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UPPERMOST ALBIAN (*STOLICZKAIA DISPAR* ZONE) AMMONITES FROM THE ANGOLAN LITTORAL

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Cape Town Kaapstad

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(With 82 figures)

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ABSTRACT

Rich, well-preserved collections of late Albian (*Stoliczkaia dispar* Zone) ammonites from the Angolan littoral provide the basis for discussion of the ontogenetic and intraspecific variation within *S.* (*Stoliczkaia*) *tenuis* Renz, *Tetragonites jurinianus* (Pictet), *Eogaudryceras italicum* Wiedmann & Dieni, *Desmoceras latidorsatum perinflatum* subsp. nov., *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinquière, *Anisoceras haasi* sp. nov., and *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. Other important elements present include *Idiohamites dorsetensis* Spath, *I. pygmaeus* sp. nov., *I.* cf. *elegantulus* Spath, *Anisoceras armatum* (J. Sowerby), *A. perarmatum* Pictet & Campiche, *A. phillipsi* sp. nov., *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), *M.* (*D.*) *subquadratum* Spath, *M.* (*Angolaites*) *simplex* (Choffat), *M.* (*A.*) *gregoryi* (Spath), *Cantabrigites? curvatum* Renz, *Hysteroceras?* cf. *ootaturense* (Stoliczka) and *Borissiakoceras* sp. nov. ? aff. *reymenti* (Brunnschweiler).

The faunas form the basis for discussion of the subdivisions of the *Stoliczkaia dispar* Zone, and a return to the simple division into subzones of *S.* (*Faraudiella*) *blancheti* below and *M.* (*Durnovarites*) *perinflatum* above is proposed.

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INTRODUCTION

Although Albian ammonites have long been known from Angola (Szajnocha 1884; Meunier 1887; Choffat *in* Choffat & De Loriol 1888), Paul Choffat was the first to record uppermost Albian ammonites when he described *Ammonites dispar* Choffat (*non* d'Orbigny) (= *Stoliczkaia tenuis* Renz) from the environs of Catumbela. Subsequently, many authors have reported on the presence of strata with *Ammonites dispar* (Mouta & Borges 1926, 1928; Mouta 1937, 1954, 1956; Mouta & O'Donnell 1933) and the presence of uppermost Albian strata in Angola is now well established. In contrast, the faunal constituents of these rocks are poorly known.

The collections which form the basis of this paper are from Porto Amboim, Cabo Ledo and Praia-Egito. The material from Porto Amboim comes from the lime kiln at the south side of the boat landing, and was collected mostly by C. W. Washburn on 22 July 1914, although some material from this locality, in the South African Museum, was described by Haughton (1924, 1925). Elements of this fauna were also described subsequently by Haas (1942), whose localities R28, R30 and 3041 have yielded an identical fauna in like preservation, with recrystallized test preserved. The fauna from Egito was collected by the senior author and comes from the coastal exposures at Praia-Egito where thinly-bedded limestone-shale alternations have yielded a rich fauna, mostly preserved as composite internal moulds. Faunas collected by the senior author from the Quissama Ridge, the promontory on which stands the Farol de Cabo Ledo, were obtained from road gravels and may represent more than one faunal horizon.

These faunas include a number of new species, and also populations, of *S.* (*Stoliczkaia*), *Mortoniceras* (*Durnovarites*), *E.* (*Eogaudryceras*), *Phylloceras* (*Hypophylloceras*), *D.* (*Desmoceras*), *Anisoceras* and *Tetragonites* which provide unique information on the intraspecific variation, development and morphology of these ammonites. Furthermore, the composition of the faunas provides an opportunity for discussion of the stratigraphic and geographic distribution of the late Albian *Stoliczkaia dispar* Zone fauna.

SYSTEMATIC PALAEONTOLOGY

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

BM British Museum (Natural History), London

SAM South African Museum, Cape Town

USNMNH U.S. National Museum of Natural History, Washington D.C.

Measurement abbreviations are as follows: D, diameter; H, whorl height; W, whorl width (intercostal unless otherwise specified); U, diameter of umbilicus between umbilical seams; $^{W}/_{H}$, whorl width/height ratio. All measurements are given in millimetres and dimensions, as a percentage of the diameter, follow in parentheses.

