

UPPER CRETACEOUS AMMONITES AND INOCERAMIDS FROM THE OFF-SHORE ALPHARD GROUP OF SOUTH AFRICA

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(With 10 figures and 2 tables)

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ABSTRACT

During dredging operations off the southern Cape coast of South Africa, concretions containing identifiable ammonites and inoceramids were recovered from three localities. The assemblage includes *Eubaculites latecarinatus* (Brunnschweiler), *Gunnarites* sp. cf. *G. kalika* (Stoliczka), *Proplacenticeras kaffrarium* (Etheridge), *Scaphites* (*Otoscapites*?) sp. indet., *Inoceramus* (*I.*) *ernsti* Heinz, and *I. frechi* Flegel; the first two are of Lower Maastrichtian, the latter all of Lower Coniacian age. Apart from permitting accurate dating of parts of the off-shore Alphard Group, four of these species are new to southern Africa. Taphonomic analysis of the inoceramid assemblage suggests a shelf habitat with moderate bottom currents and relatively slow rates of sedimentation, below the depth range of strong wave and current action.

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INTRODUCTION

Over a period of several years, concretions containing identifiable invertebrate faunas were dredged off the southern Cape coast of South Africa by the Marine Geoscience Unit of the University of Cape Town. The Coniacian ammonite *Yabeiceras manasoense* Collignon was previously described from these concretions (Klinger *et al.* 1976). Additional material has now become

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available, permitting precise dating of relevant parts of the off-shore Alphard Group, and adding to our knowledge of the geographic distribution of several taxa.

The inoceramids are a neglected faunal element of the South African Cretaceous deposits, and are here discussed more extensively in terms of biostratigraphic significance and systematics than the ammonites, which are at present the subject of current revision by Kennedy & Klinger (1975 onwards). Kauffman is preparing a monograph on the South African Inoceramidae. Taphonomic study of the inoceramids described here permits partial interpretation of the depositional environment prevailing during sedimentation of the Alphard Group.

MATERIAL

Material is from three localities (A, B and C, Fig. 1). Co-ordinates and brief descriptions of the lithologies are given below. Localities A and B are close to each other, south to south-west of Cape Infanta, and in close proximity to the locality yielding *Yabeiceras manasoense* Collignon (Klinger *et al.* 1976) (here marked as locality D; Marine Geoscience Unit, University of Cape Town, sample no. TBD 4492). Locality C is the furthest east, situated between Cape St Francis and Cape Recife.

Locality A

Lat. 35°11.7'S; Long. 20°30.0'E; depth, 197 m (Marine Geoscience Unit, University of Cape Town sample no. TBD 310). The material consists of dark, greyish green, fine-grained limestone concretions of similar lithology to that yielding *Yabeiceras manasoense* (Klinger *et al.* 1976). The sediment is highly bioturbated and lacks bedding structures. The surface of the concretion is pitted by two types of borings of Recent organisms. Faunas include rare ammonites, *Proplacenticeras kaffrarium* and *Scaphites* (*Otoscapites*?) sp. indet., abundant indeterminate juvenile bivalves, both articulated and disarticulated, and occasional juvenile gastropods. All retain original shelly material and show no signs of contemporaneous predation, encrustation, boring or scouring. Age: Lower Coniacian.

Locality B

Lat. 35°02' – 03'S; Long. 20°39' – 40.0'E; depth, 102 m (Marine Geoscience Unit, University of Cape Town, sample no. TBD 4510). The concretions consist of very fine-grained, well-sorted, relatively clean and mature quartz sand. The ubiquitous bivalve *Inoceramus* is a common element of the concretions and occurs predominantly as uncrushed, well-preserved, single, mostly left valves which retain most of the inner aragonitic nacreous shell layer intact, but only isolated fragments of the calcitic outer prismatic layer. The outer layer appears highly leached, which may imply exposure at the sediment-water interface for some time before burial.

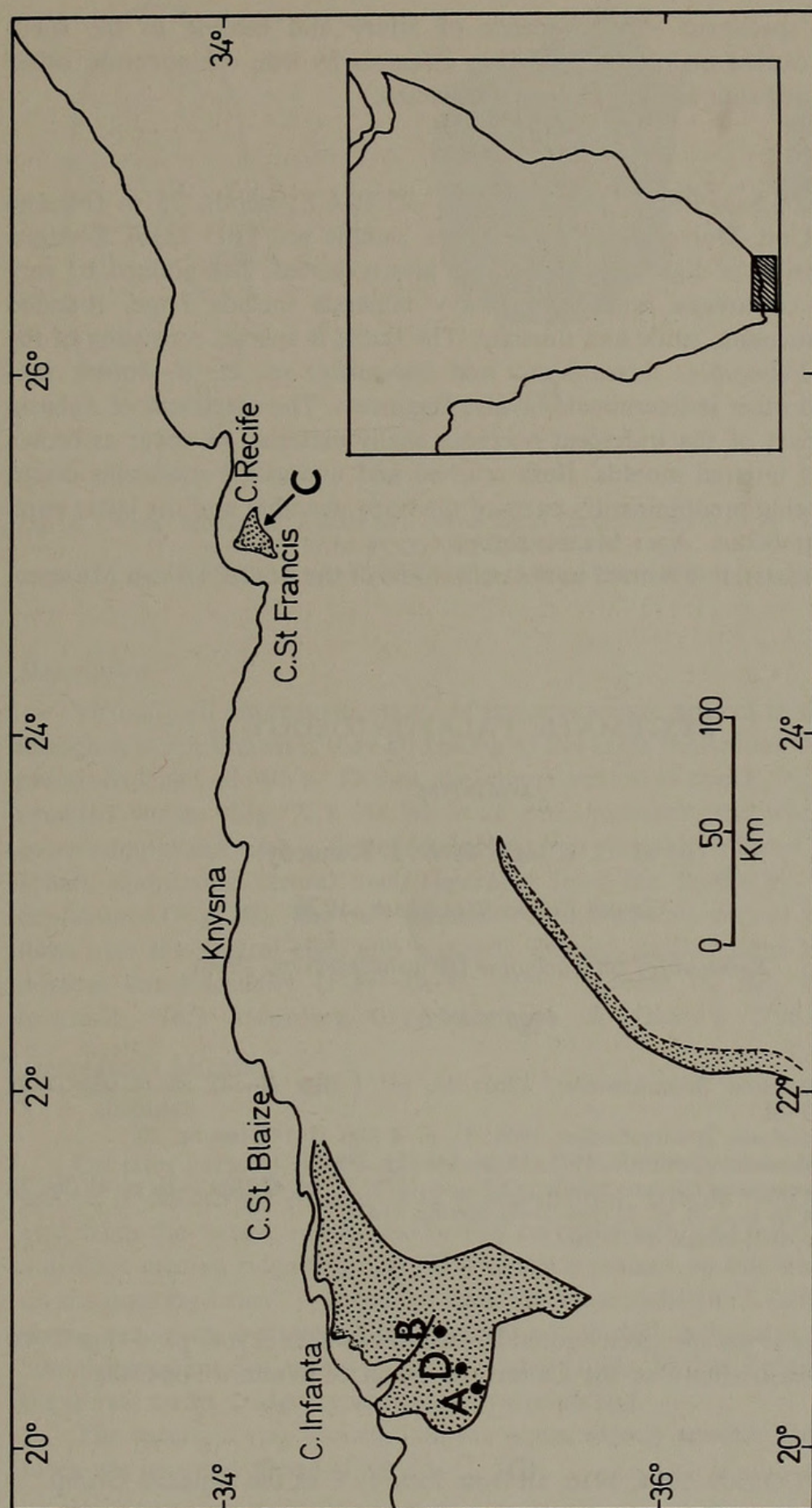


Fig. 1. Locality map of off-shore invertebrate faunas. Stippled areas indicate outcrops of Alghard Group sediments. (After Dingle 1973: 7, fig. 5.)

Several specimens show evidence of injury and healing to the shell, presumably caused mainly by predation attempts by fish, echinoderms, other molluscs or arthropods. Age: Lower Coniacian.

Locality C

Lat. 34°08,5–34°08,0S; Long. 25°10,3′–25°10,6′E; depth, 75 m (Marine Geoscience Unit, University of Cape Town, sample no. TBD 1336). Dredged material consists of light greyish yellow, poorly sorted, fine-grained to very fine-grained calcareous sandstone. Heavy minerals include large, rounded grains of glauconite, rutile and ilmenite. The fauna is sparse, consisting of the ammonites *Eubaculites latecarinatus* and *Gunnarites* sp. cf. *G. kalika*, inoceramids and other indeterminate bivalve fragments. The specimens of *Eubaculites* retain part of the iridescent nacreous shelly material, or occur as brown phosphatized internal moulds. Both crushed and uncrushed specimens occur, the former being predominantly parts of the body chamber and the latter parts of the phragmocone. Age: Maastrichtian.

All the material is housed in the collections of the South African Museum, Cape Town.

SYSTEMATIC PALAEONTOLOGY

AMMONITES

(By H. C. Klinger & W. J. Kennedy)

Genus *Eubaculites* Spath, 1926

Eubaculites latecarinatus (Brunnschweiler, 1966)

Figs 2–4, 5D

Giralites latecarinatus Brunnschweiler, 1966: 33, pl. 3 (figs 13–14), pl. 4 (figs 1–5), text-figs 17–18.

Giralites quadrisulcatus Brunnschweiler, 1966: 35, pl. 4 (figs 11–14), text-fig. 20.

Eubaculites ambindensis Collignon, 1971: 18, pl. 646 (fig. 2393).

Eubaculites latecarinatus (Brunnschweiler): Klinger, 1976: 91, pl. 40 (figs 1–2), pl. 41 (fig. 3), pl. 42 (figs 2a–b, 2, 6), pl. 43 (figs ?3–4), text-fig. 11d–e.

Eubaculites sp. [sic] Dingle, 1973: 10.

Type

Holotype is the specimen figured by Brunnschweiler (1966, pl. 4 (figs 2–4)) from the Maastrichtian of the Carnarvon Basin of Western Australia.

Material

SAM-PCO5909–5914, 5916, all from locality C in the Alphard Group.

