CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE FAMILY TETRAGONITIDAE HYATT, 1900

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(With 27 figures)

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ABSTRACT

Members of the Tetragonitidae typically form a minor portion of the ammonite fauna of the South African Cretaceous, being important only in the Upper Campanian and Lower Maastrichtian. The following species are described: *Tetragonites? heterosulcatus* Anthula, *Tetragonites subtimotheanus* Wiedmann, *Tetragonites superstes* Van Hoepen, *Tetragonites* cf. *epigonum* (Kossmat), *Saghalinites cala* (Forbes), *Saghalinites nuperus* (Van Hoepen), *Pseudophyllites indra* (Forbes), *Pseudophyllites teres* (Van Hoepen) and *Pseudophyllites latus* (Marshall). The majority of all these forms are widely distributed circum-indic species, but *T. ? heterosulcatus* has been previously recorded only from Daghestan, the Caucasus, Bulgaria and Tunisia. The material allows a revision of the poorly known *T. superstes*, *S. nuperus* and *P. teres*, whilst *T. virgulatus* van Hoepen is confirmed as a synonym of *P. indra*. Ontogenetic series of *T. subtimotheanus* are illustrated, as is the ontogeny and variation in *S. cala*. This latter material shows a range of ventral ridges and striations associated with the ventral lobe and siphuncle of unknown function.

CONTENTS

INTRODUCTION

The Tetragonitidae are a small group of ammonites, conservative in external morphology, but showing a progressive, sexlobate suture line with a formula $ELU_2U_3{=}S\ U_1I_S$. The group evolved from the Gaudryceratidae during the Aptian via *Eogaudryceras* (*Eotetragonites*); they range from the Upper Aptian

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to the Lower Maastrichtian, and have a wide distribution, being locally common in areas as far apart as Alaska, New Zealand, Japan and Antarctica. They are, however, rare in the Boreal region; only a few specimens are known from Europe and Asia north of the Alpine fold belts, and none are recorded from the Western Interior of the United States. In South Africa, species are known from the Lower/Middle Albian to Maastrichtian, and are relatively common in the Upper Campanian and Lower Maastrichtian.

The following species are described below:

Tetragonites? heterosulcatus Anthula
Tetragonites subtimotheanus subtimotheanus Wiedmann
Tetragonites superstes Van Hoepen
Tetragonites cf. *epigonum* Kossmat
Saghalinites cala (Forbes)
Saghalinites nuperus (Van Hoepen)
Pseudophyllites indra (Forbes)
Pseudophyllites teres (Van Hoepen)
Pseudophyllites latus (Marshall)

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of material:

BMNH	British Museum (Natural History), London
MHNG	Muséum d'Histoire Naturelle, Geneva
EMP	École des Mines, Paris
MHNP	Muséum d'Histoire Naturelle, Paris
SAS	South African Geological Survey, Pretoria
TM	Transvaal Museum, Pretoria
DM	Durban Museum
UPE	University of Pretoria
SAM	South African Museum, Cape Town
NMB	National Museum, Bloemfontein.

FIELD LOCALITIES

Outline details of field localities referred to in this paper are given by Kennedy & Klinger (1975); full descriptions of sections are deposited in the library of the Palaeontology Department of the British Museum (Natural History) and in the Palaeontology departments of the South African Museum and the South African Geological Survey.

DIMENSIONS OF SPECIMENS

All dimensions given below are in millimetres:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus. Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916, *see* Kullman & Wiedmann 1970) is followed in the present work:

I_S = internal lobe with septal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum	**MOLLUSCA**
Class	CEPHALOPODA Cuvier, 1797
Subclass	AMMONOIDEA Zittel, 1884
Order	LYTOCERATIDA Hyatt, 1899
Superfamily	TETRAGONITACEAE Hyatt, 1900
Family	**Tetragonitidae** Hyatt, 1900
Genus	*Tetragonites* Kossmat, 1895

Type species

Ammonites timotheanus Pictet (1848: 295, pl. 2 (fig. 6), pl. 3 (fig. 1)) by original designation.

Diagnosis

Moderately evolute tetragonitids characterized by a round to subrectangular whorl section and oblique prorsiradiate constrictions which are typically flexed over the venter and have a distinct concave ventral sinus. Suture formula $ELU_2U_3{=}S\ U_1I_S$. The external lobe (E) is deeper than the first lateral lobe (L); there is an irregularly bifid or trifid termination to the first lateral saddle (E/L) and a nearly symmetrical lateral lobe (L).

Discussion

Tetragonites can be separated from *Saghalinites* Wright & Matsumoto, 1954 on the basis of the more evolute coiling, lower expansion rate and much simpler suture of that genus. *Pseudophyllites* Kossmat, 1895 is much more inflated and involute, has a much higher expansion rate, a typically rounded, frequently compressed whorl section, no constrictions and a reticulate ornament, whilst the suture is far more highly subdivided.

The genus *Epigoniceras* Spath, 1925 with *Tetragonites epigonus* Kossmat, 1895 as type species was proposed for Lower Turonian to Maastrichtian tetragonitids which differed from earlier *Tetragonites sensu stricto* in having a retracted suspensive lobe with a much larger number of auxiliary elements. *Epigoniceras* has been accepted by Usher (1952), Wright & Matsumoto (1954), Wright (1957) and Collignon (1956, 1965*a*, 1965*b*, 1966, 1969), but Howarth (1958: 9) has successfully proved that straight, recurved and even upcurved suspensive lobes are to be found throughout the time range of the group, so that *Epigoniceras* does not bear separation from *Tetragonites* even on a stratigraphic basis. Wiedmann (1973: 609) has introduced the genus *Carinites*, with *Tetragonites* *spathi* Fabre (1940: 214, pl. 6 (fig. 1), text-fig. 26) as type species for tetragonitids with a subrectangular whorl section, persistent, irregularly spaced constrictions projected on the flanks and converging to a marked ventral peak, and a persistent, if feeble ventral keel. Wiedmann regarded the keel as a feature unknown in any other tetragonitid species, but similar 'keels' of this type are quite widespread in the material here present, occurring for instance in *Tetragonites superstes* Van Hoepen (1921: 10, pl. 2 (figs 17–20)). A distinct keel also occurs in *Tetragonites epigonus* Kossmat (e.g. Usher 1952, pl. 2 (fig. 7)) and such features are widely developed in *Saghalinites cala* (Forbes) (p. 168). This feature is not a floored keel, rather it is a raised siphonal area associated with the siphuncle. Rather similar keels are found in many ammonite groups, and appear to be variable features of specific value only, suggesting that *Carinites* may possibly be placed in the synonymy of *Tetragonites*.

Collignon (1956: 98) listed twenty-eight species and varieties of *Tetragonites* and *Epigoniceras* in his review of the genus, and since his work, Aptian to Cenomanian species have been described and discussed by Wiedmann (1962*a*, 1962*b*, 1973), Wiedmann & Dieni (1968) and Murphy (1967*a*, 1967*b*) so that over thirty names are in current usage and there are a number of other named forms, chiefly based on nuclei, which may be synonyms of better known species, or which can only be regarded as *nomen dubia*.

The authors find it difficult to believe that this host of species, many with overlapping or identical geographic and stratigraphic ranges, is indeed a true picture of the evolution of the genus, but the current material is inadequate for a satisfactory critical appraisal of the list.

Occurrence

Tetragonites first appears in the Upper Aptian, and ranges to the Maastrichtian. The genus has an almost world-wide distribution, with records from Antarctica, South Africa, Mozambique, New Zealand, Madagascar, Japan, Sakhalin, Algeria, Tunisia, the western Mediterranean, Spain, southern France, Switzerland, England, northern France, a variety of localities in central Europe, and Sinai. In North America there are records from Texas and northern Mexico, California, Oregon, British Columbia, and Alaska.

Tetragonites? heterosulcatus Anthula, 1899

Figs 1A–F, 2A–B

Lytoceras (*Tetragonites*) *heterosulcatus* Anthula, 1899: 99–100, pl. 7 (fig. 4), *non* pl. 7 (fig. 5). Pervinquière, 1907: 73.

Tetragonites heterosulcatus Drushchits, 1956: 102, pl. 7 (figs 27–28), text-fig. 44; 1960: 260, text-fig. 68. Murphy, 1967*a*: 32, text-fig. 14. Dimitrova, 1967: 31, pl. 11 (figs 1–1a), text-fig. 13.

Type

Lectotype herein designated, the original of Anthula's (1899, pl. 7 (fig. 4)) from the Akusha Shales (Aptian) of Daghestan.

Material

Three specimens, BMNH C78827–C78829, from Bed J of the Mzinene Formation, locality 171, Mlambongwenya Spruit, northern Zululand (Albian II–III).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Lectotype (from Anthula)	24,0	13,0(54)	9,0(37)	1,4	8,0(33)
BMNH C78827	49,0	24,8(51)	20,8(42)	1,2	10,9(22)
BMNH C78828	–	23,0(–)	19,0(–)	1,2	–

Description

The coiling is fairly evolute, about 40 per cent of the previous whorl being covered. The whorls expand at a moderate rate, are depressed, and have their greatest thickness below mid-flank. The umbilicus is of moderate size, 22 per cent of the diameter, and fairly deep. The umbilical wall is vertical, the umbilical shoulder abruptly rounded, the flanks flattened and subparallel, the ventrolateral shoulders abruptly rounded, the venter broad and flattened.

The surface of the shell (Figs 1A–C, 2B) bears fine growth striae and strong, flexuous prorsiradiate constrictions, fourteen or fifteen on the outer whorl, each preceded by a fine, low, rounded collar. The constrictions are narrow and quite deeply incised; they arise at the umbilical seam, pass straight up the umbilical wall, sweep forwards across the ventrolateral shoulder and are strongly prorsiradiate and markedly convex across the flanks. They flex backwards across the upper flank and ventrolateral shoulder to form a broad ventral sinus, which deepens as size increases.

The internal mould (Figs 1D–F, 2A) is smooth save for the constrictions, which are broader and deeper than on the test.

The suture, rather poorly exposed in the present material (see Drushchits 1956: 102, text-fig. 442), includes a large, asymmetrically bifid first lateral saddle (E/L), a smaller, bifid second lateral saddle (L/U_2), separated by a large bifid lateral lobe (L). There are three auxiliary saddles on the suspensive lobe (U_3), the first large and subtrifid, whilst there is a long first, and an incipient second saddle on the internal suture. The septal lobe is horseshoe shaped, and of moderate size (Fig. 1A).

Discussion

The depressed, rectangular whorl section and remarkable constrictions, becoming closely spaced and strongly recurved in adults, together with the deep ventral sinus find an exact match in the large specimens of *Tetragonites heterosulcatus* figured by Drushchits (1960) and Dimitrova (1967), whilst small speci-

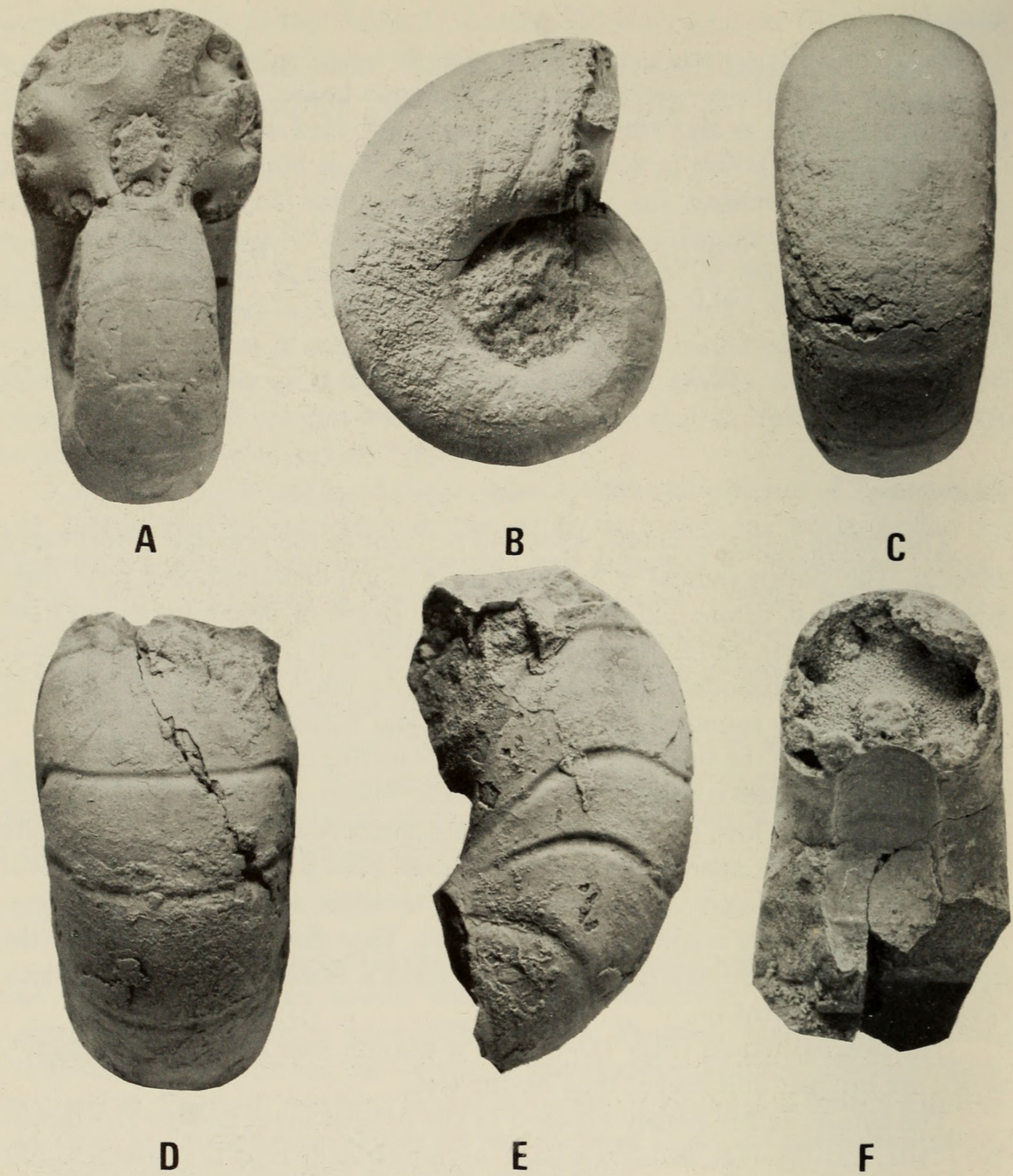


Fig. 1. *Tetragonites? heterosulcatus* Anthula. A–C. BMNH C78827. D–F. BMNH C78828. Both from Bed J of the Mzinene Formation, Albian II–III at locality 171, Mlambongwenya Spruit, northern Zululand. × 1.

mens figured by Drushchits (1956, 1960) link these with Anthula's juvenile holotype. No other *Tetragonites* species shows this combination of characters, whilst the superficially similar *Eogaudryceras* (*Eotetragonites*) such as *E. duvalianum* (d'Orbigny) (e.g. Murphy 1967*a*, pl. 1 (figs 2–3)), *E. umbilicostriatus* Collignon (1963, pl. 248 (fig. 1060)), *E. plurisulcatus* Breistroffer (= *Tetragonites duvali* Anthula (non d'Orbigny) 1899: 99, pl. 7 (fig. 3a–b)), *E. wintunius* (Anderson)

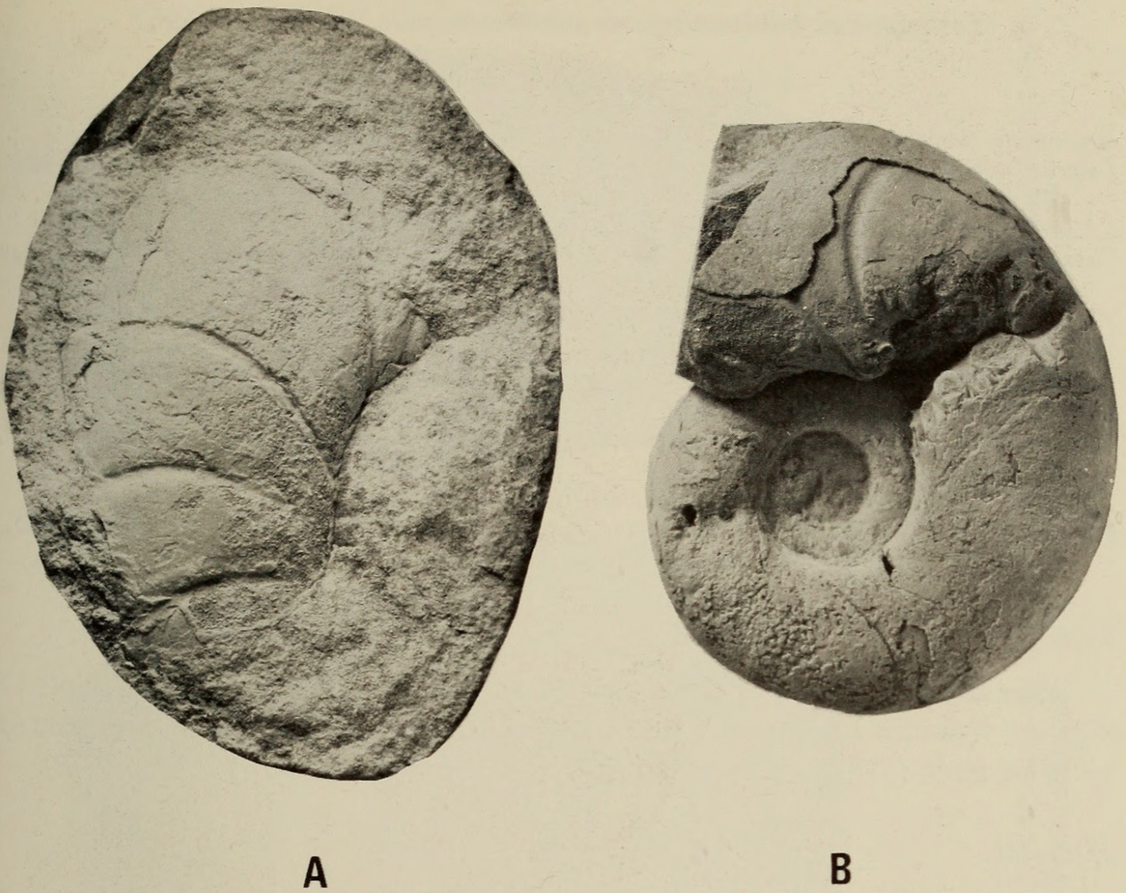


Fig. 2. *Tetragonites? heterosulcatus* Anthula. A. BMNH C78829. B. BMNH 78828. Both from Bed J of the Mzinene Formation, Albian II–III, at locality 171, Mlambongwenya Spruit, northern Zululand. × 1.

