	20.5 (65.3)	15.0 (47.8)	1.37	5.3 (16.9)
PCZ022460B	36.3 (100)	24.2 (66.7)	15.0 (41.3)	1.61	– (–)
PCZ022461C	47.5 (100)	32.5 (68.4)	22.3 (46.9)	1.46	10.6 (22.3)

All are globose individuals with a very depressed reniform whorl section, and whorl breadth to height ratio of up to 1.61. SAM-PCZ022459–61 retain recrystallized shell, with ornament perfectly preserved. It consists of growth lines and striae only. These are prorsiradiate and markedly flexuous, convex on the inner flank, concave on the middle and outer flank, projected forwards on the ventrolateral shoulder, and cross the venter in a linguoid projection. The striae and growth lines strengthen periodically where they precede very feeble constrictions on the shell surface, most obvious on the venter. They lack the strengthened ventral rib developed by some Cenomanian examples of the species described, and correspond to *forma perinflatum*. OUM KX5626 (Fig. 4F–H), the largest Upper Albian example seen is a wholly septate fragment with a maximum preserved whorl height of 62.6 mm. The penultimate whorl has a whorl breadth to height ratio of 1.05. At the greatest preserved diameter, the ratio is 0.86. The 90° whorl sector bears three strong constrictions.

The more numerous Cenomanian representatives of the species range from 23 to 150 mm in diameter:

	D	Wb	Wh	Wb:Wh	U
D997a	35.5 (100)	21.0 (59.1)	17.0 (47.9)	1.24	4.8 (13.5)
PCZ022463	23.0 (100)	11.6 (50.4)	10.6(46. 1)	1.1	3.2 (13.9)
PCZ022464	29.3 (100)	15.1 (51.5)	14.3 (48.8)	1.1	3.6 (12.3)
PCZ022465	28.2 (100)	15.0 (53.2)	14.2 (50.4)	1.1	3.5 (12.4)
PCZ022466	37.7 (100)	20.8 (55.1)	19.2 (50.9)	1.1	4.8 (12.7)
PCZ022467	39.2 (100)	22.0 (56.1)	20.0 (51.0)	1.1	5.5 (14.0)
PCZ022468	44.8 (100)	23.7 (52.9)	18.0 (40.1)	1.32	12.3 (27.5)
PCZ022462	68.0 (100)	25.5 (37.5)	31.0 (45.6)	0.82	13.0 (19.1)
SAM 2383	150.0 (100)	67.5 (45.0)	75.5 (50.3)	0.89	24.0 (16.0)

These Cenomanian representatives (Figs 3A–J, 4A–C) are all very involute at small diameters, becoming progressively more evolute as size increases. The umbilicus is of moderate depth, with a flattened, undercut wall and narrowly rounded umbilical shoulder. The whorl section is invariably

depressed, reniform, with a whorl breadth to height ratio of 1.1 to 1.32, the greatest breadth below mid-flank in the smaller specimens. Most specimens are weathered, and show neither ornament nor constrictions. SAM PCZ022454, (ex D994) is a particularly evolute juvenile, and although rather worn, has broad, distant, linguoid ventral ribs. SAM-PCZ022449a (ex A599) is a well-preserved internal mould 68 mm in diameter. There are 6–7 strong flexuous constrictions per half whorl. SAM-PCZ022458 (exD2491) is the largest specimen with the shell well preserved, and bears 6–7 distinct collar-ribs per whorl. These arise at the umbilical seam, and are prorsiradiate and flexuous, straight to feebly convex on the inner flank, concave on the mid- to outer flank, and strongly projected across the ventrolateral shoulder. They strengthen markedly into a convex linguoid peak over the venter. These main ribs are succeeded by a shallow constriction, most obvious on the ventrolateral shoulders and venter; a marked ventral lip precedes the constrictions. There are traces of low, feeble ribs on the shell surface between constrictions. SAM-PCZ022462 (ex 2383), a very large specimen is a phragmocone, still septate at 150 mm diameter. The surface is rather ill-preserved, but shows a pronounced ventral linguoid lip preceding the constrictions, plus rather feebly developed striae between. It closely resembles the large Indian specimen figured by Stoliczka (1865, pl. 74, fig. 3).

The *Desmoceras* sp. (cf. *latidorsatum,* Michelin sp.) of Crick (1907, p. 211, pl. 14, fig. 1, BMNH C18223) is illustrated here as Fig. 2M–O. It is a phragmocone 42.7 mm in diameter, retaining heavily corroded recrystallized shell, with a whorl breadth to height ratio of 1.05, the umbilicus comprising 20% of the diameter. The small specimens referred to *Desmoceras inane* by Crick (1907, p. 212, pl. 14, figs 2, 3, BMNH C18235–18237; Fig. 2A–I herein) range up to 20.7 mm in diameter, with umbilical diameters of 15–20% and whorl breadth to height ratios of 1.0. They lack ornament, and are regarded as juvenile *latidorsatum*. Crick's Manuan Creek specimen of *Desmoceras* sp. is BMNH C18274 (1907, p. 241, pl. 15, fig. 3), illustrated here as Fig. 2J–L. It is 36.8 mm in diameter, and retains heavily corroded recrystallized shell.

The whorl breadth to height ratio is 1.03; the umbilicus comprises 13% of the diameter.

BMNH C18143, the original of *Tetragonites Timotheanus* (?Mayor sp.) Stoliczka sp. of Crick (1907, p. 172, pl. 13, fig. 5), is illustrated here as Fig. 2P–R. It is not a *Tetragonites*, as recognized by Spath (1923, p. 41), but a very corroded phragmocone of *D.* (*D.*) *latidorsatum*.

Occurrence

Middle Albian to Upper Cenomanian, southern England, southern France, northern Spain, southern Germany, Switzerland, Hungary, Serbia, Poland, Sardinia, Crimea, Mozambique, Angola, KwaZulu-Natal, South Africa, Madagascar, South India, Japan, Mexico and Venezuela.