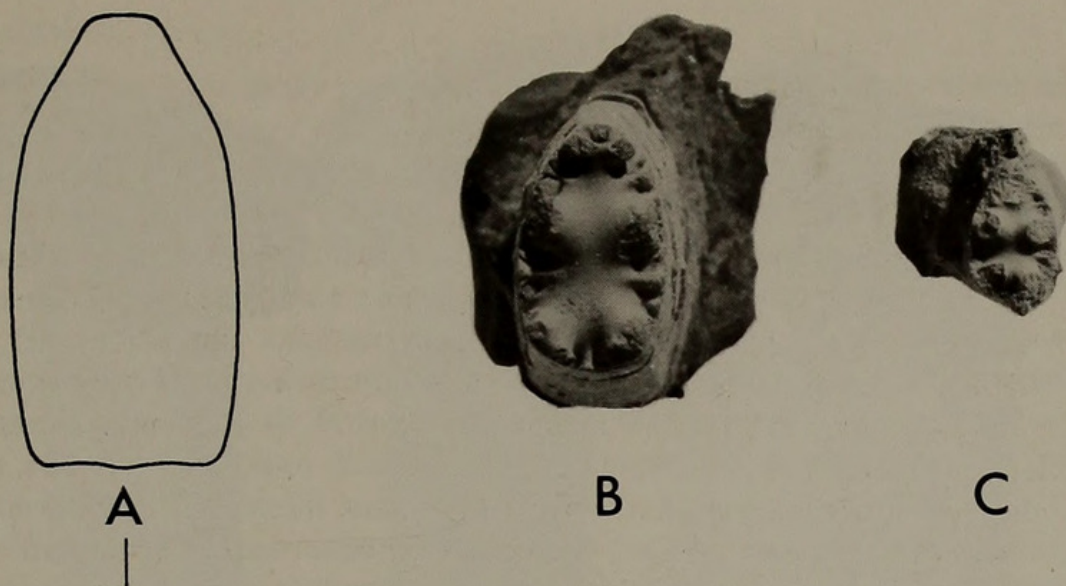


Fig. 2. Whorl section of *Eubaculites latecarinatus* (Brunnschweiler). A. SAM-PCO5908. B. SAM-PCO5909. C. SAM-PCO5913. All from locality C (TBD 1336) in the Alphard Group. $\times 1$.

Description

Virtually all ontogenetic stages of this species are present in the collection, though it is not known if they all belong to the same individual. At the earliest preserved stage, at $Wh = 12$ mm, the whorl section is ovoid, with a narrowly rounded venter (Fig. 2C). At $wh = 26$ mm, however, the whorl section is more compressed with a flattened dorsum, very weakly inflated flanks and a broad, undulating ventral keel, separated from the flanks by weak, lateral depressions (Fig. 2B). The only ornament at this size consists of weak undulations over the ventral keel, and a poorly defined median ridge traversing the dorsum longitudinally (Figs 3A–C, 5D). Increase in size at this stage is rapid, 18,3 according to Matsumoto & Obata's (1963: 4) index

$$\left(\frac{\text{increase in heights}}{\text{distance}} \times 100. \right)$$

On later parts of the phragmocone and on the body chamber, the whorl section is distinctly pyriform, with a well-defined, crenate ventral keel, separated from the flanks by a lateral furrow on either side, and a flat dorsum with a distinct median ridge (Fig. 2A, 3D) which is present on internal moulds and on the preserved shell. A specimen from the Maastrichtian of Zululand (Fig. 4) shows the adult features of the species, which still includes a total lack of lateral ornament but a slower growth index (13,4). In this Zululand specimen the dorsal median ridge appears slightly undulating.

The suture is very incised, and the septae closely spaced. The saddles and lobes are low and broad (Figs 3A–C, 5D).

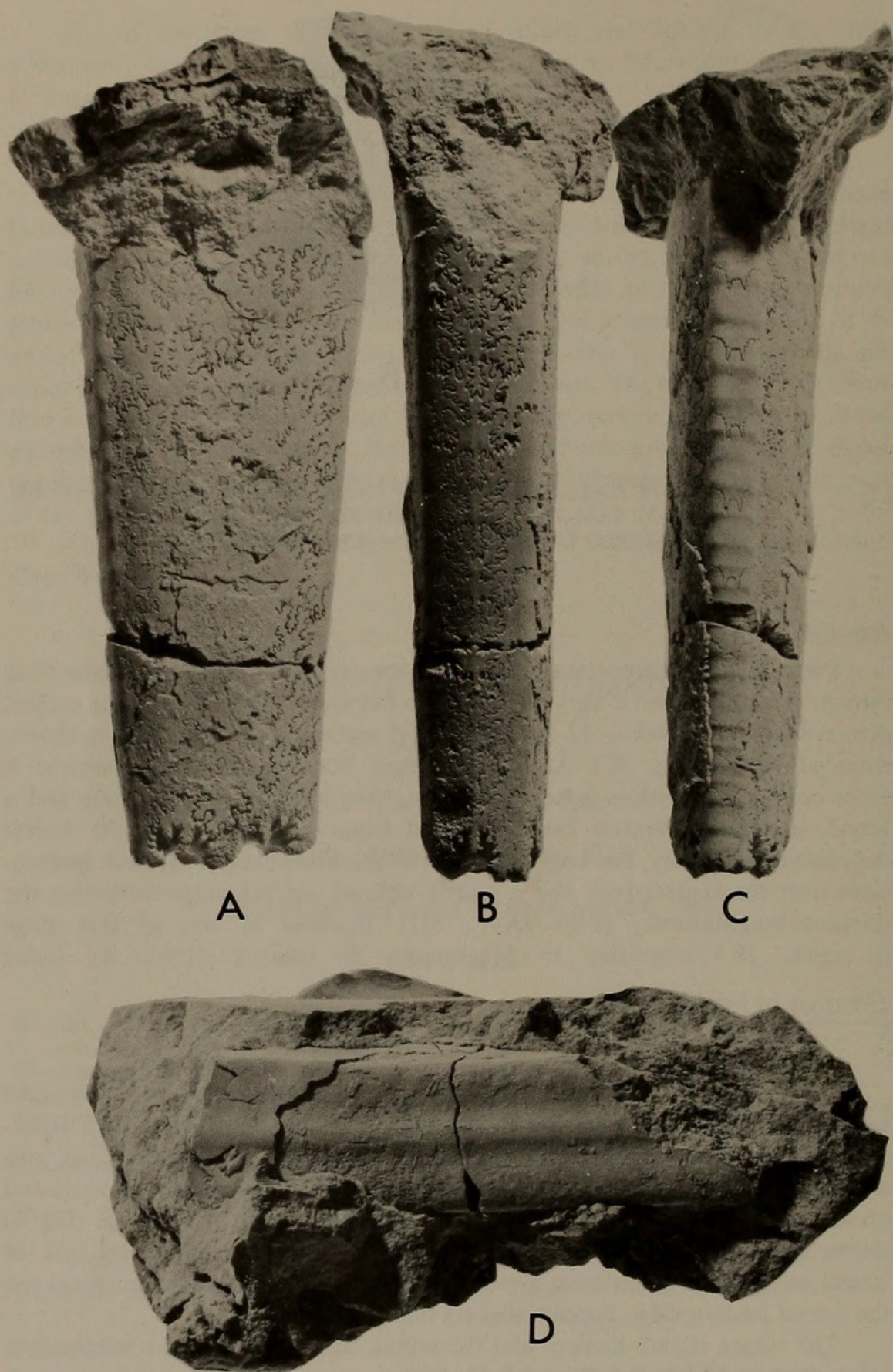


Fig. 3. *Eubaculites latecarinatus* (Brunnschweiler). A-C. Lateral, dorsal and ventral views, SAM-PCO5909. D. View of dorsal side, SAM-PCO5908. Note the prominent median ridge. (See also Fig. 4B.)

All from locality C (TBD 1336) in the Alphard Group. $\times 1$.

Discussion

This species is easily recognized in the adult stage by the pyriform whorl section, general lack of lateral ornament and the crenate, tabulate venter.

In the very early stages of growth, before the development of a distinct ventral keel, the species resembles *Baculites anceps* Lamarck and *B. subanceps* Haughton. It seems possible to derive *Eubaculites latecarinatus* from either of these two species near the Campanian/Maastrichtian boundary.

The systematic affinities and distribution of the genus *Eubaculites* were discussed recently by Riccardi (1974) and Klinger (1976). They differ, however, in their acceptance of Brunnschweiler's (1966) interpretation of the genus. The authors here follow Klinger (1976) in regarding Brunnschweiler's genera *Eubaculiceras*, *Cardabites* and *Giralites* as junior synonyms of *Eubaculites*.

Eubaculites latecarinatus is the dominant eubaculitid faunal element in the Lower Maastrichtian sediments of Zululand, and may grow up to spectacular size; incomplete specimens of c. 130 cm in length have been found in the Charters Creek Rest Camp region of St Lucia, Zululand.

The slight dorsal ridge present in *Eubaculites latecarinatus* (Figs 3D, 4B) is occasionally also found in specimens of *E. vagina* (Forbes) (Fig. 5B). The function and origin of this structure are enigmatic, but may possibly be associated with muscular attachment of the animal to the shell. Similar dorsal structures have not been observed in species of *Baculites* present in southern Africa.

Occurrence

Eubaculites latecarinatus occurs in the Maastrichtian of Western Australia, the Zone of *Pachydiscus gollevilensis* and *Pachydiscus neubergicus* of the Maastrichtian stage in Madagascar, and the first division of the Maastrichtian of Zululand *sensu* Kennedy & Klinger (1975).

Gunnarites sp. cf. *G. kalika* (Stoliczka, 1865)

Fig. 6A–B

Compare

Ammonites kalika Stoliczka, 1865: 140(100), pl. 70 (fig. 5a–b).

Holcodiscus kalika (Stoliczka): Kossmat, 1898: 41(148).

Gunnarites kalika (Stoliczka): Kilian & Reboul, 1909: 34. Spath, 1953: 33, pl. 10 (figs 1–6).