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order PHYLLOCERATIDA Arkell, 1950

Superfamily PHYLLOCERATACEAE Zittel, 1884

Family **Phylloceratidae** Zittel, 1884

Subfamily Phylloceratinae Zittel, 1884

Genus *Phylloceras* Suess, 1865

Subgenus *Hypophylloceras* Salfeld, 1924

Type species *Phylloceras onoense* Stanton, 1895

Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière, 1907
Figs 1–2, 3I

Ammonites velledae Pictet & Campiche (*non* Michelin), 1860: 268, pl. 36 (fig. 8). Stoliczka, 1865: 116, pl. 59 (figs 1–3).

Phylloceras velledae (Michelin) Kossmat 1895: 12, pl. 1 (fig. 3). Boule, Lemoine & Thévenin, 1906: 7, pl. 1 (figs 6, 11), fig. 2. Crick, 1907: 166, pl. 10 (figs 10–11). Böse, 1923: 119, pl. 7 (figs 15–17). Spath, 1925*b*: 180. Besairie, 1936: 164, pl. 16 (fig. 1). Venzo, 1936: 66, pl. 5 (fig. 4). Haas, 1942: 146, pl. 27 (fig. 1), pl. 44 (fig. 1), fig. 19. Matsumoto, 1942: 676. Almela & Revilla, 1957: 17, pl. 3 (fig. 2). Anderson, 1958: 180, pl. 16 (fig. 4).

Phylloceras velledae var. *seresitense* Pervinquière, 1907: 52; 1910: 9, pl. 1 (figs 1–3), fig. 2.

Phylloceras tanit Pervinquière, 1907: 53, pl. 3 (figs 3–9), fig. 5.

Phylloceras angolaense Haughton, 1924: 85, pl. 1 (figs 1–2); 1925: 267, pl. 12 (figs 1–2).

Phylloceras seresitense Pervinquière, Spath, 1923: 18, pl. 1 (fig. 2), pl. 2 (fig. 1). Collignon (*in* Besairie) 1936: 190, pl. 21 (figs 1–2). Fabre, 1940: 211, pl. 5 (fig. 1).

Phylloceras boulei Collignon, 1928: 144, pl. 15 (fig. 5), fig. 1.

Hyporbulites seresitensis (Pervinquière) Breistroffer, 1947: 82.

Phylloceras (*Hyporbulites*) *seresitense* Pervinquière, Collignon 1950: 66; 1963: 4, pl. 241 (fig. 1038), pl. 242 (fig. 1041).

Hyporbulites seresitensis var. *raynaudiensis* Collignon, 1956: 16, pl. 4 (fig. 1).

Neophylloceras seresitense (Pervinquière) Matsumoto, 1959: 55, pl. 12 (figs 4–5), fig. 3.

? *Phylloceras* (*Euphylloceras*) *vohipalense* Collignon, 1962: 1, pl. 215 (fig. 940).

? *Phylloceras* sp. (*Ph. velledae?*) da Silva, 1962: 26, pl. 15 (figs 1–3).

Hypophylloceras seresitense seresitense (Pervinquière) Wiedmann, 1962*a*: 142, pl. 8 (figs 1–2) fig. 8; 1962*b*: 249, pl. 16 (fig. 1).

Hypophylloceras seresitense tanit (Pervinquière) Wiedmann, 1962*a*: 142; 1962*b*: 250, fig. 2.

Phylloceras (*Hypophylloceras*) *seresitense seresitense* Pervinquière, Wiedmann, 1964: 221, pl. 15 (fig. 4), pl. 21 (fig. 1), fig. 52. Wiedmann & Dieni, 1968: 26. Kennedy & Klinger, 1977*a*: 364, pl. 4 (fig. 6), pl. 6 (fig. 4), pl. 7 (fig. 4), pl. 9. Renz, 1968: 17, pl. 1 (fig. 1).

Phylloceras (*Hypophylloceras*) *seresitense tanit* Pervinquière, Wiedmann, 1964: 226, pl. 21 (figs 2–3), fig. 54. Wiedmann & Dieni, 1968: 26, pl. 1 (fig. 6), pl. 3 (figs 1–2).

Phylloceras (*Hypophylloceras*) *seresitense boulei* Collignon, Wiedmann, 1964: 224, pl. 20 (figs 2–3), fig. 53. Renz, 1968: 18, pl. 1 (fig. 2), figs 6a, 7c. Förster, 1975: 140, pl. 1 (fig. 1), fig. 27.

