N. Jb. Geol. Paläont. Abh.	182	1	1–19	Stuttgart, April 1991

Towards a phylogenetic classification of the Cretaceous ammonites
I. Collignoniceratacea

By

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With 11 figures in the text

Cooper, M. R. (1991): Towards a phylogenetic classification of the Cretaceous ammonites. I. Collignoniceratacea. – N. Jb. Geol. Paläont., Abh., 182: 1–19; Stuttgart.

Abstract: *Pleurotexanites* from the Lower Santonian of Zululand is at the base of a phyletic line which gave rise to multituberculate texanites (*Menabites (Menabites), M. (Bererella), Australiella (Australiella), A. (Delawarella), Bevahites*), for which the new subfamily Menabitinae is proposed. Consequently, the family Texanitidae is resurrected for this and the nominate subfamily, necessitating elevation of Collignoniceratidae to superfamily rank (Collignoniceratacea). The latter taxon plus Acanthocerataceae and Sphenodiscaceae are united as the monophyletic suborder Acanthoceratina, the sister taxon of the Hoplitina (Desmocerataceae + Hoplitaceae).

Zusammenfassung: Ein neu entdeckter *Pleurotexanites* aus dem Untersanton von Zululand steht am Anfang einer Linie multituberculater Texaniten mit *Menabites (Menabites), M. (Bererella), Australiella (Australiella), A. (Delawarella)* und *Bevahites*, für die eine neue Unterfamilie (Menabitinae) vorgeschlagen wird. Deshalb müssen für diese und die Nominat-Unterfamilie die Texanitidae als Familie wiedereingeführt werden. Entsprechend erhalten die Collignoniceratidae den Rang einer Superfamilie (Collignoniceratacea), die zusammen mit den Acanthocerataceae und Sphenodiscaceae die monophyletische Unterordnung der Acanthoceratina bilden, der Schwestergruppe der Hoplitina (Desmocerataceae und Hoplitaceae).

The texanites are an important pandemic family of late Cretaceous ammonites. Typically more or less evolute, they are mostly compressed, square whorled ammonites with a nodate to entire siphonal keel and strongly ribbed ornament with up to 12 rows of tubercles. They constitute an important component of many late Cretaceous faunas, and form the basis for the Upper Coniacian to mid-Campanian ammonite zonation in a number of areas. As such, an understanding of their phylogeny is of some consequence. The purpose of this paper is (1) to record *Pleurotexanites* from the Lower Santonian of Zululand for the first time, and (2) to reassess the taxonomy of the group in the light of this discovery and other phylogenetic evidence.

0077-7749/91/0182-0001 $ 4.75

Systematic palaeontology

Order Ammonitida HYATT, 1889

Remarks: As currently viewed, this taxon includes the suborders Xipheroceratina SPATH (nom. transl. herein ex Xipheroceratida), Perisphinctina BESNOSOV & MIKHAILOVA, Haploceratina BESNOSOV & MIKHAILOVA, Hoplitina SPATH (nom. transl. herein ex Hoplitida) and Acanthoceratina HYATT (Fig. 1).

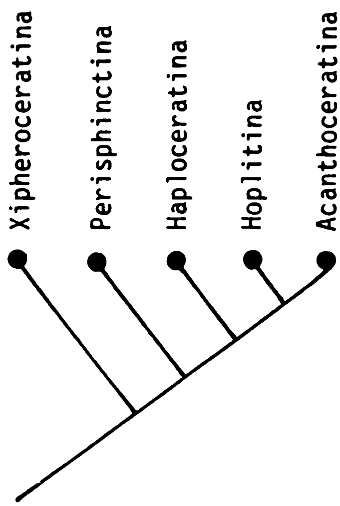

Fig. 1. Hypothesized relationships among later Ammonitida.

Suborder Acanthoceratina HYATT, 1900

(nom. transl. herein ex Acanthoceratida HYATT, 1900).

Remarks: The essence of phylogenetic taxonomy is monophyly (HENNIG 1966), which remains the only natural criterion on which to establish higher taxa. Consequently the suborder Acanthoceratina (HYATT 1900) is resurrected for the superfamilies Acanthocerataceae, Collignonicerataceae and Sphenodiscaceae (nom. transl. herein ex Sphenodiscidae), the latter introduced for weakly ornamented oxycones of the families Coilopoceratidae and Sphenodiscidae which are believed to be monophyletic (WRIGHT 1981). Acanthoceratina are descended monophyletically (WRIGHT 1981) from Hoplitina (Desmocerataceae + Hoplitaceae), the latter taxon unified by sutural characters (KULLMANN & WIEDMANN 1970; WIEDMANN & KULLMANN 1981). Hoplitina, in turn, are derived from Haploceratina (KULLMANN & WIEDMANN 1970; WRIGHT 1981) whose ancestry lies in Perisphinctina (DONOVAN et al. 1981).

Superfamily Collignoniceratacea WRIGHT & WRIGHT, 1951

(nom. transl. herein ex Collignoniceratidae WRIGHT & WRIGHT, 1951)

Remarks: The Collignoniceratidae are elevated to superfamily status to comprise the nominate family (Collignoniceratinae, Barroisiceratinae) which gave rise, independently, to Peroniceratidae (Peroniceratinae, Prionocyclinae), Texanitidae (Texanitinae, Menabitinae nov.) and Tissotiidae. It is believed to be a monophyletic grouping. Fundamental to this phylogenetic interpretation is the basic dichotomy within the Collignoniceratinae as currently perceived (Fig. 2). Thus *Collignoniceras*, the earliest known genus within the superfamily, independently gave rise to *Subprionocyclus* and *Prionocyclus* in the late Turonian (HAAS 1946; MATSUMOTO 1965). Whereas the former taxon is ancestral to Barroisiceratinae and Tissotiidae, the *Prionocyclus* stock ultimately gave rise to Peroniceratinae. These phylogenies are reflected in the nature of the siphonal keel; in *Subprionocyclus* and its descendants the keel is coarsely serrated with notches corresponding in number to external tubercles, whereas in *Prionocyclus* and its descendants the keel is finely serrated, with more notches than external tubercles (Fig. 3). As a result, the subfamily Collignoniceratinae is restricted here to the lineage *Collignoniceras* → *Subprionocyclus* → *Reesidites* and the subfamily Prionocyclinae (BREISTROFFER 1947) is resurrected for primitive unicarinate peroniceratids with a finely serrated siphonal keel, viz. *Prionocyclus*, *Lymaniceras*, *Germariceras* etc. Significantly some Peroniceratinae, e.g. certain *Gauthiericeras* (WRIGHT 1957) and *Peroniceras (Zuluiceras)* species (KLINGER & KENNEDY 1984 figs. 77, 82), preserve a finely serrated keel, confirming their ancestry in Prionocyclinae.