Genus ***Desmophyllites*** Spath, 1929

(=*Schlüteria* de Grossouvre, 1894, p. 126, *non* Fritsch in Fritsch & Kafka, 1887, p. 33; *Schlütericeras* Collignon, 1938, p. 92, *non* Hyatt, 1903, p. 110)

Type species

Desmoceras larteti Seunes, 1891, p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3, by the subsequent designation of Spath, 1921, p. 46, as type species of *Schlüteria*, of which *Desmophyllites* is the replacement name.

Desmopyhyllites diphylloides (Forbes, 1846)

Fig. 6A–S

1846 *Ammonites diphylloides* Forbes, p. 105, pl. 8, fig 8.
1850 *Ammonites diphylloides* Forbes; d'Orbigny, p. 213.
1865 *Ammonites diphylloides* Forbes; Stoliczka, p. 119 (pars), pl. 59, figs 8, 9 only.
1879 *Ammonites selwynianum* Whiteaves, p. 104, pl. 13, fig. 1.
1894 *Desmoceras pyrenaïcum* de Grossouvre, p. 168, (*pars*), pl. 37, fig. 9 only.
1898 *Desmoceras diphylloides* (Forbes); Kossmat, p. 108 (173), pl. 19 (25), figs 8, 9.
1898 *Desmoceras phyllimorphum* Kossmat, p. 110 (175), pl. 19 (25), fig. 10.
1901 *Desmoceras salsense* de Grossouvre, p. 463.
1907 *Puzosia* (*Latidorsella*) *diphylloides* Forbes; Pervinquière, p. 140, pl. 6, figs 1–7.
1921 *Schlüteria woodsi* Spath, p. 45, pl. 7, fig. 1.
1921 *Desmoceras simplex* van Hoepen, p. 19, pl. 3, figs 11–16, text-fig. 10.
1921 *Desmoceras crassum* Van Hoepen, p. 20, pl. 4, figs 3, 4; text-fig. 11.
1922 *Schlüteria simplex* van Hoepen; Spath, p. 129.
1922 *Schlüteria simplex* van Hoepen; Spath, p. 129.
1922 *Schlüteria crassa* van Hoepen; Spath, p. 129.
1931 *Desmoceras diphylloides* Forbes; Basse, p. 23, pl. 2, figs 3, 4.
1931 *Desmoceras* (*Latidorsella*) *diphylloides* var. *Besairiei* Collignon, p. 15, pl. 2, figs 8, 9; pl. 2, figs 5–8.
1938 *Schlüteria larteti* (Seunes); Collignon, p. 42, pl. 7, fig. 3; text-figs k, l.
1952 *Schlüteria selwyniana* (Whiteaves); Usher, p. 63, pl. 5, figs 3, 4; pl. 6, figs 1–3.
1953 *Desmophyllites diphylloides* (Forbes); Spath, p. 21, pl. 2, figs 5, 6.
1955 *Desmophyllites diphylloides* (Forbes); Matsumoto & Obata, p. 121, pl. 24, figs 1–5; pl. 30, fig. 1.
1958 *Desmoceras selwynianus* Anderson, p. 215, pl. 40, fig. 2.
1958 *Desmophyllites siskiyouensis* Anderson, p. 215, pl. 35, fig. 3; pl. 41, figs 1–3.
1959 *Desmophyllites diphylloides* (Forbes); Matsumoto, p. 9, pl. 3, fig. 3; text-fig. 2.
1961 *Desmophyllites diphylloides* Forbes; Collignon, p. 61, pl. 25, figs 1, 2; text-fig. 2.
1961 *Desmophyllites diphylloides* Forbes var. *besairiei* Collignon, p. 63, pl. 25, figs 4–6; text-fig. 3.
1961 *Desmophyllites diphylloides* Forbes var. *inermis* Collignon, p. 63, pl. 24, figs 4, 5; pl. 25, fig. 3.
1961 *Desmophyllites diphylloides* Forbes var. *lata* Collignon, p. 64, pl. 25, figs 7, 8; text-fig. 4.
1961 *Desmophyllites phyllimorphus* (Kossmat); Collignon, p. 65, pl. 26, fig. 1; text-fig. 5.
1961 *Desmophyllites larteti* (Seunes); Collignon, p. 66, pl. 26, fig. 2; text-fig. 6.
1963 *Desmophyllites phyllimorphus* (Kossmat); Jones, p. 34, pl. 10, figs 4–6.

1965 *Desmophyllites diphylloides* (Forbes); Howarth, p. 388, pl. 11, fig. 3.
1966 *Desmophyllites diphylloides* (Forbes); Collignon, p. 84, pl. 489, fig. 1973.
1966 *Desmophyllites diphylloides* Forbes var. *besairiei* Collignon; Collignon, p. 9, pl. 458, fig. 1870.
1966 *Desmophyllites diphylloides* Forbes var. *inermis* Collignon; Collignon, p. 9, pl. 458, fig. 1871.
1966 *Desmophyllites diphylloides* Forbes var. *lata* Collignon; Collignon, p. 27, pl. 466, fig. 1900.
1971 *Desmophyllites phyllimorphus* Kossmat; Collignon, p. 36, pl. 655, fig. 2414.
1971 *Desmophyllites diphylloides* Forbes; Collignon, p. 37, pl. 655, fig. 2415.
1971 *Desmophyllites larteti* Seunes; Collignon, p. 37, pl. 655, fig. 2416.
1977 *Desmophyllites diphylloides*; Kennedy, text-figs 31, 33.
1980 *Desmophyllites diphylloides* (Forbes); Blasco de Nullo, Blasco & Proserpio, p. 483, pl. 2, figs 9–15.
1983 *Desmophyllites diphylloides* Forbes; Collignon, p. 191.
1985 *Desmophyllites diphylloides* (Forbes, 1846); Henderson & McNamara, p. 54, pl. 4, figs 1–4.
1989 *Desmophyllites*; Kennedy, text-fig. 17d.
1992 *Desmophyllites diphylloides* (Forbes, 1846); Kennedy & Henderson, p. 405, pl. 6, figs 1–9; pl. 16, figs 1–3, 7–8; pl. 17, 4–7; text-fig. 3f (with full synonymy).
1993a *Desmophyllites diphylloides* (Forbes, 1846); Kennedy & Cobban, p. 120, pl. 1, figs 1–8; text-fig. 5c.
1993b *Desmophyllites diphylloides* (Forbes, 1846); Kennedy & Cobban, p. 411, text-fig. 5, 21.
1995 *Desmophyllites diphylloides* (Forbes, 1846); Kennedy in Kennedy, Bilotte & Melchior, p. 397, pl. 4, figs 1, 2, 6, 7, 14; text-fig. 16.
1995 *Desmophylllites diphylloides* (Forbes, 1846); Kennedy, p. 241, pl. 1, figs 1, 2.
1997 *Desmophyllites diphylloides* (Forbes, 1846); Arkadiev & Bogdanova, p. 120, pl. 48, fig. 2.
1997 *Desmophyllites diphylloides* (Forbes); Alabushev & Wiedmann, p. 22, pl. 6, figs 3–5.
2000 *Desmophyllites diphylloides* (Forbes, 1846); Arkadiev, Atabekian, Baraboshkin & Bogdanova, p. 108, pl. 12, fig. 1.
2004 *Desmophyllites diphylloides* (Forbes, 1846); Ifrim, Stinnesbeck & Lopez-Oliva, p. 1594, text-figs 8c–d, 9e, f.