? *Phylloceras* (*Hypophylloceras*) *seresitense vohipalense* Collignon, Förster, 1975: 139, fig. 26.

? *Phylloceras serum* var. *perlobata* Zwierzycki (*non* Sayn), 1913: 323, figs a–c.

? *Phylloceras* ex aff. *ramosi* Meek, Collignon, 1928: 1, pl. 1 (figs 2–4).

? *Phylloceras* aff. *tanit* Pervinquière, Matsumoto, 1942: 674, fig. 2.

Phylloceras cf. *seresitense* Pervinquière, Wright & Wright, 1951: 12.

? *Phylloceras* cfr. *semistriatum* Choffat (*non* d'Orbigny), 1903: 17, pl. 1 (fig. 10).

Material

Ten specimens, SAM-6527, USNMNH 236897–236904, 237013, all with recrystallized shell preserved, and all from Porto Amboim.

Description

The coiling is very involute, with a narrow, crater-like umbilicus (6–7% of the diameter). The whorl section is strongly compressed, elliptical ($^{W}/_{H}$ = 0,55–0,67). The flanks are slightly convex, with maximum width just below midflank, converging to a narrow, evenly rounded venter. Ornament comprises fine, flexuous lirae, very faint or completely effaced on the inner half of the flanks (faint growth striae suggest they were prorsiradiate there), recurving at about midflank so as to pass straight or slightly backwards across the venter. On USNMNH 236897 there are about 128 lirae per half-whorl. None of the present specimens shows the sutures.

Measurements

No.	D	H	W	$^{W}/_{H}$	U
USNMNH 236897	37	21(57)	13(35)	0,62	2,6(7)
,,	26,5	15,5(58)	±8,5(32)	0,55	
USNMNH 236898	52	30,5(59)	17,5(34)	0,57	3(6)
,,	35	19(54)	11(31)	0,58	?
USNMNH 236900	15	8(53)	5(33)	0,63	1,1(7)
,,	11	5,5(50)	3,7(34)	0,67	?
USNMNH 236901	17	10(59)	6,5(38)	0,65	1,0(6)
USNMNH 236902	21	12(57)	7,7(37)	0,64	?