Material

SAM-PCO5907 from locality C in the Alphonse Group.

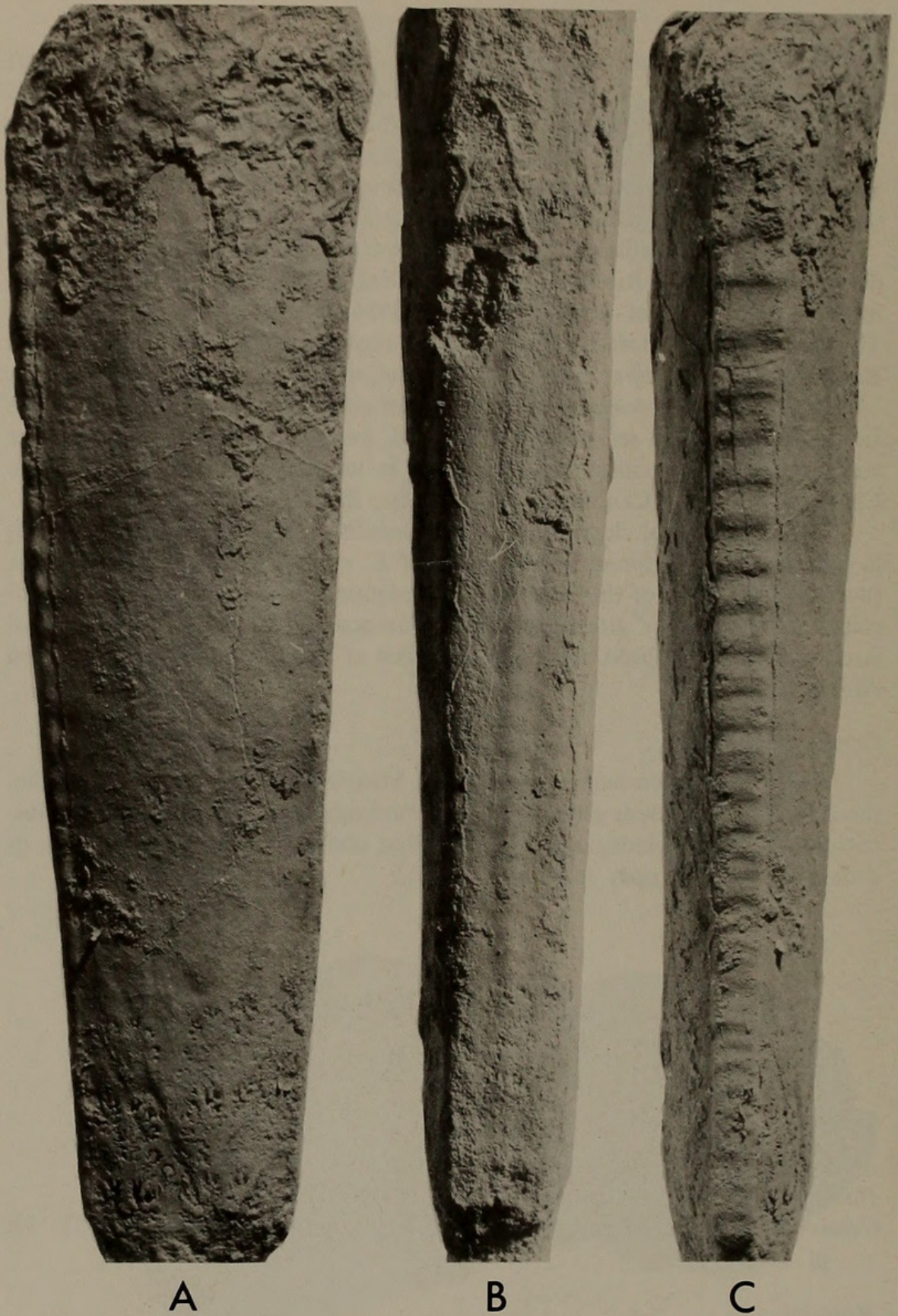


Fig. 4. *Eubaculites latecarinatus* (Brunnschweiler). A-C. Lateral, dorsal and ventral views, SAS-H163D, from locality 20 in Zululand. Note the median dorsal ridge. $\times 1$.

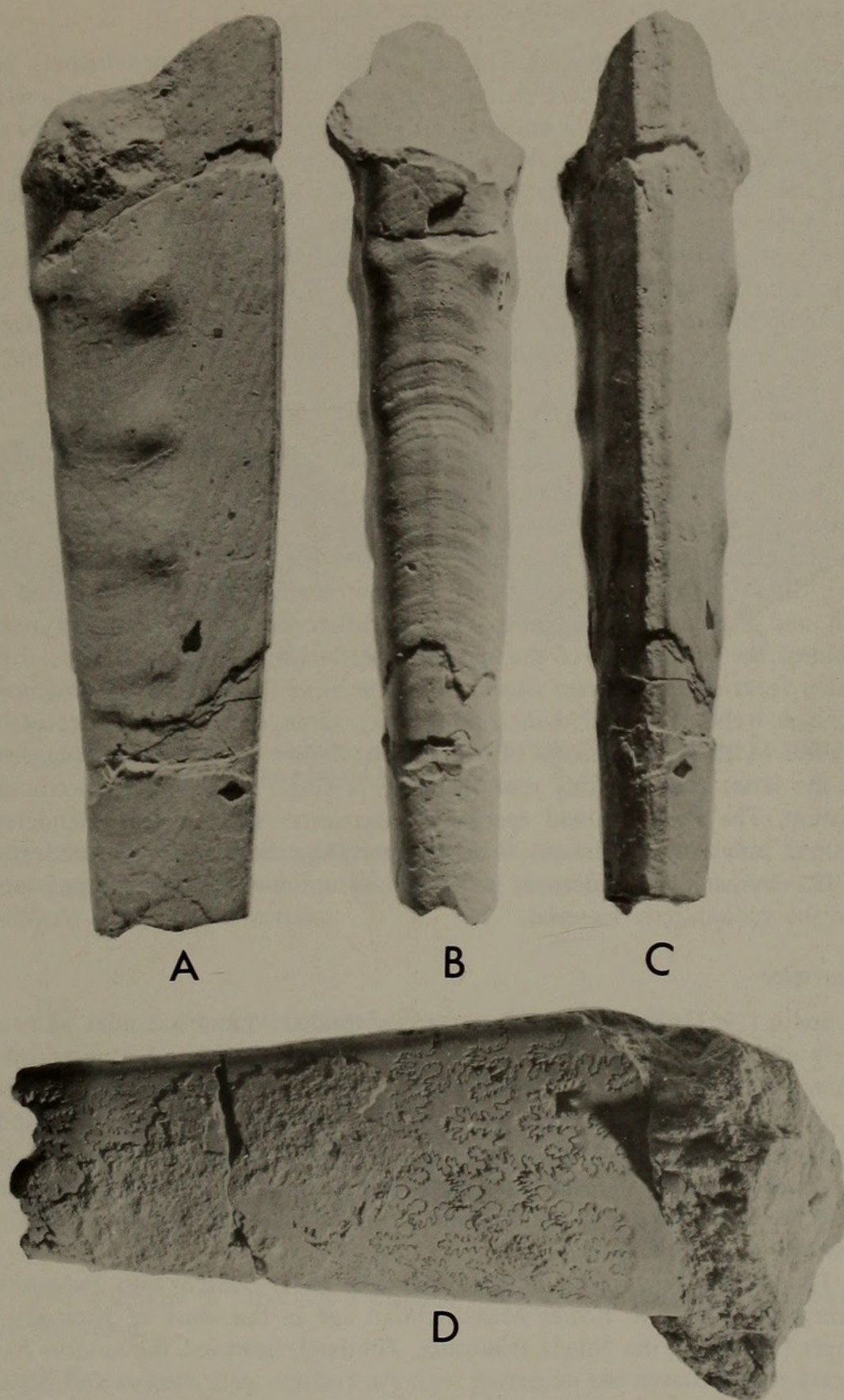


Fig. 5. A-C. *Eubaculites vagina* (Forbes). BMNH C51141. Plaster cast of Indian specimen. Note also the median dorsal ridge. $\times 1$. D. *Eubaculites latecarinatus* (Brunnschweiler). Lateral view, SAM-PCO5909. (See also Fig. 3A.)

From locality C (TBD 1336) in the Alphard Group. $\times 1$.

Description

The specimen consists of part of an impression of approximately one quarter of a whorl. The whorl section is distinctly compressed, higher than wide, with virtually parallel flanks and a slightly narrower, rounded venter. Ribs are feebly prosiradiate across the flanks, and pass straight across the venter (Fig. 6). Fine, though distinct crenations appear on the ribs towards the ventrolateral part of the flanks, and continue over the venter. Towards the apertural end of the fragment a few thicker ribs occur, apparently lacking crenations, although the material is too poorly preserved to be certain of this. A thin, sinuous but crenate rib branches off from the first of these thickened ribs at about midflank, presumably reflecting the presence of a constriction on the internal mould.

Discussion

The present specimen is virtually identical to Stoliczka's figure of the holotype, and, were the material more complete, the authors would have no doubt in definitely referring it to Stoliczka's species.

The genus *Gunnarites* is best known from the subantarctic islands from which Spath (1953) described a host of new species and varieties based on slight, and often overlapping morphological differences. Howarth (1966) greatly simplified the systematics of the species described by Spath, and reduced the number from eight to three: *Gunnarites antarcticus* (Weller), *G. bhavaniformis* (Kilian & Reboul), and *G. kalika* (Stoliczka), arranged in order of decreasing umbilical width and coarseness of ribbing. Henderson (1970: 54) even suggested that the latter may possibly represent only a single species with spectacular variation. The New Zealand species of *Gunnarites* described by Henderson (1970), *G. zelandicus* (Marshall), *G. denticulatus* (Marshall), *G. spathi* Henderson, and *G. varicostatus* Henderson, however, showed no such transitional series as in the subantarctic material.