(1938, pl. 16 (figs 2–5)). *E. shoupi* Murphy (1967*b*: 22, pl. 3 (figs 7–9)) and *E. jallabertianus* (Pictet) (1848: 302, pl. 4 (fig. 2a–b)) have straight or flexuous constrictions, never develop a strong ventral sinus, and have markedly different relative proportions.

The generic affinity of the species is enigmatic. Murphy (1967*a*, 1967*b*) in the most recent revision of this species placed it in *Tetragonites*. Wiedmann (1973) has subsequently referred the species to *Eotetragonites* because it lacks an umbilical lobe; this divergence reflects the difficulties sometimes encountered in placing forms in the two genera where differing criteria—sutures vs. form of constriction—are used. In consequence the authors have questioned reference of this species to *Tetragonites* until a full review of the *Tetragonites*/*Eotetragonites* plexus is available.

Occurrence

Upper Aptian of Daghestan, the Caucasus and Bulgaria, Aptian of Tunisia, and Lower/Middle Albian of Zululand.

Tetragonites subtimotheanus subtimotheanus Wiedmann, 1962

Figs 3A–C, 4A–F, 5A–H, 6A–G

Ammonites timotheanus Stoliczka, 1865: 146, pl. 73 (figs 3–4, 6) *non* 5.
Lytoceras (*Tetragonites*) *timotheanus* Kossmat, 1895: 133, pl. 17 (figs 11, 13). Collignon, 1928: 18, pl. 1 (fig. 18).
Lytoceras timotheanum Anderson, 1902: pl. 7 (figs 145–148).
Tetragonites timotheanus Crick, 1907: 172, pl. 10 (fig. 15–15a), *non* pl. 13 (fig. 5–5a) (=*Desmoceras latidorsatum* (Michelin)).
Tetragonites aff. *T. timotheanus* Imlay, 1960: 100, pl. 12 (figs 24–28).
Tetragonites subtimotheanus Wiedmann, 1962*a*: 131, 172. Collignon, 1963: 22, pl. 249 (fig. 1071). *Pars*. Murphy, 1967*a*: 62, pl. 5 (figs 11, 13), *non* pl. 6 (figs 5, 8) (= *T. blaisoni* Collignon), text-figs 34–35.
Tetragonites rectangularis alaskaensis Murphy, 1967*a*: 46, pl. 6 (figs 9–10, 14), pl. 7 (figs 2, 9), text-figs 22–23.
?*Tetragonites madagascariensis* Murphy, 1967*a*: 68.
Tetragonites subtimotheanus subtimotheanus Wiedmann, 1973: 592, pl. 1 (fig. 5 ?), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8 ?), text-fig. 2.

Type

The holotype is the original specimen figured by Kossmat (1895) as pl. 17 (fig. 15), from the lower part of the Utatur Group of southern India. Designated by Wiedmann (1962*a*: 171).

Material

Fourteen specimens from the Mzinene Formation of the Mzinene River and Skoenberg regions: BMNH C78834 from locality 70 (Middle Albian), NMB D367a–b from Bed 7 at locality 51, SAS H207/8/9 from Bed 8 or 9 at locality 51, and BMNH C78835 from Bed 9 or 10 at the same locality (Upper Albian), BMNH C78831 from locality 61 (Albian VI), and C78832–C78833 (Lower–Middle Cenomanian) from locality 62, SAS 689, SAS 1034 and BMNH C18142 are probably from the Lower to Middle Cenomanian of the same locality, whilst a further specimen, SAS 10869, is probably from the Upper Albian of the Mzinene River. UPE 270–271 and BMNH C78836 are from locality 64 (Albian V). A juvenile, BMNH C78837, best referred to as *T.* sp. juv. cf. *subtimotheanus*, comes from locality 106 (Albian V).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (after Kossmat 1895)	35,0	19,0(54)	14,0(40)	1,35	10,0(29)
Indian specimens (after Murphy 1967*a*)					
MHNG 9 Odium, larger specimen	51,7	31,1(60)	21,5(41)	1,45	14,6(28)

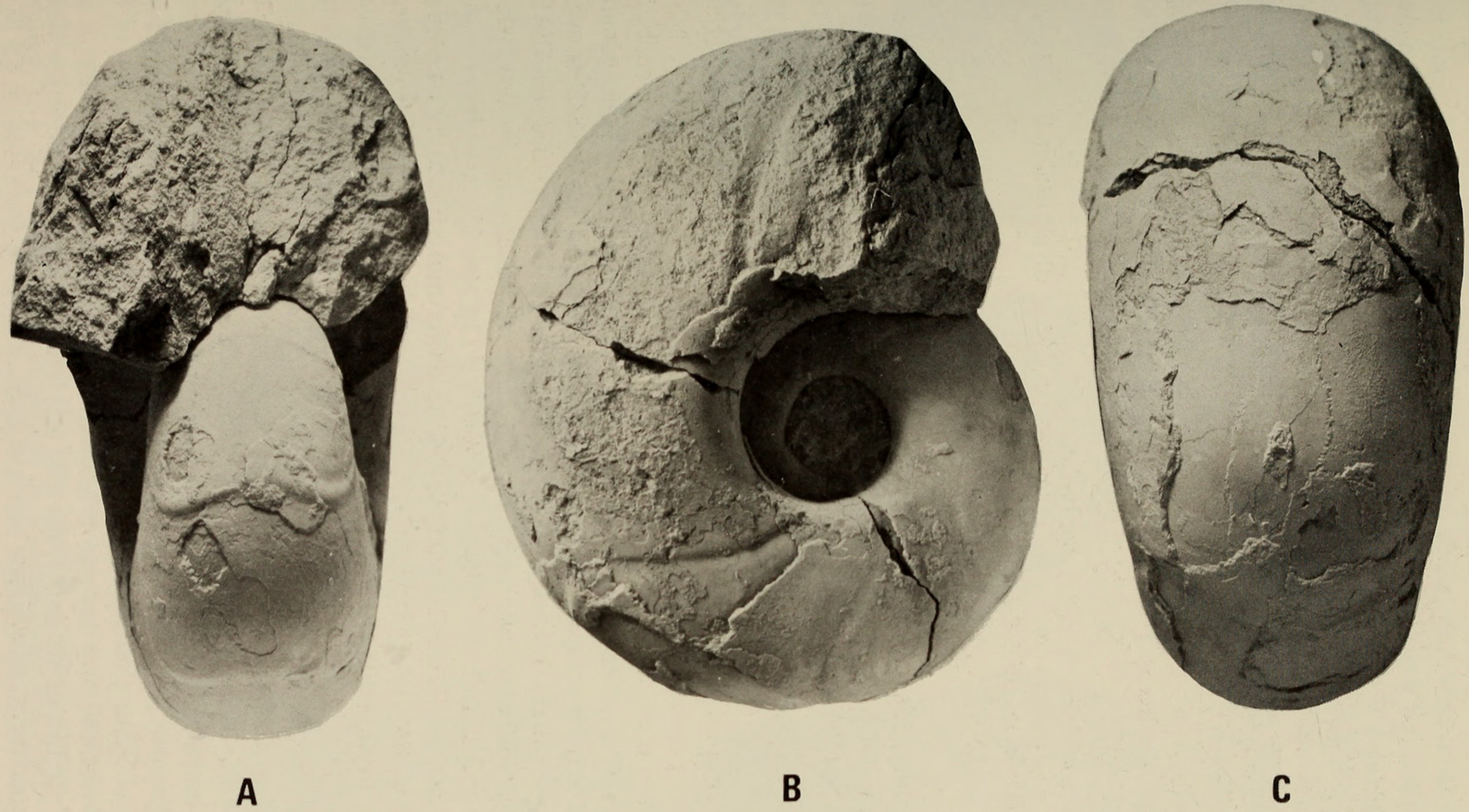


Fig. 3. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. BMNH C78834, from the Mzinene Formation, Albian II, on the farm Izwehelia, north north-east of Hluhluwe, Zululand. × 1.

		D	Wb	Wh	Wb/Wh	U
MHNG 9 Odium, smaller specimen 1		32,4	18,5(57)	13,1(40)	1,41	10,1(31)
MHNG 9 Odium, smaller specimen 2		20,3	11,3(56)	8,3(41)	1,36	6,4(32)
Indian specimens (after Kossmat)	a	80,0	45,0(56)	41,0(51)	1,09	16,0(20)
	b	27,0	14,5(54)	10,5(39)	1,38	8,0(30)
BMNH C18142		24,1	13,5(±56)	10,4(43)	1,29	7,0(29)
BMNH C78832		—	18,8(—)	14,2(—)	1,32	—
BMNH C78833		—	13,2(—)	10,1(—)	1,30	—
BMNH C78834	at	50,5	23,7(47)	23,1(46)	1,02	13,9(27)
	at	68,5	38,5(56)	32,8(48)	1,17	19,5(28)
	at	84,0	45,2(54)	37,5(44)	1,20	21,5(25)
SAS A1034		29,4	15,5(53)	12,2(41)	1,27	9,2(31)
SAS A689		19,5	9,9(51)	7,2(37)	1,37	6,2(31,7)
SAS 1869		64,3	36,2(56)	27,3(42)	1,32	15,1(23)
UPE 271		47,5	26,0(55)	22,5(47)	1,15	10,0(21)

Description

The coiling is involute, over two-thirds of the previous whorl being covered. The whorls are trapezoidal, very depressed when young (whorl breadth to whorl height ratio is up to 1,37), becoming somewhat rounded and less depressed when adult (breadth : height ratios of 1,2 to 1,09) and expanding fairly slowly. The greatest breadth is at the umbilical shoulder. The umbilicus is deep, and of moderate size, 28–32 per cent of diameter in the middle growth stages, but becoming proportionally smaller—25 per cent of diameter or less—in larger specimens. The umbilical wall is flat and subvertical, the umbilical shoulder abruptly rounded. The flanks are distinctly flattened and convergent, the ventrolateral shoulder abruptly rounded, and the venter broad and flattened.

The shell surface is finely striate. These striae pass straight across the umbilical wall, running normal to the umbilical seam. They sweep forwards across the umbilical shoulder, and are strongly prorsiradiate over the flank and markedly concave. They flex backwards over the ventrolateral shoulder and form a pronounced sinus over the siphonal area. As size increases, the flexure of the striae increases and they become very concave on both flanks and venter.

There are five or six collar-like ribs and associated constrictions per whorl in smaller specimens; adults bear seven to eight, with some crowding on the body chamber. Collars are faint on the flanks, but strengthen considerably on the shoulder and venter. They are rounded, with a gentle adapical and steep adapertural slope. The constrictions parallel growth striae; they arise at the umbilical seam, are deep across umbilical and ventrolateral shoulders, but relatively weak on flank and venter.

The internal mould is smooth, save for the constrictions, which are far more prominent than on the test. They arise at the umbilical seam, pass straight up the umbilical wall and forwards across the umbilical shoulder, where they are strongly marked. They are concave and strongly prorsiradiate on the flanks and

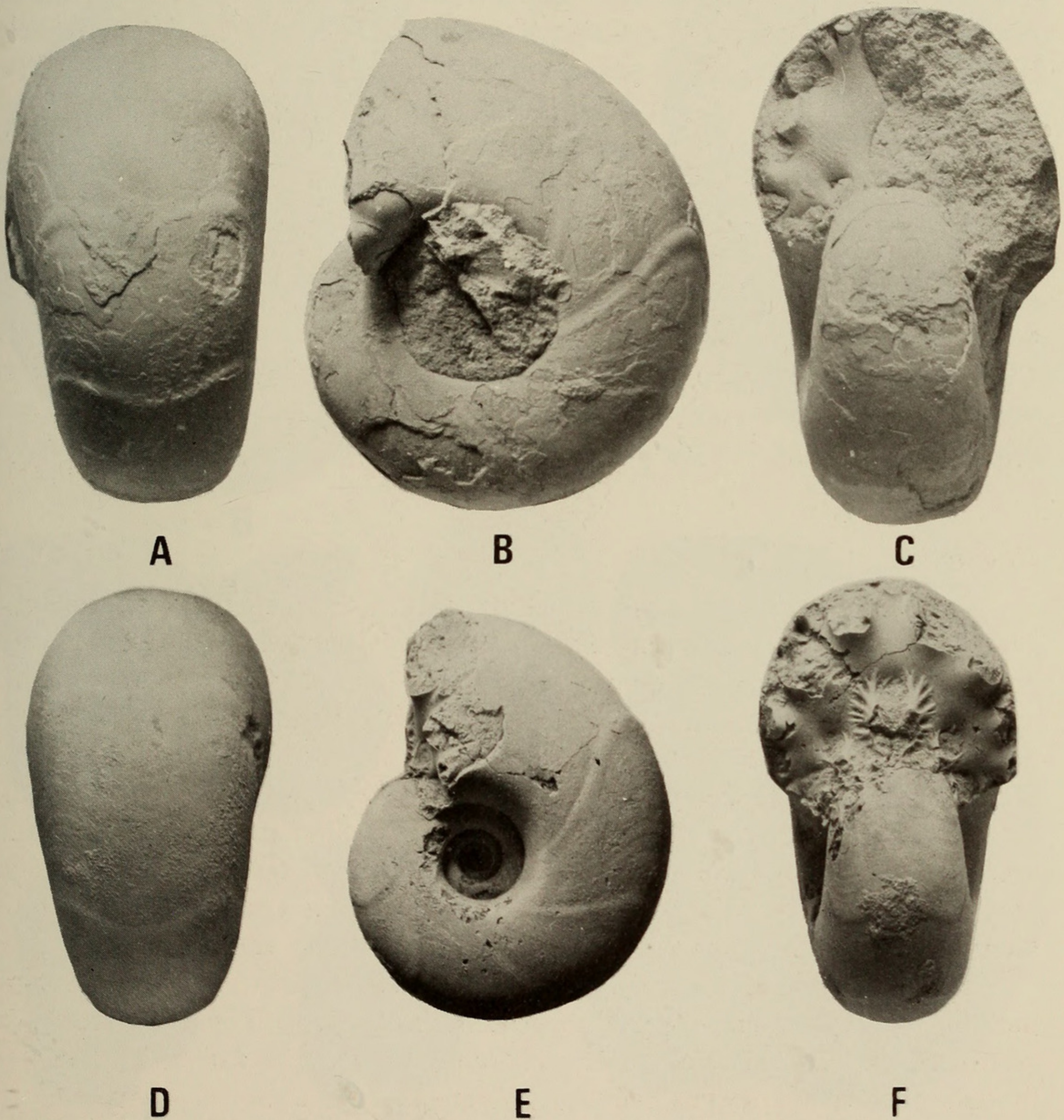


Fig. 4. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C. BMNH C78834, from the Mzinene Formation, Albian II, on the farm Izwehelia, north north-east of Hluhluwe, Zululand. D–F. BMNH C78836, from bed 4 of the Mzinene Formation, Albian V, at locality 71 on the southern tributary of the Munywana Creek, Zululand. This specimen shows a well-preserved septal lobe. × 1.

flex backwards over the shoulder with a striking ventral sinus. The constrictions become broader and more strongly flexed as size increases.

The adult aperture shows features very similar to the collars associated with constrictions, being marked by a thickened lip.