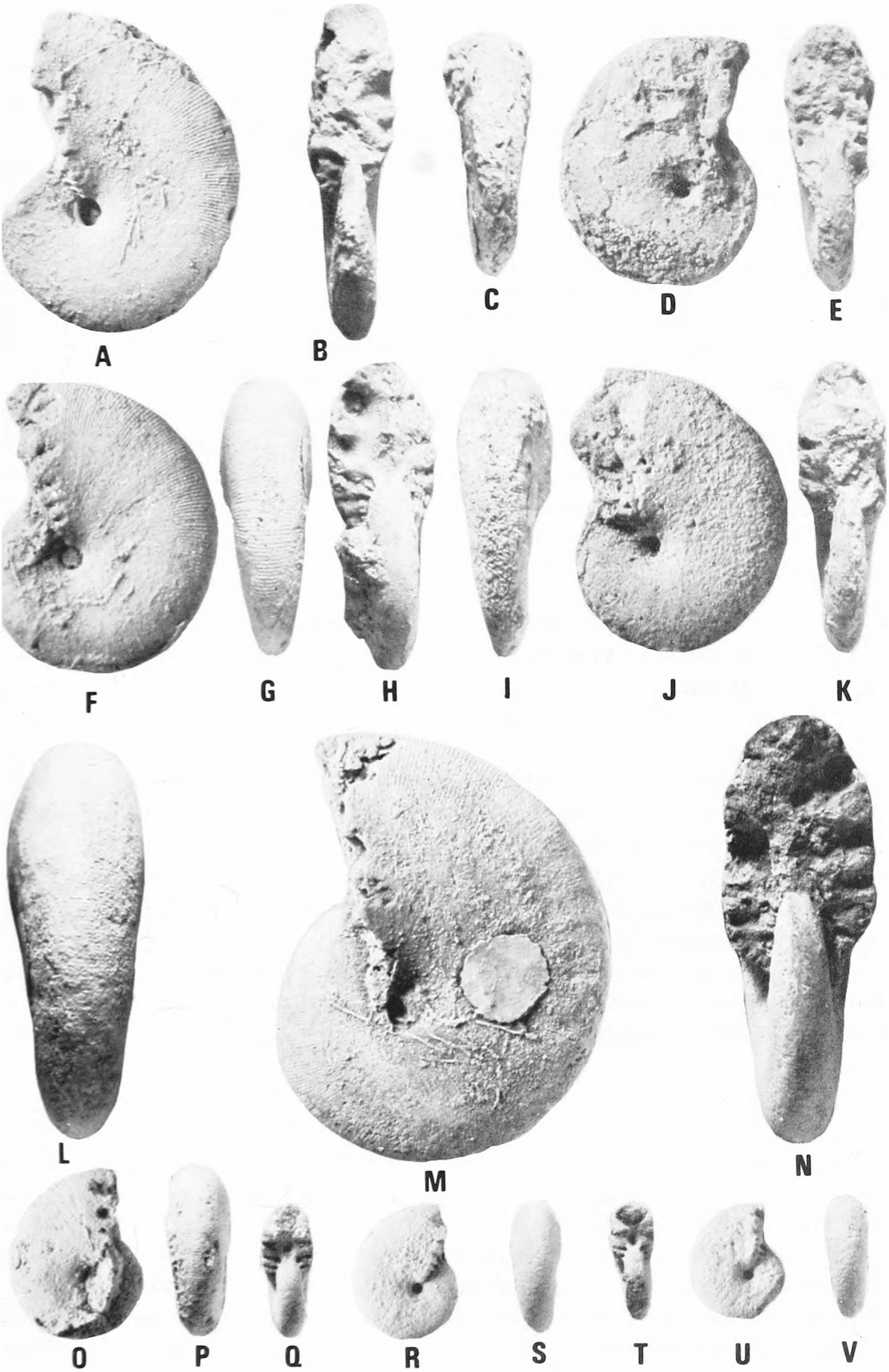

Fig. 1. *Phylloceras* (*Hypophylloceras*) *seresitense* Pervinquière. A–B. USNMNH 236899. C–E. USNMNH 236904. F–H. USNMNH 236897. I–K. USNMNH 236903. L–N. USNMNH 236898. O–P. USNMNH 236902. Q–S. USNMNH 236901. T–V. USNMNH 236900. ×1.

Intraspecific variation

Wiedmann (1964: 221) recognized three subspecies within *P.* (*H.*) *seresitense*:

P. (*H.*) *seresitense seresitense*—whorl section moderately compressed, whorl width to height ratio up to 0,65. Umbilicus very narrow.

P. (*H.*) *seresitense boulei* Collignon—whorl section very compressed ($^{W}/_{H}$ = 0,50–0,57), with very narrow umbilicus.

P. (*H.*) *seresitense tanit*—whorl section compressed, but with moderately open umbilicus.

The most noteworthy variation in the population before the writers is in the degree of inflation of the whorls. As can be seen from Figure 2 the variation in this respect ($^{W}/_{H}$ = 0,55–0,67) includes individuals of all of Wiedmann's (1964) subspecies and, since they are all broadly contemporaneous (ranging from Aptian to Cenomanian), appear to have little biological significance. The authors find, therefore, the application of the subspecies *boulei* and *tanit* inappropriate to the present collection.

Discussion

The holotype of *Phylloceras angolaense* Haughton is in the South African Museum, SAM–6527. The specimen is entirely septate and is replaced by crystalline calcite.

The shell is strongly compressed and very involute, with a very narrow, deep umbilicus. The flanks are slightly convex, almost flat, and converge towards the narrow, evenly rounded venter (Fig. 3I). Maximum width is about one-quarter of the way up the flanks. Ribbing is very faint on the inner half of the flanks, although growth striae suggest it was prorsiradiate here. On the outer half of the flanks, the ribs recurve so as to become almost radial. The ribbing is very fine, with fourteen ribs in a distance of 10 mm along the venter on the adoral quarter of the outer whorl.

There are no features by which *P. angolaense* may be satisfactorily distinguished from *P. seresitense* and consequently the authors follow Wiedmann (1962*a*, 1962*b*) in regarding it as a junior subjective synonym of Pervinquière's species.

