

ON THE AFFINITIES OF *MADAGASCARITES ANDIMAKENSIS*
COLLIGNON, 1966, AND ALLIED UPPER CRETACEOUS
HETEROMORPH AMMONITES

By

HERBERT CHRISTIAN KLINGER

Division of Earth Sciences, South African Museum, Cape Town

&

WILLIAM JAMES KENNEDY

Geological Collections, University Museum, Oxford

(With 17 figures)

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ABSTRACT

Coiling in the Santonian heteromorph ammonite genus *Madagascarites* Collignon, 1966 (type species *M. andimakensis* Collignon, 1966), was originally compared to that of *Nipponites* Yabe, 1904. This is shown to be incorrect. *Hyphantoceras ingens* Collignon, 1966, is regarded as a synonym of *M. andimakensis*. Material from the Turonian of Japan ascribed to the genus *Madagascarites* clearly does not belong to this genus and is referred to *Ryuella* gen. nov., with *Madagascarites ryu* Matsumoto & Muramoto, 1967, as type species. *Heteroceras amapondense* van Hoepen, 1921, which was also tentatively referred to *Madagascarites*, is here referred to *Eubostriochoceras (Amapondella)* subgen. nov. of which it is the type species.

CONTENTS

	PAGE
Systematic descriptions and discussions	227
Acknowledgements	246
References	246

SYSTEMATIC DESCRIPTIONS AND DISCUSSIONS

We (Klinger & Kennedy in prep.) are at present revising the Upper Cretaceous heteromorph ammonites from Zululand described by Klinger (1976) on the basis of additional and new material. Our views on the systematics and phylogeny of these heteromorphs will be discussed fully in this revision. For the present we restrict ourselves to the affinities of the poorly known genus *Madagascarites* Collignon, 1966, and allied forms.

The genus *Madagascarites* Collignon, 1966, with type species *Madagascarites andimakensis* Collignon, 1966 (p. 26, pl. 465 (figs 1897–1898)) from the Middle Santonian of Madagascar was introduced (Collignon 1966: 26) as follows: 'MADAGASCARITES ANDIMAKENSIS nov. gen. nov. sp. G.T. Il s'agit d'une Ammonite à déroulement aussi désordonné que celui de *Nipponites* . . . mais en différant par l'ornementation, puisque *Nipponites* n'a pas des côtes tuberculées.

Ici, les côtes serrées, annulaires, minces et tranchantes, sont groupées par 5-7 environ, et sont encadrées de côtes à boucles à 4 tubercules, comme chez *Hyphantoceras ingens* nov. sp. Mais les côtes à boucles commencement dès le début et ne sont pas limitées à la chambre d'habitation. Le mode de déroulement est aussi bien différent et permet, à mon sens, de séparer ces divers échantillons, celui d'Antsoha se rattachent naturellement à *Hyphantoceras*, au moins pour le moment, car des séries d'exemplaires de toutes tailles pourraient peut-être permettre de les rattacher les uns aux autres dans le genre *Madagascarites* qui serait alors caractérisé aussi bien par son ornementation que par son mode particulier de déroulement.'



Fig. 1. *Madagascarites andimakensis* Collignon, 1966. The holotype, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 734, Sud Ambiky (Belo sur Tsiribihina), Madagascar. This specimen cannot, at present, be traced in the collections of the Université de Bourgogne in Dijon. $\times 1$.

According to Collignon's diagnosis, *Madagascarites* thus has (irregular) coiling as in *Nipponites*, but ornament throughout as on the body chamber of *Hyphantoceras ingens*.

Apart from the holotype, Collignon (1966: 26, pl. 465 (fig. 1898)) figured a second specimen consisting of part of a helical whorl and the succeeding, ascending body chamber.

Several questions have to be addressed:

1. The relationship between *Madagascarites* and *Nipponites*.
2. The relationship between *Madagascarites andimakensis* and *Hyphantoceras ingens*.
3. Affinities with *Hyphantoceras*.
4. The identity of *Madagascarites ryu* Matsumoto & Muramoto, 1967.
5. The affinities of *Hyphantoceras (Madagascarites?) amapondense* (van Hoepen).



Fig. 2. *Madagascarites andimakensis* Collignon, 1966. The holotype, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 734, Sud Ambiky (Belo sur Tsiribihina), Madagascar. This specimen cannot, at present, be traced in the collections of the Université de Bourgogne in Dijon. $\times 1$.

The holotype of *Madagascarites andimakensis* has two early whorls, which are situated at an angle to each other (Figs 1–4). Having examined the holotype, Klinger (1976: 71) suggested that this may be due to post-mortem fracture of the shell; the totally crushed, ascending body chamber may confirm this. These early whorls suggest helical coiling, either contiguous or slightly separated, and are succeeded by a final helical whorl and an ascending body chamber that reaches at least to the top of the early whorls—a mode of coiling analogous to that of the Upper Campanian genus *Anaklinoceras* Stephenson, 1941.

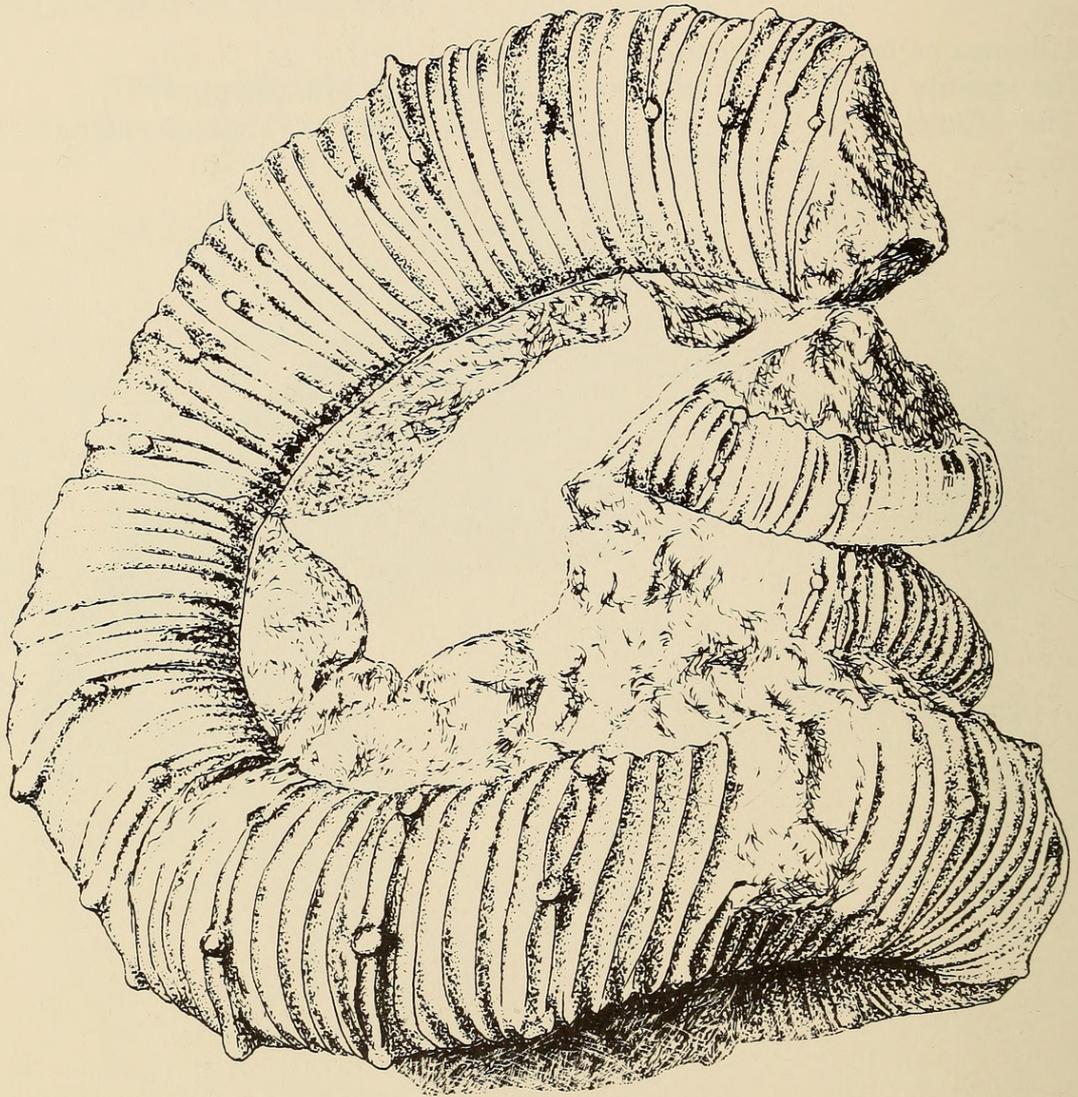


Fig. 3. *Madagascarites andimakensis* Collignon, 1966.
Line drawing based on Figure 1. $\times 1$.