Types

The lectotype, by the subsequent designation of Matsumoto & Obata (1955, p. 122) is no. C22682 in the collections of the Natural History Museum, London, the original of Forbes, 1846, pl. 8, fig. 8; paralectotypes are BMNH C22683–5, all from the Upper Maastrichtian Valudavur Formation of Pondicherry, South India (Fig. 6A–J)).

Material

The holotype of *Schlüteria woodsi* Spath, 1921, p. 45, pl. 7, fig. 1, an unregistered specimen in the collections of the Durban Museum, together with the 'immature specimen (diameter = 17 mm)' mentioned by Spath.

The holotype of *Desmoceras simplex* van Hoepen, 1921, p. 19, pl. 3, figs 11, 12, and two paratypes, the original of van Hoepen's pl. 3, figs 13–16, text-fig. 10, and a further specimen in the collections of the Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria.

The holotype and paratype of *Desmoceras crassum* Van Hoepen, 1921, p. 20, pl. 4, figs 3, 5; text-fig. 11, in the collections of the Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria.

SAM-PCP022484a,b (ex D1703a,b)SAM-PCP022485a–c (ex D1712a–c)PCP022486 (ex D1703c) PCP 6724PCP022487 (ex 4805)PCP 022488 (ex 4365)PCP022489 (ex7028) PCP022490 (ex7069)

All specimens are from the Middle Santonian to lowest Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975, p. 281), cliff and foreshore exposures 1 km north of the mouth of the Mzamba River in northern Eastern Cape Province, coordinates 31°05′50″S, 30°10′30″E. The section is described in detail by Klinger & Kennedy (1980).

Dimensions

	D	Wb	Wh	Wb:Wh	U
PCP022488 (ex 7028a)	22.0 (100)	10.3 (46.8)	11.2 (50.9)	0.91	1.8 (8.2)
PCP022490 (ex 7069)	23.0 (100)	10.6 (46.1)	11.6 (50.4)	0.91	1.8 (7.8)
PCP6271	33.5 (100)	– (–)	17.0 (50.7)	–	2.7 (8.1)
PCP6270	35.0 (100)	14.0 (40.0)	17.5 (50.0)	0.8	2.5 (7.1)
PCP022491 (ex D1702)	36.0 (100)	14.3 (39.7)	19.0 (52.8)	0.75	2.9 (8.1)
PCP 022492 (ex Z116 (4))	61.5 (100)	26.5 (43.1)	32.5 (52.8)	0.82	5.0 (8.1)
PCP022493 (ex D1693)	90.5 (100)	– (–)	49.5 (54.7)	–	13 (14.4)

Description

Specimens vary from 8.5 to 90 mm in diameter. Coiling is involute, with a tiny, deep umbilicus. The whorl section is compressed, with whorl breadth to height ratios of 0.75–0.91. The umbilical wall is rounded and undercut, the umbilical shoulder narrowly rounded. The greatest whorl breadth is below mid-flank. The inner and middle flanks are flattened and subparallel, the ventrolateral shoulders and venter broadly rounded. The shell surface is ornamented by growth lines and striae, straight and prorsiradiate on the inner and middle flanks, flexed forwards and concave on the outer flank and ventrolateral shoulder, and crossing the venter in a narrow, convex, linguoid projection. The ventrolateral shoulders and venter bear up to four periodic low, rounded collar ribs per half whorl, succeeded by shallow constrictions on the outer flank, ventrolateral shoulders and venter. The constrictions are much better developed on the internal mould, where they extend to the umbilical shoulder. They are narrow, straight, and prorsiradiate on the inner flank, flex forwards and are concave on the outer flank and ventrolateral shoulder, and project forwards into a narrow convex ventral peak.

The suture (Van Hoepen, 1921, text-figs 10, 11) is deeply and intricately incised, with narrow-stemmed bifid E/A and A/U2, and A deeply and intricately incised and trifid.