Occurrence

Spath (1953) regarded the subantarctic Graham Land localities as being largely of Upper Campanian age, with the possibility of basal Maastrichtian elements occurring locally. Howarth (1966: 68), on the other hand, considered the subantarctic *Gunnarites*-yielding localities to be of late Lower to Middle Campanian age. Henderson (1970: 78) concluded that the Graham Land fauna may in part be uppermost Campanian or possibly basal Maastrichtian, due to the occurrence of three Graham Land kossmaticeratids above *Hoplito-placenticer* in New Zealand.

The present occurrence of *Gunnarites* sp. cf. *G. kalika* with *Eubaculites latecarinatus* points to Lower Maastrichtian age in the sense of Kennedy & Klinger (1975). On the Nibela Peninsula, Zululand, however, the authors have recently found *Gunnarites* occurring with *Pachydiscus gollevillensis* and *Saghalinites cala* in their Campanian IV below the level of abundant *Eubaculites* and

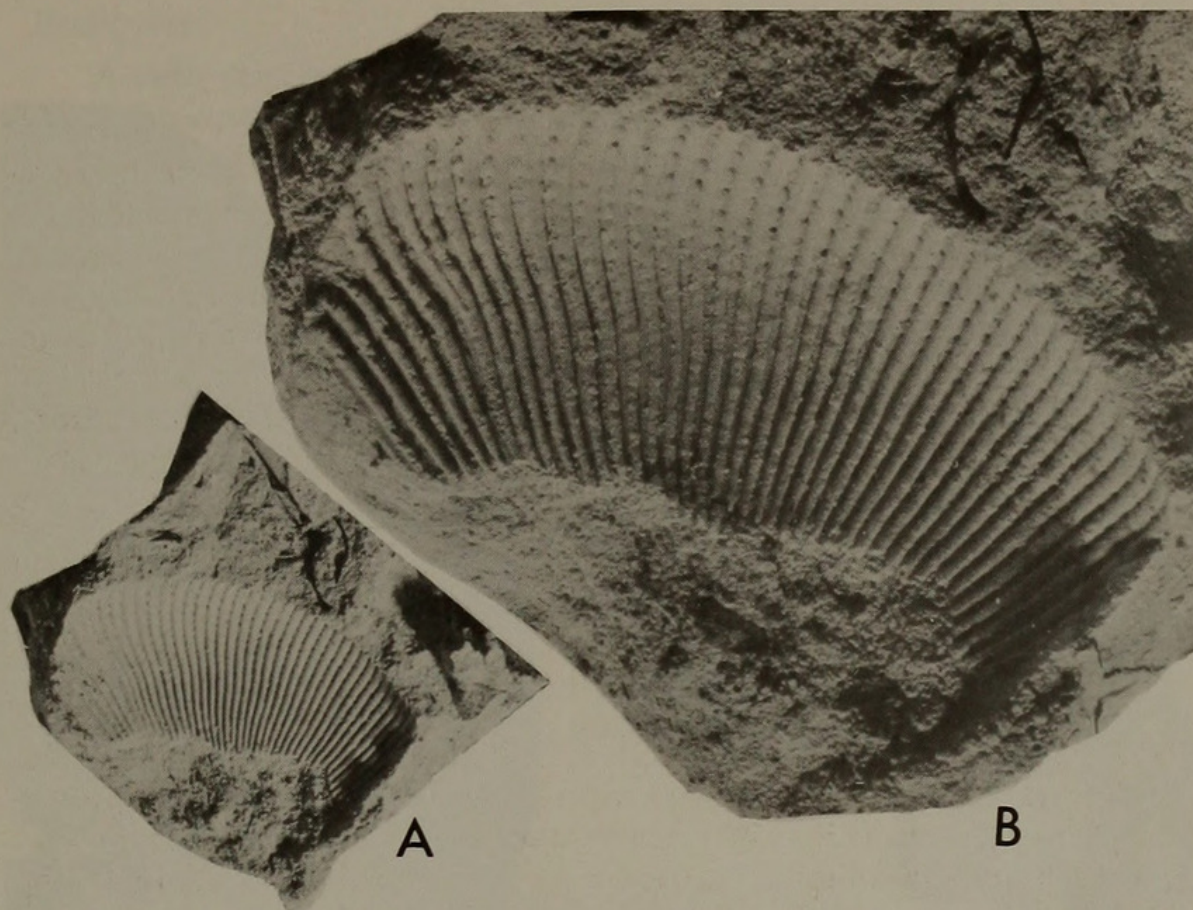


Fig. 6. *Gunnarites* sp. aff. *G. kalika* (Stoliczka). SAM-PCO5907. From locality C (TBD 1336) in the Alphard Group. A $\times 1$, B $\times 2.4$.

above that of *Hoplitoplacenticeras* and *Maorites*. This highlights the continuing problem of correlating the European Maastrichtian standard with the Southern hemisphere sequence.

Proplacenticeras kaffrarium (Etheridge, 1904)

Fig. 7

Placenticeras kaffrarium Etheridge, 1904: 89, pl. 3 (fig. 16).

Placenticeras umkwelanensis Etheridge, 1904: 89, pl. 3 (figs 17–20).

Placenticeras subkaffrarium Spath, 1921: 247, pl. 21 (fig. 2).

Placenticeras whitfieldi (auctorum, non Hyatt): Besairie, 1930, pl. 46 (fig. 1); Venzo, 1936: 107 (49), pl. 11 (7) (fig. 12).

Type

The holotype is Etheridge's original figured specimen from Umkwelane Hill, Zululand.

Material

SAM-PCO5908 from locality A in the Alphard Group.

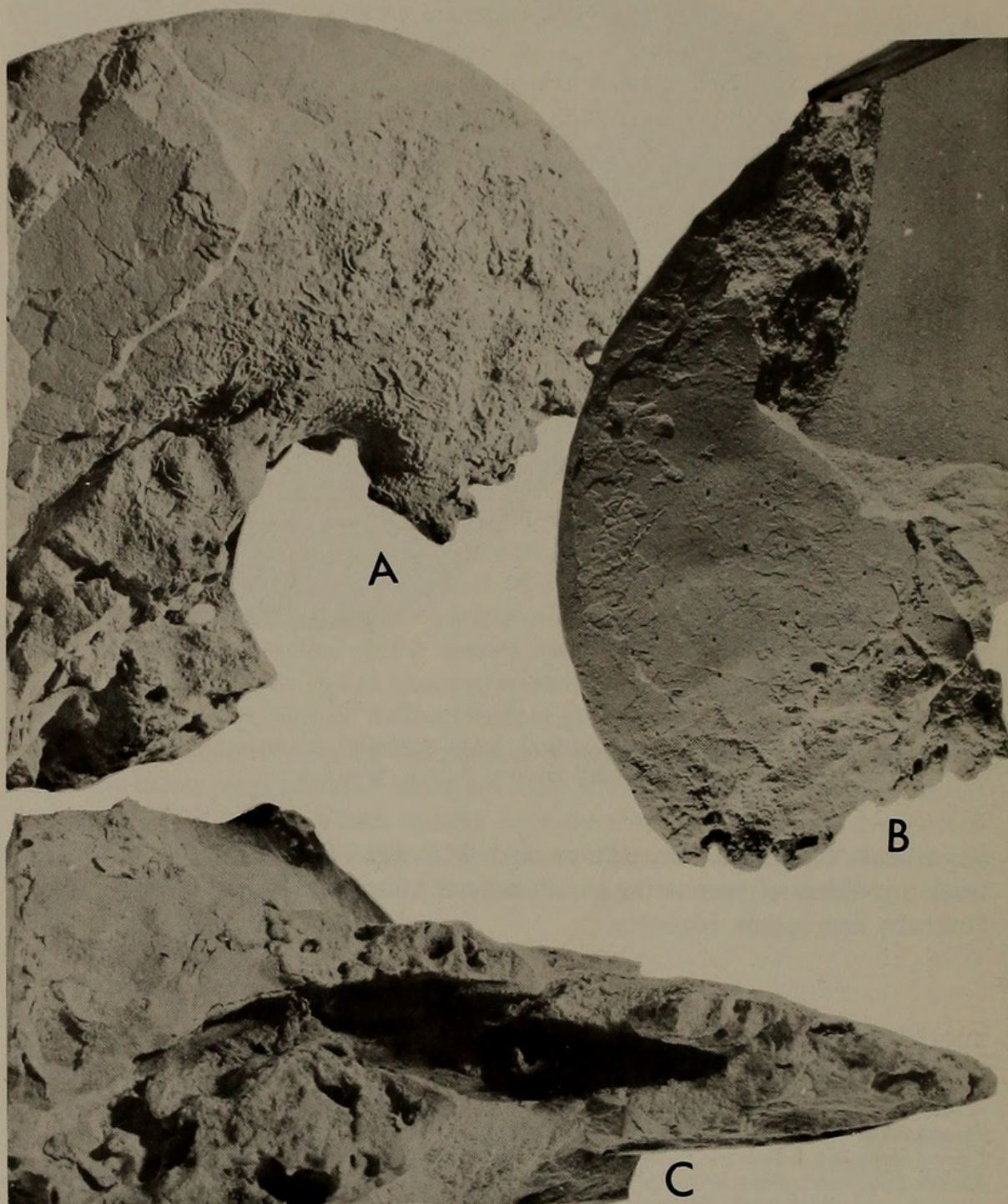


Fig. 7. *Proplacenticerias kaffrarium* (Etheridge). SAM-PCO5908.
From locality A (TBD 310) in the Alphard Group. $\times 1$.
A-B. Lateral views. C. Ventral view.

Description

A badly corroded body chamber fragment with part of the shell preserved shows the typical lenticular whorl section and flat venter on both inner and outer whorls which characterizes the '*umkwelanensis*' variants of this species. The sides are smooth, save for faint auricular swellings on the outer parts.

Discussion

P. umkwelanensis, *P. kaffrarium* and *P. subkaffrarium* were all originally described from Umkwelane Hill in Zululand and, as the authors have already suggested (Kennedy & Klinger 1975), represent no more than a single variable species; subsequent collecting in this area revealed the presence of all intermediates in the same concretion. This wide variation mirrors that now known to characterize placenticeratids, as in *Hoplitoplacenticeras plasticum* Paulke and *Placenticeras syrtale* (Morton) (Wolleben 1967).