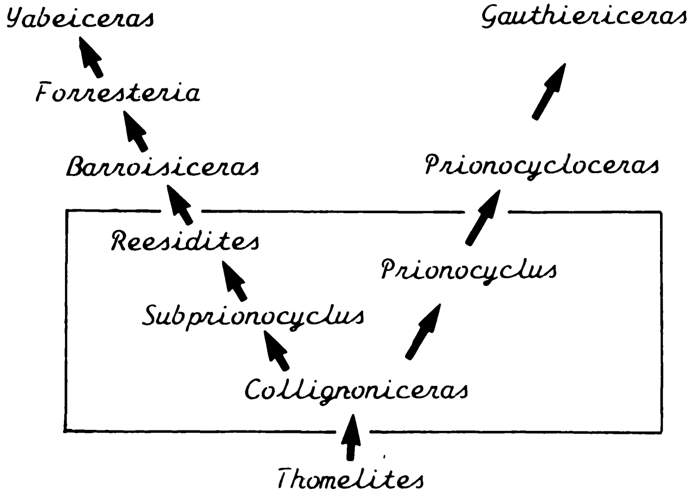

Fig. 2. Phylogenetic relationships among stem Collignoniceratinae auctorum (boxed) and near allies.

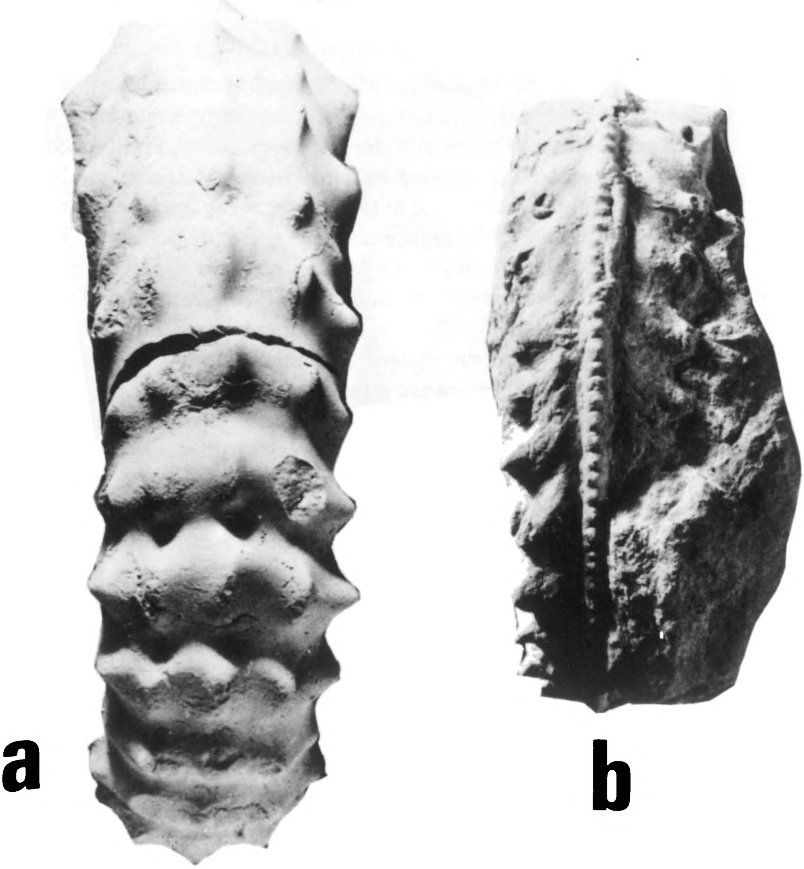

Fig. 3. Ventral views of (A) *Collignoniceras woollgari* (MANTELL) an (B) *Prionocycloceras carvalhoi* (HOWARTH), showing the different nature of the siphonal keels.

Family Texanitidae COLLIGNON, 1948

Remarks: The most recent review of the family (KLINGER & KENNEDY 1980) derives texanites polyphyletically from both collignoniceratine and peroniceratine ancestors, thus making the group taxonomically unsound. Contrary to this view, the writer follows WRIGHT (1957, 1979, 1981) and MATSUMOTO (1959, 1970) in deriving texanites monophyletically from *Subprionocyclus* of the Collignoniceratinae, a view supported by coarse undulations to the siphonal keel of many early texanites.

Fig. 4. *Subprionocyclus branneri* (Anderson), x1. Note the similarity to *Protexanites bourgeoisi* (D'Orbigny). After Wright (1979).

As suggested by Matsumoto (1970) and shown by Wright (1979), the *Protexanites* condition is foreshadowed by *Subprionocyclus branneri* (Anderson) (Fig. 4) and *Protexanites* (Fig. 5) of the Texanitinae evolved, therefore, from Collignoniceratinae by an increase in size, a slight increase in inflation, and the development of straighter ribs and an entire siphonal keel. This phylogeny is confirmed by undulations to the siphonal keel of *P. bourgeoisi* which correspond in number to the external tubercles (Matsumoto 1966), as in *Subprionocyclus*. The claim (Klinger & Kennedy 1980, p. 17) that *P. bourgeoisi* and other coarsely ornamented *Protexanites* " . . . appear closer to '*Fraudatoroceras' besairiei*", i.e. *Peroniceras*, is, in the writer's opinion, based upon superficial characters.

Protexanites (Anatexanites) Matsumoto (1970) is a relatively large offshoot of *Protexanites* which adds a lateral tubercle in maturity. It is thus different from *Paratexanites* which achieves the quadrituberculate condition by splitting of the ventrolateral (submarginal) tubercle (Klinger & Kennedy 1980). The aberrant *Defordiceras* Young (1963) is from an uncertain stratigraphic horizon and is too poorly known to fit positively into any phylogenetic scheme. However, its loss of siphonal keel in maturity is matched by a number of texanites, e.g. *Pleurotexanites, Plesiotexanites, Paratexanites* and *Submortoniceras*, and its trituberculate condition suggests affinities with *Protexanites* (Matsumoto 1970).

Protexanites (*Miotexanites*) Matsumoto (1970) is a diminutive offshoot of *Protexanites* with weak flank ribs and indistinct umbilical and submarginal tubercles. In the writher's opinion it is probably a *Protexanites* microconch but, until this hypothesis is tested, *Miotexanites* is presumed to have descended from *Protexanites* by a weakening of flank ornament and a reduction in size. With a continuation of these evolutionary trends it gave rise, in the late Santonian, to virtually smooth *Haboroceras* (Toshimitsu 1988) (?also a microconch).