Discussion

The type material of *Desmophyllites diphylloides* was revised by Kennedy & Henderson (1992, p. 405, pl. 6, figs 1–9; pl. 16, figs 1–3, 7–8; pl. 17, 4–7; text-fig. 3f), and is based on juveniles up to 40 mm in diameter ; the lectotype is illustrated here as Fig. 6A–D, a paralectotype as Fig. 6E–J. The Mzamba material of the same diameter differs in no significant respects. Henderson & McNamara (1985, p. 54, pl. 4, fig 1–4) described an assemblage of over 30 specimens, septate to a diameter of 80 mm. These specimens show constrictions weakening markedly at the largest diameters, as in the present material, including the holotype of *Schlueteria woodsi* Spath, 1921 (p. 45, pl. 7, fig. 1), illustrated here as Fig. 6R,S. We follow Matsumoto (1959, p. 9) and Henderson & McNamara (1985, p. 54) in regarding *selwynianum* Whiteaves (1879), *pyrenaicum* de Grossouvre, 1894 (*pars*; see also Kennedy in Kennedy, Bilotte & Melchior, 1995, p. 397, pl. 4, figs 1, 2, 6, 7, 14; text-fig. 16), *phyllimorphum* Kossmat, 1898, and the varieties of *diphylloides* recognized by Collignon (1931, 1938, 1961, 1966,1971) as a synonyms. That *woodsi* of Spath is no more than an adult *diphylloides* is noted above. *Desmoceras crassum* of van Hoepen (1921, p. 20, pl. 4, figs 3, 4; text-fig. 11) is based on juveniles 30.2–36 mm in diameter with whorl breadth to height ratios of 0.78–0.8 that differ in no significant respects from the type series. The type material of *Desmoceras simplex* van Hoepen, 1921 (p. 19, pl. 3, figs 11–16; text-fig. 10) ranges from 25.7–44 mm in diameter, internal moulds showing well-marked sinuous constrictions, as in Californian and French specimens referred to *diphylloides* (Matsumoto, 1959, pl. 3, fig. 3; Kennedy in Kennedy *et al.,* 1995, pl. 4, fig. 6).

Desmophyllites larteti (Seunes, 1891) (p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3 (see Hancock & Kennedy, 1993, p. 154, pl. 2, figs 1–3, 10, 11, 14; pl. 3, figs 1, 4, 5) is much more compressed, with an arched venter and 4–5 markedly biconcave constrictions per half whorl.

Occurrence

Lower Santonian to Upper Maastrichtian, South India, Madagascar, Eastern Cape Province, South Africa, Western Australia, Japan, Alaska, British Columbia, California, Arkansas, Mexico, Argentina, Angola, Tunisia, United Arab Emirates, Crimea and southeastern France.

Genus ***Damesites*** Matsumoto, 1942

(ICZN name no. 1349)

(= *Kotoceras* Yabe, 1927, p. 36 (ICZN rejected name no. 1264, *non* Kobayashi, 1934, p. 391; *Neokotôceras* Anderson, 1958, p. 219)

Type species

Desmoceras damesi Jimbo, 1894, p. 172, pl. 1, figs 2, 3; ICZN Opinion 555, 1959.

Damesites sugata (Forbes, 1846)

Figs 7A–J

1846 *Ammonites Sugata* Forbes, p. 113, pl. 10, figs 2a–c.

1864 *Ammonites Sugata* Forbes; Stoliczka, p. 60, pl. 32, figs 4–6; pl. 33, figs 1, 2.

Non 1890 *Desmoceras sugata* Forbes; Yokoyama, p. 185, pl. 20, fig. 11 (=*Damesites damesi intermedius* Matsumoto, 1942).

1898 *Desmoceras Sugata* Forbes; Kossmat, p. 111 (176), pl. 18 (24), fig. 11; pl. 19 (25), fig.1).

1921 *Hauericeras*? *sugata* (Forbes); Spath, p. 46, pl. 6, fig. 3.

1921 *Desmoceras compactum* van Hoepen, p. 21, pl. 4, figs 5–7; text-fig. 12.

1922 *Hauericeras*? *sugata* (Forbes); Spath, p. 131.

?1931 *Desmoceras sugata* (Forbes); Basse, p. 21, pl. 2, figs 19, 20.

1942 *Damesites sugata* (Forbes); Matsumoto, p. 27, text-fig. 1f.

1955 *Damesites sugata* (Forbes); Matsumoto & Obata, p. 128, pl. 26, figs 4, 5; pl. 27, figs 3, 4; text-fig. 3.

1961 *Damesites sugatus* Forbes; Collignon, p. 67, pl. 27, figs 1–2; text–fig. 7.

1965 *Damesites sugatus* Forbes; Collignon, p. 20, pl. 421, fig. 1750–1751.

?1980 *Damesites compactus* (van Hoepen); Summesberger, p. 278, pl. 1, figs 3–4; text-fig. 4.

1989 *Damesites sugata* (Forbes, 1846); Haggart, p. 195, pl. 8.4, figs 14–23 (with additional synonymy).

1991 *Damesites sugata* (Forbes, 1846); Kennedy & Henderson, p. 471, text-figs 1, 2.

1993 *Damesites sugata* (Forbes, 1846); Alabushev & Wiedmann, p. 554, text-figs 1, 2.

?1996 *Damesites damesi* (Jimbo, 1894); Cooper & Greyling, p. 19, figs 7i–l.

2003 *Damesites sugata* (Forbes, 1846); Cooper, p. 155, text-figs 6e–f, 7d.

1997 *Damesites sugata* (Forbes); Alabushev & Wiedmann, p. 22, pl. 6, figs 6, 7; pl. 11, fig. 2; text-figs 4a, 7.

Types

The lectotype is BMNH C22647, the original of Forbes, 1846, pl. 10, figs 2a–c, illustrated here as Fig. 7D, E. There are three paralectotypes, BMNH C22675 (Fig. 7F, of which BMNH C3561a is a further fragment) and BMNH 24196a, b, while BMNH C3561b may be a further paralectotype. The type material is from Vridachellum (Verdachellum), South India.

Material

The original of *Hauericeras sugata* (Forbes) of Spath, 1921, p. 46, pl. 6, fig. 3, in the collections of the Durban Museum. The holotype of *Desmoceras compactum* van Hoepen, 1921, p. 21, pl. 4, figs 5–7; text-fig. 12, in the collections of the Ditsong Museum of Natural History (formerly Transvaal Museum), Pretoria. Both are from the Middle Santonian to lowest Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975, p. 281), cliff and foreshore exposures 1 km north of the mouth of the Mzamba River in northern Eastern Cape Province, coordinates 31°05′50″S, 30°10′30″E. The section is described in detail by Klinger & Kennedy (1980). SAM-PCZ022494 (formerly Z1061), from the Coniacian or Santonian St Lucia Formation on the north bank of the Munywana Creek on the farm Insleep, in northern KwaZulu-Natal.