Unfortunately, the holotype of *M. andimakensis* cannot, at present, be located in the Collignon collection at Dijon (J.-H. Delance—pers. comm. 31 August 1994). When last seen and photographed by Klinger in 1973, it was displayed in General Collignon's study. We suspect that it may have been misplaced during the transfer of the Collignon collection to Dijon. However, another specimen (757), with a label in Collignon's handwriting and which

identifies it as *Madagascarites andimakensis* (Figs 5–6A), is present amongst the undescribed material at Dijon. This specimen is much smaller than the holotype and lacks the early whorls. The last part of the phragmocone is poorly preserved and tubercles, if present, are either very weak or absent. Tubercles are only prominent on the ascending part of the body chamber.

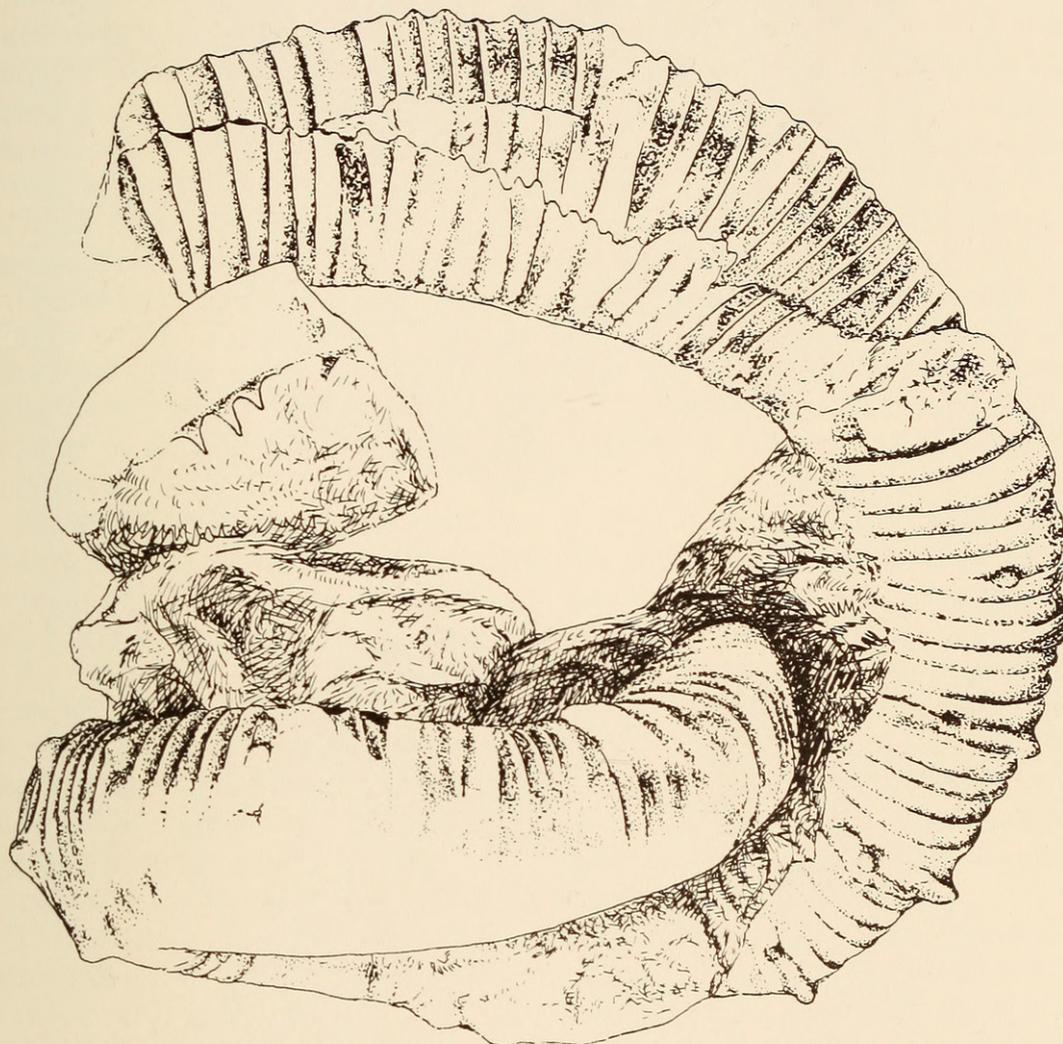


Fig. 4. *Madagascarites andimakensis* Collignon, 1966.
Line drawing based on Figure 2. $\times 1$.

1. As discussed above, the preserved early whorls of the holotype of *Madagascarites andimakensis* suggest a helical mode of coiling in the early, but not earliest, part of the phragmocone, and ends in a final helical whorl, followed by an ascending body chamber, which may embrace the helical phragmocone. Coiling in well-preserved *Nipponites* is very distinctive, consisting of a series of U-shaped sections, comparable to the sutures on a tennis ball, and ends in a looped or U-shaped body chamber, suspended below the phragmocone (Okamoto 1989; herein Fig. 7). The genus is thus far only known from the Middle Turonian to Lower Coniacian with records from Japan, Saghalien, Kamchatka and Oregon (see Matsumoto 1977). Similarities between the coiling of *Madagascarites* and *Nipponites*, as suggested by Collignon (1966: 26), cannot be sustained.