Most workers (Wright 1957, 1981; Young 1963; Matsumoto 1970) would derive *Paratexanites* from *Protexanites* by splitting of the submarginal row of

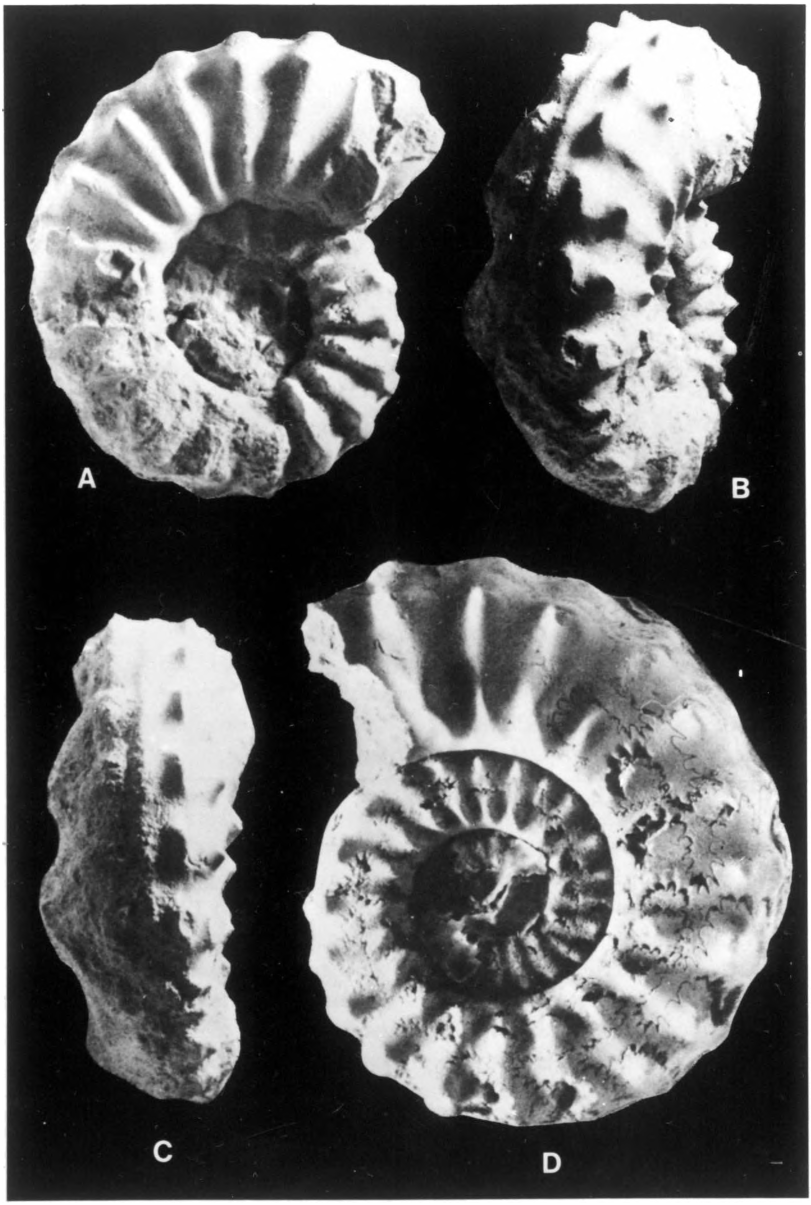

Fig. 5. *Protexanites bourgeoisi* (d'Orbigny), x1. A-C, Specimen in the D'ORBIGNY collection, Natural History Museum (Paris), from Villedieu (Loir-et-Chér); D, Specimen in the GROSSOUVRE collection, Natural History Museum (Paris), from an unknown locality.

tubercles. KLINGER & KENNEDY (1980), however, note the spiral coalescence of the external rows of tubercles in the holotype of *Paratexanites australis* KLINGER & KENNEDY (1980, p. 19, fig. 8) so as to produce irregular, wavy, lateral keels, and a superficially tricarinate venter. Although these lateral keels are absent from several of the paratypes (KLINGER & KENNEDY 1980, fig. 10), they claim every transition between *P. australis* and *Peroniceras (Peroniceras) tridorsatum* (SCHLÜTER), and advocate an ancestry in Peroniceratinae. Yet, they also note that in the late, or suppressed, division of the ventrolateral tubercle, *P. australis* " . . . appears to be morphological (sic) intermediate between *Protexanites* s.s. and *Paratexanites*" (p. 27). This latter observation is significant since at least one of the paratypes (KLINGER & KENNEDY 1980, figs. 12-13) remains trituberculate throughout and seems to be identical to *Protexanites cucaitaensis* ETAYO-SERNA (compare ETAYO-SERNA 1979, pl. 15, figs. 3-4 with KLINGER & KENNEDY 1980, figs. 12-13), suggesting the two species are synonyms. However, with respect to the Colombian species, ETAYO-SERNA (1979, p. 103) noted that from the ventrolateral tubercles the ribs continue " . . . onto the venter as a broad triangular ridge at the end of which one or two clavate, bead like tubercles are present". Thus *Protexanites cucaitaensis* may be a *Paratexanites*. However, this confusion further serves to emphasize the similarities between *Protexanites* and *Paratexanites* and to support an ancestry independent of *Peroniceras*. This is confirmed by coarse undulations to the siphonal keel of many *Paratexanites* species which may be so strong as to appear as a central row of clavi (KLINGER & KENNEDY 1980; KENNEDY et al. 1981, fig. 5F). In the writer's opinion, therefore, *Paratexanites* is descended from earlier *Protexanites* by an increase in inflation and splitting of the submarginal tubercle to produce the quadrituberculate condition. MATSUMOTO & KANIE (1982, pl. 2, figs. 3-5) figure a probable microconch of this genus.

Whereas WRIGHT (1957) and KLINGER & KENNEDY (1980) would derive *Texanites* from *Paratexanites* by acquisition of a lateral tubercle, thereby attaining the pentatuberculate condition, MATSUMOTO (1970) suggested an ancestry in *Plesiotexanites*. However, since *Plesiotexanites collignoniforme* KLINGER & KENNEDY and *Texanites vanhoepeni* KLINGER & KENNEDY occur side-by-side at the base of the Santonian in Zululand they are, at best, sister taxa and generic separation is justified (KLINGER & KENNEDY 1980). Significantly, *Texanites vanhoepeni* (KLINGER & KENNEDY 1980, p. 144, figs. 109-117) shows an undulatory keel which, in some cases, forms a row of weak clavi which correspond in number to the marginal tubercles. This confirms an ancestry independent of the Peroniceratinae. As recently shown by SUMMESBERGER (1987), *Neoselwynoceras* COLLIGNON (1970) is based upon a pathologically deformed *Texanites*.

By the development of overhanging umbilical walls, an increase in involution, a strong tendency for ornament to weaken or become effaced in maturity, and the multiplication of tubercles in the external row due to bifurcation and intercalation of ribbing, *Texanites* gives rise to *Submortoniceras* (YOUNG 1963; MATSUMOTO 1970; KLINGER & KENNEDY 1980).