Dimensions

	D	Wb	Wh	Wb:Wh	U
Type *compactum*	34.6 (100)	16.3 (47.1)	20.1 (58.0)	0.81	2.8 (8.1)
SAM PCZ022494 (ex Z1061)	45.3 (100)	20.0 (44.2)	23.2 (51.2)	0.86	3.9 (8.6)

Description

The Durban Museum specimen (Spath, 1921, p. 46, pl. 6, fig. 3; Fig. 7A–C herein) is 32.5 mm in diameter, and retains recrystallized shell. Coiling is very involute, the umbilicus comprising less than 10% of the diameter, the umbilical wall flattened and outward inclined, the umbilical shoulder narrowly rounded. The whorl section is compressed, with a whorl breadth to height ratio of 0.8 approximately, the flanks very feebly convex, subparallel, the greatest breadth just below mid-flank. The ventrolateral shoulders are broadly rounded, the venter feebly convex with a strong siphonal keel. There are traces of delicate growth lines, most obvious on the outer flank and ventrolateral shoulder. They are prorsiradiate, near-straight on the flanks, very feebly concave on the inner flank, very feebly convex at mid-flank and concave on the outer flank, projecting forwards on the ventrolateral shoulders and venter, where they join the siphonal keel.

SAM-PCZ022494 (Fig. 7G–J herein) is a well-preserved individual 45.3 mm in diameter, retaining extensive traces of partially exfoliated shell. Coiling is very involute, the umbilicus comprising 8.6% of the diameter, the umbilical wall flattened and outward-inclined, with a narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.86. The flanks are flattened and subparallel, the ventrolateral shoulders broadly rounded, the venter feebly convex, with a strong siphonal keel. The exfoliated shell bears traces of growth lines only. The internal mould bears narrow prorsiradiate constrictions, four of which are detectable in an approximately 120° sector of whorl (Fig. 7H). They are near-straight on the flanks, very feebly concave on the umbilical shoulder and inner flank, very feebly convex at mid-flank, and more markedly concave on the outer flank and ventrolateral shoulder, projecting strongly forwards on the venter to join with the siphonal keel.

Discussion

On the basis of the type material and other specimens from South India revised by Kennedy & Henderson (1991, p. 471, figs 1, 2), together with abundant material from the Middle Coniacian of Pilmisi, Ariyalur, Tamil Nadu (OUMNH Collections), *Damesites sugata* is a compressed species with a whorl breadth to height ratio of 0.63 to 0.82, with near-straight prorsiradiate constrictions that are very feebly concave on the inner flank, very feebly concave at mid-flank, more markedly concave on the outer flank and ventrolateral shoulder (not convex as stated by Kennedy & Henderson, an error) and projected forwards on the venter.

The holotype of *Desmoceras compactum* van Hoepen, 1921 (p. 21, pl. 4, figs 5–7; text-fig. 12) is 18.2 mm in diameter, with a whorl breadth to height ratio of 0.83 and an umbilical diameter of 10% according to van Hoepen. He separated his species from *sugata* on the basis of his species having a lower keel, the greatest whorl breadth at the external edge of the flanks and constrictions that are slightly convex towards the middle of the flanks. A slight convexity in the constriction at mid-flank is shown by the paralectotype of *sugata*, BMNH C22675 (Fig. 7F), and we regard *compactum* as a probable synonym of *sugata*. Matsumoto & Obata (1955, p. 132) thought the holotype of *compactum* too small for satisfactory comparison with other species of the genus. Collignon (1961, p. 70, pl. 26, fig. 4; text-fig. 8) referred a series of much larger specimens up to 68 mm in diameter to *compactum*. They have whorl breadth to height ratios of 0.80–0.88, and are thus stouter than most *sugata* at the same diameter. Haggart (1989, p. 196) suggested that *Damesites damesi* (Jimbo, 1894) *intermedius* Matsumoto, 1954 (p. 270, pl. 22 (6), fig. 4) is a further synonym of *sugata*. The constrictions of the holotype are close to those of one of the present specimens (Fig. 7H).

Cooper & Greyling (1996, p. 19, Fig. 7i–l) referred two specimens from the Lower Campanian part of the Mzamba Formation 3 km north of the classic cliff outcrop of the Formation to *Damesites damesi* (Yabe, 1904). Their smaller specimen, 28.8 mm in diameter has a whorl breadth to height ratio of 0.63, their larger specimen, approximately 92 mm in diameter, has a whorl breadth to height ratio of 0.68. The specimens are described as having constrictions that seem to be biconcave and projected strongly forwards on across the venter, with weak spiral ornament on the body chamber, creating a reticulate pattern. They may be further specimens of the present species.

Occurrence

Coniacian to Campanian, South India, Madagascar, Eastern Cape Province, South Africa, Angola, southeastern France, Austria?, British Columbia, Canada and Washington State and California in the U.S.A.

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Fig. 1. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838). The neotype, no. B46095, *ex* d'Orbigny Collection 5773-B1, in the collections of the Muséum National d'Histoire Naturelle, Paris, from the condensed Albian of Escragnolles, Var, France. Figures are ×1.