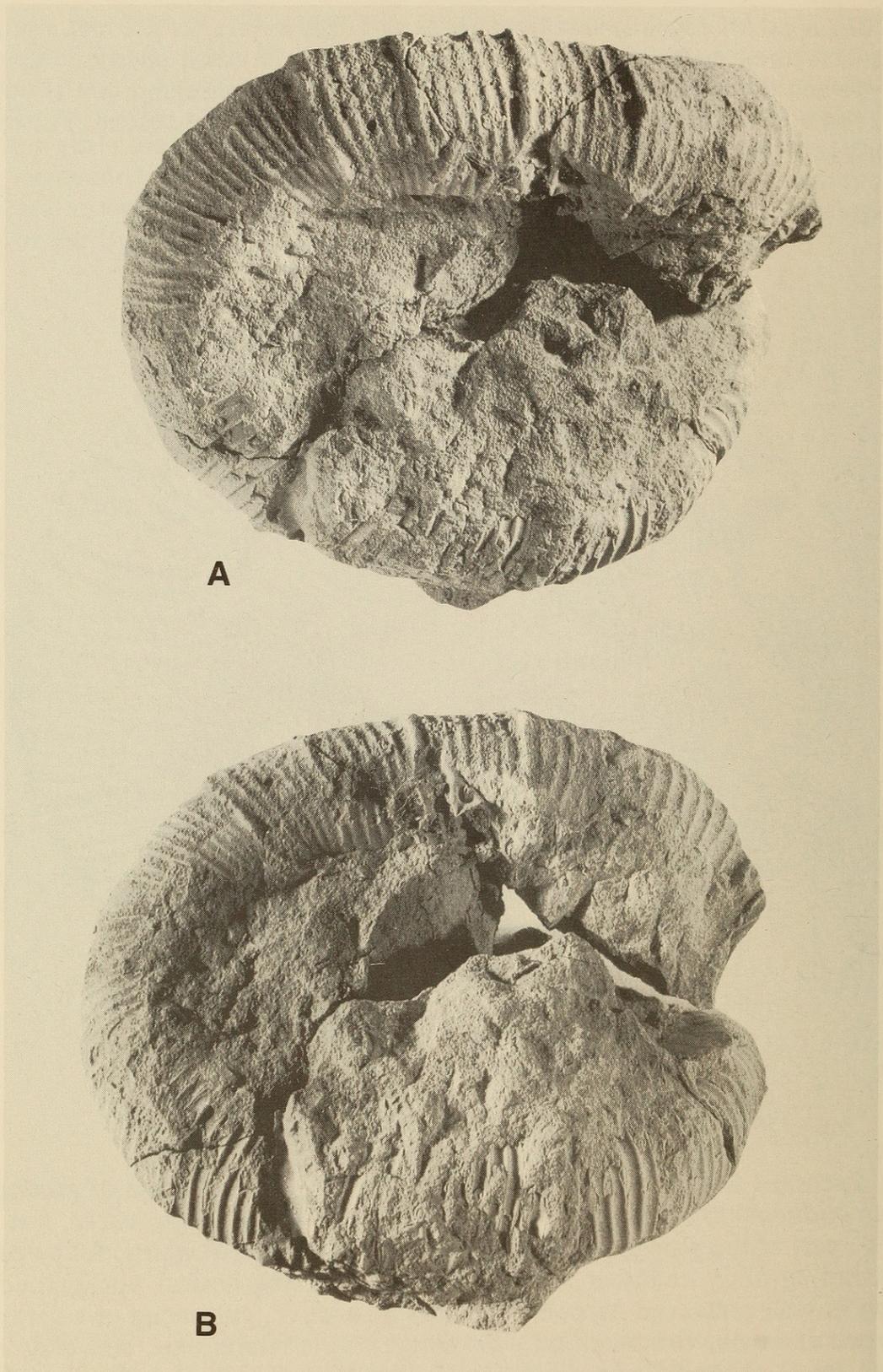


Fig. 5. *Madagascariites andimakensis* Collignon, 1966. Undescribed specimen from the Middle Santonian, zone of *Texanites hourqi* at gisement 757, km 8500 Coupe S. Beantaly, Souromarinaro (Belo sur Tsiribihina), Madagascar. A. View from top, looking down on ascending part of body chamber. B. Lateral view, with ascending part of body chamber pointing upwards. Both $\times 1$.

2. *Madagascarites andimakensis* and *Hyphantoceras ingens* have identical body chamber ornament. This consists of several simple, non-tuberculate ribs separating looped ribs with four rows of tubercles. According to Collignon (1966: 26), these looped, quadrituberculate ribs already occur on the early whorls of *M. andimakensis* but only appear on the body chamber of *H. ingens*.

Both species are dated as Middle Santonian, but the types are from different localities. However, we have a specimen (SAM-GMC737, Fig. 6B-C) identified as *H. ingens* by General Collignon from the same locality as the figured paratype of *M. andimakensis*. *Hyphantoceras ingens* and *M. andimakensis* are thus, in part at least, coeval. The early whorls of *H. ingens* are not known, but the last part of the body chamber of the holotype (Fig. 8) and specimen SAM-GMC737 (Fig. 6B-C) show signs of an upward curvature, suggesting a final mode of coiling similar to that of *M. andimakensis*.

The holotype of *H. ingens* (Fig. 8) is nearly twice the size of that of the holotype of *M. andimakensis* (Figs 1-4). SAM-GMC737 (Fig. 6B-C) shows indications of the onset of upward coiling of the body chamber at a diameter similar to that of the holotype of *M. andimakensis*. On the other hand, the third specimen of *M. andimakensis* (Figs 5, 6A) is only about one-half the size of the holotype.

These observations suggest that the holotype of *H. ingens* is merely a large form of *Madagascarites andimakensis*. In addition, the third, and smallest specimen of *M. andimakensis* appears to lack tubercles on the phragmocone—a feature originally thought to be characteristic of *Hyphantoceras ingens*.

We believe *H. ingens* and *Madagascarites andimakensis* to be synonyms, as suggested earlier (Klinger & Kennedy 1977: 79) and, as first revising authors, select the name *andimakensis* for the species. Thus interpreted, *M. andimakensis* shows a wide range in adult size, some specimens being twice as large as others, presumably a reflection of dimorphism. In addition, the ontogenetic stage at which ornament changes (from uniform simple ribbing to simple ribs separating periodic quadrituberculate major ribs) is quite variable.

3. *Hyphantoceras*, as interpreted in terms of the type species *Hyphantoceras reussianum* (d'Orbigny, 1850) (see Kaplan & Schmid 1988; Metzdorf 1993, for full reviews) (Figs 9, 16D), has flared quadrituberculate ribs throughout and we would prefer to retain this name for those ornamented forms with helical coiling, a low apical angle, and a retroversal body chamber.

Madagascarites can probably be derived from *Hyphantoceras* on the basis of the common presence of flared quadrituberculate ribs. An origin could be less probably sought in *Schlueterella* of the group of *S. compressus* Klinger,

Fig. 6 (see overleaf). A. *Madagascarites andimakensis* Collignon, 1966. Undescribed specimen from the Middle Santonian of gisement 757 at km 8 500 Coupe S. Beantaly, Sourmarinara (Belo sur Tsiribihina), Madagascar. Lateral view, showing last part of helical phragmocone whorl and ascending part of body chamber at top. B-C. Undescribed specimen of *Hyphantoceras ingens* SAM-GMC733, ex Collignon collection, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 733, Coupe d'Ambikity, Andimaka (Belo sur Tsiribihina), Madagascar, the same locality as the paratype of *M. andimakensis* Collignon (1966, pl. 465 (fig. 1898)). All $\times 1$.

Fig. 7 (see overleaf). *Nipponites mirabilis* (Yabe). Cast of specimen figured by Matsumoto (1977, pl. 56 (fig. 1)), GK H5846 from locality T1022p, Saku-gakko-no-sawa, Saku area, Hokkaido. $\times 1$.