The monospecific *Texanites (Ankilizatella)* COLLIGNON (1970) is based on a mid-Campanian species which preserves the wide umbilicus of *Texanites* and the smooth, compressed outer whorls of *Submortoniceras*. Although questionably included in the synonymy of *Submortoniceras* (KLINGER & KENNEDY 1980), the relatively narrow umbilicus of *Submortoniceras* is one of its prime distinguishing characters. Consequently, *Texanites (Ankilizatella)* is best retained as a subgenus of *Texanites*. KLINGER & KENNEDY (1980) followed MATSUMOTO (1959, 1970) in including *Butticeras* (ANDERSON 1958) and *Jimenesites* (CARRASCO 1967) in the synonymy of *Submortoniceras*. They also questioned the necessity for *Submortoniceras (Antsirasirella)* COLLIGNON (1970) considering it, like *Butticeras*, to be based upon species of *Submortoniceras* in which the attenuation of adult ornament is taken to extremes, with the loss of all but the umbilical and external rows of tubercles. Whereas in *Butticeras* the venter is rounded and without a siphonal keel in maturity, in *Submortoniceras (Antsirasirella)* it is flattened (KLINGER & KENNEDY 1980). In the writer's opinion, *Submortoniceras* is sexually dimorphic, microconchs having been figured by YOUNG (1963, pl. 60, figs. 2, 3, 7, 9, 10), KENNEDY et al. (1981, fig. 26) and TOSHIMITSU (1988, pl. 29, fig. 1).

The phyletic line *Protexanites* → *Paratexanites* → *Texanites* → *Submortoniceras* seems secure and forms the basis for the subfamily Texanitinae. Offshoots of this line include *Protexanites (Anatexanites)*, *Miotexanites, Haboroceras, Defordiceras* and *Texanites (Ankilizatella)*. KLINGER & KENNEDY (1980) consider *Plesiotexanites, Reginaites* and *Neogauthiericeras* an independant offshoot of this lineage. Since these taxa are not relevant to the present discussion, lengthy discussion is unwarranted but an ancestry in *Paratexanites* seems to be confirmed by the similarity of the inner whorls of *Plesiotexanites kawasakii* (KAWADA) and *Paratexanites australis* KLINGER & KENNEDY (compare MATSUMOTO 1970, pl. 41, figs. 1 a-d with KLINGER & KENNEDY 1980, figs. 10 a-c).

As noted by WRIGHT (1957) and many subsequent workers (YOUNG 1963; MATSUMOTO 1970; KLINGER & KENNEDY 1980), there is a second phyletic line within the texanites which includes the following taxa introduced by COLLIGNON (1948): *Menabites (Menabites), M. (Australiella), M. (Bererella), M. (Delawarella)* and *Bevahites*. These are unified by a multiplicity of tubercles in the external row, sometimes outnumbering those of the marginal row by as much as 3:1 (KLINGER & KENNEDY 1980).

Both YOUNG (1963) and MATSUMOTO (1970) recorded Santonian occurrences of *Australiella*, which they treated as generically distinct from *Menabites*, and derived this genus from *Protexanites* of the *planatus* (LASSWITZ) group. KLINGER & KENNEDY (1980), however, suggested that such Santonian occurrences were stratigraphically misplaced, and that *Australiella* did not appear prior to the Campanian.

MATSUMOTO (1970) introduced the new genus *Pleurotexanites* for *Protexanites superbus* COLLIGNON (1966, p. 64, pl. 480, fig. 1952) (Fig. 6) and *P.*

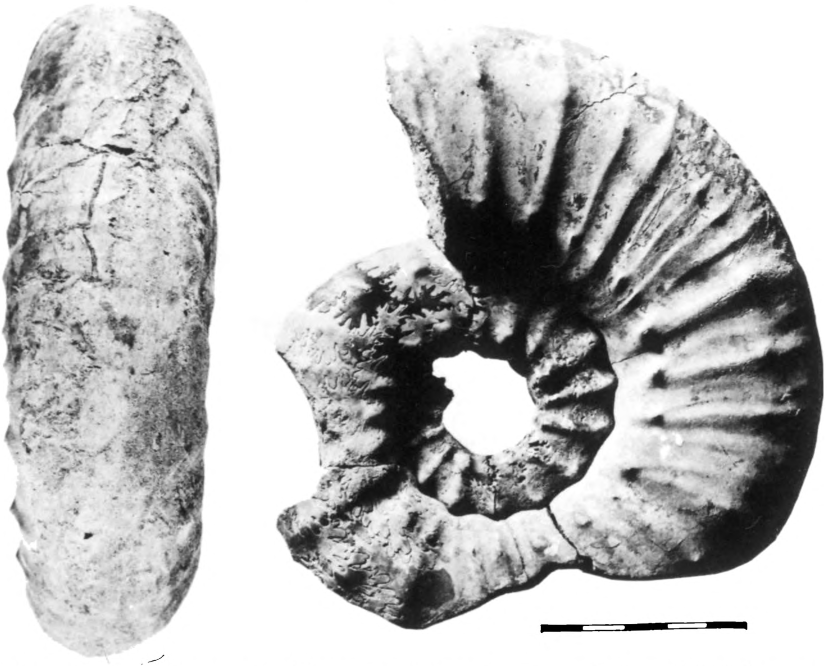

Fig. 6. *Pleurotexanites superbus* (Collignon). Lateral and ventral views of the holotype, showing the rounding of the venter and loss of ornament in maturity. The bar scale is 5 cm.

obatai Collignon (1966, p. 66, pl. 481, figs. 1953-1954) from the mid-Santonian of Madagascar, distinguished by being compressed and trituberculate, with a multiplicity of tubercles in the external row, and a nodate siphonal keel. He suggested (Matsumoto 1970, p. 299) that " . . . *Pleurotexanites* and *Australiella* were probably in sisterhood relationship, having been derived commonly from *Protexanites* but deviating from each other in shell-form and ornament". Klinger & Kennedy (1980), on the other hand, considered *Pleurotexanites* ancestral to *Australiella*. On the basis of derived characters, i.e. a multiplicity of tubercles in the external row, the writer concurs. The Zululand examples of *Pleurotexanites* described below support an ancestry in *Protexanites* of the *planatus* (Lasswitz) group, contrary to the view that it is descended from *Paratexanites* (Klinger & Kennedy 1980). As a result of this fundamental dichotomy within texanite phylogeny, the writer proposes:

Subfamily Menabitinae nov.

Diagnosis: Texanites with 3-5 rows of tubercles, those of the external row outnumbering those of the marginal row by at least 2:1. Primitively compressed and trituberculate, with a nodate to undulatory siphonal keel, later inflated and pentatuberculate with an entire siphonal keel. In some growth stages there is a tendency for the ventrolateral tubercles to form horns. Age: Lower Santonian - mid-Campanian.