P. kaffrarium ranges through the Lower Coniacian of Zululand and, as with Wolleben's *Placenticeras*, shows changing population structures with time, compressed '*umkwelanensis*' variants being commonest at low levels.

A further discussion is deferred, pending the authors' full revision of this rich material.

Scaphites (*Otoscapites*?) sp. indet.

Figs 8–9

Material

SAM-PCO5917–5918 locality A on the Alphard Group.

Description

Coiling in the early ammonitic part is very loose, with the whorls just touching (Fig. 9A), and a very shallow dorsal zone of impression. The whorl section increases rapidly in size, changing in shape from initially rounded, through ovoid depressed to laterally compressed and dome-shaped (Fig. 9A) on the late part of the ammonitic whorl. The section, however, is rounded throughout with no clearly defined umbilical or ventrolateral edges.

Ornament is best seen on the internal mould of SAM-PCO5917 (Fig. 8A). On the phragmocone this consists of strong, umbilical bullae which give rise to groups of two or three ribs which loop over the venter, with some additional intercalated ribs. Towards the shaft of the uncoiled body chamber, ornament weakens considerably and the mould is nearly smooth. A small fragment of the terminal hook (Fig. 8B) shows that all ornament weakens on the recurved part. The aperture is not preserved.

The suture is shown in Figure 9B, and is typically quadrilobate, scaphitoid, with a prominent incision, p, in the saddle L/U.

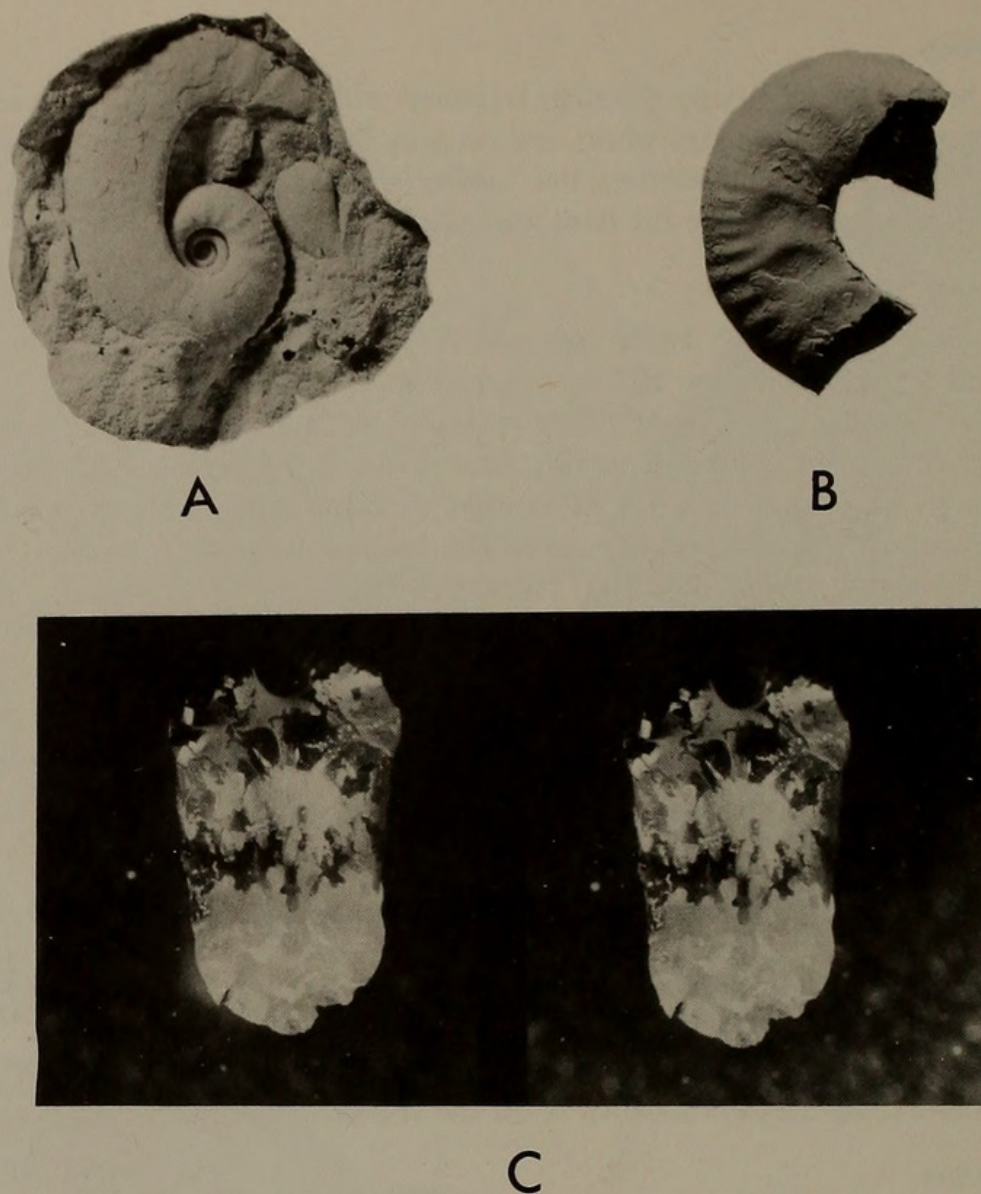


Fig. 8. *Scaphites* (*Otoscapites*?) sp. indet. SAM-PCO5917. From locality A (TBD 310) in the Alphard Group. A. Silica rubber mould. $\times 2$. B. Fragment of recurved body chamber. $\times 2$. C. Stereopair photograph of inner whorls. $\times c. 15$.

Discussion

The present specimen, although specifically indeterminate, appears to occupy a position between the genera *Otoscapites* and *Pteroscaphites*.

Ornament is of the type of *Scaphites aequalis*, as found in *Pteroscaphites minutus* Moreman (see especially Wiedmann 1965, pl. 58 (fig. 5)), but the relatively slow increase in whorl diameter and mode of coiling of the body chamber compare better with *Otoscapites*, e.g. *O. puerculus* (Jimbo) (see especially Tanabe 1975, pls. 10–11).

On the basis of the present material, erection of a new species is not advisable, and it seems adequate merely to record the first occurrence of a representative of the *Pteroscaphites*–*Otoscapites* plexus from southern Africa.

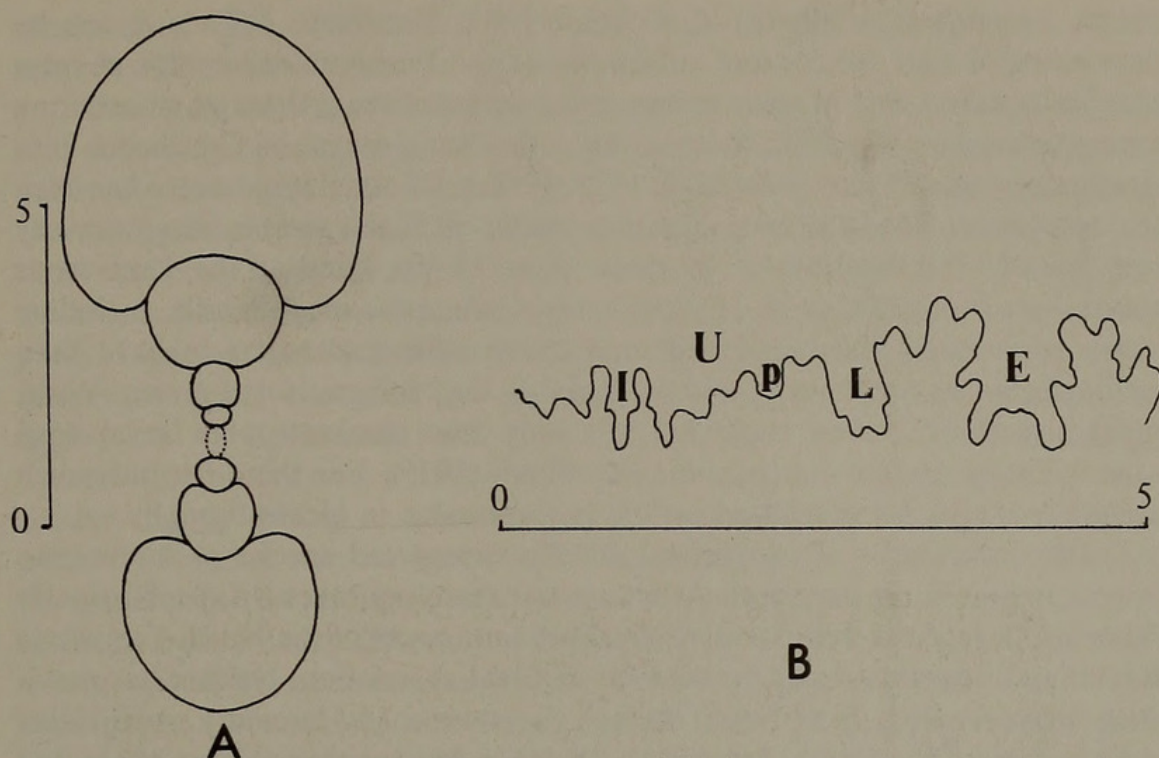


Fig. 9. *Scaphites* (*Otoscapites*?) sp. indet. From locality A (TBD 310) in the Alphard Group. A. Whorl section, SAM-PCO5918. B. Suture line, SAM-PCO5917.

For a full discussion on the affinities of *Pteroscaphites* and *Otoscapites*, as well as the possible sexual dimorphic implications, readers are referred to Wiedmann (1965).

Occurrence

Otoscapites and *Pteroscaphites* occur mainly in the Turonian and Coniacian, but according to Wiedmann (1965: 449, text-fig. 16) may occur as late as the Campanian, and probably arose in the Upper Albian.

The co-occurrence with *P. kaffrarium* suggests a Lower Coniacian date for this species.