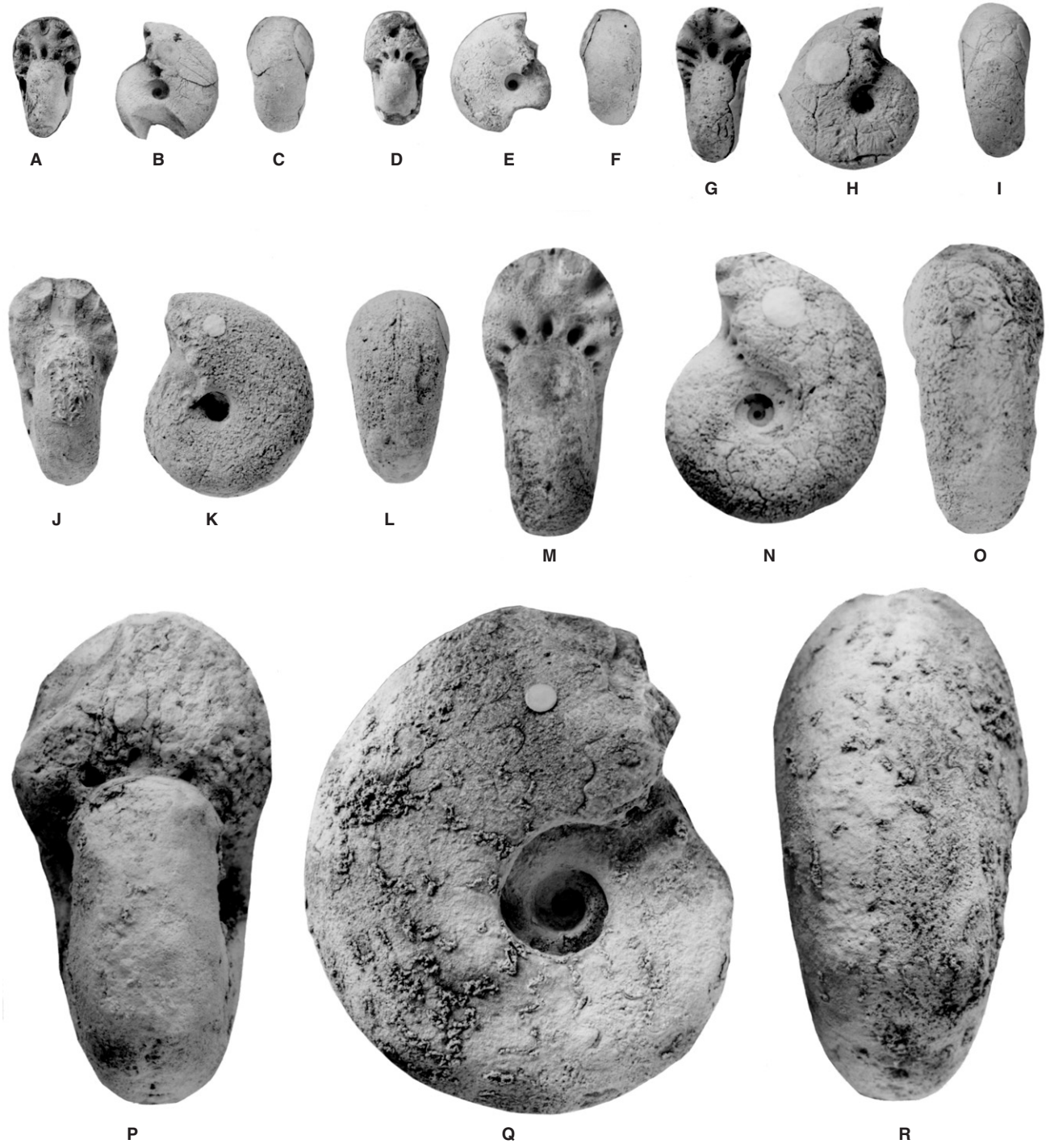


Fig. 2. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838). **A–C**, BMNH C18235, the original of specimen (b) of *Desmoceras inane* Stoliczka of Crick, 1907, p. 212-3 pl. 14, fig. 2. **D–F**, BMNH C18236, the original of *Desmoceras inane* Stoliczka of Crick, 1907, pl. 14, fig. 2. **G–I**, BMNH C18237, the original of Crick 1907, pl. 14, fig. 3. **J–L**, BMNH C18274, original of *Desmoceras* sp. of Crick, 1907, p. 15, fig. 3.**M–O**, BMNH C18223, the original of *Desmoceras* sp. (cf. *latidorsatum* Michelin sp.) of Crick, 1907, pl. 14, fig. 1. **P–R**, BMNH C18143, the original of *Tetragonites Timotheanus* (? Mayor sp.) Stoliczka sp. of Crick, 1907, p. 172, pl. 13, fig. 5. The originals of A–I, M–R, are inferred to be from the Lower to Middle Cenomanian Mzinene Formation of the Skoenberg, localities 61–63 of Kennedy & Klinger (1975). The original of J–L is from Crick's south branch of the Manuan (Munywana) Creek locality, and is probably Upper Albian. Figures A–F, J–R are ×1; Figures G–I are ×2.