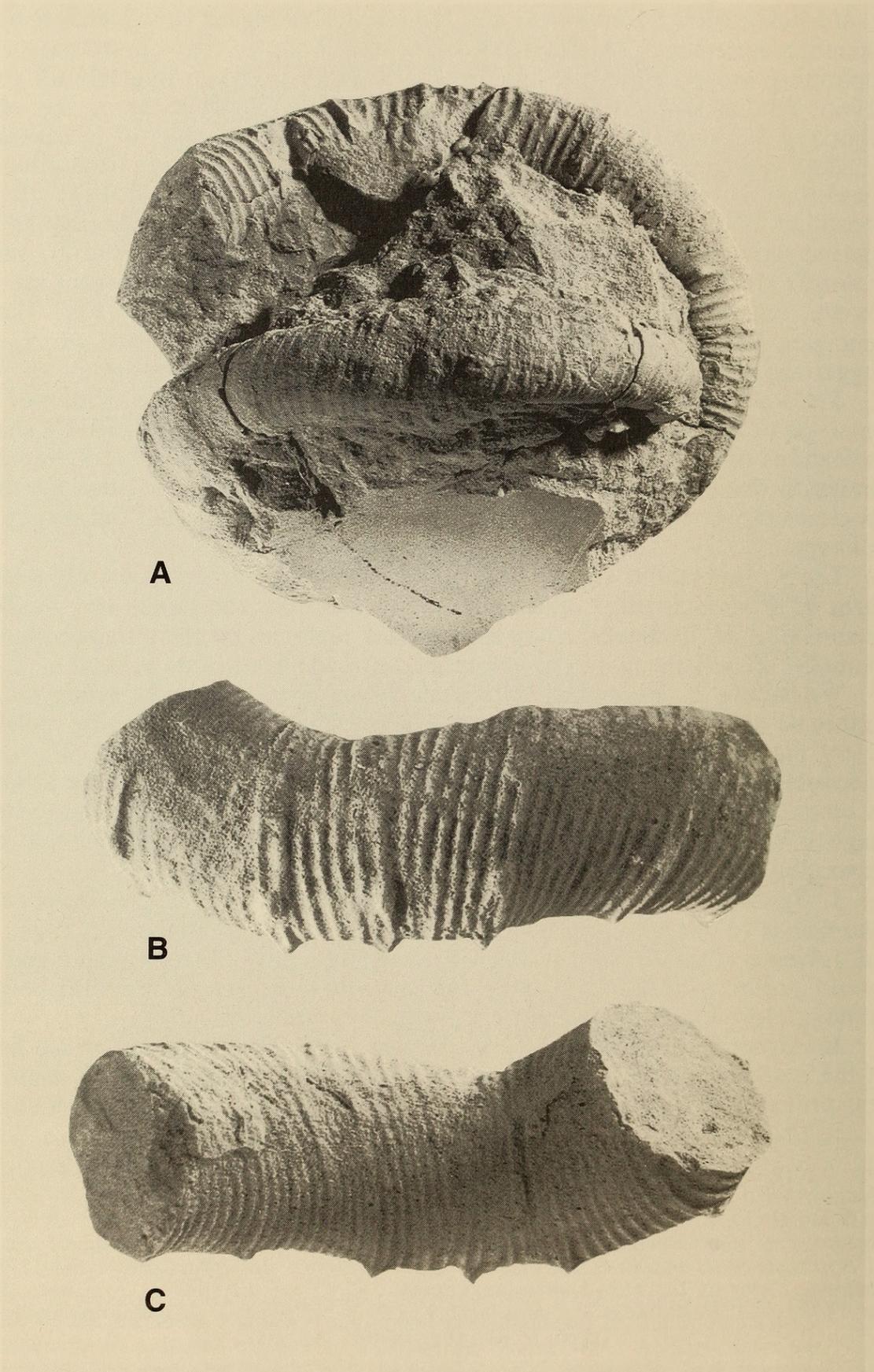


Fig. 6



Fig. 7

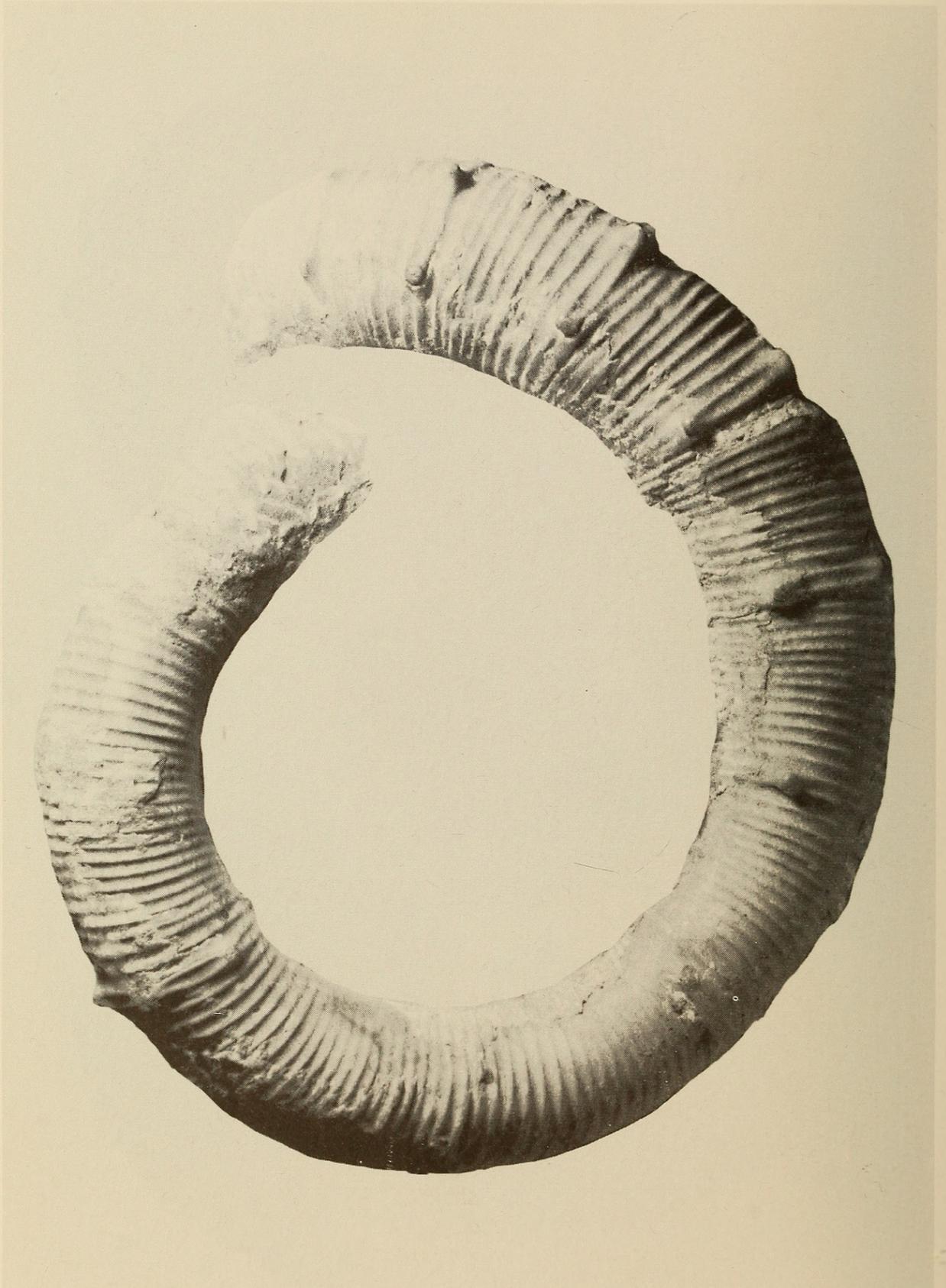


Fig. 8. The holotype of '*Hyphantoceras ingens*' Collignon, 1966, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 230, Ansoha (Antsalova), Madagascar.
× 0.85.



Fig. 9. *Hyphantoceras reussianum* (d'Orbigny, 1850). Cast of the original of Schlüter (1876, pl. 32 (fig. 18)). Unregistered specimen in the collections of the Geological and Palaeontological Institute, Göttingen, Germany. $\times 1$.

1976, of the Lower Santonian. The quadrituberculate ornament of the latter (see especially Immel *et al.* 1982: 25, pl. 9 (fig. 3), pl. 10 (figs 1–4), pl. 11 (fig. 3)) is remarkably similar to that of *M. andimakensis*, although the modes of coiling are quite different.

4. Matsumoto & Muramoto (1967: 362, pl. 19 (fig. 3), pl. 22 (fig. 1), pl. 23 (figs 1–4)) described *Madagascarites ryu* from the uppermost Turonian of Hokkaido. The species (Figs 10–11) has coiling as in *Nipponites bacchus* Matsumoto & Muramoto, 1967, with the major part of the shell consisting of U-shaped sections, terminating in a hook-shaped body chamber suspended below the early part of the shell. Tanabe *et al.* (1981) showed details of coiling in *M. ryu*, especially of the early growth of the shell, which include an initial straight shaft (Fig. 11). But instead of simple ribbing as in *Nipponites*, *M. ryu* has quadrituberculate major ribs and finer intermediary ribs (Figs 10–11). It is, in fact, a *Nipponites* with *Hyphantoceras*-like ornamentation, and not a representative of *Madagascarites*. We presume that *Madagascarites ryu* arose from

Hyphantoceras in a manner analogous to that of *Nipponites* from *Eubostrioceras japonicum* (Yabe, 1904), as suggested by Okamoto (1989: 133). Apart from differences in coiling, there is a considerable time gap between Late Turonian *Madagascarites ryu* and Middle Santonian *M. andimakensis*. We regard them as heterochronous homoeomorphs in terms of ornament (but not coiling) and do not consider them to be congeneric.

We here propose the genus *Ryuella* gen. nov. for this Japanese species, with type species *Madagascarites ryu* Matsumoto & Muramoto, 1967. The diagnosis is as follows: coiling in major part of phragmocone as in *Nipponites*, consisting