BIVALVES

(By E. G. Kauffman)

Family *Inoceramidae* Giebel, 1852

Inoceramid bivalves have long been used in regional biostratigraphy because of their abundance, wide facies distribution, and common co-occurrence with ammonites in Cretaceous strata. More recently, Inoceramidae have evolved an important role in global and intercontinental correlation, and are now a mainstay of wide-ranging Cretaceous biostratigraphic systems. Where a detailed radiometric scale is available, as in the Western Interior Cretaceous of

North America (Obradovich & Cobban 1975; Kauffman 1977c), it can be demonstrated that species and subspecies of the Inoceramidae evolve at rates that are equal to, and in some cases even more rapid than, those of co-occurring ammonites and planktonic foraminifera—the ‘main stays’ of Cretaceous biostratigraphy (Kauffman 1970, 1972, 1975, 1978a). Of equal importance has been the recognition that the biogeographic range of Inoceramidae was normally very broad—intercontinental in more than 75 per cent of the Cretaceous species—and exceeded that of most other Cretaceous macrofossils, including many ammonites. Further, inoceramid species dispersal seems to have been ‘geologically instantaneous’, and as rapid as that for any fossil group. Wide, rapid dispersal has been attributed to a long-lived planktotrophic larval stage—as in living *Mytilus edulis* Linné (Kauffman 1975). For these reasons much attention is now being focused on the Inoceramidae in biostratigraphy.

The occurrences of two geographically widespread species of *Inoceramus* in concretions from the South African coast therefore takes on special significance. Both species have extensive distribution in rocks of the North Temperate Realm and provide a basis for detailed regional correlation. Neither has previously been reported from South Africa; *Inoceramus* (*Inoceramus*) *ernsti* Heinz is known from the South Temperate Realm in Madagascar (Heinz 1933), but *I. frechi* Flegel was previously thought to be restricted to the North Temperate Realm, mainly northern Europe. Collectively, these inoceramids suggest a Lower Coniacian age for the concretions, and this is compatible with the age as determined by co-occurring ammonites.

There is no good English language description of either of the *Inoceramus* species present in the Alphonse Group collections, and none anywhere that discusses interior shell morphology in detail, warranting redescription of the taxa here.

Genus *Inoceramus* Sowerby, 1814

Type species

Inoceramus cuvierii Sowerby (ICZN opinion 473, 1957, see Cox 1969: N315).

Description

Small to moderately large; slightly to highly inequivalve, left valve largest and most inflated; shell sub-erect (typical) to moderately prosocline. Beaks—umbo inflated and projecting, especially left valve, normally prosogyrous, incurved, situated anteriorly; some species with small anterior ear below beaks. Posterior auricle prominent, triangular and commonly flared posteriorly, separated from disc by distinct auricular sulcus. Posteroventral sulcus or flattened area occurs on most species, situated posterior and parallel to rounded umbonal fold. Anterior face commonly broad, flat to slightly

concave, in some cases bounded by low ridge to form pseudolunule; some species with shallow sulcus on anterior face.

Ornament of weak to very strong rugae, normally subequally developed and subevenly spaced, ranging to irregular and unequal; crowded, evenly to subevenly developed flat lamellae and/or raised growth lines commonly occur in interrugal depressions. Shell consisting of outer prismatic layer and thinner, inner nacreous layer. Shell thin except dorsally, where moderately to greatly thickened (especially prismatic layer) and folded along hinge and ligamental plate. Ligament multivincular, producing numerous, moderately excavated, narrow, vertically elongated pits separated by rounded, narrower ridges of flat interspaces on ligamental plate (Woods 1912, text-figs 66, 80 show typical examples). Commissure smooth, slightly to moderately sinuous and in some species slightly gaping on anterior face below beaks and anterior ear (where present); forming narrow byssal slit. Muscle impressions consisting of large, elongated posterior adductor 'scar' situated near posteroventral margin, a thin, entire or nearly entire (interrupted dorsolaterally) pallial line, and commonly a large pedal-byssal muscle insertion area beneath the small, curved but unnotched, umbonal septum. Some species with second small pedalbyssal retractor scar situated anterodorsally just below beak (see Kauffman & Powell 1977, fig. 3, especially fig. 3D). Thin linear tracks of accessory mantle suspender muscles occur inside the posterior auricle of many species, outside of the pallial line.

Discussion

The name '*Inoceramus*' has been broadly and inconsistently applied to a variety of inoceramid lineages which possess suites of morphologic characters, internal as well as external, that would be recognized in other bivalve groups as being of generic and subgeneric grade. Kauffman & Powell (1977) discuss this problem, and support a multigeneric taxonomy for the family such as that proposed by Cox (1969), though more extensively incorporating interior shell features such as musculature, ligamenture, dentition, the umbonal septum and various internal ribs, folds, etc., which are produced in selected lineages.

Inoceramus is thus redefined here in the restricted sense to comply with this taxonomic philosophy and the definition of Cox (1969: N315); it is expanded to include interior shell features to the extent that they are known. The *Inoceramus cuvierii*-*I. lamarcki* lineage serves as the model for this genus.

Variations in external shell morphology serve to define subgenera of *Inoceramus* (Cox 1969). *Inoceramus ernsti* is an extension of the *I. cuvierii*-*I. lamarcki* lineage and possesses all the characteristics of the subgenus (*Inoceramus*) Sowerby. The more prosocline shells of *I. frechi*, with their enlarged posterior auricle, less truncated anterior face, more equivalve shells, non- to poorly defined posteroventral sulcus, and more widely spaced ligament pits, probably represent a distinct subgenus, as yet undefined. Consequently no subgenus is listed for *Inoceramus frechi* Flegel in this respect.

Inoceramus (Inoceramus) ernsti Heinz, 1928

Fig. 10G-P

Inoceramus ernsti Heinz, 1928: 73-74. Tröger, 1967: 128-130, pl. 14 (figs 1-4, 6). Kauffman, 1977b, pl. 11 (fig. 5).

Inoceramus lamarcki Parkinson: Woods, 1911: 307-327 (part), text-fig. 85 (lectotype designated by Tröger, 1967: 128). ?Pergament, 1971 (part), pl. 4 (fig. 1) only.

Tethyoceramus (Proteoceramus) ernsti (Heinz), 1933: 250, pl. 19 (fig. 1a-b).

Material

Nine complete or nearly complete left valves, SAM-PCO5919A-H, some with shell margins broken, all with nacre intact. One right valve, complete except for posteroventral margin; nacreous layer preserved. All shells medium-sized adults. Scattered fragments and partial valves. All from locality B in the Alaphard Group.

Description

Measurements for South African specimens are given in Table 1. Moderate size for genus, attaining heights of 150-175 mm, lengths of 125 mm, and widths of 45 mm (right valve) to 75 mm (left valve) on described specimens. South African specimens smaller than average for species. Moderately biconvex; inequivalved; left valve moderately more inflated, larger than right valve, with markedly greater projection of beak and umbo above hinge line. Maximum inflation of both valves dorsocentral, just above midshell and point where valves show weak to moderately prominent geniculation (Fig. 10L-M, P); average H/W 1.83 for left valve, 2.2 for right valve. Valves inequilateral, subrect, slightly prosocline, with subrectangular to roughly ovate outline. Dorsal margin (hinge line) straight, moderately long, equalling one-half the shell length, posteriorly extended along auricle. Posterodorsal corner obtusely subangular, rarely acute or forming right angle where auricle slightly flared (Fig. 10I). Anterior margin straight to slightly convex except below beak, where slightly concave. Ventral margin moderately and asymmetrically rounded, posteroventrally flattened. Posterior margin moderately and more evenly curved. Beaks bluntly pointed, anterior; beaks-umbos highly inflated, projecting moderately above hinge line of left valve and strongly incurved, slightly above hinge line of right valve. Early umbo devoid of ornamentation; umbo weakly rugate ventrally. No anterior auricle or marginal projection. Posterior auricle small, subtriangular, gently sloping, moderately to poorly defined by shallow auricular sulcus; auricle smooth dorsally, weakly rugate nearer disc.

Disc ornamentation (Fig. 10G) consisting of weakly to moderately developed, subsymmetrical, subregular rounded rugae which become more prominent over geniculation and irregular, much weaker or absent ventral to geniculation. Raised growth lines absent, or sparse and irregularly developed between rugae near midshell. Nature of fine concentric ornamentation unknown.