None of the present specimens shows the external suture, but the septal faces

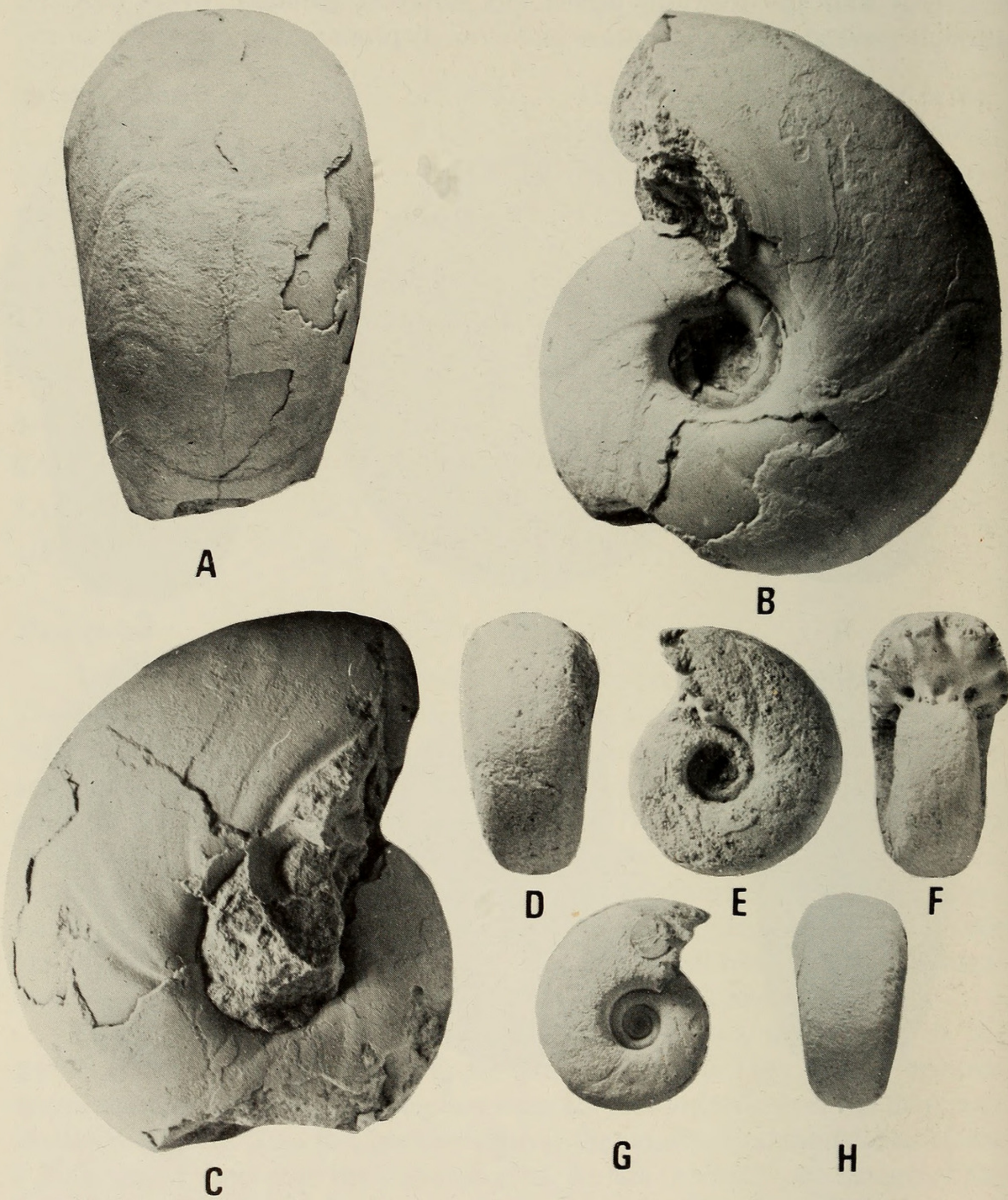


Fig. 5. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C. SAS A10869, from the Upper Albian Mzinene Formation on the Mzinene River, Zululand. D–F. SAS A1034. G–H. BMNH C18142 figured by Crick (1907, pl. 10 (fig. 15–15a)). All from the Lower or Middle Cenomanian Mzinene Formation, Skoenberg, on the Mzinene River, Zululand. × 1.

of a number of specimens show two large internal saddles on either side of the dorsal lobe and a prominent septal lobe (Fig. 4F). Some specimens, including that figured by Crick (1907, pl. 10 (fig. 15–15a)) show, in addition, a tiny third internal saddle.

Discussion

A series of *Tetragonites* ranging from Middle Albian to Middle Cenomanian are linked together by their involute coiling, depressed trapezoidal whorls and markedly flexuous constrictions, collar ribs and growth striae. Although variable in their relative proportions and the degree of incision and flexure of constrictions, reference to a single species seems acceptable. The specimens match closely with *Tetragonites subtimotheanus subtimotheanus* as figured by Stoliczka (1865, pl. 73 (figs 3–3a, 4–4a)), Kossmat (1895, pl. 7 (fig. 13–13a)) and Wiedmann (1973: 592, pl. 1 (fig. 5?), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8?)). The latter author (Wiedmann 1973: 594) discusses fully how *T. subtimotheanus subtimotheanus* differs from related forms. *T. timotheanus* (Pictet 1848: 295, pl. 2 (fig. 6), pl. 3 (fig. 1)) has a similar juvenile shell, remaining evolute throughout, and loses its constrictions early in ontogeny. *Tetragonites rectangularis* Wiedmann (1962*a*: 178, pl. 14 (fig. 3), text-fig. 39) has a broad, rectangular whorl section at first, losing its distinct ventro-lateral shoulders at a diameter of around 30 mm, whilst the constrictions are straighter, less crowded and decline earlier. *Tetragonites kitchini* Krenkel (1910: 226, pl. 22 (fig. 8)) has a subrectangular whorl section

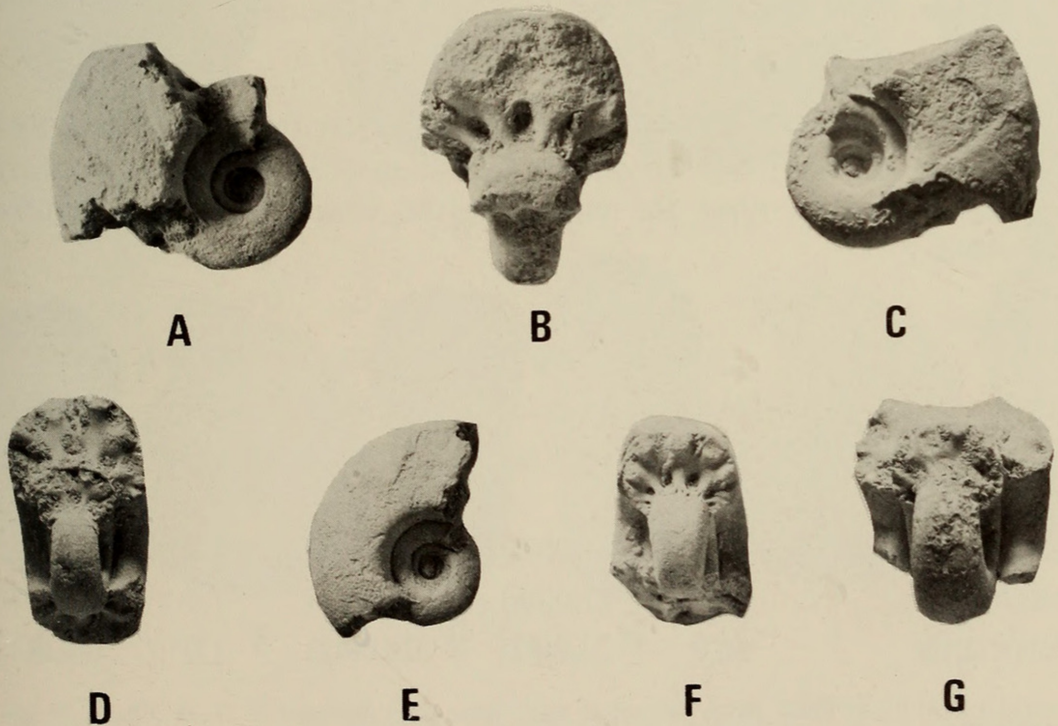


Fig. 6. *Tetragonites subtimotheanus subtimotheanus* Wiedmann. A–C, G. BMNH C78832. D–F. BMNH C78833. Both from the Lower or Middle Cenomanian Mzinene Formation, Skoenberg, on the Mzinene River, Zululand. × 1.

which persists to greater diameters, and generally five constrictions per whorl.

Tetragonites subtimotheanus subspecies *maclearni* Wiedmann (1973: 595, pl. 4 (fig. 1), pl. 5 (figs 1–3), text-fig. 3) has been distinguished from the typical form on the basis of the development of an oval, rather than broadly rounded whorl section in adults (compare Wiedmann 1973, text-figs 2a–e, 3a–b).

Occurrence

This species is known from the upper Lower Albian to Lower Cenomanian of the Queen Charlotte Islands, British Columbia and the Chitina Valley, Alaska, the Upper Albian of Oregon, the Upper Albian and Lower Cenomanian of Madagascar and southern India, and the Middle Albian to Lower (and Middle?) Cenomanian of Zululand.

Tetragonites superstes Van Hoepen, 1921

Figs 7A–D, H–J, 8, 12A–C

Tetragonites superstes Van Hoepen, 1921: 10, pl. 2 (figs 17–20), text-fig. 6. Spath, 1922: 119, pl. 6 (fig. 6).
Tetragonites cf. *epigonum* Spath, 1921*b*: 42.
Epigoniceras superstes Collignon, 1956: 87, pl. 11 (fig. 3a–b); 1969: 14, pl. 517 (fig. 2034).

Type

The holotype is TM 564, the original of Van Hoepen (1921, pl. 2 (figs 17–18)) from the Umzamba Formation (Late Santonian to Early Campanian) at locality 1, the mouth of the Umzamba River, Transkei (Pondoland).

Material

Seven specimens, TM 525, TM 564–566, BMNH C19416, SAM–K7029, SAM–K7096, all from the Umzamba Formation (Late Santonian to Early Campanian), locality 1, at the mouth of the Umzamba River, Transkei (Pondoland).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype TM 564	40,0	18,2(45)	17,3(43)	1,05	10,4(26)
Paratype TM 566	32,4	15,5(48)	14,2(44)	1,09	8,3(26)
From Collignon 1956: 87					
MNHP 2098	44,0	21,0(48)	19,0(43)	1,1	13,0(30)
MNHP 2099	44,0	21,0(48)	18,0(41)	1,1	13,0(30)
MNHP 2100	52,0	22,0(42)	22,0(42)	1,0	14,0(27)

Description

The shell is small and involute with a moderately high expansion rate. The whorl section is depressed (whorl breadth : height ratio 1,05 to 1,15) with the greatest breadth just below mid-flank. The umbilicus is about 26 per cent of the diameter, rather deep, with a subvertical wall of moderate height. The umbilical shoulder is abruptly rounded, the flanks gently rounded, merging with broadly rounded shoulders and venter. The whorl section is thus between subrectangular and elliptical. The surface of the test bears very fine prorsiradiate growth striae, whilst the internal mould is smooth. Some individuals show faint spiral ridges, one over the siphonal area and a pair on each shoulder (Figs 7D, H, 12C).

Constrictions are faint on the mould, and virtually invisible when the shell is preserved. They appear to be absent on juveniles, but up to four per half-whorl are present during the later growth stages, as in TM 566. The mature aperture, present on a number of specimens (Fig. 7A, C) is also constricted. These apertural constrictions are deep and quite wide, originating at the umbilical seam. They pass normally across the inner part of the umbilical wall and are strongly prorsiradiate across the flanks, flexing backwards across the ventro-lateral shoulders and passing across the venter with a shallow, concave ventral sulcus.

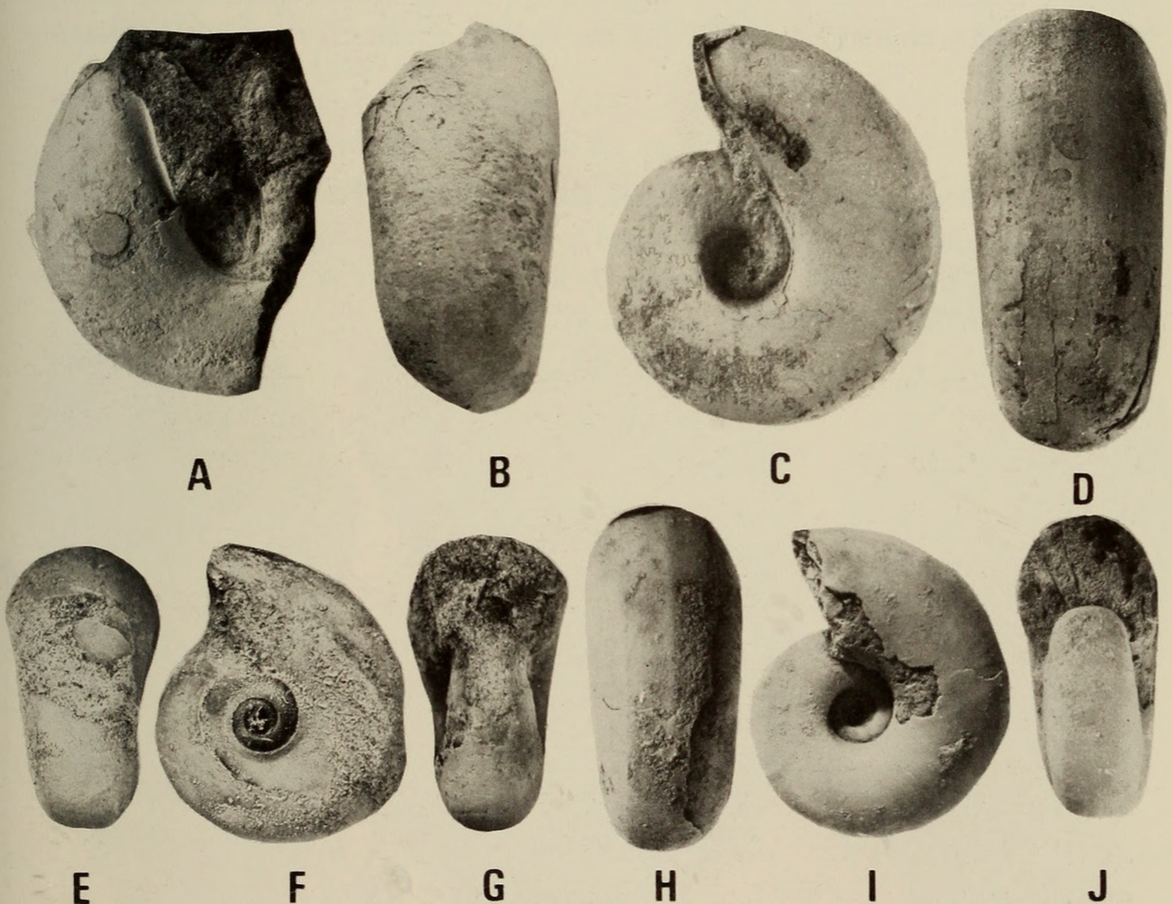


Fig. 7. A–D, H–J. *Tetragonites superstes* Van Hoepen. A–B. BMNH C19416 (original of Spath 1922, pl. 6 (fig. 6)). C–D. Holotype, TM 564. H–J. TM 566, a paratype. E–G. *Tetragonites* cf. *epigonus* Kossmat. An unregistered specimen in the collections of the Durban Museum. All specimens are from the Umzamba Formation, of late Santonian to early Campanian age, at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

The suture line (Fig. 8) has a large, asymmetric trifid first lateral saddle (E/L), a smaller trifid second lateral saddle (L/U_2), and a suspensive lobe with a large trifid first auxiliary saddle. The first lateral lobe (L) is large and irregularly subdivided. The first of the four auxiliary lobes is trifid.

Discussion

Tetragonites superstes most closely resembles *Tetragonites popetensis* Yabe (1903: 48, pl. 7 (figs 4a–b, 6)), a Campanian to Maastrichtian species known from Japan and California. In Yabe's species the position of the constrictions is rather clearly marked on the shell surface by rounded ribs,which are markedly flexed. The shell is also more evolute (U = 31 % at a diameter of 34 mm in the type).

Differing proportions and number and style of constrictions readily separate *Tetragonites superstes* from contemporary species such as *Tetragonites glabrus* Jimbo and its variety *problematica* Matsumoto (1942: 672, figs 1–1b, 2a–2b), *Tetragonites garuda* (Forbes) (1846: 102, pl. 7 (fig. 1a–c)), *Tetragonites mitraikyense* Collignon (1956: 86, pl. 11 (fig. 2–2b)), *Tetragonites beantalyensis* Collignon (1956: 83, pl. 10 (fig. 1–1b)) and the various species revised by Henderson (1970).

Occurrence

All present material comes from the Umzamba Formation of Transkei (Pondoland), and cannot be dated more accurately than Late Santonian to Early Campanian. The species is also known in Madagascar where it occurs from Lower to Middle Campanian.

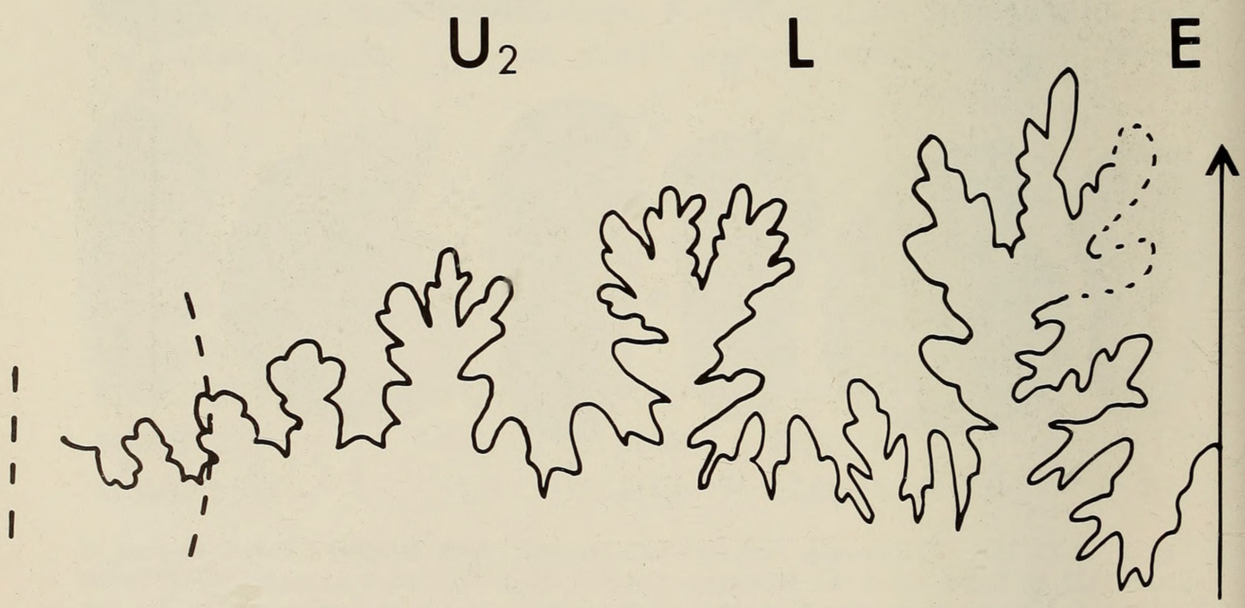


Fig. 8. External suture of *Tetragonites superstes* Van Hoepen. TM 564. × 10.

Tetragonites cf. *epigonus* Kossmat, 1895

Figs 7E–G, 9A–C

Compare:

Ammonites timotheanus Stoliczka, 1865: 146, pl. 73 (fig. 5 only).

?Desmoceras pyrenaicum De Grossouvre, 1894: 168, pl. 25 (fig. 2), *non* pl. 37 (fig. 9), text-fig. 73.

Lytoceras (*Tetragonites*) *epigonus* Kossmat, 1895: 135, pl. 17 (figs 4a–c, 5a–b, 10). Kilian & Reboul, 1909: 14.