Phylloceras velledae (Michelin) (Wiedmann 1964: 209, pl. 11 (fig. 1), pl. 13 (fig. 4), pl. 21 (fig. 4), fig. 49) typically differs from the present species in having more convex flanks, with much coarser, more flexuous lirae, and a suture which shows diphyllic saddles in immaturity rather than tetraphyllic saddles as in *P.* (*H.*) *seresitense*.

Hypophylloceras yeharai Nakai & Matsumoto (1968: 4, pl. 1 (figs 1–3), pl. 3 (fig. 1)) is based upon crushed material said to differ from *P.* (*H.*) *velledae* in its more compressed whorls (? enhanced by crushing) and less numerous and broader lirae. Kennedy & Klinger (1977*a*) have recently demonstrated the wide range of variation within contemporaneous populations of *P.* (*H.*) *velledae* and

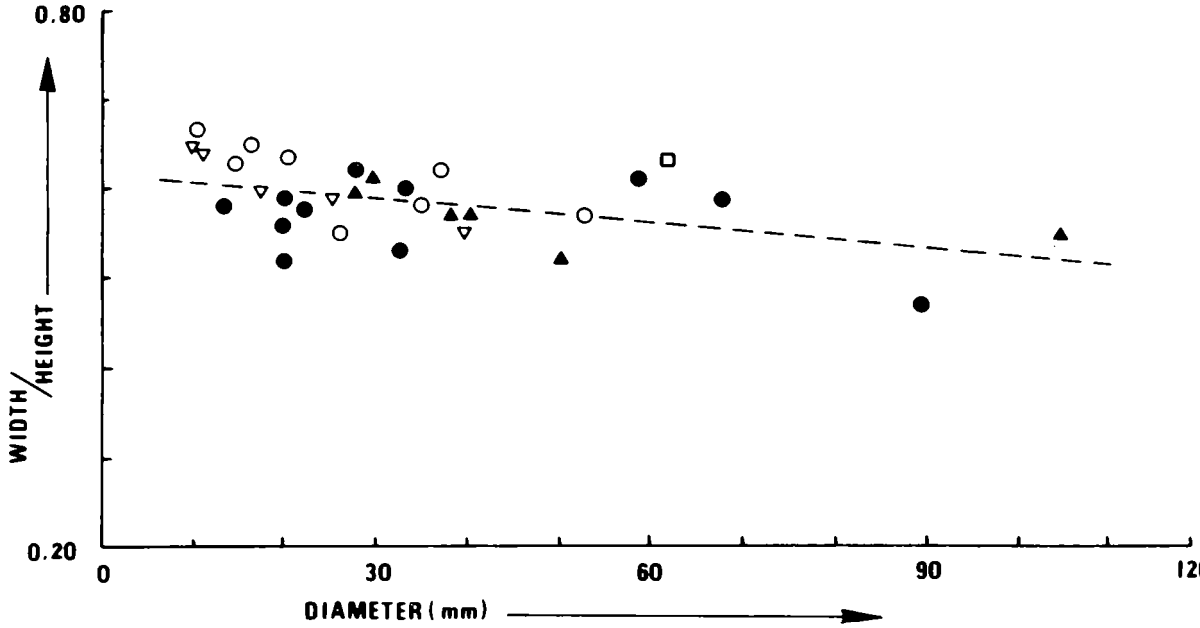

Fig. 2. Plot of inflation (whorl width/height ratio) versus diameter for *Phylloceras seresitense* Pervinquière, showing the unsatisfactory separation of subspecies. Circles = present Angolan material; dots = *P. seresitense tanit* Pervinquière; square = holotype of *P. angolaense* Haughton; open triangles = *P. seresitense seresitense* Pervinquière; black triangles = *P. seresitense boulei* Collignon. (Data after Stoliczka 1865, Spath 1923, Wiedmann 1962, Collignon 1963, Wiedmann & Dieni 1968, Renz 1968, Förster 1975, and Kennedy & Klinger 1977.)

figured examples (1977*a*: pls 10–11) as coarsely ribbed as the Japanese material, suggesting that *P.* (*H.*) *yeharai* may be within the limits of variation of *P.* (*H.*) *velledae*.

Occurrence

Phylloceras (*Hypophylloceras*) *seresitense* ranges from Upper Aptian to Middle Cenomanian, and is known from southern France, Switzerland, southern England, Spain, Tunisia, Algeria, Sardinia, the Balearics, southern India, Japan, Alaska, California, Mexico, Angola, Zululand, possibly Tanzania, and Madagascar.