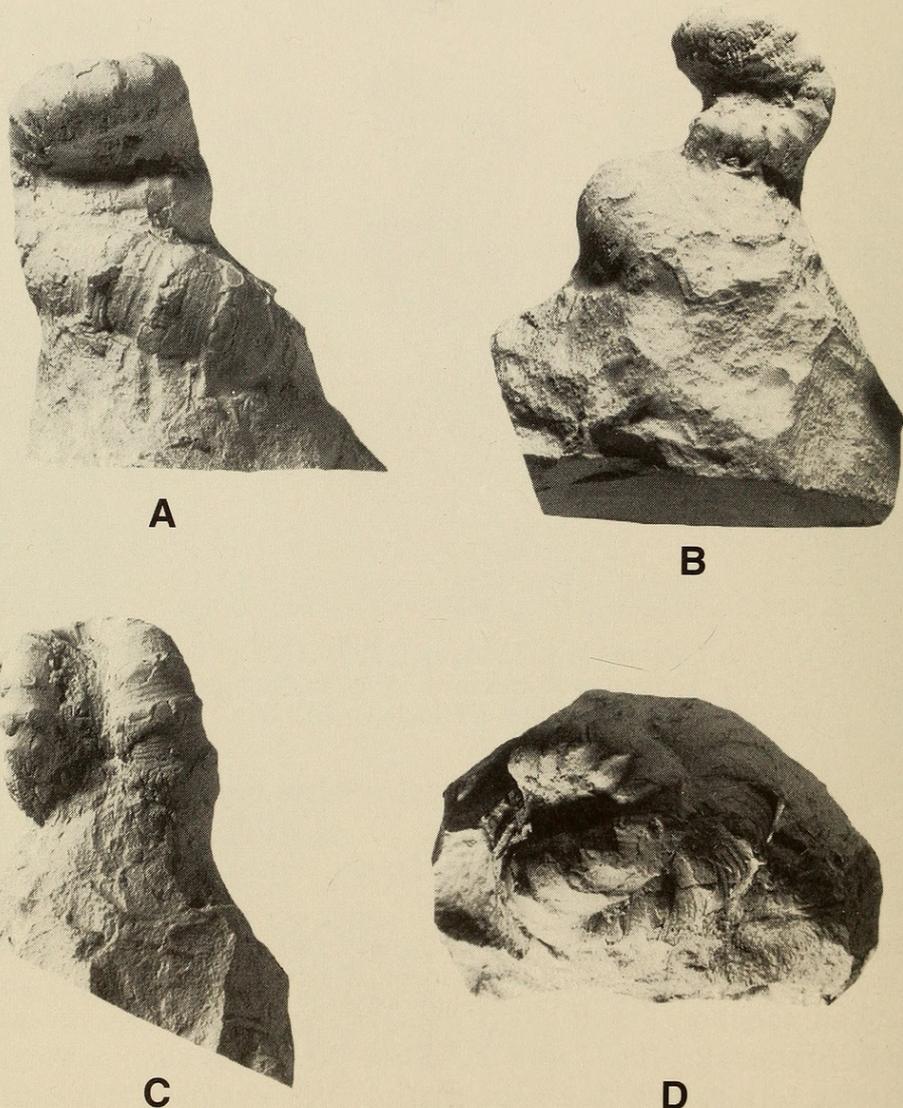


Fig. 10. *Ryuella ryu* (Matsumoto & Muramoto, 1967). Plaster cast of a paratype figured by Matsumoto & Muramoto (1967, pl. 23 (fig. 1a-c)), Muramoto collection 9100B, from the uppermost Turonian, zone of *Reesidites minimus* at Ikushumbets, Hokkaido. $\times 1$.

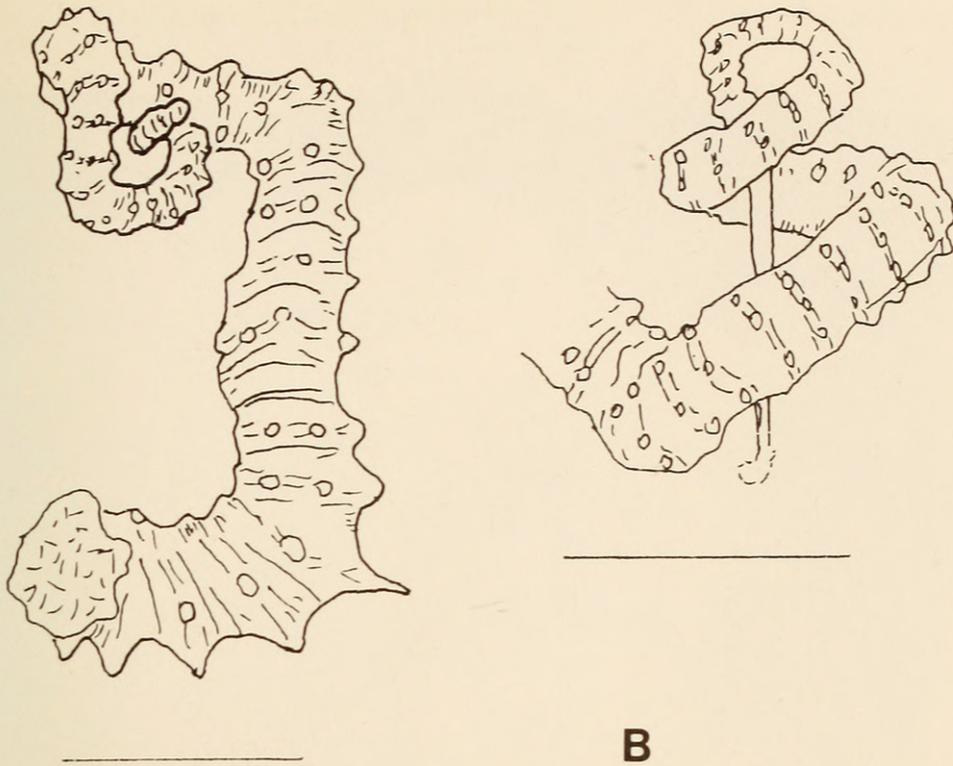


Fig. 11. *Ryuella ryu* (Matsumoto & Muramoto, 1967). A. Sketch of phragmocone showing typical *Nipponites*-like coiling. Scale = 10 mm.
 B. Sketch of early stage of ontogeny. Scale = 5 mm.
 Both after Tanabe *et al.* 1982, text-fig. 4.

Fig. 12 (*see overleaf*). *Eubostriochoceras* (*Amapondella*) *amapondense* (van Hoepen, 1921). A-C. SAM-4820, the specimen described and figured by Woods (1906: 340, pl. 44 (fig. 3a-c)) as *Hamites* (*Anisoceras*). E-F. Cast of the holotype, Transvaal Museum collections, both from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, probably uppermost Santonian or basal Campanian. D. Specimen labelled *Hyphantoceras* ex Collignon collection from the Santonian of gisement 147-148, Mitraiky, north of Manimbilo, Madagascar.
 All $\times 1$.

Fig. 13 (*see overleaf*). A-C. *Eubostriochoceras* (*Amapondella*) *amapondense* (van Hoepen, 1921). SAM-PCZ7328 from locality 105, Zululand, St Lucia Formation, Campanian I.
 All $\times 1$.

Fig. 14 (*see overleaf*). A. *Eubostriochoceras* (*Amapondella*) *amapondense* (van Hoepen, 1921). Catalogue and locality data as in Figure 13. B-C. *Eubostriochoceras* (*E.*) *auriculatum* (Collignon, 1965). SAM-GMC335 from the lower Coniacian at gisement 335, Beantaly (Belo sur Tsiribihina), Madagascar.
 All $\times 1$.

Fig. 15 (*see overleaf*). A-E. *Eubostriochoceras* (*Amapondella*) *amapondense* (van Hoepen, 1921). A-B. SAM-PCZ12881 (ex H126E/1) from Bed E, locality 105, Zululand, St Lucia Formation, Campanian I. C-D. SAM-PCZ12882 (ex Cape of Good Hope Geological Commission collection) from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, probably uppermost Santonian or basal Campanian. E. '*Allocrioceras*' sp. SAS-Z2071. Latex peel showing hamitid early irregular whorls and part of body chamber with bituberculate flared ribs. From an unknown horizon at locality 105.
 All $\times 1$.