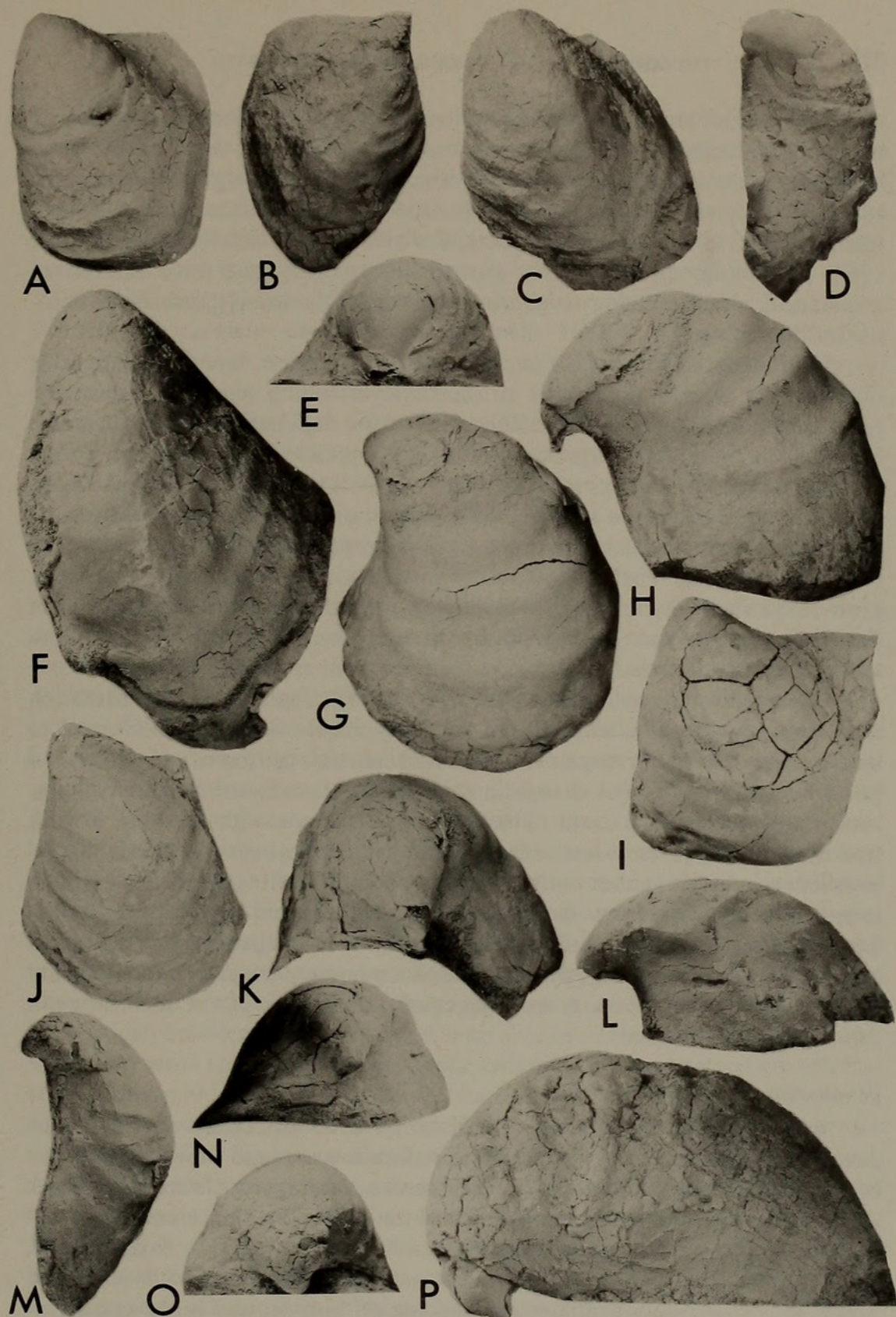


Fig. 10. A-F. *Inoceramus frechi* Flegel. A, D-E. Suberect left valve, left lateral, anterior, dorsal views respectively, SAM-PCO5919I. B. Incomplete right valve, SAM-PCO5919I. C. Typically inclined left valve, SAM-PCO5919K. F. Left valve showing typical development and trace of rugae, SAM-PCO5919J.

All from locality B (TBD 4510) in the Alphard Group.

A-E $\times 1$, F $\times 2$.

G-P. *Inoceramus (Inoceramus) ernsti* Heinz. G-H, K. Oblique, left lateral, anterior and dorsal views respectively, left valve lacking lateral auricle, with typical ornament, SAM-PCO5919B. I, L, N. Left lateral, anterior and dorsal views respectively, left valve with unusually large posterior auricle, PCO5919E. J, M, O. Left lateral, anterior and dorsal views respectively, small typical left valve, PCO5919G. P. Anterior view, largest left valve, PCO5919D.

All from locality B (TBD 4510) in the Alphard Group. All $\times 1$.

Growth line and rugae trace typically irregular, moderately curved anteriorly, becoming flattened to broadly curved ventrally (Fig. 10J), with angular bend over weakly developed umbonal fold; trace markedly straight along the flat to very weakly sulcate posterior shell flank, forming second angular bend over low posterior fold bounding the auricular sulcus. The lectoholotype (Tröger 1967, pl. 14 (fig. 6)) best shows growth line trace. Rugae trace variable in population, rarely ranging to subrounded with only weakly defined postero-ventral flattening (Fig. 10G).

Shell moderately thin (1–2 mm) over most of the disc; inner nacreous layer only slightly thinner than outer prismatic layer; along hinge line, prismatic layer rolled and moderately thickened to form ligamental plate. Ligament multivincular; individual ligamental pits poorly preserved. Musculature poorly known. Umbonal septum medium sized, curved but not notched ventrally, containing vertical striae on inner face, marking site of a pedalbyssal muscle insertion. Pallial line weakly impressed, thin, complete anteriorly, but unknown elsewhere on shell. Posterior adductor insertion track marked by two weak grooves on shell interior, slightly diverging ventrally, situated along posterior flank at site of flattening in growth line trace. Actual adductor insertion area, and pedalbyssal musculature of disc not preserved on known specimens.

Principal ontogenetic variation involves: (i) change in ornamentation from smooth (juvenile) umbone, to regularly rugate adult midshell area, to weakly and irregularly rugate (or smooth) ventral (gerontic?) shell beyond point of geniculation; (ii) change in shell shape, as reflected in growth lines: moderately prosocline, ovate to submytiloid in shape with rounded growth line trace during juvenile and early adult growth, changing to suberect, slightly prosocline subrectangular outline (mid- and late adult growth stages) with irregular growth line trace (flattened posteroventrally and bounded by angular bends). Adult variation mainly reflected in degree of irregularity of growth line trace (subrounded and slightly irregular to moderately irregular), development of rugae (weak to moderate) and degree of geniculation of the shell (none to moderately well defined).

Discussion

Inoceramus (Inoceramus) ernsti Heinz is a cosmopolitan species which occurs almost exclusively with Lower Coniacian strata and biotas (Oberturon of German authors) in Europe, North America, Madagascar, north and South Africa, and possibly on the Pacific coast of the USSR (as *?Inoceramus lamarcki lamarcki* Parkinson, in part, Pergament, 1971, pl. 14 (fig. 1)). Tröger (1967, fig. 43) notes that *I. (I.) ernsti* co-occurs only with *Inoceramus deformis* Meek and *I. inconstans* Woods in northern and central Europe, and in the upper half of the 'Oberturon'. Based on the co-occurrence of these last two inoceramids with Lower Coniacian (and never older) ammonites and foraminifera elsewhere in the world, this suite of species is now widely regarded as Lower Coniacian in age. American occurrences of *I. (I.) ernsti* (Kauffman 1977b; 1975 as *I. erectus*

in part) range questionably from the highest ammonite zone of the Turonian (*Scaphites corvensis*) and definitely through the lower half of the Lower Coniacian to the top of the *Inoceramus erectus* zone. The lectoholotype from England lacks locality data and was only questionably referred to the latest Turonian *Holaster planus* zone of the Upper Chalk (Woods 1911: 325). It could just as well have come from younger levels, being a float specimen.

Several described species are very closely similar, and related to *I. (I.) ernsti*. Primary among these are *I. madagascariensis* Heinz (1933, pl. 19, (fig. 2); pl. 20 (fig. 2); Coniacian), *I. inaequalvis* Schlüter (Heinz 1933, pl. 18 (fig. 1a-c); Turonian), *I. selwyni* McLearn (1926, pl. 21 (figs 8-9); Middle, Upper Coniacian), and *I. erectus* Meek (Kauffman 1977b, pl. 11 (figs 3-4); Meek 1877, pl. 13 (figs 1, 1a); pl. 14 (fig. 3); Lower Coniacian). With large populations, and careful study of adult variation in the species, some of these may prove to be conspecific. *I. erectus* Meek, 1877, has priority among the possible conspecific taxa. Small morphologic differences separate the species as currently known. Compared to *I. (I.) ernsti* as redefined by Tröger (1967), (i) *Inoceramus inaequalvis* is smaller, narrower, and has twice the number of rugae; these are more regularly developed and more closely spaced; there is no well-defined growth geniculation, and the posterior auricle is smaller; most descriptions depict *I. inaequalvis* as less inequivalved than *I. (I.) ernsti*, with greater projection of the beak on the left valve above the hinge line; (ii) *I. madagascariensis* has similar but more strongly defined rugae with a more rounded, symmetrical growth line trace, no growth geniculation, and with two to four strongly raised growth lines subregularly spaced between the rugae; *I. (I.) ernsti* lacks these lines; (iii) *Inoceramus erectus* is most closely similar to *I. (I.) ernsti*, but is nearly equivalve (see Meek's 1877 types), has a more rounded, symmetrical growth line trace (though with a posteroventral flattening), a broader and more rounded to ovate shell, fine juvenile ornamentation consisting of small regular rugae and/or coarse raised growth lines, and more numerous and closely spaced adult rugae, commonly with coarse, raised growth lines irregularly spaced between them; (iv) *Inoceramus selwyni* is also more equivalve with a broader, more rounded to subquadrate shell form, a more curved growth line trace showing only slight posteroventral flattening, and more strongly developed rugae. This younger Coniacian form is obviously derived from *I. (I.) ernsti*.

Compared to the co-occurring South African specimens of *I. frechi* Flegel, *I. ernsti* is much more erect, more inequivalve, with fewer, coarser, more widely spaced rugae, and with a distinctive growth line trace. The small, close, regular rugae of *I. frechi* are not found on the umbo of *I. (I.) ernsti*, which generally lacks ornamentation.

Temporal relationships of these closely related taxa suggest an evolutionary series beginning with Lower to Middle Turonian *I. apicalis* Woods, through Upper Turonian *I. inaequalvis*, to *I. ernsti* (latest Turonian?-Lower Coniacian). *I. erectus* (Lower Coniacian), to higher Coniacian forms such as *I. madagascariensis* and *I. selwyni*.

Stratigraphic occurrence

Lower Coniacian of South Africa, possibly ranging to highest Turonian elsewhere.

TABLE 1. Biometry of South African *Inoceramus* (*Inoceramus*) *ernsti*: hypotypes.

Catalogue no.	valve L = left R = right	H (mm)	L (mm)	W (mm)	AL (mm)	$\angle i$ (degrees)	no. rugae in	
							1st 25 mm AL	2nd 25 mm AL
PCO5919A	L	54,2	41	30,9	57,5	65	3	4
PCO5919B	L	55	44,1	35,5	56,7	58	2	2
PCO5919C	L	51,3	34,1*	36,2	52,5	68	3	3
PCO5919D	L	73	47	38,4	74,1	75	3	3
PCO5919E	L	44,1	36,2	23,2	45,9	68	4	5
PCO5919F	L	38,7	34,8	20,5	42	65	4	3
PCO5919G	L	42,2	31,5	17,8	42	79	2	4
PCO5919H	R	47,6	37,4	21,6	46,8	76	3	3
Mean values			H/L	H/W	H/AL			
	L		1,33	1,83	0,97	68,3	3	3**
	R		1,27	2,20	1,02	76		

H—height perpendicular to hinge line; L—length parallel to hinge line; W—width (inflation) of single valve; AL—length of shell along growth axis; $\angle i$ —angle of inclination; *—partially crushed; **—average no. rugae in 3rd 25 mm AL (3 specimens) = 3; in 4th 25 mm AL (1 specimen) = 2.