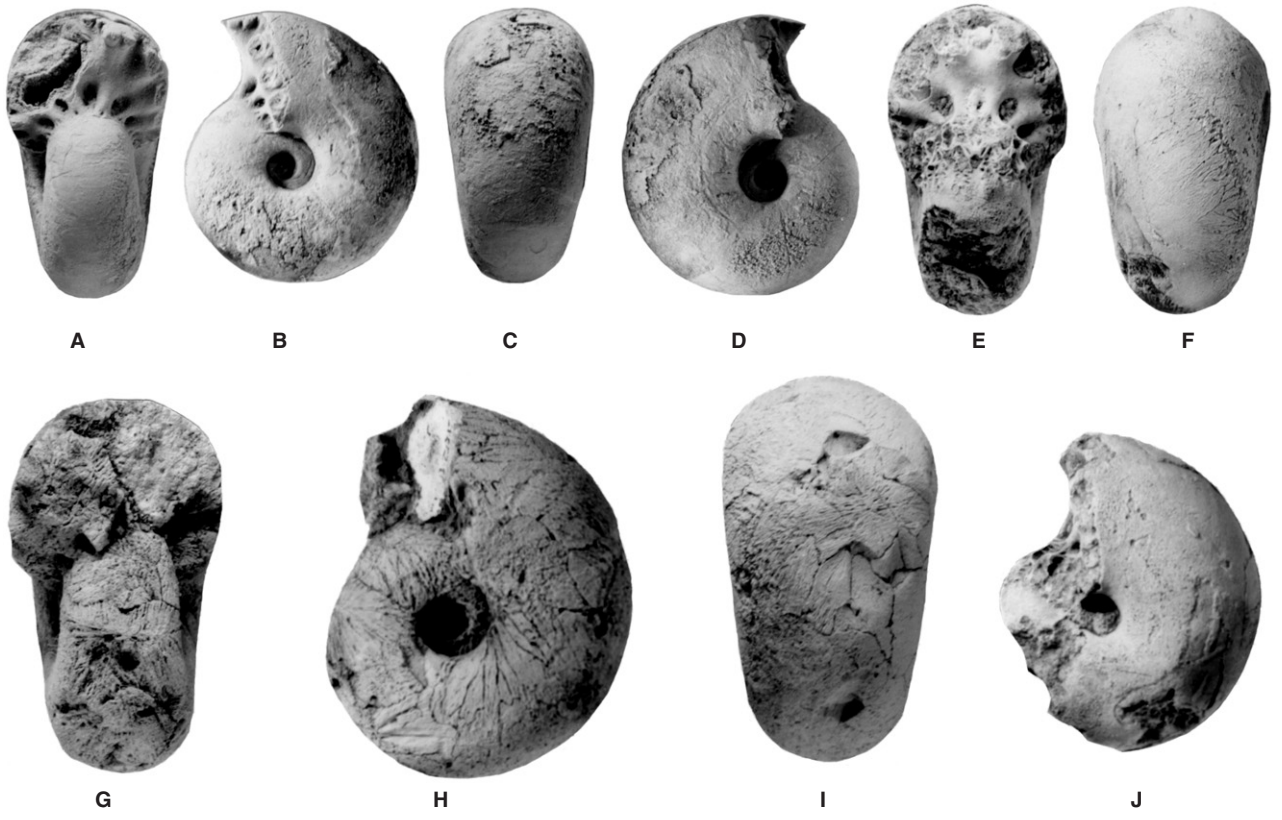
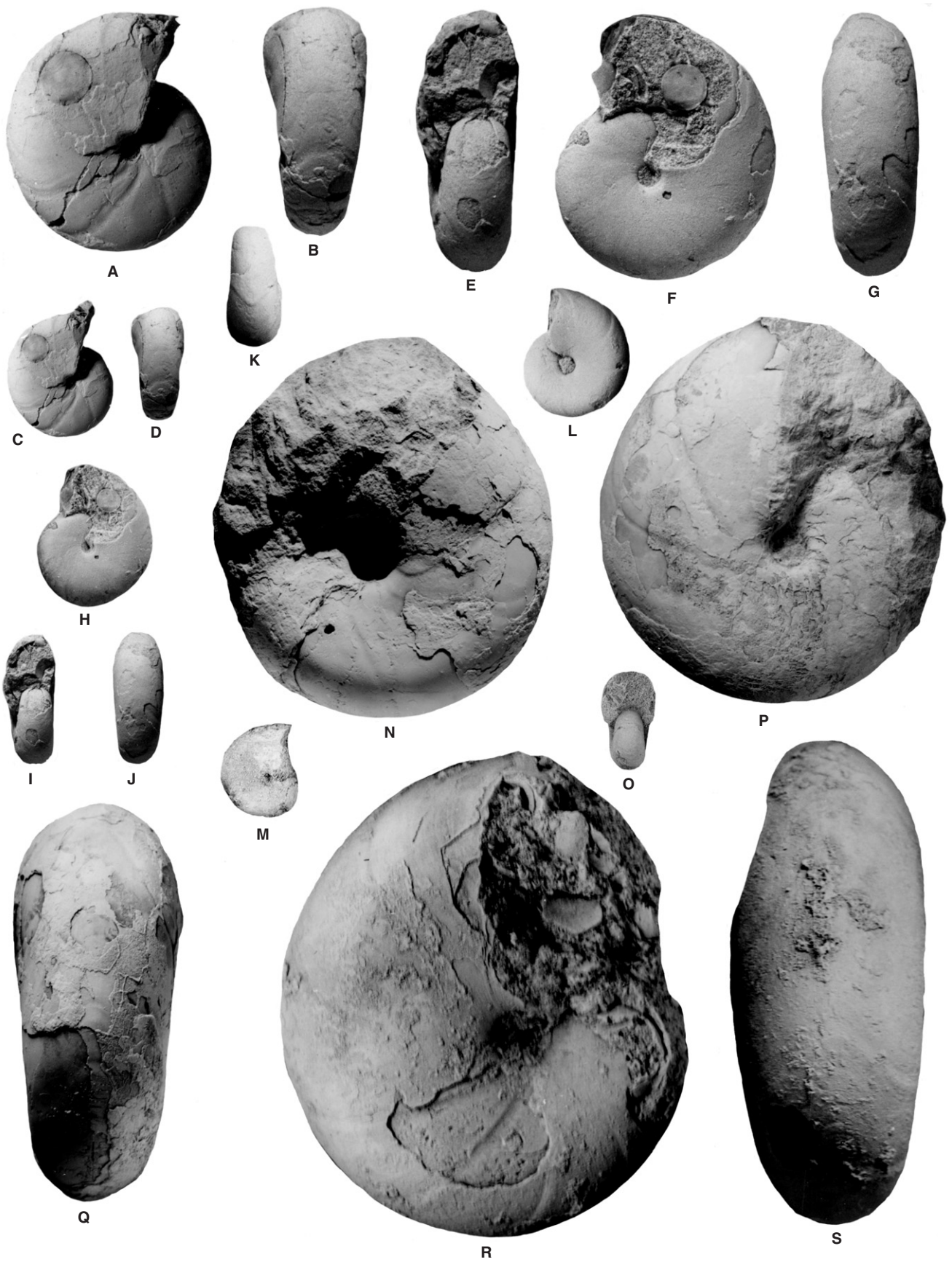


Fig. 3. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838). **A–D**, SAM PCZ22497; **E**, **F**, **J**, SAM PCZ022452 (ex A1079); **G–I**, SAM PCZ022450 (ex A785). All specimens are from the Lower to Middle Cenomanian Mzinene Formation at locality 62 of Kennedy & Klinger (1975), the Skoenberg, northern KwaZulu-Natal. Figures are ×1.