?Tetragonites timotheanus Whiteaves, 1903: 329.

Tetragonites cf. *epigonus* Yabe, 1903: 49, pl. 7 (fig. 3).

non *Lytoceras* (*Tetragonites*) *epigonum* Boule, Lemoine & Thévenin, 1906: 13, pl. 3 (fig. 1–1a). This specimen is an Albian desmoceratid. Marshall, 1926: 149, pl. 21 (fig. 10), pl. 29 (figs 6–7) = *Tetragonites marshalli* Collignon. Anderson, 1958: 187, pl. 65 (figs 4–5), pl. 67 (fig. 3–3a) = *Tetragonites popetensis* Yabe.

Lytoceras (*Tetragonites*) *epigonum* Pervinquière, 1907: 76, pl. 3 (figs 27–28), text-figs 15–16. Basse, 1928: 461, pl. 30 (figs 1–3). Collignon, 1931: 14, pl. 2 (figs 5–7), pl. 3 (fig. 4).

Tetragonites epigonus Paulcke, 1906: 174.

?Tetragonites sp. indet. Spath, 1921*b*: 42, pl. 7 (fig. 3).

? Epigoniceras epigonum Spath, 1925: 29, pl. 1 (fig. 2a–b).

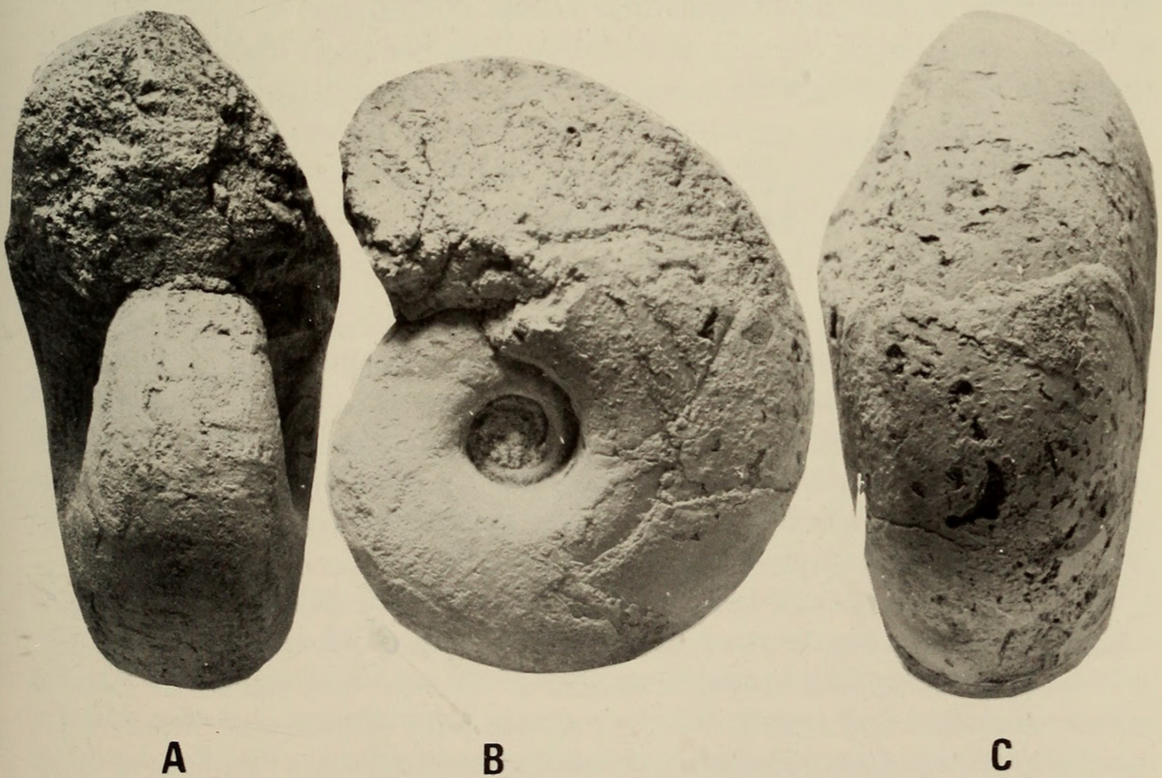


Fig. 9. *Tetragonites* cf. *epigonus* Kossmat. BMNH C78838, from the St Lucia Formation, Campanian IV–V, at locality 73, on the lower reaches of the Mzinene River, Zululand. × 1.

? Lytoceras (Tetragonites) aff. *epigonus* Basse, 1939: 45.
Epigoniceras epigonum Matsumoto, 1942: 671. Usher, 1952: 55, pl. 2 (figs 6–7), pl. 3 (fig. 1), pl. 31 (fig. 13). Collignon, 1956: 85; 1965*a*: 8, pl. 417 (fig. 1723); 1966: 3, pl. 456 (fig. 1855).
Tetragonites jurianus angolanus Haas, 1952: 12–15, figs 21, 23–25 only.
Tetragonites cf. *epigonus* Howarth, 1958: 9, pl. 1 (fig. 12a–b).
Tetragonites epigonus Matsumoto, 1959: 153, text-fig. 75.

Type

Lectotype (herein designated) is the original of the larger of Kossmat's (1895, pl. 17 (fig. 4a–c)) figured specimens.

Material

Two specimens; a dubious juvenile in the collections of the Durban Museum, figured by Spath (1921*b*, pl. 7 (fig. 3)) from the Umzamba Formation of Late Santonian or Early Campanian age, locality 1, the mouth of the Umzamba River, Transkei (Pondoland), and a further specimen, BMNH C78838 from the St Lucia Formation at locality 73 on the lower Mzinene River (Coniacian IV–V).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
BMNH C78838. Maximum diameter is 71 mm. Proportions at:					
	65,0	–	31,3(48)	–	14,5(22)
	51,5	28,5(55)	26,0(50)	1,09	12,0(23)
From Kossmat (1895: 135)					
	59,0	27,0(46)	26,0(44)	1,04	15,0(25)
	23,0	11,0(44)	10,0(43)	1,1	7,0(30)

Description

The coiling is involute, the whorls expanding at a moderate rate. The whorl section is slightly depressed, with the greatest breadth close to the umbilical shoulder. The umbilicus is small (22 % of the diameter) and relatively deep, with a high, subvertical wall. The umbilical shoulder is abruptly rounded whilst the sides are somewhat flattened and convergent, the ventro-lateral shoulders distinct and the rather wide venter broadly rounded.

The shell surface is corroded, and no trace of ornament remains. Traces of seven constrictions are, however, visible on the outer whorl, each associated with a low, rounded rib. The constrictions arise at the umbilical seam, pass straight up the umbilical wall, sweep forwards across the umbilical shoulder and are markedly prorsiradiate and slightly concave across the flanks; they flex distinctly backwards over the ventro-lateral shoulders, and there is a broad, shallow ventral sinus. The sutures are not exposed.

Discussion

The juvenile specimen noted by Spath (1921*b*; 1922, pl. 4 (fig. 1a–c)) is difficult to place with certainty, but the lack of ornament, relative proportions, umbilical wall and flank shape all match closely with Kossmat's (1895, pl. 17 (fig. 5a–b)) smaller specimen. The authors' other specimen, although poorly preserved, has proportions, whorl section and constrictions, all of which suggest reference to Kossmat's species.

Occurrence

Tetragonites epigonus is a long-ranging form known from the Turonian to the Campanian. Its geographic distribution includes Antarctica, Angola, Madagascar, Japan, southern India, British Columbia, south Patagonia, north Africa and southern France. In South Africa the Pondoland occurrence can be dated no more firmly than Late Santonian to Early Campanian. The Zululand example is firmly dated as Coniacian IV–V.

Genus *Saghalinites* Wright & Matsumoto, 1954

Type species

Ammonites cala (Forbes, 1846: 104, pl. 8 (fig. 4a–c)) by original designation of Wright & Matsumoto (1954: 110).

Diagnosis

Very evolute tetragonitids with a low expansion rate, the whorls being slightly depressed. The whorl section is typically rounded when young, becoming distinctly octagonal during later growth stages in most species. The shell surface is smooth, or bears only growth striae. Constrictions are consistently present, and may be weak to strong, straight or sinuous. The suture is relatively simple, with trifid major saddles, and a retracted suspensive lobe.

Discussion

The name *Saghalinites* was introduced by Shimizu in 1934 as a *nomen nudum*; validation extends from the work of Wright & Matsumoto in 1954. Originally proposed as a subgenus of *Epigoniceras* Spath, 1925, the work of Howarth (1958), Matsumoto (1959) and Wiedmann (1962*a*, 1962*b*, 1973) suggests that *Epigoniceras* does not bear separation from *Tetragonites sensu stricto*, as noted elsewhere (p. 151). Howarth and Matsumoto have treated *Saghalinites* as a subgenus of *Tetragonites*, whilst Birkelund (1965) and Wiedmann (1962*a*), amongst others, have given it full generic status. Wiedmann (1973: 589) has subsequently suggested that *Saghalinites* is no more than a synonym of *Tetragonites*. In the authors' views, however, the features of the type species and other well-known Santonian to Maastrichtian species referred to the genus indicate a distinct monophyletic offshoot from contemporaneous *Tetragonites* which merits generic separation; the group appears as distinctive as the bulk of the genera of Tetragonitaceae.

Saghalinites is readily separable from *Pseudophyllites* Kossmat, 1895, in that that genus is inflated, very involute, and typically has a rounded whorl, higher than wide, and is ornamented by longitudinal and transverse striae, whilst the suture line is highly subdivided and there are no constrictions.

Tetragonites Kossmat, 1895, is also typically more inflated, with a higher expansion rate, and more involute coiling.

The origin of *Saghalinites* clearly lies in *Tetragonites*, from which it evolved in the Late Santonian (or possibly the Coniacian, according to Collignon (1956: 82)).

The following species and varieties have been referred to the genus:

1. *Saghalinites cala* (Forbes) (1846: 104, pl. 8 (fig. 4a–c)). Campanian to Maastrichtian.
2. *Saghalinites nuperus* (Van Hoepen) (1921: 13, text-fig. 8, pl. 3 (figs 3–4)). Santonian to Lower Campanian.
3. *Saghalinites zeugitanus* (Pervinquière) (= *Tetragonites cala* var. *zeugitana* Pervinquière, 1907: 79, pl. 3 (fig. 3a–b)). ? Santonian.
4. *Saghalinites zelandicus* Shimizu, 1935 (= *Gaudryceras politissimum* Marshall (*non* Kossmat), 1926: 143, pl. 20 (fig. 3), pl. 28 (figs 1–2), but is, in fact, a crushed *Anagaudryceras particostatum* (Marshall); fide Henderson 1970).
5. *Saghalinites kingianus* (Kossmat, 1895) (= *Ammonites cala* Stoliczka (*non* Forbes), 1865: 153, (*pars*) pl. 75 (fig. 4)). ? Santonian to Campanian.
6. *Saghalinites kingianus* (Kossmat) var. *involutor* Paulcke (1906: 174, pl. 17 (figs 3–4)). Campanian.
7. *Saghalinites wrighti* Birkelund (1965: 30, pl. 1 (fig. 5), pl. 2 (figs 1a–c, 5a–c), pl. 3 (fig. 1), text-figs 14–25). Maastrichtian.

Occurrence

Saghalinites first appears in the Santonian and ranges to the Lower Maastrichtian. Species have a wide geographic distribution; there are records from Antarctica, south Patagonia, Zululand, Madagascar, South Africa, Japan, Sakhalin, southern India and Greenland.

Saghalinites cala (Forbes, 1846)

Figs 10A–B, 11A–B, 12D–G, 13A–B, E–K, ? C–D, 14A–F, 15A–F

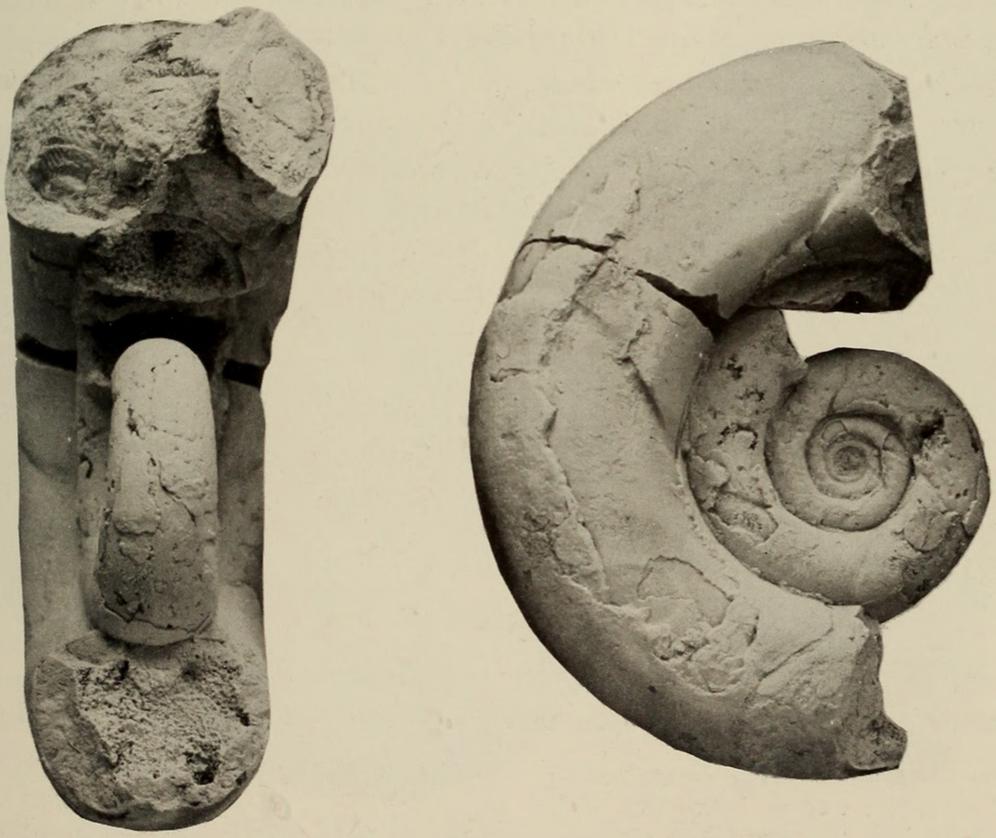
Ammonites cala Forbes, 1846: 104, pl. 8 (fig. 4a–c). *Non* Kossmat, 1895: 153, pl. 75 (fig. 4) =*Saghalinites kingianus* (Kossmat).
Lytoceras (*Tetragonites*) *cala* Kossmat, 1895: 136, pl. 17 (fig. 12a–d).
non *Tetragonites* cf. *cala* Anderson, 1902: 84. Yabe, 1915: 16, pl. 1 (fig. 7), pl. 3 (fig. 2) =*Saghalinites nuperus* Van Hoepen.
?*Tetragonites* aff. *cala* Woods, 1906: 335, pl. 41 (fig. 7a–c).
Tetragonites cala (Forbes) var. *zeugitana* Pervinquière, 1907: 79, pl. 3 (fig. 30), text-fig. 18.
non *Tetragonites cala* Kilian, 1922: 176.
Tetragonites cala Shimizu, 1935: 181.
Saghalinites cala Spath, 1953: 9. Collignon, 1956: 99.
Tetragonites (*Saghalinites*) *cala* Howarth, 1958: 10, pl. 1 (fig. 11a–b).

Type

The lectotype is Forbes's original figured specimen, BMNH C51057, from the Valudayur Beds (Campanian–Maastrichtian) of Pondicherry, southern India.

Material

The authors have numerous specimens, as follows: SAS H163/E1, E2 and E6, H163/3, H163B/2, 4 and 5, H163C/2 and 12, H163G/1, all from locality 20 south of Lake Mfuthululu, east-south-east of Mtubatuba (Maastrichtian I–II); BMNH C78840–43 from locality 113 at the south-eastern corner of the Nibela Peninsula, Lake St Lucia (Campanian IV); SAS Z2267–2267e from this locality and to the area to the immediate west; SAS H104/1 from locality 117 at the north-eastern tip of the southern Peninsula (Campanian IV); SAS Z2242 and 2248a–b, H119/11, H115/10 and 11 from locality 119; BMNH C78862 and C78863 from locality 120; BMNH C78861 from locality 121, The Coves, on the eastern shores of the southern Peninsula (Campanian III–IV); BMNH C18857–60 from locality 124 north of Fanies Island Rest Camp on the eastern shores of the southern Peninsula (Campanian III–IV); BMNH C78856 from locality 126, south of the Camp (Maastrichtian II); BMNH C78853–C78855 from locality



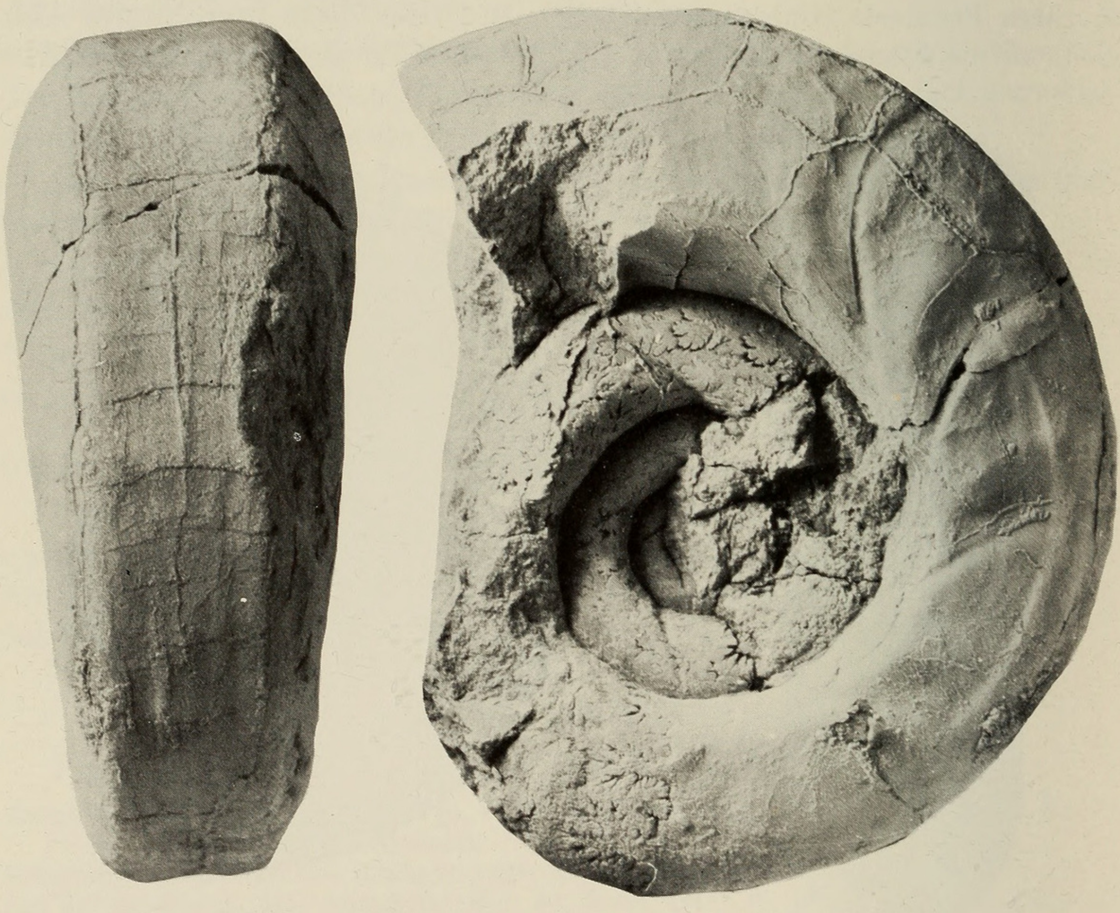
A B

Fig. 10. *Saghalinites cala* (Forbes). BMNH C51058, the original of Kossmat (1895, pl. 17 (fig. 12a–d)), from the Valudayur Beds (Campanian–Maastrichtian) of Pondicherry, southern India. × 1.