Discussion: The earliest menabite is *Pleurotexanites* which appears at the base of the Santonian in Zululand. The Malagasy material of this genus comes from the Middle Santonian (COLLIGNON 1966), while the Upper Santonian example of *Australiella* aff. *pattoni* YOUNG figured by MATSUMOTO (1970, p. 300, pl. 43, fig. 3, text-fig. 27) has an undulatory keel and is here identified as *Pleurotexanites* sp. juv. The strongly depressed whorls of the Santonian or Campanian *Australiella austinensis* YOUNG (1963, p. 115, pl. 64, figs. 3-4 m, pl. 65, fig. 6, pl. 67, figs. 4-6, text-fig. 28e) favour the younger age and KLINGER & KENNEDY (1980) seem to be correct in restricting *Australiella* to the Campanian.

Menabites s.s. first appears in the Lower Campanian (KLINGER & KENNEDY 1980) and, prior to development of the pentatuberculate condition, is barely separable from *Pleurotexanites*. It is distinguished by its flat flanks, quadrate whorl section, simple strong pillar-like main ribs, entire siphonal keel and pentatuberculate condition in maturity. Although KLINGER & KENNEDY (1980, fig. 266) would derive it from *Bevahites*, the bifurcation and intercalation of ribs characteristic of the latter taxon is not found in typical *Menabites* which has strong simple ribs on the inner whorls (COLLIGNON 1948, pl. 17, figs. 3-4, pl. 18, fig. 1). Consequently, *Menabites* is here derived from *Pleurotexanites*, independant of *Bevahites*, by the acquisition of an entire siphonal keel and 5 rows of flank tubercles in maturity. *Menabites* (*Bererella*) is a localized mid-Campanian offshoot of *Menabites* distinguished by its sparse weak ribs (COLLIGNON 1948; WRIGHT 1957; KLINGER & KENNEDY 1980).

Australiella is easily derived from *Menabites* by an increase in inflation, resulting in a strongly depressed whorl section, bulging flanks, and a broadly rounded venter to the early and middle growth stages (Fig. 7). In addition, at the trituberculate stage the ventrolateral tubercles are exaggerated and horn-like.

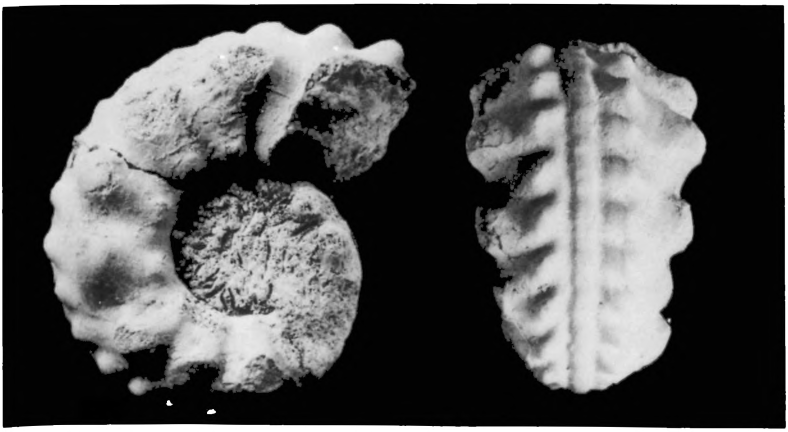

Fig. 7. *Australiella* sp. juv., x1. An individual from the upper Lower Campanian of Zululand, in the Durban Museum, showing exaggerated ventrolateral horns, inflated form and broadly rounded venter.

At many localities *Australiella* and *Delawarella* occur side-by-side. Whereas the inner whorls are similar (Young 1963; Klinger & Kennedy 1980), *Delawarella* attains a much larger adult size than the relatively ornate *Australiella*. In addition, it displays a loss of tuberculation in maturity, accompanied by a narrowing of the umbilicus and densicostate outer whorls, sometimes with flexuous ribs which bifurcate from the umbilical bullae, resulting in a convergent resemblance to *Submortoniceras* (Klinger & Kennedy 1980). This relationship is suggestive of sexual dimorphism but, until the hypothesis is tested, *Delawarella* is assumed to have descended from *Australiella* (Klinger & Kennedy 1980) and, consequently, is treated as a subgenus of the latter taxon.

Although *Bevahites* is alleged to appear in the Lower Santonian of France (Fabre-Taxy 1963), the first specifically identifiable material comes from the Upper Santonian (Collignon 1948: Young 1963; Klinger & Kennedy 1980). It is worth noting, however, that Collignon (1966) makes no reference to Upper Santonian *Bevahites* in his atlas of the Malgash faunas and, in fact, this material is re-assigned to the Lower Campanian (Besairie & Collignon 1972).

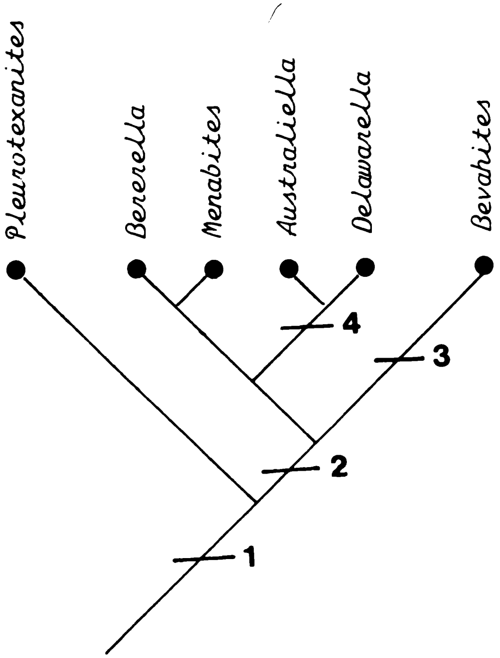

Fig. 8. Hypothesized relationships within the Menabitinae nov. 1, Evolute, trituberculate, flat-sided quadrate whorls, simple main ribs, multiplicity of tubercles in external row, nodate to undulatory siphonal keel with nótches corresponding in number to external tubercles; 2, keel entire, pentatuberculate in maturity; 3, venter narrow, flank costae frequently bifurcate and with intercalatories, marginal and submarginal tubercles approximated; 4, early whorls inflated, with strongly depressed whorl section, broadly rounded venter, and exaggerated ventrolateral horns.