Fig. 4. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838). **A–C**, OUM KX4644, from the Lower to Middle Cenomanian Mzinene Formation at locality 62 of Kennedy & Klinger (1975), the Skoenberg, northern KwaZulu-Natal. **D**, **E**, OUM KX4808, from the Middle Albian Mzinene Formation at locality 53 of Kennedy & Klinger (1975, p. 288), derelict dam site on Indabana 13162, 2.2 km south of the farm Izwehelia, north of Hluhluwe, 27°52′24″S, 32°19′02″E. **F–H**, OUM KX5026, from the Upper Albian Mzinene Formation at locality 65 of Kennedy & Klinger (1975, p. 289), dam site excavations 1300 m southwest of the farm Izwehelia, coordinates 27°51′38″S, 32°19′30″E. All figures are x1.

Fig. 5. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin, 1838). BMNH C2607 (ex King Collection) from the Utatur Group of Odium, Tamil Nadu, South India. Figures are ×1.

Fig. 6. *Desmophyllites diphylloides* (Forbes, 1846). **A–D**, the lectotype, BMNH C22682, the original of Forbes, 1846, pl. 8, fig. 8; **E–J**, paralectotype BMNH C22683, both from the Upper Maastrichtian Valudavur Formation, of Pondicherry, South India. **K**, **L**, SAM-PCZ7069; **M**, **O**, Spath's smaller specimen,in the collections of the Durban Museum; **N**, **P**, **Q**, SAM Z116, from the Santonian–Lower Campanian Mzamba Formation of Mzamba Cliff, Eastern Cape Province. **R**, **S,** the holotype of *Schlüteria woodsi* Spath, 1921, the original of Spath, 1921, p. 45, pl. 7, fig. 1 in the collections of the Durban Museum. Figures A, B, E, F, G are ×2; Figs C, D, H–S are ×1.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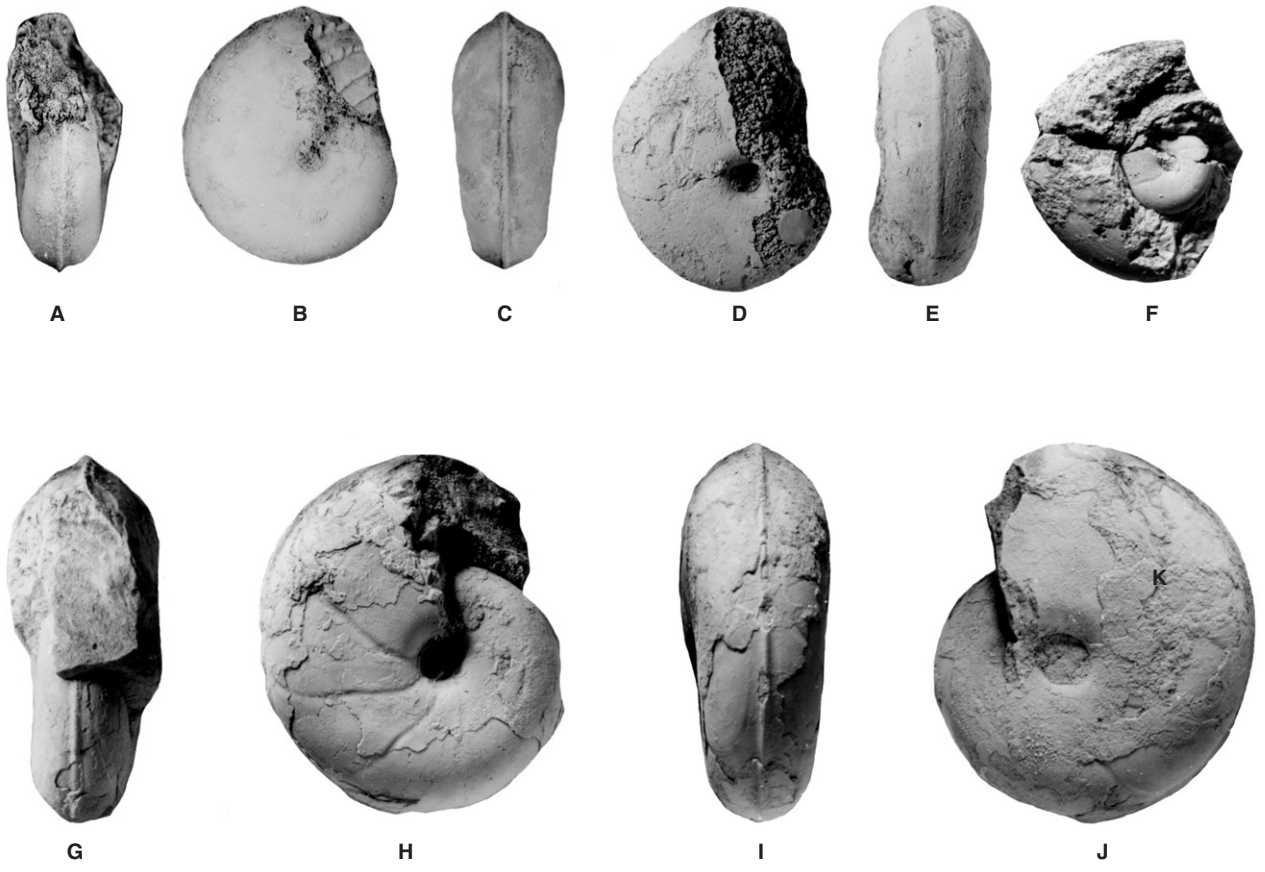

Fig. 7. **A–J**, *Damesites sugata* (Forbes, 1846). **A–C**, the original of Spath, 1921, p. 46, pl. 6, fig. 3, in the collections of the Durban Museum., from the Santonian–Lower Campanian Mzamba Formation of Mzamba Cliff, Eastern Cape Province. **D**, **E**, the lectotype, BMNH C22647, the original of Forbes, 1846, pl. 10, fig. 2; **F**, paralectotype, BMNH C22675, both from Vridachellum (Verdachellum), South India. **G–J**, SAM PCZ022494, from the Coniacian or Santonian St Lucia Formation on the north bank of the Munywana Creek on the farm Insleep, in northern KwaZulu-Natal. All figures are ×1.