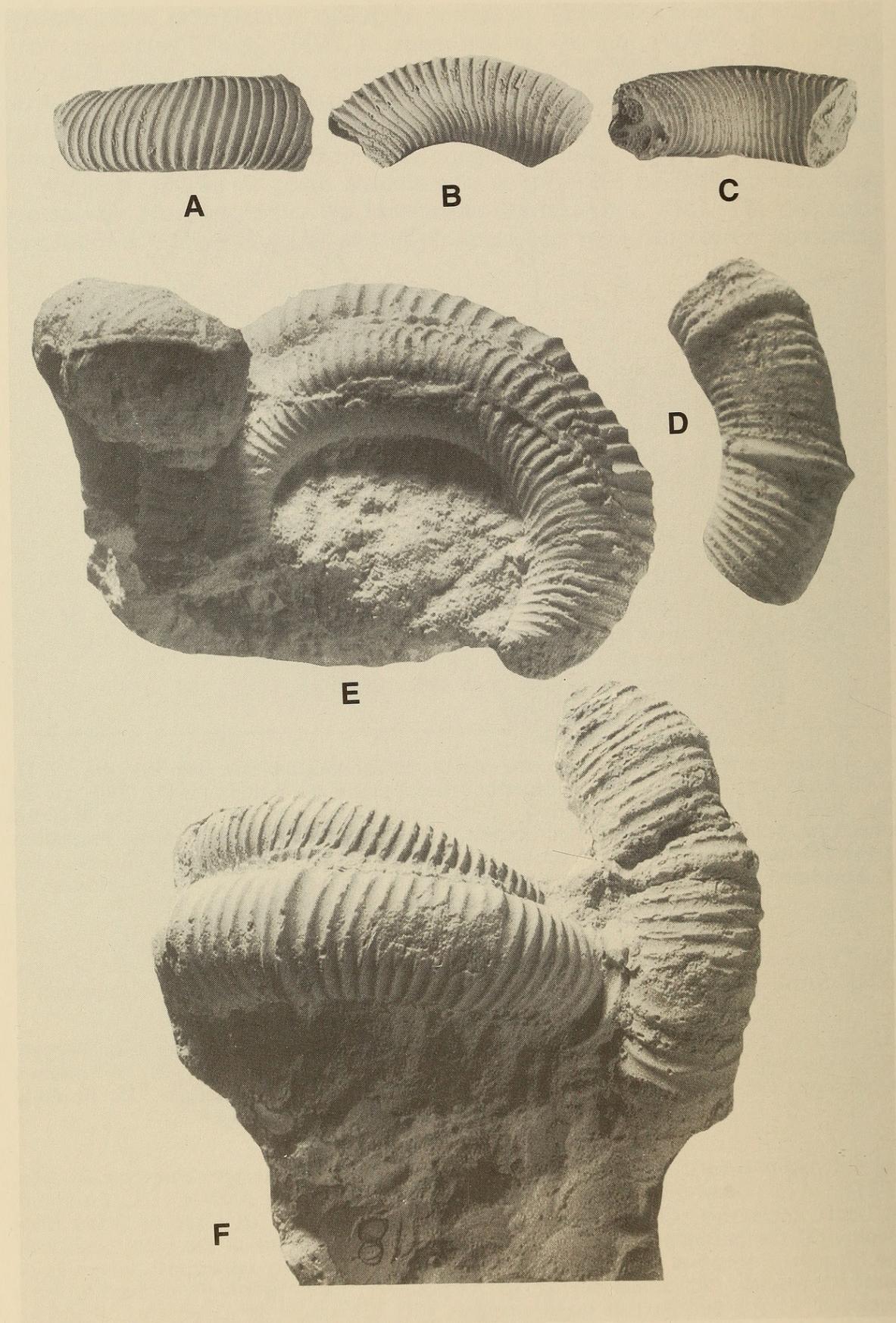


Fig. 12

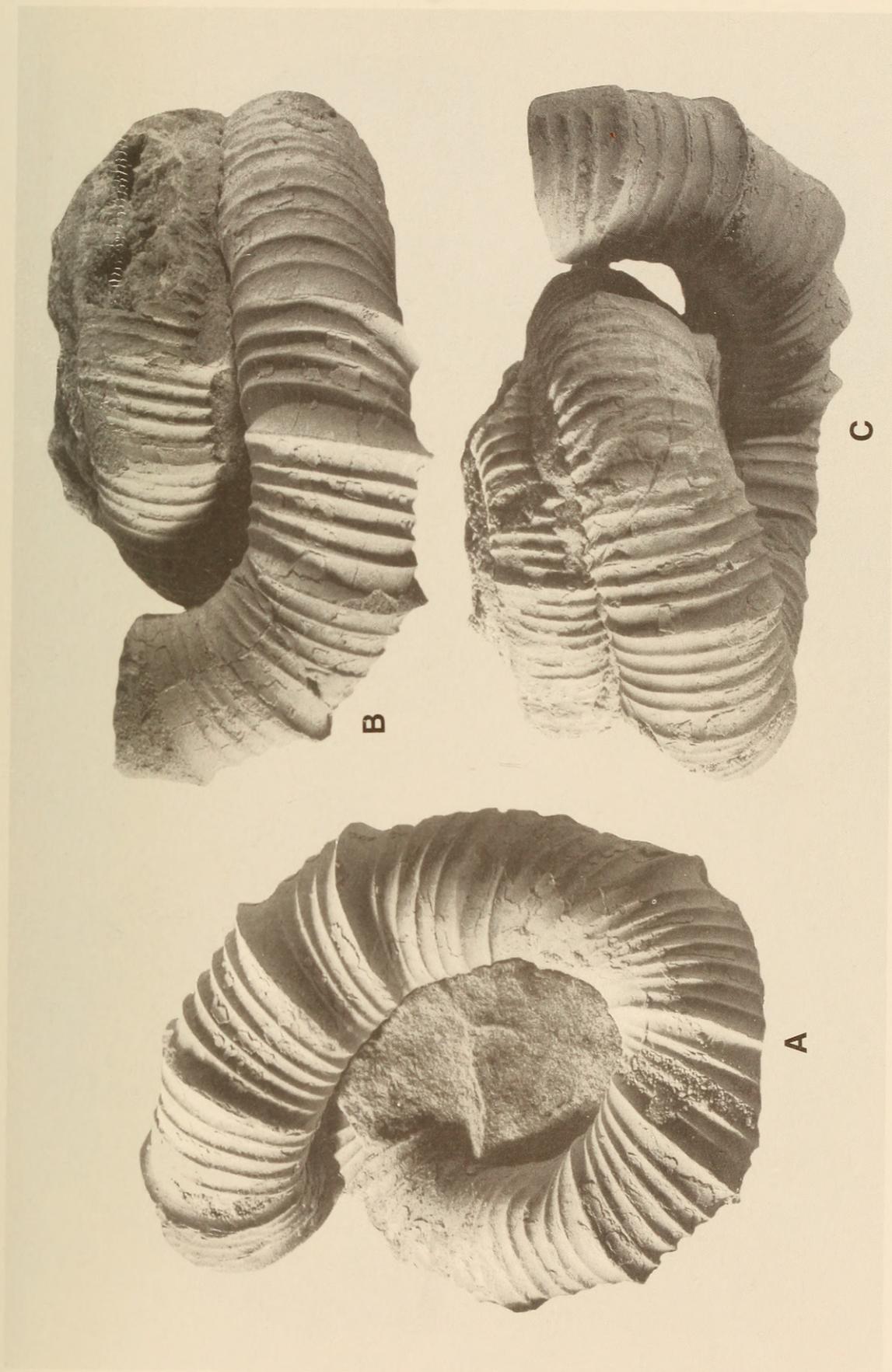


Fig. 13

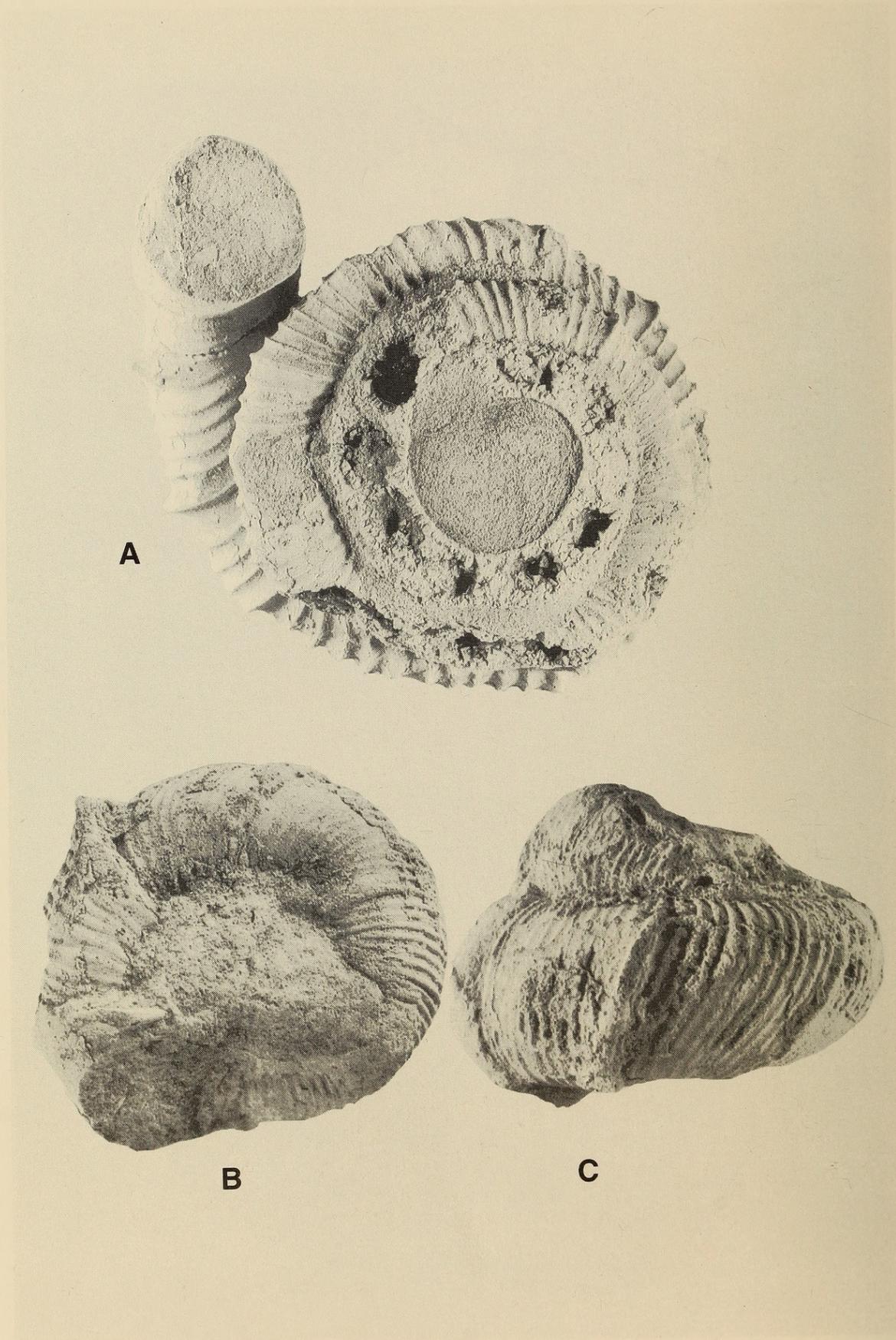


Fig. 14

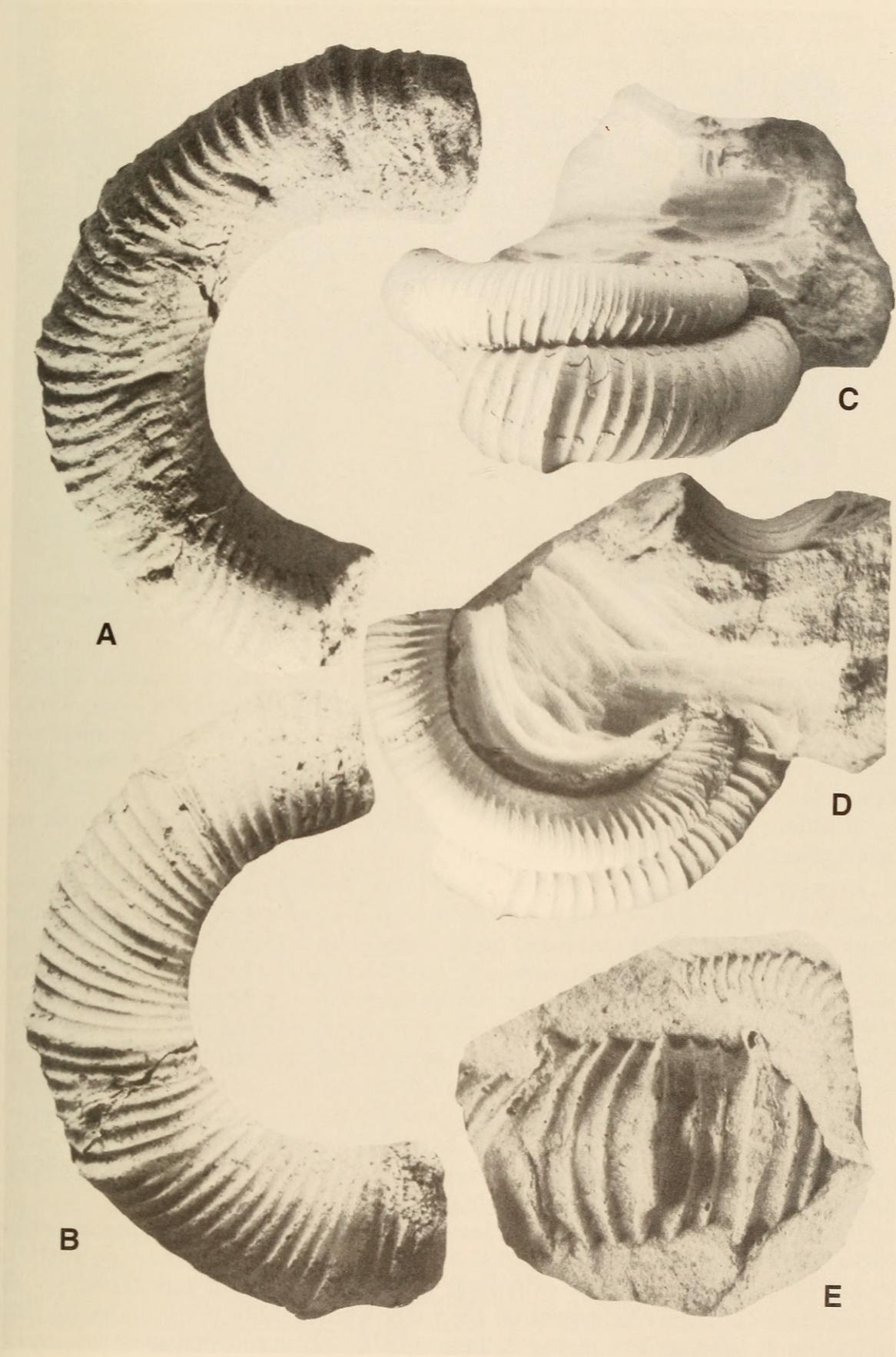


Fig. 15

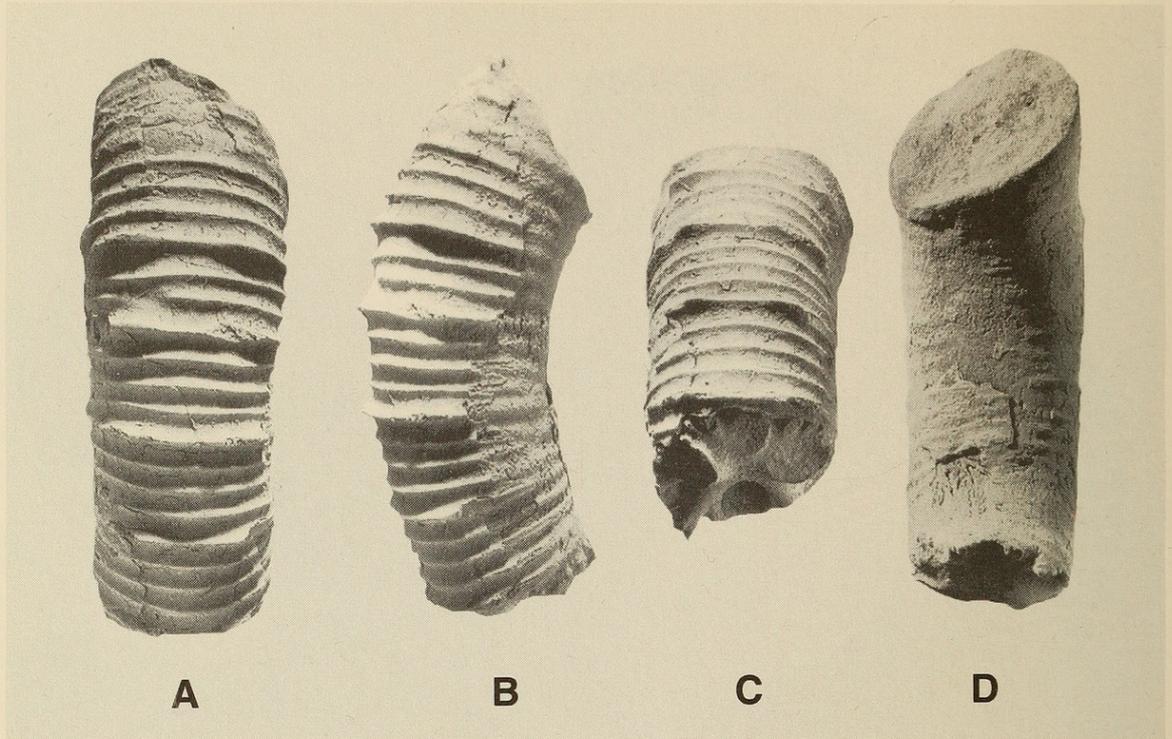


Fig. 16. '*Allocrioceras*' sp., SAM-Z2071 from locality 105, Zululand, St Lucia Formation, uppermost Santonian or basal Campanian. Note the distinct bituberculate flared ribs. $\times 1$.

of an initial straight shaft, followed by a helical whorl and a series of closely connected U-shaped sections, ending in a retroversal body chamber hook. Ornament as in *Hyphantoceras* with major quadrituberculate ribs and intermediary, fine, non-tuberculate ribs. The genus is thus far only known from the Upper Turonian of Hokkaido.