The type species of *Bevahites* is characterized by a quadrate to compressed whorl section with 5 rows of tubercles from small diameters, approximated marginal and submarginal tubercles, external clavi close to the siphonal keel, and with frequent bifurcation and intercalation of ribs. It differs from *Menabites* in early attainment of the pentatuberculate condition, and in the frequent bifurcation and intercalation of ribs. This suggests *Bevahites* is a parallel development (Fig. 8) which acquired the pentatuberculate condition independent of *Menabites*. Support for this hypothesis is provided by forms such as *Bevahites* gr. *subquadratus* (KLINGER & KENNEDY 1980, fig. 216) which are weakly quadrituberculate, with the marginal row of tubercles on the upper flank, closely matching the condition in the larger Zululand specimen of *P. superbus* (Fig. 10).

Genus *Pleurotexanites* MATSUMOTO, 1970

Type species: *Protexanites superbus* COLLIGNON, 1966; by original designation.

Diagnosis: Relatively small evolute menabites with a uniformly subrectangular whorl section varying from slightly depressed in the immature stages to compressed in maturity. Ornament comprises strong, distant, rectiradiate to prorsiradiate primaries which arise singly from umbilical bullae and terminate in spinose ventrolateral tubercles; the latter are outnumbered 2:1 by the external row of clavi. The siphonal keel is nodate to undulatory. On the final body chamber ornament weakens, the venter rounds, and the external tuberculation and siphonal keel are lost. Age: Santonian.

Remarks: Although KLINGER & KENNEDY (1980) derived *Pleurotexanites* from *Paratexanites*, they curiously treated it as a subgenus of *Protexanites*. MATSUMOTO (1970) is followed here in regarding it as generically distinct.

Pleurotexanites superbus (COLLIGNON, 1966)

Figs. 6, 9-11

1966 *Protexanites superbus* COLLIGNON. – p. 64, pl. 480, fig. 1952.
1970 *Pleurotexanites superbus* (COLLIGNON). – MATSUMOTO, p. 232.
1980 *Protexanites (Pleurotexanites)*. – KLINGER & KENNEDY, p. 5.

Material: Two specimens. DM-PCZ341 and 4406, both housed in the palaeontological collections of the Durban Museum.

Stratigraphic horizon: The material was found loose on the foreshore of False Bay, at Locality 84 of KENNEDY & KLINGER (1975). Its Lower Santonian age is confirmed by associated *Plesiotexanites collignoniforme* KLINGER & KENNEDY, *Texanites vanhoepeni* KLINGER & KENNEDY, *Baculites capensis* WOODS, *Damesites sugata* (STOLICZKA) and *Pseudoschloenbachia* cf. *umbulazi* (BAILY).

Fig. 9. *Pleurotexanites superbus* (COLLIGNON), x1. Lateral, ventral and ventrolateral views of DM-PCZ4406, from the Lower Santonian of Zululand.

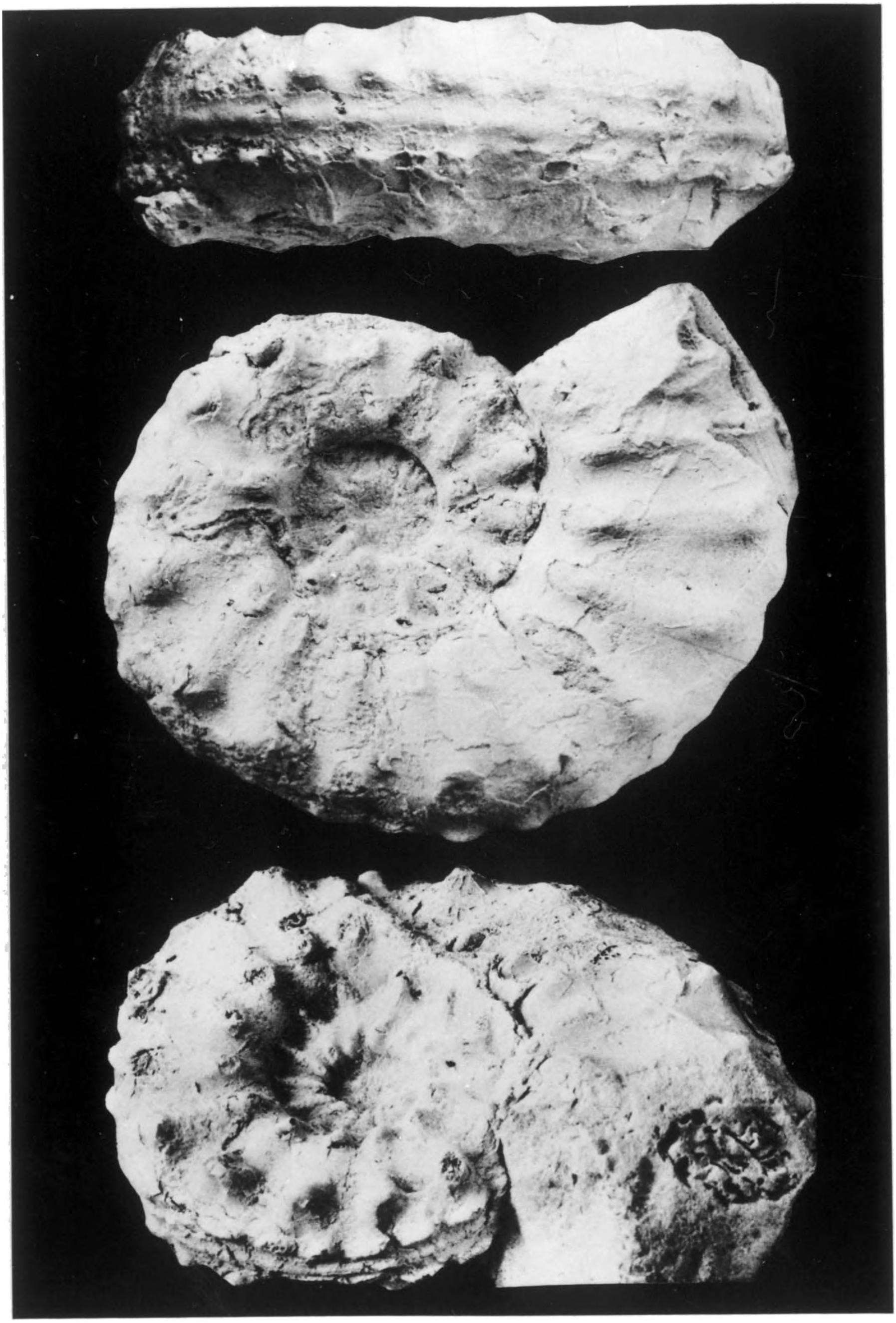

Fig. 9 (Legend see p. 12)