Inoceramus frechi Flegel, 1905

Fig. 10A–F

Inoceramus frechi Flegel, 1905: 25. Scupin, 1907: 693.

Andert, 1911: 51 (19), pl. 1 (fig. 8a–b); pl. 7 (fig. 6).

Scupin, 1912, 1913: 208, pl. 11 (fig. 10), pl. 12 (fig. 2).

Andert, 1934: 120–122, pl. 5 (figs 5–8, 9a–c), pl. 6 (fig. 1).

Dobrov & Pavlova, 1959: 137, pl. 9 (fig. 4). Tsagarelli, 1963: 79, pl. 7 (fig. 3).

Inoceramus cf. *frechi* Flegel; Heine, 1929, pl. 6 (fig. 31).

Inoceramus sp. nov. (*I. mukawaensis* Otatsume MS.) Nagao & Matsumoto, 1939: 293–295, pl. 32 (fig. 1a–d, non fig. 3a–b).

Mytiloides? *frechi* (Flegel), Kauffman, 1977b: pl. 9 (fig. 21).

Material

SAM–PCO5919, I–M, three nearly complete, medium-sized left valves, most of nacre attached; two right valves, one moderate size, the other in late juvenile to early adult growth stage; from locality B on the Alphonse Group.

Description

Moderate size, attaining height of 100 mm, length of 80 mm, width of 40–45 mm or more; measurements of South African material in Table 2. Moderately inequivalved; left valve moderately more inflated, larger than right valve, with somewhat greater dorsal projection of beak and umbo. Moderately biconvex, H/W for left valve averaging 1,83, for right valve 2,29;

maximum inflation dorsocentral. Valves inequilateral, moderately prosocline (left valve) to suberect or slightly prosocline (right valve) (Fig. 10C typical). Angle of inclination averaging 59° on South African specimens, 66° on Andert's (1934) hypotypes from north Germany. Valve outline subquadrate to submytiloid; dorsal margin (hinge line) straight, moderately long, situated posterior to beak along auricle, dorsoposterior corner normally rounded to obtusely subangular, in some specimens flared posteriorly (Andert 1934, pl. 5 (fig. 7)). Anterior, posterior margins slightly diverging ventrally; posterior margin gently rounded, anterior margin straight to slightly concave below beaks; ventral margin moderately, irregularly rounded, somewhat flattened posteroventrally. Anterior flank steep, slightly concave to flattened, in some specimens bounded by low fold to form pseudolunule. No anterior auricle; dorsoanterior margin just below beaks slightly projecting in some specimens. Subtriangular posterior auricle well defined (Fig. 10A), gently sloping to flattened distally, with weakened ornamentation similar to that of disc; auricle separated from disc by shallow to moderately deep auricular sulcus. Posteroventrally directed umbonal fold low, asymmetrical, steepest posteriorly, rugae and growth lines make irregular bend across umbonal fold (Fig. 10C, F). Flank posterior to umbonal fold flattened to very broadly sulcate; rugae trace straight across this area. A low, rounded fold separates auricular sulcus from posteroventral sulcus or flattened area.

Beaks bluntly pointed (Fig. 10A, C) anterior; beaks-umbos moderately (left valve) to slightly (right valve) projecting above hinge line, moderately prosogyrous, incurved. Umbonal ornamentation finer but similar to that on disc.

Ornamentation consisting of numerous, rounded to subangular, subequally developed, subevenly spaced, asymmetrical concentric rugae with rare, irregularly raised growth lines between them. Rugae somewhat irregular on older parts of shell. Growth line trace slightly flattened on anterior face, slightly to strongly flattened posterior to umbonal fold; with subangular bends over umbonal and subauricular folds (Fig. 10C, F). Shell thin; hinge plate moderately thickened. Ligamenture (known only from Andert 1934, pl. 5 (fig. 9b)) multivincular, producing vertically elongated, subrectangular, moderately deep pits along ligamental plate separated by slightly smaller, flattened to broadly rounded interspaces. Musculature poorly preserved on known specimens; pallial line entire, thin, but only partially observed; posterior adductor muscle track weakly defined along posterior flank of umbonal fold. Adductor and pedalbyssal insertion areas not yet observed.

Ontogenetic change mainly involves increase in size and spacing of rugae, and change from erect to more inclined shells between juvenile and adult growth stages. Principal adult morphological variation involves shell shape (suberect to submytiloid; see Andert 1934, pl. 5 (figs 5-9), growth line trace (subrounded with only slight posteroventral flattening to irregular, with prominent posteroventral flattening and angular bends over umbonal and auricular folds), and development of posterior auricle (rounded to flared).

Discussion

This is a cosmopolitan species, and is known from North America, Japan?, probably eastern Russia (? as *I. stantoni*, part, in Pergament 1971, see pl. 60 (fig. 3a-b)), throughout northern and western Europe, sparsely in the Caribbean and Mediterranean Tethys, and now off South Africa. *Inoceramus frechi* occurs primarily in beds attributed to the Lower Coniacian.

In northern Europe, several related and/or co-occurring species are similar, and possibly even conspecific. *Inoceramus winkholdioides* Andert (1934, pl. 8 (figs. 1a-b)) is an associated species mainly known from compressed internal moulds; it appears to be somewhat more erect, and to have a much more angular growth line (rugae) trace than *I. frechi*. *Inoceramus glatziae* Flegel (Andert 1934, pl. 6 (figs 2-4)) and *I. multiformis* Pergament (1971, pl. 33 (fig. 3)) are similar in form but have a much more irregular ornamentation with finer, closer rugae and raised growth lines. Some specimens of *I. kleini* Müller are remarkably similar (see Andert 1934, pl. 4 (fig. 9)); but typical *I. kleini* are smaller, more prosocline and have regularly spaced growth lines between the rugae. Descendant species which are closely similar are *Inoceramus stantoni* Sokolow (Stanton 1899, pl. 75 (figs 9-10)) and the probably conspecific species *I. uwajimensis* Yehara (Nagao & Matsumoto 1939, pl. 34 (figs 1-3)), both from Middle and/or Upper Coniacian and possibly Lower Santonian levels. These species have a more prosogyrate beak-umbo, a more prosocline shell and a narrower, but longer and more indistinct posterior auricle than does *I. frechi*. Regular, fine growth lines are common between the rugae on *I. stantoni*. The Lower Coniacian *I. incurvatus* Tröger is broader and more strongly rugate than *I. frechi*, but related.

Stratigraphic occurrence

Lower Coniacian in South Africa, in so far as known. Elsewhere the species may range into latest Turonian in North Germany (Oberturon alpha). It is not yet definitely reported from younger Coniacian strata.

ENVIRONMENTAL AND ECOLOGICAL INTERPRETATION OF INOCERAMIDAE

Unlike the ammonites, which in general are ambiguous indicators of sedimentary environment, the inoceramids from locality B permit partial interpretation of the prevailing bathymetric current conditions, and also give indications of their ecologies.

Complete left valves of inoceramids dominate the collection; as both species of *Inoceramus* are strongly inequivalve, with the left being the largest and the heaviest, this occurrence suggests winnowing of dead shells by moderate bottom currents, with selective removal of the lighter right valves. The disarticulated but relatively complete nature of the valves supports this interpre-

tation. Preservation of the nacre and lack of significant crushing of the specimens further suggest early diagenetic cementation of the concretions at or just below the sediment-water interface, before crushing by compaction of a thick sediment overburden.

Thus, taphonomic analysis of the inoceramid bivalves collectively suggests a shelf habitat with moderate bottom currents and relatively slow rates of sedimentation, below the depth range of strong wave and current action. The matrix of the concretions, a very fine-grained, well-sorted relatively clean and mature quartz sand, is compatible with interpretation of an inner shelf environment.

Inoceramus (I.) ernsti Heinz, is an inflated, markedly inequivalve species with a broad, flattened to slightly concave anterior face, a sinuous anterior byssal slit, and two or more small pedalbyssal retractor muscle insertion areas situated on the anterodorsal part of the shell interior and under the umbonal septum. These characteristics suggest a wholly epifaunal mode of life with the shell strongly attached by byssal threads along the anterior face. The inequivalve condition suggests that the species may have lain semi-recumbent on the anterior face of the left valve with the commissure at an angle of 60–80 degrees to the substrate.

Inoceramus frechi Flegel is somewhat more prosocline and mytiloid in form, moderately inequivalve (left valve larger and more convex), has a flat to slightly concave anterior face (smaller and less well defined than that of *I. (I.) ernsti*) and has a weakly defined byssal slit and pedalbyssal musculature. The only known byssal muscle is beneath the umbonal septum. We speculate that this species was also wholly epifaunal, lying semi-reclined on the anterior face of the left valve, loosely attached by a thin row of byssal threads as in living *Mytilus*.

Thus, both inoceramid species show adaptation to epibyssate habitats and the ability to withstand moderate, but not severe currents without being uprooted. It is assumed that byssal attachment was originally to shell fragments, and ultimately to other living *Inoceramus* shells, resulting in clustered populations.

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TABLE 2. Biometry of South African *Inoceramus frechi*: hypotypes.

Catalogue no.	valve L = left R = right	H (mm)	L (mm)	W (mm)	AL (mm)	$\angle i$ (degrees)	no. rugae in	
							1st 25 mm AL	2nd 25 mm AL
PCO5919I .	L	40,1	29,2	21,4	42,5	57	8	5
PCO5919J .	L	34,5	24,1	17	35,4	61	5	5
PCO5919K .	L	42,5	32,9	26,9	46	54	c. 9-10	6
PCO5919L .	R	42,5	30,4	16,4	43,5	66	7	4
PCO5919M .	R	20	17,2	10,1	20,5	55	9	—
			H/L	H/W	H/AL			
Mean values .	L		1,37	1,83	0,95	57,3		
	R		1,28	2,29	0,98	60,5	7,7	5,0

See Table 1 for key to abbreviations.

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