132; BMNH C78844 and SAS specimens A1252, 2087, H60F/6, 60H/6 and 16217 from locality 133; BMNH C78845–C78852, and SAS specimens H63/2, 10, 13–14, 22–25, H61/1, 2, 5, 7, 9, 12, 18, H64/1–4, 6, 9, and Z2210a–k from locality 134 in the area of Charters Creek Rest Camp, Lake St Lucia (Maastrichtian I); and SAS H66/1 from locality 135, Makakatana Bay, Lake St Lucia (Maastrichtian I). There is a single juvenile specimen, SAM–4808, from the Umzamba Formation at locality 1, the mouth of the Umzamba River, Transkei (Pondoland) (Late Santonian to early Campanian) which may belong here.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Lectotype					
BMNH C51057	32,3	13,7(42)	9,9(31)	1,38	14,4(45)
BMNH C51058	78,8	30 (38)	23,9(30)	1,25	37,4(47)
SAS H60/12	66,8	—	20,5(30)	—	31,2(46)



A B

Fig. 11. *Saghalinites cala* (Forbes). SAS H163b/2, from the St Lucia Formation, Maastrichtian I–II, at locality 20, south of lake Mfuthululu, east south-east of Mtubatuba, Zululand. The specimen shows coarse lateral folds associated with constrictions, a distinctly sulcate venter, and spiral ridges on both flank and venter. × 1.

Lectotype		D	Wb	Wh	Wb/Wh	U
SAS H61/11		76,5	29,2(38)	21,9(28)	1,33	36,1(47)
SAS H163/D		89,0	38,5(43)	28,2(31)	1,36	40,5(45)
BMNH C78855	at	28,2	11,1(39)	9,4(33)	1,18	12,4(44)
	at	63,0	23,3(37)	18,5(29)	1,25	30,0(47)
BMNH C78843		91,8	–	29,7(32)	–	42,0(46)
BMNH C78863		99,5	–	31,8(32)	–	46,4(46)
SAS Z2270k		60,5	21,5(35)	18,5(31)	1,16	28,5(47)
SAS A1214		88,5	31,5(36)	28,0(32)	1,12	43,0(49)

Description

The bulk of the material occurs either as composite or internal moulds.

Juveniles, up to 30 mm diameter (Figs 12E–F, 13A–D, G–K)

The coiling is evolute, slowly expanding, the whorl section depressed and rounded, the whorl breadth : height ratio being around 1,2, the greatest breadth some distance below mid-flank. The umbilicus is broad, 44 per cent of the diameter, shallow, with a low, rounded, undercut wall. The flanks are rounded, and there is a broad, rounded venter. The surface of the mould is smooth, with six prominent, narrow constrictions. The constrictions arise at the umbilical seam, pass straight up the umbilical wall, and straight across the inner flanks in a markedly prorsiradiate direction, flexing gently backwards across the upper flank and shoulder to form a shallow concave sinus over the siphonal area.

Middle growth stages, 30 to 60 mm diameter (Figs 12D, 14A–F)

The coiling remains evolute, but the whorl section becomes more depressed, the whorl breadth : height ratio being up to 1,25 and the whorl section changing from depressed oval to polygonal.

The umbilical wall increases in height, is flat, and inclined outwards, the umbilical shoulder is abruptly rounded, the whorl sides flattened and convergent, the ventrolateral shoulder abruptly rounded, the venter, broadly rounded at first, becomes flattened, and in some cases concave. Constrictions become increasingly flexed, sweeping forwards over the inner flanks, flexing backwards at mid-flank and developing a broad, shallow but distinct ventral sinus. The number of constrictions increases, with up to eight per whorl in some specimens.

Many specimens show a range of structures associated with the siphonal band (Fig. 14A, D), as discussed below.

60 mm Onwards (Figs 11A–B, 12G)

The largest specimens present are still incomplete at 100 mm and are the largest known representatives of the genus. Up to two-thirds of the outer whorl is body chamber in these specimens. The whorl section is polygonal, as in middle growth stages, but there is an increase in the degree of ventral concavity, and many specimens develop a low, but distinct, rounded siphonal ridge and related structures.

Constrictions become stronger, deeper, closer spaced and more markedly flexed on body chambers, and there is a tendency for the lower part of the flank between constrictions to become irregularly swollen (Fig. 11A–B). In other specimens, broad, flexuous folds are present on the flanks, and seem to represent an exaggerated development of this feature. Yet other specimens show low, rounded, spiral ridges on their flanks (Fig. 13E–F).

The few external moulds of the outer shell surface available suggest that it

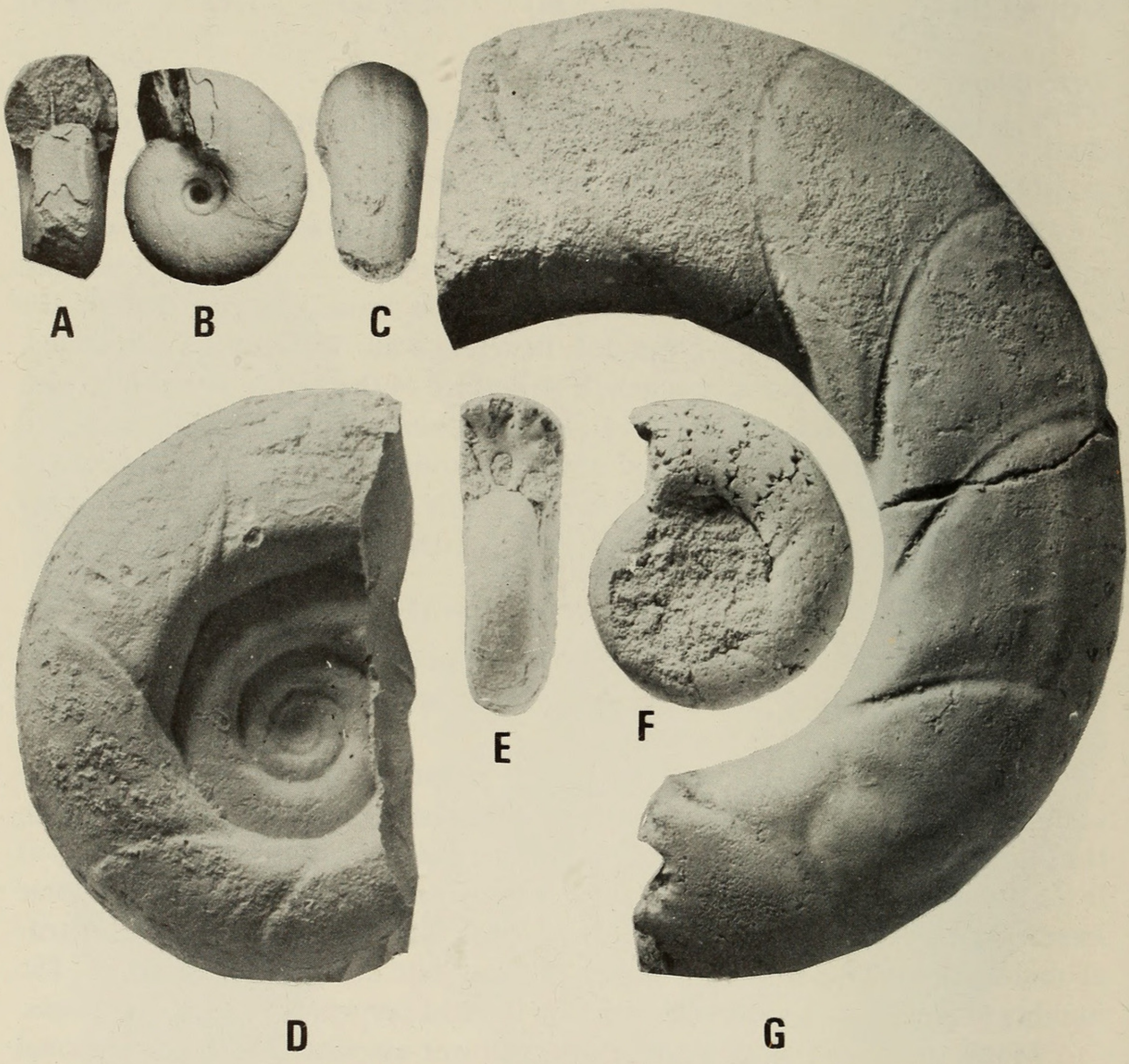


Fig. 12. A–C. *Tetragonites superstes* Van Hoepen. TM 7029, from the late Santonian–early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. D–G. *Saghalinites cala* (Forbes). D. A silicone mould taken from BMNH C78841, from the St Lucia Formation, Campanian IV, at the south-eastern corner of the Nibela Peninsula, Lake St Lucia, Zululand. E–F. BMNH C78856, from the St Lucia Formation, Maastrichtian II, at locality 126, south of Fanies Island Rest Camp, on the eastern shores of the southern Peninsula, Lake St Lucia, Zululand. G. BMNH C78863, from the St Lucia Formation, Campanian III–IV, locality 120, The Coves, on the eastern side of the southern Peninsula, Lake St Lucia, Zululand. A–D, G, × 1; E–F, × 2.

bore faint growth striae, parallel to the constrictions, whilst the constrictions are themselves rather less conspicuous on the shell exterior, being associated with a low, collar-like rib (Fig. 12D).

The external suture line (Figs 14A–C, 15) is rather simple, with a large first lateral saddle (E/L), and a smaller second lateral saddle (L/U_2), both of which are irregularly trifid. The suspensive lobe is strongly retracted, the auxiliary lobes and saddles decreasing rapidly in size. The lateral lobe (L) is markedly bifid.

The internal suture has a deep dorsal lobe and a narrower lateral lobe

Fig. 13. *Saghalinites cala* (Forbes). A–B, G–K. BMNH C78855, from the St Lucia Formation, Maastrichtian I, at locality 132, near Charter's Creek Rest Camp, Lake St Lucia, Zululand. E–F. BMNH C78851, from the St Lucia Formation, Maastrichtian I, near Charter's Creek Rest Camp, Lake St Lucia, Zululand. The specimen is an internal mould of a body chamber lacking constrictions, and showing lateral and ventral spiral ridges. C–D. SAM–4808, best referred to as *Saghalinites* cf. *cala* (Forbes) ?, from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. A–B, × 2; C–K, × 1.

extending to about half the depth. The first saddle is tall and narrow, the second much smaller (Fig. 14B, F).

Discussion

The large number of specimens available show very variable adult features, especially the nature and development of constrictions and lateral folds on the body chamber, the degree of concavity of the venter and the extent of the siphonal band. In spite of this, the authors feel confident in referring their specimens to Forbes' species on the basis of the comparable and distinctive ontogenetic changes, the markedly similar polygonal whorl section of adults, distinctly sigmoidal constrictions and overall comparable relative proportions.

Comparable variability in whorl section and venter form has been described in *Saghalinites wrighti* from the Maastrichtian of west Greenland (Birkelund 1965: 30 et seq., especially text-figs 14–20). *S. cala* and *S. wrighti* can, however, be differentiated on the basis of the absence of constrictions on the early whorls of *S. wrighti*, the fewer constrictions on the later whorls, and their straight rather than flexuous course.

S. cala can readily be separated from both *S. nuperus* and the doubtful *S. kingianus* on the basis of its sinuous rather than straight constrictions, and the development of a polygonal whorl section during later growth stages rather than the rounded section retained by these forms.

Pervinquière's *Lytoceras* (*Tetragonites*) *cala* var. *zeugitana* (1907: 79, pl. 3 (fig. 30a–b)) is based on a specimen only 13 mm in diameter and was separated from the typical form on the basis of the more angular, trapezoidal whorl section and more flexuous constrictions. It seems doubtful if it indeed merits separation in view of the great variability as described above, but since it is said to be of Santonian age, it may conceivably be the juvenile of some other species.

As already noted, many of the present specimens show beautifully ventral structures resembling those described by Grandjean (1910: 502–503), Neaverson (1927), Hölder (1955), Vogel (1959: 510–511), Jordan (1968: 28) and Birkelund (1965: 36).

On internal moulds of body chambers (Figs 11A, 13E–F), the chief structure is a low, flat-topped ridge, marked off on either side by a distinct narrow groove and extending from the aperture to the last septum. When intersected by constrictions, the ridge is weakened, but nevertheless continuous across the constriction. It thus appears that this structure corresponds to the presence of a pair of parallel ridges on the shell interior. On the phragmocone during later growth stages (Fig. 14A, D), this ridge is usually subdued, or its site marked by a band corresponding in width to the ventral lobe. The band is bisected by a continuous median groove, and the surface is covered by fine, longitudinal striae which converge slightly when traced in an apical direction from one suture to the next. In some cases, concave transverse striae are present in the area enclosed by the siphonal lobe, giving rise to a distinctive reticulate pattern (*Schleppstreifen* of Hölder 1955: 374), whilst the ventral band in some juveniles is ornamented by a curious chevron-like striation. The interpretation of these structures is far from clear; Jordan (1968) suggested that the ventral ridge represents the trace of a muscle system controlling a pre-septal gas and fluid-filled space, but it is difficult to reconcile this with the extension of the band throughout the length of the body chamber. The striations of the siphonal band on the phragmocone are typically interpreted as the site of muscle or ligament insertion associated with

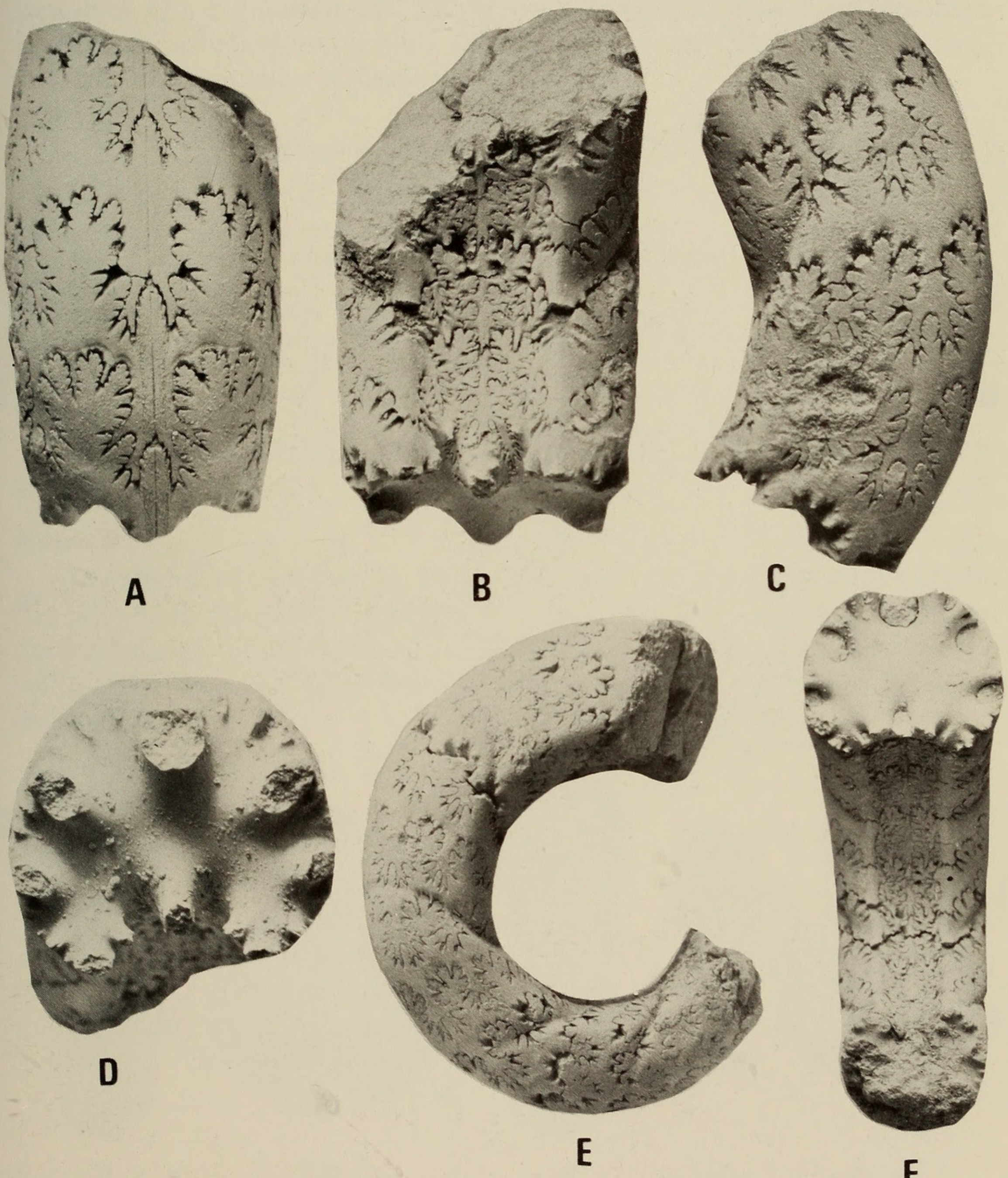


Fig. 14. *Saghalinites cala* (Forbes). BMNH C78855, from the St Lucia Formation, Maastrichtian I, at locality 132 near Charter's Creek Rest Camp, Lake St Lucia, Zululand. A and D show details of ventral structures; B and F the internal suture. A–D, × 2; E–F, × 1.