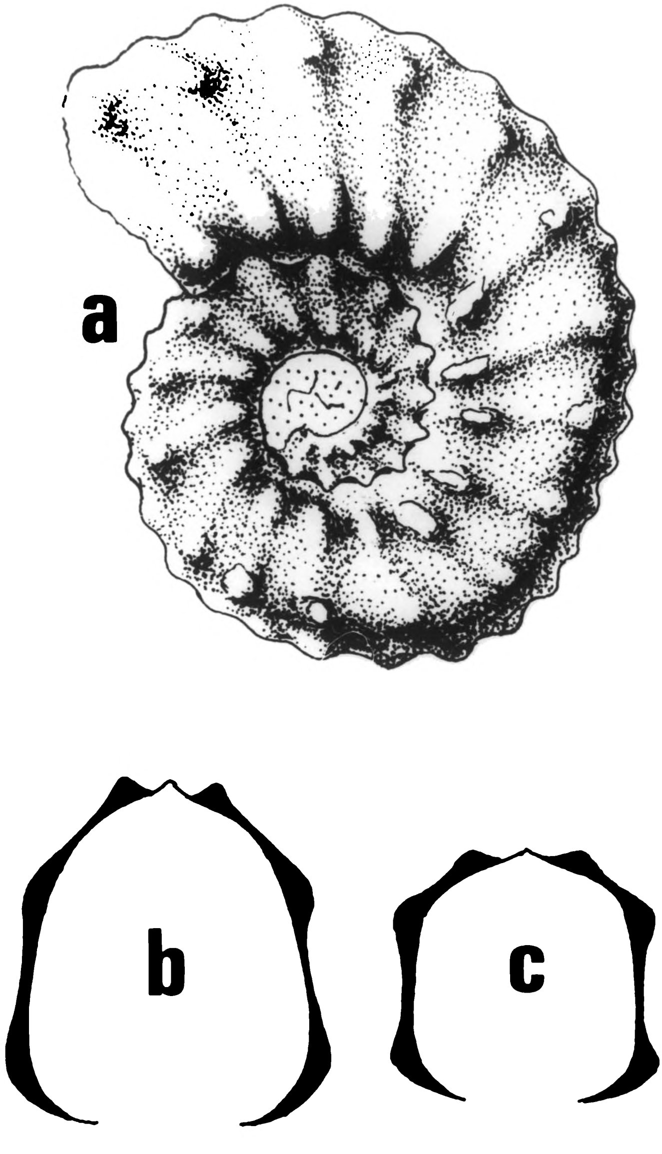

Fig. 10. *Pleurotexanites superbus* (Collignon). A, Reconstruction of DM-PCZ4406; B, Whorl section of DM-PCZ341; C, Whorl section of DM-PCZ4406. All x1.

Fig. 11. *Pleurotexanites superbus* (Collignon), x0,15. Lateral, ventral and ventrolateral views of DM-PCZ341 from the Lower Santonian of Zululand. Note how the submarginal tubercle has shifted to a high flank position.

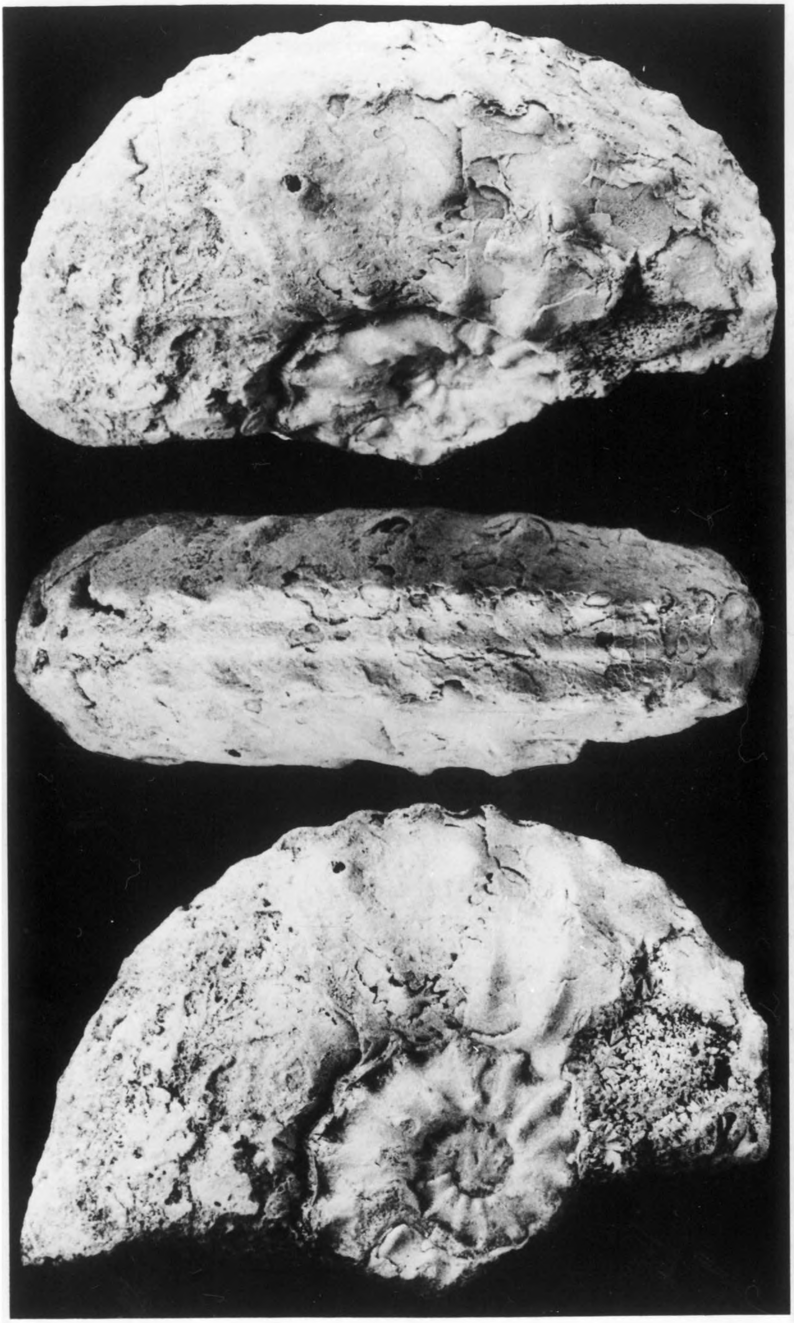

Fig. 11 (Legend see p. 14)

Description: The smaller specimen (Figs. 9, 10A, C) comprises part of a body chamber which preserves recrystallized test on the inner whorls, but only with patches of test on the outer whorl. It is moderately large (91 mm diameter), evolute, with a compressed, subquadrate whorl section (W/H = 0,88), and wide, shallow umbilicus (approximately 36% of the shell diameter). The umbilical wall is steep, with an evenly rounded shoulder and the broad, flat, subparallel flanks converge slightly towards the venter, with maximum width below midflank. Ornament comprises strong prorsiradiate ribs which arise singly from distinct umbilical bullae and form prominent spinose marginal tubercles at the ventrolateral shoulder. The ribs are much narrower than the interspaces, with 17 on the outer whorl. The strongly clavate external tubercles outnumber those of the marginal row 2:1, and are situated relatively close to the slightly undulating but entire siphonal keel.