Order LYTOCERATIDA Hyatt, 1889

Superfamily LYTOCERATACEAE Neumayr, 1875

Family **Tetragonitidae** Hyatt, 1900

Genus *Tetragonites* Kossmat, 1895

Types species *Ammonites timotheanus* Pictet, 1848

Discussion

Wiedmann (1973) has provided the most recent discussion of the Albian to Cenomanian members of this genus, recognizing three species groups. The group of *T. rectangularis* possesses persistent constrictions and a straight umbilical suture, and includes *T. rectangularis* Wiedmann, *T. subtimotheanus*

Wiedmann, *T. kitchini* (Krenkel), *T. subbeticus* Wiedmann, *T. marrei* Thomel and *T. blaisoni* Collignon. In the group of *T. timotheanus* (Pictet), constrictions are present only at an early growth stage, whilst the umbilical suture is retracted. To this group Wiedmann (1973) assigned *T. timotheanus* (Pictet), *T. balmensis* Breistroffer, and *T. nautiloides* (Pictet). Forms lacking constrictions at all growth stages are referred to the group of *T. jurinianus* (Pictet).

Tetragonites (*Tetragonites*) *collignoni* Breistroffer, 1940

Ammonites timotheanus Stoliczka (*non* Mayor), 1865: 146, pl. 73 (figs 3–4, 6).

Tetragonites collignoni Breistroffer, 1940: 110. Murphy, 1967*a*: 66, pl. 5 (figs 2–5), fig. 36. Förster, 1975: 147, pl. 1 (fig. 5) (with synonymy).

Tetragonites subtimotheanus Wiedmann, 1962*a*: 131; 1973: 592, pl. 1 (fig. 5), pl. 2 (fig. 2), pl. 3 (figs 1–5), pl. 7 (fig. 8), fig. 2 (with synonymy).

Tetragonites blaisoni Collignon, 1964: 31, pl. 324 (fig. 1448). Wiedmann, 1973: 601, pl. 1 (fig. 4), pl. 6 (figs 5–7), fig. 7 (with synonymy).

Material

One specimen, USNMNH 236916, preserved as an internal mould, from Porto Amboim.

Description

Shell involute, somewhat inflated, with a depressed, trapezoidal whorl section ($^{W}/_{H}$ = 1,21). Umbilicus narrow (22% of the diameter), deep, with steep, almost vertical umbilical walls. Umbilical shoulder evenly rounded, with flattish flanks converging towards a broad, slightly convex venter which rounds somewhat in maturity. There are two distinct constrictions in a distance equal to the whorl height on the last portion of the outer whorl (representing part of the body chamber), although the number of constrictions per whorl is unknown. The constrictions are markedly prorsiradiate across the inner flanks, recurving strongly in the region of the ventrolateral angulations to cross the venter with a prominent concave sinus.

Measurements

No.	D	H	W	$^{W}/_{H}$	U
USNMNH 236916	44	21,5(49)	±26(59)	1,21	±9,5(22)

Discussion

Problems concerning the specific identification of constricted tetragonitids become very clear from the recent literature concerning this group (Wiedmann 1962*a*, 1962*b*, 1973; Collignon 1963, 1964; Murphy 1967*a*, 1967*b*; Wiedmann & Dieni 1968; McLearn 1972; Förster 1975; Kennedy & Klinger 1977*b*). Förster (1975) has suggested that *T. subtimotheanus* and *T. blaisoni* are junior subjective synonyms of *T. collignoni*. Wiedmann (1973) rejected the latter name because it

was based upon a pyritic nucleus only 14 mm in diameter (although he retains *T. kitchini* and *T. subbeticus* as valid species even though the types are only 18 and 16 mm in diameter respectively), considering it a *nomen dubium*. Because the authors are at present unhappy with Wiedmann's (1973) fine delimitation of *T. subtimotheanus* Wiedmann, *T. rectangularis* Wiedmann, *T. blaisoni* Collignon, and *T. kitchini* (Krenkel), all of which are broadly contemporaneous, they have some sympathy with Förster's (1975) view in assigning the present material to *T. collignoni*.