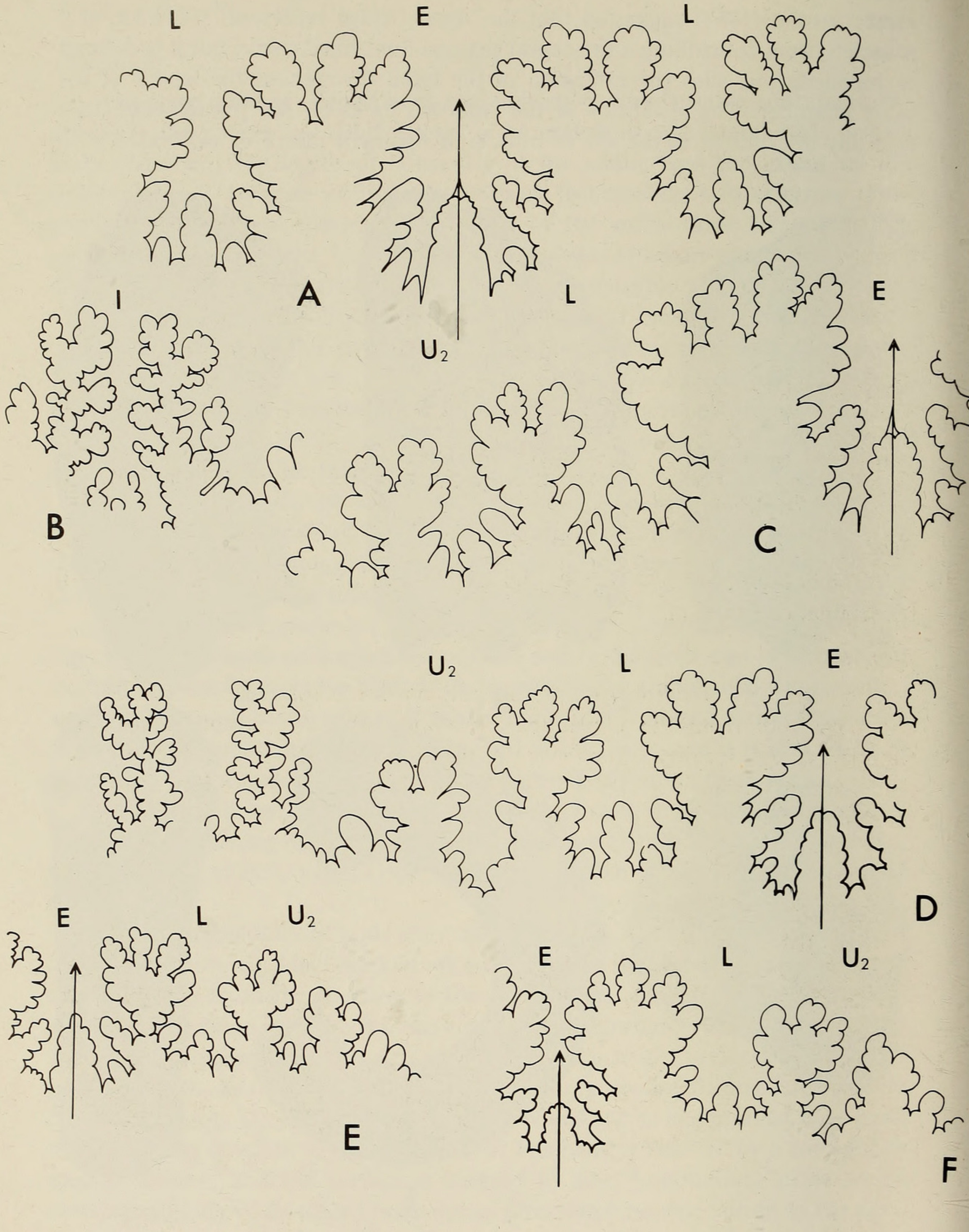


Fig. 15. External and internal sutures of *Saghalinites cala* (Forbes). A–E. BMNH C78545. F. BMNH 78844. All × 6.

the attachment of the siphuncle to the shell, but again there is no convincing evidence for this.

Occurrence

Saghalinites cala is common in Zululand, ranging from the Upper Campanian (Campanian IV) to the Lower Maastrichtian (Maastrichtian II). The doubtful Pondoland occurrence cannot be dated more precisely than Late Santonian to Early Campanian. The type, from southern India, is of Santonian or Campanian age, whilst there are also records from the Campanian of Antarctica and the ?Santonian of Tunisia.

Saghalinites nuperus (Van Hoepen, 1921)

Figs 16A–E, 17A–B, 18

Tetragonites cf. *cala* Yabe, 1915: 16, pl. 1 (fig. 7), pl. 3 (fig. 2).
Tetragonites nuperus Van Hoepen, 1921: 13, pl. 3 (figs 3–4), text-fig. 8. Besairie, 1930: 224, pl. 21 (fig. 3–3a).
Tetragonites cala Basse, 1931: 17, pl. 1 (figs 27–28), pl. 10 (fig. 7).
Saghalinites nuperus Collignon, 1956: 95, pl. 11 (fig. 1a–b); 1966: 3, pl. 456 (fig. 1856); 21, pl. 463 (fig. 1893).

Type

The holotype is TM 532, the original of Van Hoepen (1921, pl. 3 (figs 3–4)) by original designation.

Material

In addition to the holotype, the authors have seen three paratypes, TM 536 and 539, both from the Umzamba Formation of Late Santonian to Early Campanian age, locality 1, the mouth of the Umzamba River, Transkei (Pondoland), and a specimen, BMNH C78839, from locality 84, False Bay, Zululand (Santonian I).

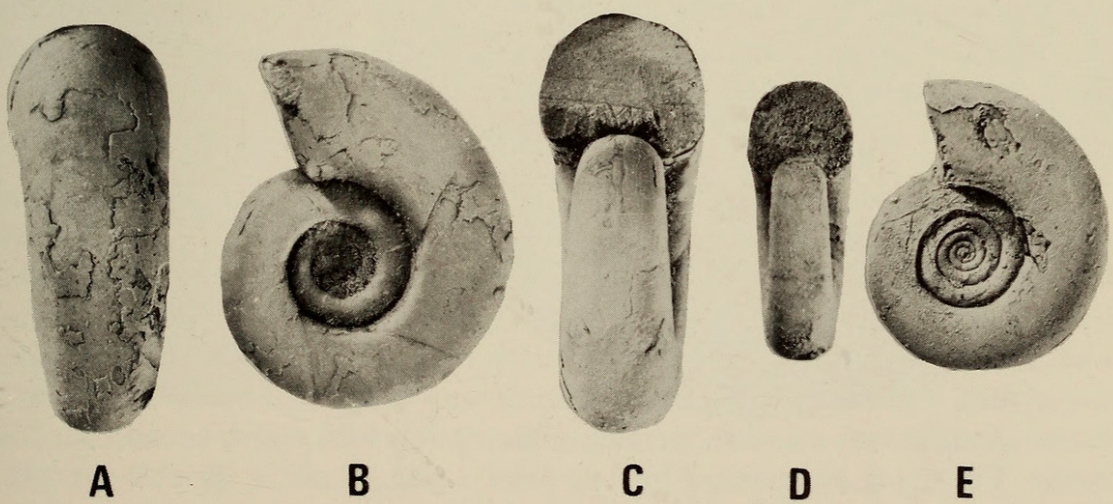


Fig. 16. *Saghalinites nuperus* (Van Hoepen). A–B. The holotype, TM 532. C–E. Paratype, TM 535. Both specimens are from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

Dimensions

	D	Wb	Wh	Wb/Wh	U
Holotype	37,6	15,0(40)	14,0(37)	1,1	15,5(41)
Paratype TM 539	25,2	10,2(40)	9,0(35)	1,13	10,6(42)
Paratype TM 536 (crushed)	15,0	6,0(40)	5,6(37)	1,1	6,2(41)
BMNH C78839	92,0	42,0(46)	35,8(39)	1,17	32,5(35)
From Collignon 1955: 95					
MHNP 2173	53,0	21,0(40)	19,0(36)	1,1	21,0(40)
MHNP 2177	59,0	25,0(42)	21,0(36)	1,19	27,0(46)
MHNP 2179	72,0	31,0(43)	25,0(35)	1,24	30,0(42)

Description

Early whorls, 10–30 mm

The shell is of medium size, evolute, only 25 per cent of the previous whorl being covered, slowly expanding, with a wide umbilicus (*ca.* 40% of diameter). The whorl section is rounded at first in the smallest paratypes, but is depressed throughout later growth, becoming somewhat less depressed as diameter increases; the greatest breadth is a little below mid-flank. The umbilicus is shallow, with a low subvertical wall which merges into a rounded shoulder, which in turn grades imperceptibly into the rounded convergent flanks. The venter is broadly rounded.

The test is ornamented by very fine, dense striae which arise at the umbilical seam, run at first normal to the seam but then sweep strongly forwards over the shoulder and are gently convex and strongly prorsiradiate on the flanks. They sweep gently back across the ventro-lateral shoulder to form a gentle concave ventral sinus. The internal mould is smooth. Four to five constrictions per whorl are present, and occur from a diameter of 5 mm onwards, although initially rather faint. They are rather narrow, and follow a course parallel to the growth striae. On the test, their site is marked by a faint collar.

Adults

The larger specimen, 98,5 mm in diameter, is the largest described individual referred to this species and appears to be adult. The coiling is moderately involute, with depressed whorls and a moderately high expansion rate, a relatively deep umbilicus equal to 35 per cent of the diameter, with a high, subvertical wall. The umbilical shoulder is fairly abruptly rounded, the flanks gently inflated, convergent, with the greatest breadth some way below mid-flank. The ventro-lateral shoulders are rounded, merging imperceptibly with a fairly broad, rounded venter. The test is ornamented by fine, dense striae, of rather variable strength. These arise at the umbilical seam, run normally across the inner part of the umbilical wall, but sweep strongly forwards on the shoulder. They are straight and strongly prorsiradiate on the inner flank, weakly convex at mid-flank, flexed gently backwards across the shoulder and pass across the venter with a slight convex peak. There are five well-developed constrictions on the last half-whorl, which run parallel to the growth striae. On the mould they are relatively deeply incised at the umbilical shoulder, and are narrow and sharply demarcated on flank and venter. They are rather less prominent on the test.

The suture line (Fig. 18) is rather simple, with a large, trifid first lateral saddle (E/L) and a smaller, virtually identical second lateral saddle (L/U_2). The lateral lobe (L) is bifid, the first auxiliary lobe trifid. The suspensive lobe is retracted with several auxiliaries.

Discussion

The holotype and paratypes of this species are rather small, but the larger individuals figured by Collignon (1956, 1966) and the present adult specimen

A B

Fig. 17. *Saghalinites nuperus* (Van Hoepen). BMNH C78839, from the St Lucia Formation, Santonian I, locality 84, False Bay, St Lucia, Zululand. × 1.

show that this species retains a rounded whorl section throughout ontogeny, whilst constrictions become more closely spaced as diameter increases.

Saghalinites nuperus is thus readily separated from *S. cala* and *S. wrighti*, both these species developing a polygonal whorl section at large diameters. The constrictions of *S. cala* are, in addition, markedly flexed with a concave ventral sinus, rather than the peaked constrictions of the adult *S. nuperus*.

Saghalinites kingianus is a difficult species to interpret, being based upon a composite drawing taken from more than one specimen. It appears, however, to lack constrictions to a diameter of 40–50 mm, and when they do appear they are strongly prorsiradiate and straight rather than gently curved as in *S. nuperus*. Until further material is described and adequately figured, *S. kingianus* is perhaps best regarded as a *nomen dubium*.

Paulcke's *Saghalinites kingianum* var. *involutor* (1906: 175, pl. 17 (figs 3–4)) is based on two juveniles having the following dimensions:

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Example 1	11,0	9,0(81)	6,0(54)	1,5	3,5(31)
Example 2	22,0	17,0(77)	12,0(55)	1,42	7,0(32)

It thus differs markedly from *S. nuperus* in relative proportions and, like the typical form, lacks constrictions at this size.

Occurrence

The type material from Pondoland is from an unknown horizon within the Umzamba Formation of Late Santonian to Early Campanian age. Detailed collecting by one of the authors (H.C.K.) at the type section yielded one fragment of *S. nuperus* in the uppermost Santonian just below the Santonian/Campanian boundary. The species is also recorded from the Lower and Middle Santonian and possibly the Upper Santonian/Lower Campanian of Madagascar, and is known from the 'Senonian' of Japan.

Genus *Pseudophyllites* Kossmat, 1895

Type species

Ammonites indra Forbes, 1846 by original designation.

Diagnosis

Tetragonitids with moderately involute whorls when young, expanding to become very involute when adult. Early whorls depressed, with greatest breadth close to mid-flank, later whorls becoming rounded and varying from slightly compressed to slightly depressed. No constrictions; surface of test ornamented by fine transverse growth lines and spiral striae which combine to produce a typical reticulate pattern. Suture very finely divided with asymmetrically trifid or asymmetrically bifid major saddles having subphylloid terminations; suspensive lobe retracted.

Discussion

Pseudophyllites is readily separated from *Saghalinites* Wright & Matsumoto, 1954 in that that genus is very evolute, has a low expansion rate, a rounded to polygonal whorl section, a simpler suture line and prominent constrictions. *Tetragonites* Kossmat, 1895 typically has a rounded to squarish whorl section, a simpler suture, and generally bears striking constrictions throughout ontogeny.

The origin of *Pseudophyllites* clearly lies in *Tetragonites*, from which it evolved in the Late Santonian. Collignon (1956) lists six species which have been referred to that genus, and a further species, *Pseudophyllites skoui* Birkelund (1965: 37, pl. 3 (figs 2–6), text-figs 26–33), has since been added. Species are separated chiefly upon details of whorl section and suture line.

Occurrence

Pseudophyllites species are best known from the Campanian and Maastrichtian, the geographic distribution including Antarctica, South Africa, Madagascar, southern India, New Zealand, northern Australia, Japan, Sakhalin, southern and central Europe, west Greenland, Alaska, British Columbia, California and Brazil. The genus is also said to occur in the upper Santonian of Madagascar (Collignon 1956).

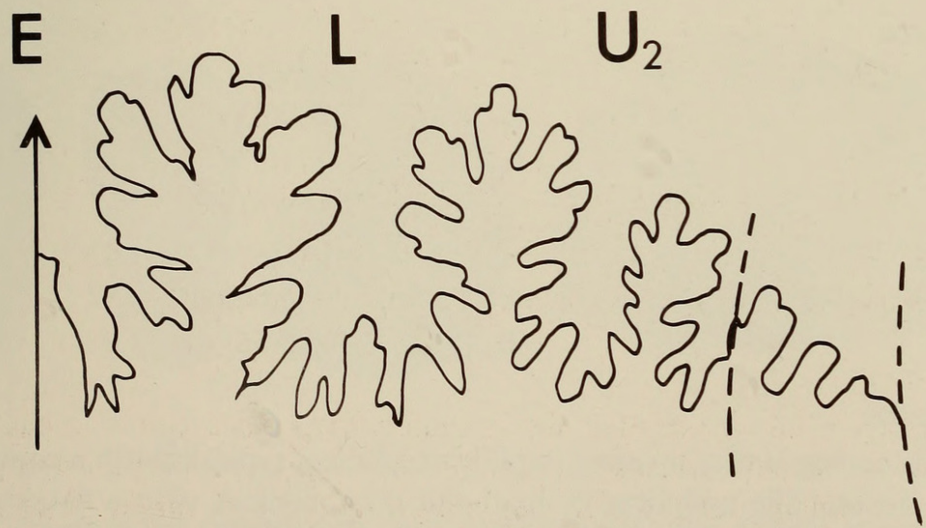


Fig. 18. *Saghalinites nuperus* (Van Hoepen). External suture of TM 532. × 10.