The larger specimen (Fig. 10 B, 11) is wholly septate and attained a much larger adult size than the holotype (Fig. 6). Whereas its inner whorls are identical to the smaller specimen from the same locality, its outer whorl is more compressed and polygonal due to the submarginal tubercles shifting from a ventrolateral position to a high-flank position, and the flanks converge more strongly to the relatively narrower venter. In these respects it closely approaches *Bevahites* of the *subquadratus* group such as have been figured by Klinger & Kennedy (1980, fig. 216) but differs in lacking nodes at midflank.

Measurements:

No.	D	H	W	W/H	U
DM-PCZ4406	91	34,0 (37)	30,0 (33)	0,88	32,5 (36)
DM-PCZ341	136	55,5 (41)	44,0 (32)	0,79	51,0 (38)
DM-PCZ341	95	41,5 (44)	40,3 (42)	0,97	32,0 (34)
*P. superbus**	160	62,0 (39)	50,0 (31)	0,81	63,0 (39)
*P. superbus**	88	36,0 (41)	28,0 (32)	0,78	30,0 (34)

* After Collignon (1966).

Remarks: The smaller specimen, DM-PCZ4406, compares favourably with the inner whorls of the holotype of *P. superbus*, differing only in being slightly more inflated and with an undulatory rather than nodate siphonal keel. The differences in siphonal keel are not considered taxonomically important since similar differences are encountered in other texanites (Klinger & Kennedy 1980; Kennedy et al. 1980) and are suscribed to intraspecific variation. Like the holotype, the smaller Zululand example of *P. superbus* also shows a tendency for ornament to weaken on the outer whorl, but not to the extent seen in the holotype. The larger Zululand specimen is entirely septate and retains ventral tuberculation and keel to a much larger adult size than the holotype. These differences fall within the range of variation encountered in other texanites (Klinger & Kennedy 1981).

Pleurotexanites obatai (Collignon) (1966, p. 66, pl. 481, figs. 1953-1954) differs in its consistently square whorl section (W/H = 1,00) and rectiradiate flank costae, presumably also with siphonal nodes.

Description: The smaller specimen (Figs. 9, 10A, C) comprises part of a body chamber which preserves recrystallized test on the inner whorls, but only with patches of test on the outer whorl. It is moderately large (91 mm diameter), evolute, with a compressed, subquadrate whorl section (W/H = 0,88), and wide, shallow umbilicus (approximately 36% of the shell diameter). The umbilical wall is steep, with an evenly rounded shoulder and the broad, flat, subparallel flanks converge slightly towards the venter, with maximum width below midflank. Ornament comprises strong prorsiradiate ribs which arise singly from distinct umbilical bullae and form prominent spinose marginal tubercles at the ventrolateral shoulder. The ribs are much narrower than the interspaces, with 17 on the outer whorl. The strongly clavate external tubercles outnumber those of the marginal row 2:1, and are situated relatively close to the slightly undulating but entire siphonal keel.

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Measurements:

No.	D	H	W	W/H	U
DM-PCZ4406	91	34,0 (37)	30,0 (33)	0,88	32,5 (36)
DM-PCZ341	136	55,5 (41)	44,0 (32)	0,79	51,0 (38)
DM-PCZ341	95	41,5 (44)	40,3 (42)	0,97	32,0 (34)
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Remarks: The smaller specimen, DM-PCZ4406, compares favourably with the inner whorls of the holotype of *P. superbus*, differing only in being slightly more inflated and with an undulatory rather than nodate siphonal keel. The differences in siphonal keel are not considered taxonomically important since similar differences are encountered in other texanites (KLINGER & KENNEDY 1980; KENNEDY et al. 1980) and are suscribed to intraspecific variation. Like the holotype, the smaller Zululand example of *P. superbus* also shows a tendency for ornament to weaken on the outer whorl, but not to the extent seen in the holotype. The larger Zululand specimen is entirely septate and retains ventral tuberculation and keel to a much larger adult size than the holotype. These differences fall within the range of variation encountered in other texanites (KLINGER & KENNEDY 1981).

Pleurotexanites obatai (COLLIGNON) (1966, p. 66, pl. 481, figs. 1953-1954) differs in its consistently square whorl section (W/H = 1,00) and rectiradiate flank costae, presumably also with siphonal nodes.

'Australiella' pattoni YOUNG (1963, p. 116, pl. 65, figs. 4-5, pl. 66, figs. 1-2, 5-6, pl. 68, figs. 1-3, 6, text-figs. 24 b, 26 h, 33 a, c, 34 d, g) is based upon wholly septate material up to 100 mm diameter. Its quadrate whorl section and flat flanks preclude it from *Australiella* as interpreted here and, on the basis of its Campanian age and presumed pentatuberculate state in maturity, it is assigned to *Menabites* s. s. Although KLINGER & KENNEDY (1980) claim that *Menabites* s.s. can be separated from *Australiella* by the relatively early development of the pentatuberculate condition, the type species *M. menabensis* COLLIGNON (1948, p. 7, pl. 17, figs. 3-4, pl. 18, fig. 1) " . . . est de toutes les Ammonites de ce group (non compris les sous-genres) celle qui conserve le plus longtemps le stade trituberculе". According to COLLIGNON (1948), *M. menabensis* attains the pentatuberculate stage only at 60-100 mm diameter, although *M. gignouxi* COLLIGNON (1948, p. 15, pl. 22, fig. 2) shows a lateral tubercle at only 25 mm diameter. The stage at which the pentatuberculate condition is attained is thus a poor character on which to separate menabites. Since *Pleurotexanites* is not yet reported from the Campanian, all square-whorled, flat-sided, trituberculate menabites from this level are assumed to be *Menabites* s.s. in which the pentatuberculate condition was attained late in ontogeny. *Menabites (Menabites) pattoni* differs from *P. superbus* only in having stronger, more rectiradiate main ribs, an entire siphonal keel, a slightly depressed whorl section, and a slightly wider umbilicus at comparable diameter. The Japanese *Australiella* aff. *pattoni* YOUNG (MATSUMOTO 1970, p. 300, pl. 43, fig. 3) is based on a specifically indeterminate juvenile fragment of *Pleurotexanites*.

Acknowledgements

I am grateful to GERARD AUTRAN (Nice) and JACQUES THIERRY (Dijon) for providing me with photographs of the holotype of *Pleurotexanites superbus*, JACQUES SORNAY (Paris) for access to the collections of the Natural History Museum, Paris, and BETSIE GREYLING for assistance. The University of Durban-Westville is thanked for a grant in aid of fieldwork.

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Bei der Tübinger Schriftleitung eingegangen am 14. November 1989.

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