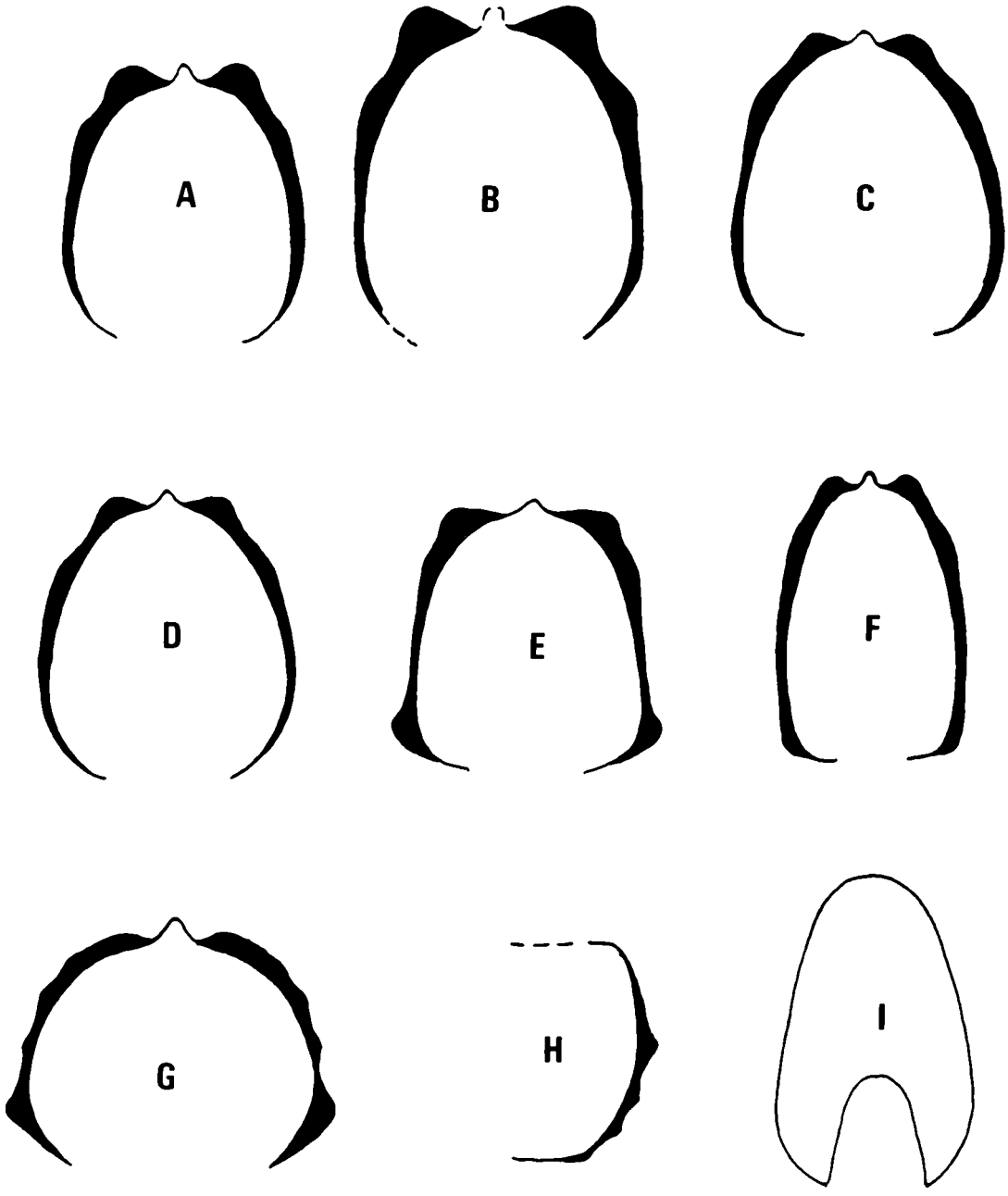

Fig. 3. A–D. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). A. SAM–PCA4613. B. SAM–PCA4774. C. SAM–PCA4590. D. SAM–PCA4609. E–F. *Drakeoceras* cf. *dellense* Young. E. SAM–PCA4662. F. SAM–PCA4800. G. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath), SAM–PCA4587. H. *Mariella* (*Mariella*) cf. *oehlerti* (Pervinquière), SAM–PCA4798. I. *Phylloceras* (*Hypophylloceras*) *seresitense* (Pervinquière), the holotype of *P. angolaense* Haughton, SAM–6527. ×1.