Pseudophyllites indra (Forbes, 1846)

Figs 19A–F, 20–22

Ammonites indra Forbes, 1846: 105, pl. 11 (fig. 7). Stoliczka, 1865: 112, pl. 58 (fig. 2a–b). Whiteaves, 1879: 105, pl. 13 (fig. 2–2a).
?*Gaudryceras colloti* De Grossouvre, 1894: 229, pl. 27 (fig. 8a–b).
Pseudophyllites indra Kossmat, 1895: 137, pl. 16 (figs 6–9), pl. 17 (figs 6–7), pl. 18 (fig. 3). Whiteaves, 1903: 331. Woods, 1906: 334, pl. 41 (fig. 6a–b). ?*Non* Kilian & Reboul, 1909: 14, text-fig. 3 = ?*P. latus*. Spath, 1921*b*: table opposite page 50; 1922: 119 (*pars*). *Non* Marshall, 1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5) = *P. latus*. Nagao & Saito, 1934: 359, text-fig. 10. Collignon, 1938: 24, text-fig. E. Usher, 1952: 57, pl. 3 (figs 2–13), pl. 21 (fig. 17). Collignon, 1956: 90. Matsumoto, 1959: 134. Jones, 1963: 25, pl. 7 (figs 6–7), pl. 8, pl. 29 (figs 7–12), text-fig. 10. Collignon, 1969: 12, pl. 516 (fig. 2032).
Lytoceras indra Boule, Lemoine & Thévenin, 1906: 2, pl. 1 (fig. 1–1b).
Tetragonites virgulatus Van Hoepen, 1921: 11, pl. 3 (figs 1–2), text-fig. 7.
?*Pseudophyllites amphitrite* Maury, 1930: 167, pl. 27 (fig. 1), pl. 28 (fig. 1).
Parapachydiscus catarinae Anderson & Hanna, 1935: 19 (*pars*), pl. 3 (figs 2–3).
Pseudophyllites aff. *indra* Spath, 1940: 43.

Type

Lectotype herein designated, BMNH C51068, figured by Forbes (1846, pl. 11 (fig. 7)) from the Valudayur Group near Pondicherry, southern India.

Material

Six specimens, BMNH C19417 and C19418, TM 531 and 526 (the latter two being the types of *Tetragonites virgulatus* Van Hoepen) from the Late Santonian to Early Campanian, Umzamba Formation at locality 1, the mouth of the Umzamba River, Transkei (Pondoland), SAS H126/2 from locality 106 at the mouth of the Nyalazi River (Campanian I), and SAS H150, from locality 16, south of Mtubatuba (age uncertain).

Dimensions

		D	Wb	Wh	Wb/Wh	U
Lectotype						
BMNH C51068	at	109,3	—	61,5(56)	—	19,4(17)
	at	94,5	44,5(47)	50,0(53)	0,89	15,5(16)
C19417		296,0	148,5(50)	171(57)	0,87	42,0(14)
C19418		70,5	—	35,7(51)	—	13,0(18)
H126/2	at	98,5	53,0(54)	51,5(52)	1,02	18,6(18)
	at	77,5	40,3(52)	43,8(56)	0,92	14,3(18)
H150		109,0	60,0(55)	60,0(55)	1,0	—

Description

The coiling is very involute, rapidly expanding, typically with a compressed whorl section. The umbilicus is small and deep, conical, with a flat, outwards sloping wall. The umbilical shoulder is abruptly rounded, with initially rather flattened, convergent flanks, and an arched, rounded venter. The test is ornamented by fine striae and ridges which arise at the umbilical seam, sweep slightly backwards across the umbilical wall, flex backwards over the shoulder, pass across the flanks in a prorsiradiate direction and may be faintly convex. They sweep backwards across the ventro-lateral shoulder, and cross the venter with a broad, faint, concave ventral sinus. In addition, there are faint, closely spaced spiral striae which combine with the transverse ornament to produce a reticulate pattern on the shell surface.

Internal moulds are smooth, or may bear faint traces of the reticulate ornament. The suture line (Fig. 22) is highly subdivided, with a rather variably sub-

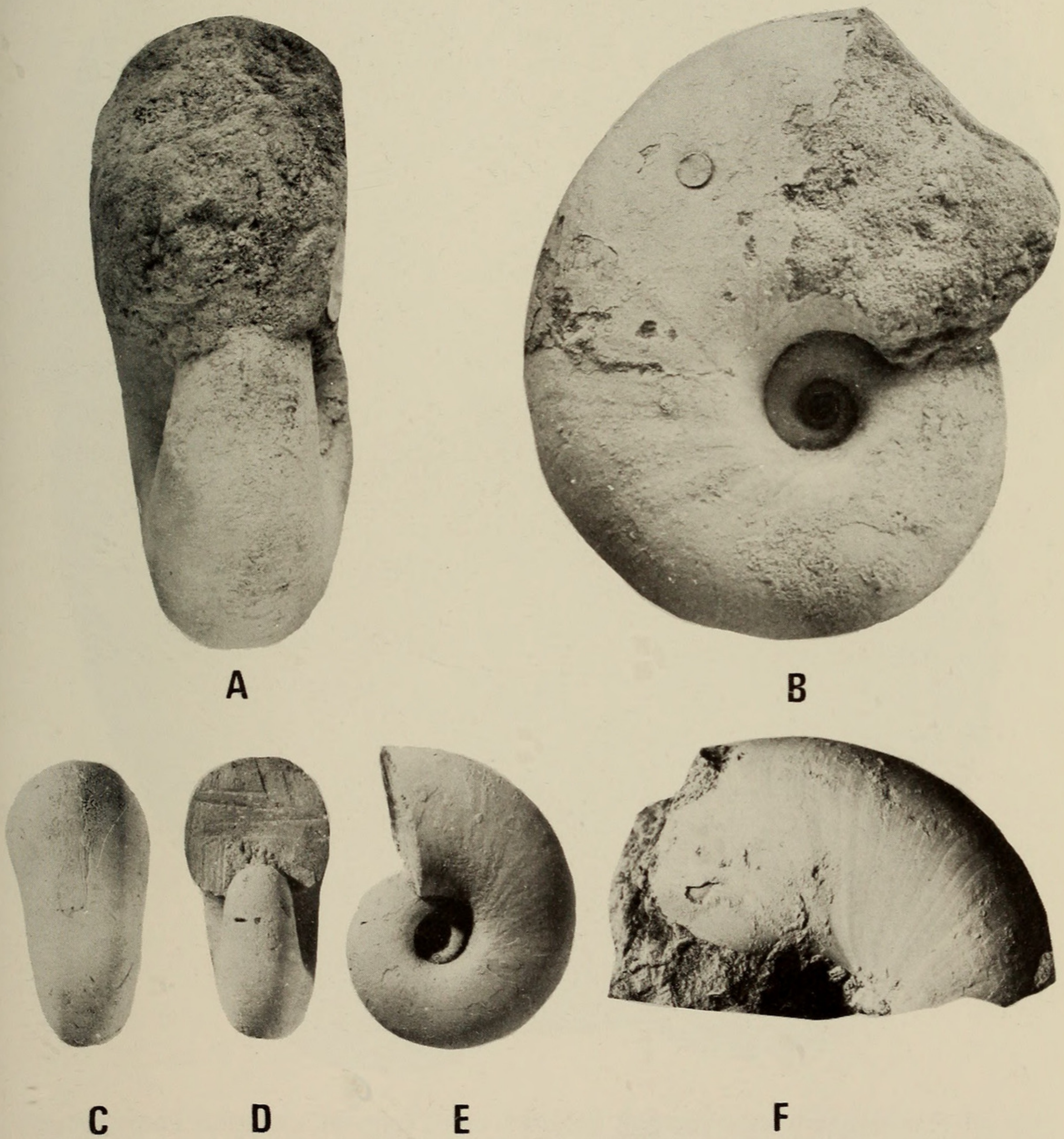


Fig. 19. *Pseudophyllites indra* (Forbes). A–B. BMNH C19418. C–E. TM 431, the holotype of *Tetragonites virgulatus* Van Hoepen. F. TM 526, a paratype of *T. virgulatus*. All specimens are from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland. × 1.

Fig. 20. *Pseudophyllites indra* (Forbes). BMNH C19417, from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. Reduced × 0,5. (British Museum photograph.)

Fig. 21. *Pseudophyllites indra* (Forbes). BMNH C19417, from the Umzamba Formation, of late Santonian to early Campanian age at locality 1, the mouth of the Umzamba River, Pondoland. Reduced × 0,5. (British Museum photograph.)

divided ventral saddle (E) which is often lanceolate in broad outline, a large, irregularly trifid first lateral saddle (E/L), a smaller bifid, second lateral saddle (L/U_2), a deeply incised bifid lateral lobe (L) deeper than the ventral lobe (E), and a retracted suspensive lobe with a large bifid first auxiliary saddle. Saddle terminations are typically subphylloid. The septal face shows two lateral saddles on either side of the internal lobe, and there is a massive septal lobe, well displayed on several of the present specimens.

Discussion

This classic species is characterized by a high expansion rate and rapid increase in whorl height, flattened flanks, fairly narrow venter, and a small, conical umbilicus in which the umbilical wall slopes outward to an abruptly rounded umbilical shoulder.

Pseudophyllites latus (Marshall) (1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5)), of which *Pseudophyllites whangaroaensis* (Marshall) (1926: 153, pl. 20 (fig. 2), pl. 21 (fig. 11), pl. 32 (figs 5–6)), *Pseudophyllites peregrinus* Spath (1953: 7, pl. 1 (figs 6–9)) and *Pseudophyllites skoui* Birkelund (1965: 37, pl. 3 (figs 2–6), text-figs 26–33) are synonyms, is a species known from the Campanian to Maastrichtian of New Zealand, Antarctica, Madagascar and Greenland. From Henderson's (1970: 12 et seq.) recent discussion this form has a generally broader venter than *P. indra*, but shows identical ontogenetic changes and style of shell ornament. The sutures are said to differ, however, the ventral saddle of *P. indra* being lanceolate, that of *P. latus* being spatulate. The umbilical walls also differ, that of *P. indra* sloping distinctly outwards, that of *P. latus* being subvertical.

P. teres (Van Hoepen), a species based chiefly on small specimens, has been separated from *P. indra* on the basis of the compressed, flattened and subparallel flanks and consequently subrectangular whorl section, whilst the umbilical wall is subvertical.

Gaudryceras colloti De Grossouvre (1894: 229, pl. 37 (fig. 8a–b)) from the Upper Campanian of the Basses-Pyrenées, in southern France, is based upon a specimen just under 60 mm in diameter, with the following proportions:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
58,0	27,0(46)	29,5(51)	0,92	10,5(18)

It is preserved as a composite mould, and is deformed. The ornament is of *Pseudophyllites* type, and it is best regarded as a synonym of *Pseudophyllites indra*.

Ammonites postremus Redtenbacher (1873: 115, pl. 26 (fig. 3a–d)) is based upon a series of specimens, the figure showing what may be a *Pseudophyllites*. It has a subrectangular whorl section and vertical umbilical wall; both features clearly separate it from *P. indra*.

Tetragonites virgulatus Van Hoepen (1921: 11, pl. 3 (figs 1–2), text-fig. 7) is based on juvenile *P. indra*; the types are figured here as Figure 19C–E.

Pseudophyllites amphitrite Maury (1930: 167, pl. 27 (fig. 1), pl. 28 (fig. 1)) is based upon a specimen having the following dimensions:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
210	75(35)	120(51)	0,63	45(21)

The ornament matches that of *P. indra*, whilst there is a comparable ventral profile. The whorls are highly compressed, however, but this appears to be due to *post-mortem* crushing; the species is also best considered a synonym of *P. indra*. *Pseudophyllites nereidideditus* Maury (1930: 169, pl. 29 (fig. 1)) appears to be a crushed *Pseudophyllites teres*, as discussed below. The umbilicus and relative proportions readily separates it from *P. indra*.

Occurrence

Pseudophyllites indra ranges from the late Santonian to early Maastrichtian. Its geographic distribution includes South Africa (Zululand and Pondoland), Madagascar, southern India, northern Australia, Japan, Sakhalin, Alaska, British Columbia, California and possibly south-eastern France and Brazil.

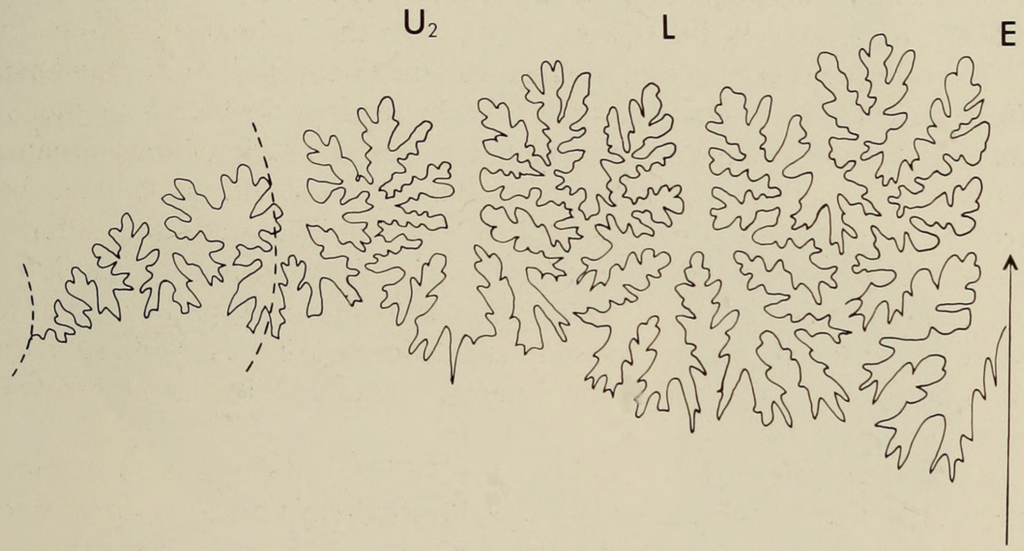


Fig. 22. External suture of *Pseudophyllites indra* (Forbes). TM 531. × 5.

Pseudophyllites teres (Van Hoepen, 1920)

Figs 23A–B, 24A–B

Tetragonites teres Van Hoepen, 1920: 144, pl. 25 (figs 1–2).
Pseudophyllites indra Spath, 1922: 119 (*pars*).
?Pseudophyllites nereidideditus Maury, 1930: 169, pl. 29 (fig. 1).
Pseudophyllites teres Collignon, 1956: 94, pl. 9 (fig. 2–2b); 1969: 14, pl. 517 (fig. 2034).

Type

The holotype is Van Hoepen's original specimen, TM 562, by original designation.

Material

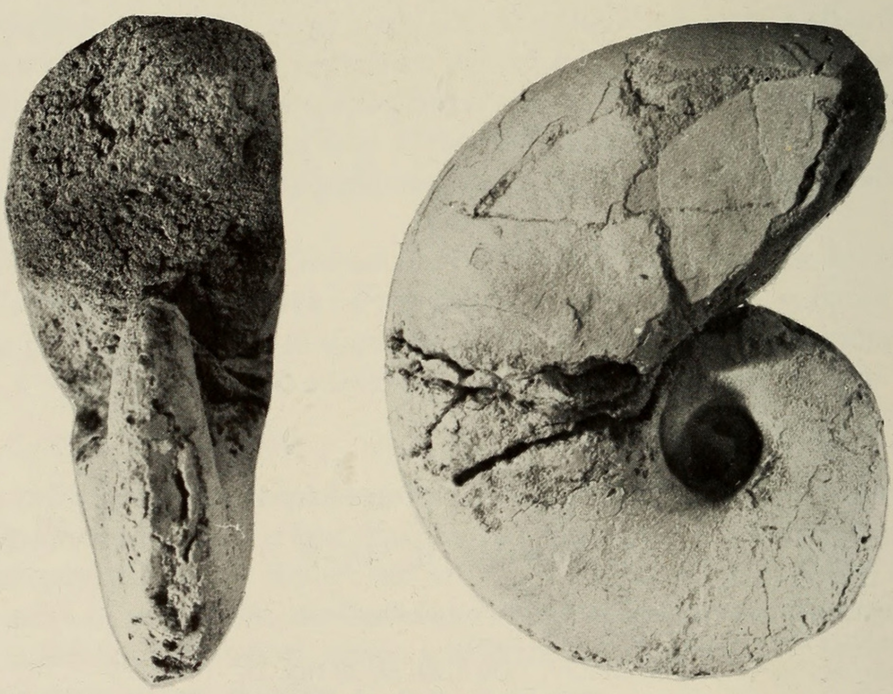
Two specimens, the holotype and BMNH C19415, both from the late Santonian to early Campanian Umzamba Formation at locality 1, the mouth of the Umzamba River, Pondoland.

Dimensions

	D	Wb	Wh	Wb/Wh	U
Holotype					
TM 562 (*a*)	69	—	39(57)	—	14(20)
(*b*)	57	26(46)	31(54)	0,84	—
From Collignon (1956: 94)					
MHNP 2160	51,0	25,0(49)	26,0(51)	0,96	11,0(22)
MHNP 2163	78,0	39,0(50)	42,0(54)	0,93	16,0(21)
MHNP 2164	98,0	43,0(44)	52,0(53)	0,83	19,0(19)
MHNP 2166	115,0	54,0(47)	63,0(55)	0,86	21,0(18)

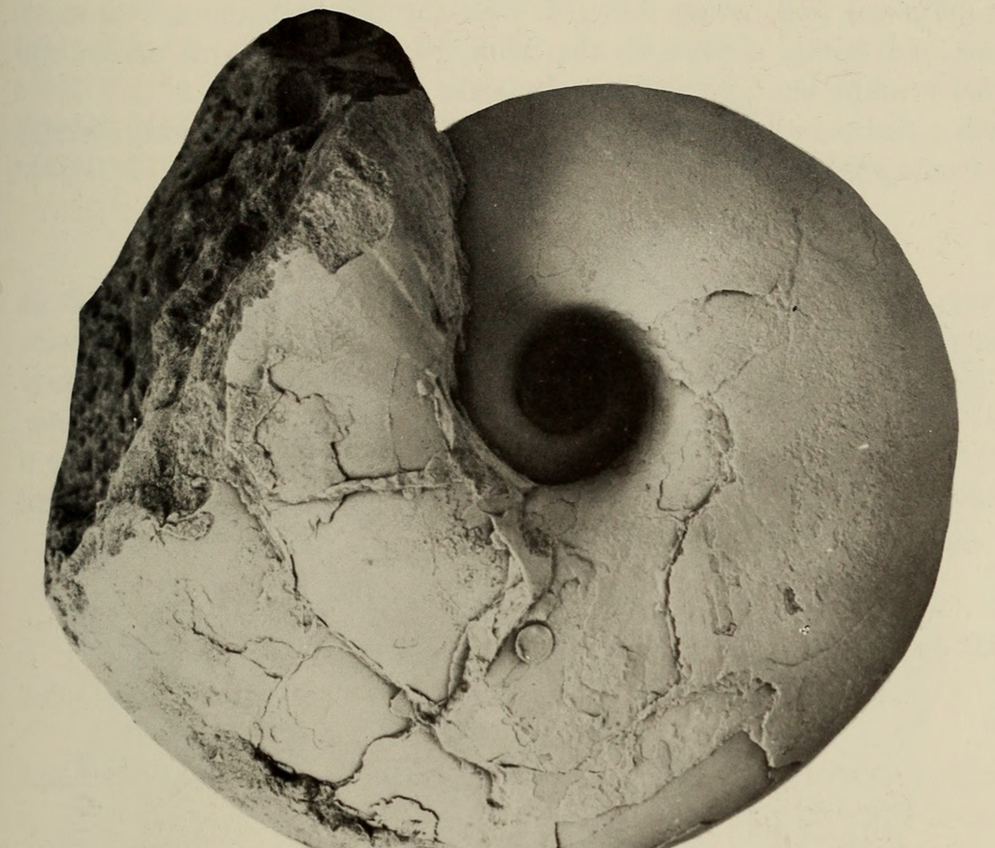
Description

The coiling is involute, rapidly expanding, and compressed (whorl breadth to whorl height ratio is less than 0,96, decreasing with age). The umbilicus is small (20 % of diameter), deep, with a high, subvertical wall and abruptly rounded



A B

Fig. 23. *Pseudophyllites teres* (Van Hoepen). TM 535, the holotype from the Umzamba Formation, of late Santonian to early Campanian age, locality 1, the mouth of the Umzamba River, Pondoland. × 1.