It differs from *Nipponites* by the *Hyphantoceras*-like ornament, and from the latter genus by its distinctive coiling.

5. Klinger (1976: 71, pl. 32 (fig. 5a-b), pl. 33 (figs 2-3), text-fig. 10d-e) identified Van Hoepen's (1921: 17, pl. 4 (figs 1-2)) *Heteroceras amapondense* from the uppermost Santonian and basal Campanian of Pondoland and Zululand as *Hyphantoceras* (*Madagascarites*?) *amapondense*. The lower Campanian Madagascan species described as *Anaklinoceras*? *stephensoni* by Collignon (1969: 50, pl. 532 (fig. 2096)) was regarded as a synonym of the former. Klinger's reasons for this identification were that the ascending body chamber of *H. amapondense* was reminiscent of that of *Madagascarites*, whereas the ornamentation of the late growth stage with periodic flared ribs, was reminiscent of *Hyphantoceras*. This tentative generic and subgeneric designation was followed by Summesberger (1979, 1980), Lewy (1983), Klinger (1985), Immel (1987), Kennedy & Cobban (1991) and Wright (1996).

Comparison with the type species of *Hyphantoceras* and *Madagascarites* shows that *Heteroceras amapondense* belongs to neither genus. It lacks the quadrituberculate ornament of both; instead, it has *Hamites*- or *Eubostrychoceras*-like ornament on the early whorls, with periodic flared ribs appearing at later growth stages. Klinger (1976: 72) stated that well-preserved *H. amapondense* had flared ribs with two rows of fine tubercles and that the

early whorls showed irregular coiling (e.g. Klinger 1976, pl. 33 (figs 2–3)) (herein Fig. 15E). Newly collected specimens of *H. amapondense* show that this is not so. Coiling in the early stages of *H. amapondense* is helical (see Lewy 1983, figs 4–6), and the flared ribs never bear tubercles. Fragments with tuberculate, flared ribs and irregular early whorls that occur with *H. amapondense* were regarded as late Upper Santonian or basal Campanian representatives

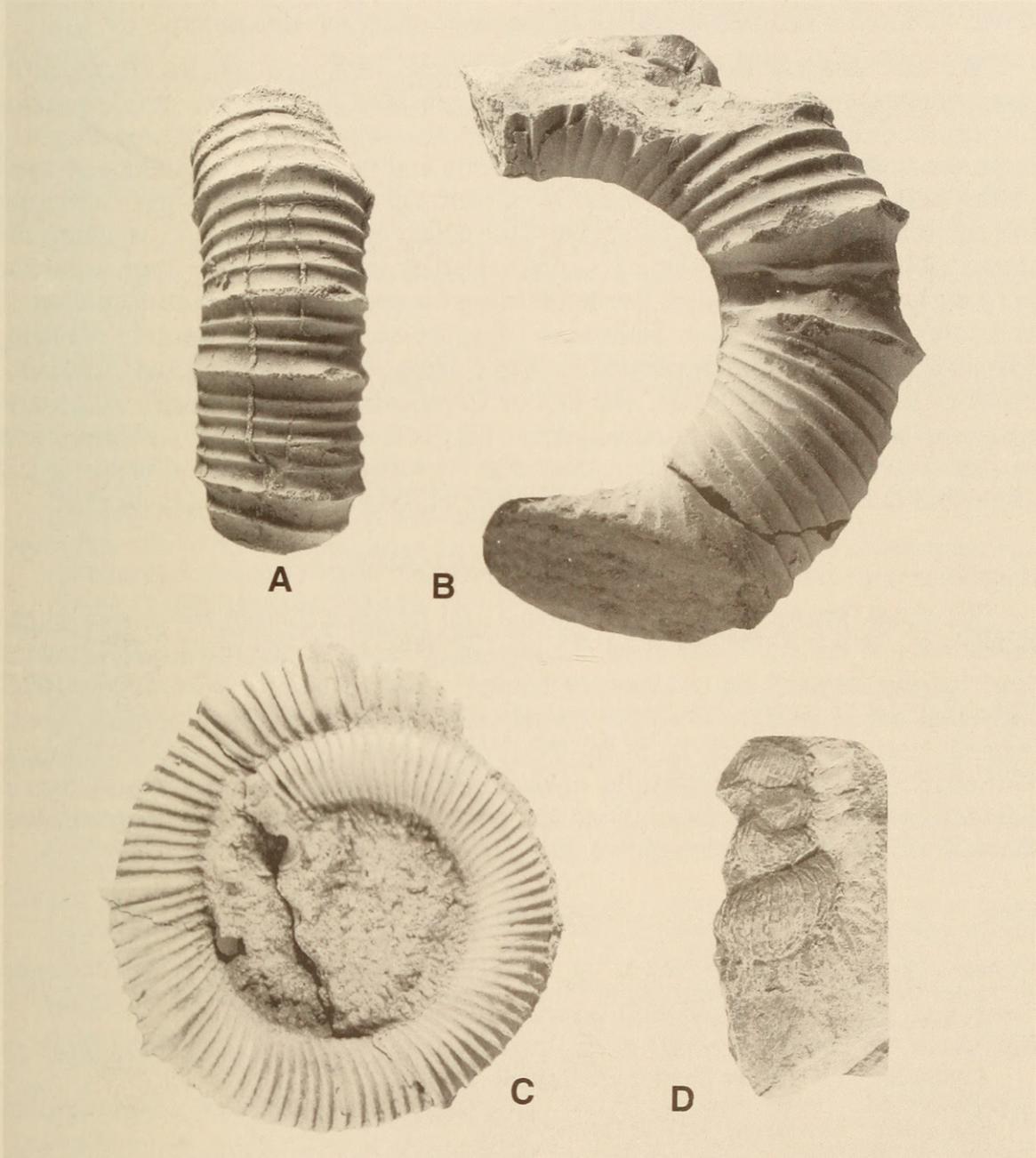


Fig. 17. A–C. *Eubostriochoceras (Amapondella) amapondense* (van Hoepen, 1921). A. Specimen labelled 'Hyphantoceras', SAM-GMC252, ex Collignon collection from gisement 252, Coupe de Bevaho (Belo sur Tsiribihina), Lower Campanian, Zone of *Anapachydiscus wittekindi* and *Eulophoceras jacobi*. B. SAS-Z1455 from locality 105, Zululand, St Lucia Formation, uppermost Santonian or basal Campanian. C. SAM-PCP6890 from bed 7 at locality 1, the type section of the Mzamba Formation, Santonian III. D. SAM-PCZ12883 *Hyphantoceras reussianum* (d'Orbigny, 1850) from the abandoned limestone quarry Annelise near Bad Rothenfelde, northern Germany. All $\times 1$.

of *Allocrioceras* by Cooper (1994: 362). Whether these are indeed *Allocrioceras* or Santonian–Campanian homoeomorphs is impossible to tell at this time. Some fragments (Fig. 15E) consist of hamitid early whorls and planispiral later whorls as in some *Didymoceras*, e.g. *Didymoceras binodosum* (Kennedy & Cobban (see Cobban & Kennedy in press). The early whorls of *H. amapondense* differ in no significant respects from those of *Eubostriochoceras* species, and we interpret it as a late subgenus of the latter characterized by the development of flared ribs and a distinctive coiling of the body chamber at maturity.

We here propose the subgenus *Amapondella*, with type species *Heteroceras amapondense* van Hoepen, 1921. The diagnosis is as follows: major part of phragmocone coiled in a low helix with the whorls touching or slightly impressed; the body chamber curves upwards and embraces the flanks and apex of the helix. Early ornament consists of uniform ribbing only; later ornament has intercalated, flared ribs and occasional constrictions. The stage at which the flared ribbing starts appearing is quite variable; in some it may appear on the very early parts of the helix. Variation in size is probably due to dimorphism. It is known from the Upper Santonian of south-west France, Israel, Austria, Mississippi, Upper Santonian and Lower Campanian Pondoland and Zululand, offshore south coast of Natal, and Lower Campanian of Madagascar. *Eubostriochoceras auriculatum* (Collignon, 1965) (Fig. 14B–C) is possibly a related form in that it acquires flared ribs on the body chamber, but it has an acute apical angle and lacks the ascending body chamber of *Amapondella amapondensis*.

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