A B

Fig. 24. *Pseudophyllites teres* (Van Hoepen). BMNH C14915, from the Umzamba Formation, of late Santonian to early Campanian age, locality 1, the mouth of the Umzamba River, Pondoland. × 1.

shoulder. The greatest breadth is at the umbilical margin, the inner flanks being flattened and subparallel, with broadly rounded shoulders and venter. Ornament is not well preserved, but consists of fine, dense growth striae which pass back across the umbilical wall, sweep forwards over the shoulder and are strongly prorsiradiate and faintly convex on the flank, passing backwards across the shoulder and running almost normally across the venter.

There is a marked apertural constriction. The suture line is poorly visible, but of the *Pseudophyllites* type.

Discussion

The largest specimens the authors have seen of this species are adult at approximately 100 mm diameter, and at this size the compressed whorls with flattened, subparallel sides, plus the umbilicus with subvertical wall, clearly differentiates this species from *Pseudophyllites indra*, *P. latus* and *P. postrematus*. *Pseudophyllites nereidideditus* Maury (1930: 196, pl. 29 (fig. 1)) appears to be a large crushed example possibly referable to this species. The dimensions given by Maury are as follows:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
210,0	70,0(33)	115,0(55)	0,61	45,0(21)

Occurrence

Santonian–Campanian of Pondoland (Umzamba Formation) and Madagascar. *?* Maastrichtian of Brazil.

Pseudophyllites latus (Marshall, 1926)

Figs 25–26

Pseudophyllites indra Kilian & Reboul, 1909: 14. Marshall, 1926: 152, pl. 20 (fig. 1), pl. 29 (figs 3–5).
Tetragonites latus Marshall, 1926: 149, pl. 20 (fig. 6), pl. 32 (figs 1–2).
Pseudophyllites whangaroaensis Marshall, 1926: 153, pl. 20 (fig. 2), pl. 21 (fig. 11), pl. 32 (figs 5–6).
Pseudophyllites peregrinus Spath, 1953: 7, pl. 1 (figs 6–9). Collignon, 1956: 92, text-fig. 12.
Pseudophyllites latus Henderson, 1970: 12, pl. 1 (fig. 10), pl. 2 (fig. 3), text-fig. 4a–c.
Pseudophyllites skoui Birkelund, 1965: 37, pl. 3 (figs 2–6), text-figs 26–33.

Type

The lectotype, designated by Henderson (1970: 14) is the original of Marshall (1926, pl. 32 (fig. 1)), from the Mata Series (Campanian) of New Zealand.

Material

One specimen only, SAS Z1114, from locality 106 at the mouth of the Nyalazi River (Campanian I).

Dimensions

	D	Wb	Wh	Wb/Wh	U
SAS Z1114	172,0	96,4(56)	94,8(55)	1,02	28,5(17)
From Collignon (1956: 93)					
MHNP 2152	80,0	44,0(55)	40,0(50)	1,1	16,0(20)
MHNP 2154	90,0	51,0(57)	48,0(53)	1,1	16,0(18)
MHNP 2155	127,0	73,0(57)	69,0(54)	1,05	24,0(19)
MHNP 2157	181,0	113,0(62)	101,0(56)	1,1	33,0(18)

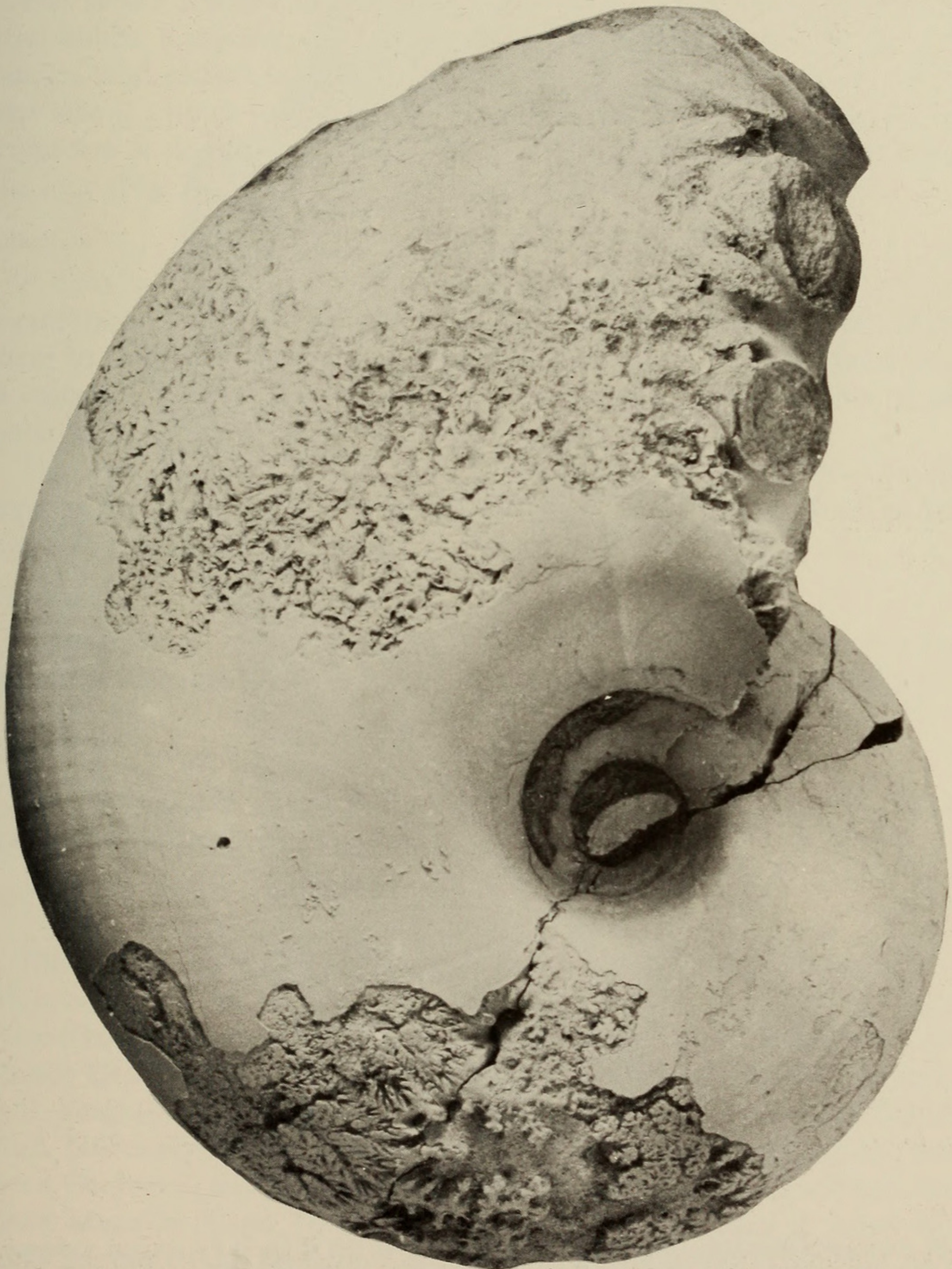


Fig. 25. *Pseudophyllites latus* (Marshall). SAS Z1114, from the St Lucia Formation, Campanian I, locality 106, at the mouth of the Nyalazi River, Zululand. × 0,8.

Description

The specimen is wholly septate, and retains much of the original aragonitic shell. The coiling is very involute, more than four-fifths of the previous whorl being covered, with a slightly depressed whorl section throughout ontogeny. The whorls expand rapidly, the greatest breadth being at the umbilical shoulder. The umbilicus is deep, conical and narrow (17 % of diameter), with a high, flat,

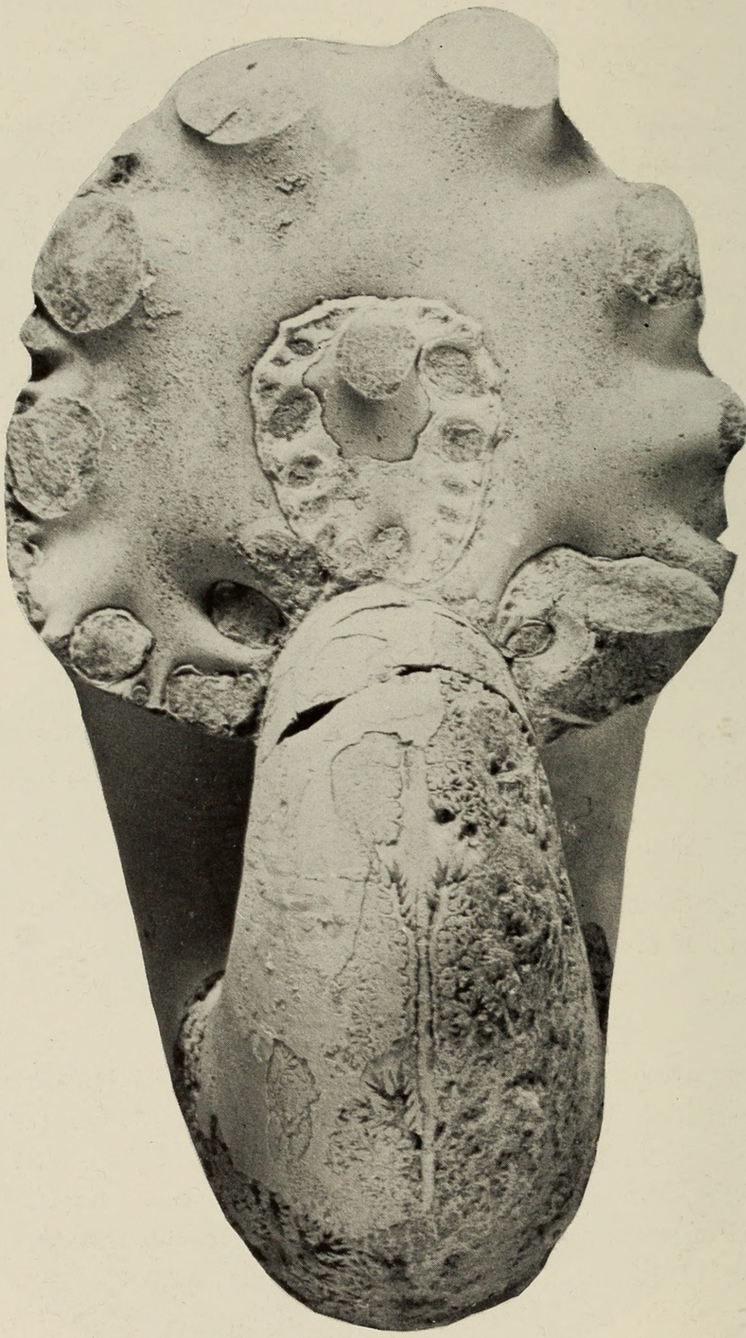


Fig. 26. *Pseudophyllites latus* (Marshall). SAS Z1114, from the St Lucia Formation, Campanian I, locality 106, at the mouth of the Nyalazi River, Zululand. The specimen shows the reticulate ornament clearly, and has the septal lobe well preserved. × 0.8.

subvertical wall. The umbilical shoulder is abruptly rounded, the flanks broadly rounded and convergent, merging with a broadly rounded venter. Ornament consists of fine transverse growth striae and longitudinal ridges which combine to produce a reticulate pattern which is particularly conspicuous on the venter. The transverse striae arise at the umbilical seam, pass straight up the umbilical wall with a shallow concavity, are slightly prorsiradiate and weakly convex across the flanks, and sweep backwards across the ventrolateral shoulders to form a shallow, broad ventral sinus.

The suture consists of a broad, short, moderately subdivided spatulate ventral saddle, a massive, highly subdivided bifid first lateral saddle (E/L) and a smaller bifid second lateral saddle (L/U_2) separated by a symmetrical bifid lateral lobe (L) which is deeper than the external lobe (E). The suspensive lobe includes five or six auxiliary lobes; there are two internal saddles and a massive septal lobe (Fig. 26).

Discussion

P. latus is readily separated from *P. indra* on the basis of its broader whorls, less rapidly increasing height, and much steeper umbilical wall. It differs from *P. teres* in being broader and having convergent rather than subparallel flanks. The spatulate rather than lanceolate ventral saddle is also distinctive. *P. postrematus* has a distinctly rectangular whorl section, as noted above.

The authors agree with Henderson (1970) in regarding *Pseudophyllites peregrinus* Spath, *P. skoui* Birkelund and *P. whangaroaensis* Marshall as synonyms of *P. latus*.

Occurrence

Campanian of New Zealand and Antarctica, Upper Santonian and Campanian of Madagascar, Maastrichtian of Greenland, and Campanian of Zululand.

STRATIGRAPHY

The stratigraphic distribution in south-eastern Africa of the species described herein is illustrated in Figure 27.

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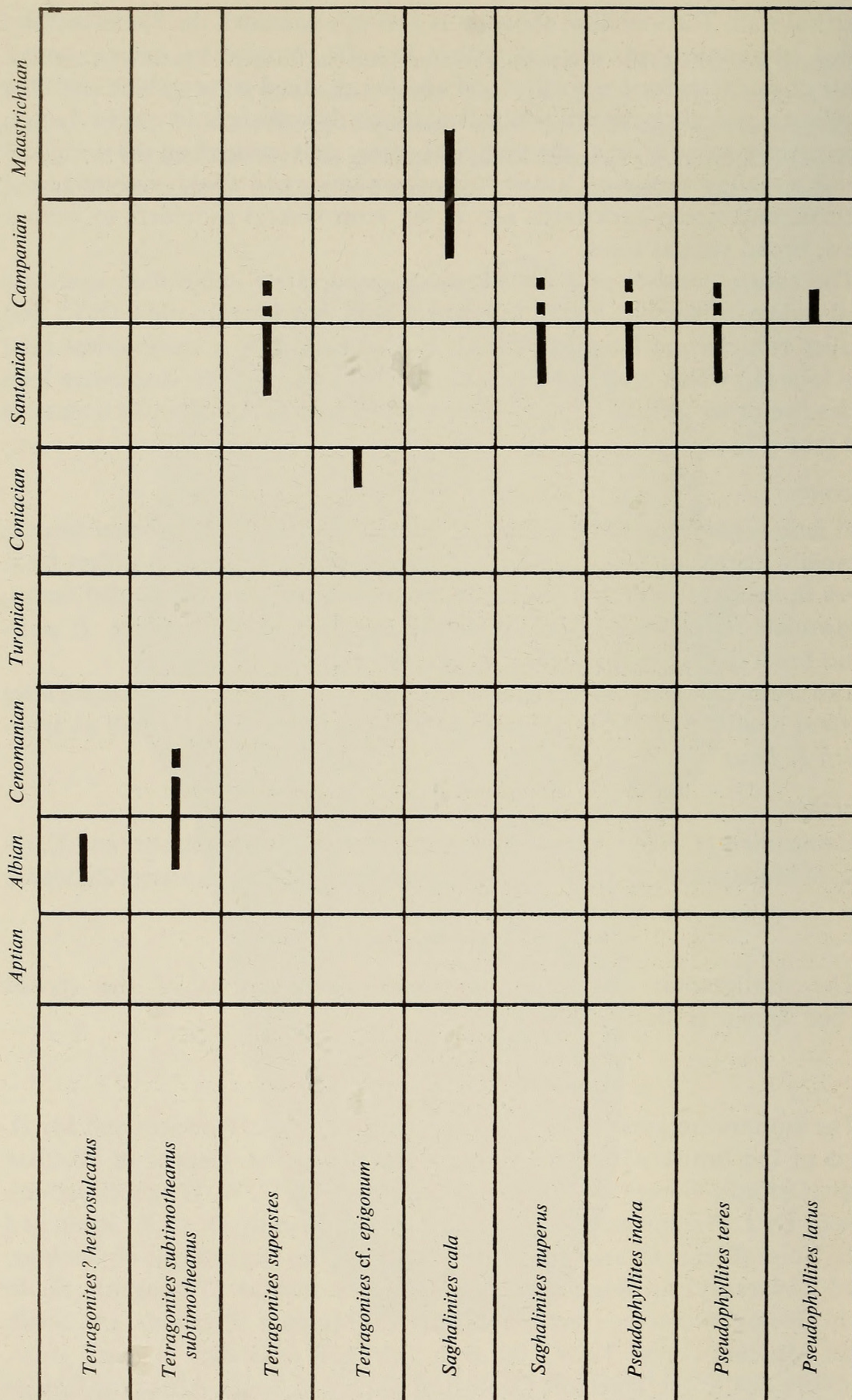

Fig. 27. Stratigraphic distribution of tetragonitids in south-east Africa.

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