Occurrence

Tetragonites collignoni ranges from the Lower Albian to the Middle Cenomanian, and is known from Madagascar, southern India, Zululand, Alaska, British Columbia, and Oregon.

Tetragonites (*Tetragonites*) *kitchini* (Krenkel, 1910)
Fig. 4

? Ammonites timotheanus Whiteaves (*non* Mayor), 1876: 41, pl. 3 (fig. 2).
Desmoceras (*Puzosia; Latidorsella?*) *kitchini* Krenkel, 1910: 226, pl. 22 (fig. 8).
Tetragonites kitchini (Krenkel), Wiedmann 1962*a*: 171. Murphy, 1967*a*: 33, pl. 2 (figs 11–14), figs 15–16. Wiedmann, 1973: 599, pl. 1 (fig. 7), pl. 6 (figs 1, ?2–4), figs 5, ?6.
Tetragonites hulenensis Murphy, 1967*a*: 54, pl. 6 (figs 16–19), pl. 7 (figs 3, 6–8, 10), figs 28–30. Murphy, 1967*b*: pl. 4 (figs 8–9).
? Tetragonites aff. *kitchini* (Krenkel), McLearn 1972: 26, pl. 4 (figs 4–5).

Material

A single specimen, SAM–PCA3125, from low in the coastal cliffs immediately north of the estuary at Praia-Egito (low *dispar* Zone).

Description

The shell is moderately involute (umbilicus 31,5% of the diameter) and partially retains recrystallized shell. The whorl section is subtrapezoidal, almost subquadrate, as wide as high ($^{W}/_{H}$ = 1,00), with slightly converging flanks and a flattish, slightly convex venter. The umbilicus is rather narrow and deep, with steep umbilical walls and subrounded umbilical shoulders. The ventrolateral shoulders are evenly rounded. Maximum width is at the umbilical shoulder.

Fig. 4. *Tetragonites kitchini* (Krenkel). Lateral and ventral views of SAM–PCA3125, partially retaining recrystallized test. ×1.

There would appear to have been about seven slightly flexuous (prorsiradiate concave in the terminology of Murphy (1967*a*)), strongly prorsiradiate constrictions on the outer whorl, which cross the venter with a concave-adoral sinus. The suture line was not observed.

Measurements

No.	D	H	W	W/H	U
SAM-PCA3125	54	25(46)	25(46)	1,00	17(31,5%)

Discussion

Tetragonites kitchini differs from all other contemporaneous species of constricted *Tetragonites* in having less strongly inflated whorls with an almost quadrate whorl section. However, there appear to be intermediate forms to *T. subtimotheanus* Wiedmann and *T. rectangularis* Wiedmann, and the population structures of these species require investigation to fully validate their specific separation.

Occurrence

Tetragonites kitchini is known from the upper Lower Albian of Tanzania, California, Alaska, and perhaps British Columbia, and from the Middle or Upper Albian of Madagascar, and the uppermost Albian of Angola.

Tetragonites (*Tetragonites*) *jurinianus* (Pictet, 1847)
Figs 5–6

Ammonites jurinianus Pictet (*in* Pictet & Roux), 1847: 297, pl. 3 (fig. 3). D'Orbigny, 1850: 124.
Ammonites timotheanus Pictet & Campiche (*non* Mayor), 1860: 289 (pars).
Lytoceras (*Tetragonites*) *epigonum* Boule, Lemoine & Thévenin (*non* Kossmat), 1906: 186, pl. 3 (fig. 1).
? *Lytoceras* (*Tetragonites*) *timotheanum* Pervinquière (*non* Mayor), 1907: 74 (pars.), pl. 3 (fig. 24 only).
Lytoceras (*Tetragonites*) *jurinianum* (Pictet) Jacob, 1908: 19, pl. 1 (fig. 12).
Latidorsella latidorsata Jacob (*non* Michelin), 1908: 35, pl. 5 (fig. 1 only).
Lytoceras (*Tetragonites*) *zacatecanus* Böse, 1923: 127, pl. 9 (figs 11–17).
Tetragonites jurinianus (Pictet) Spath, 1923: 26. Roman, 1938: 43. Breistroffer, 1940: 112. Wiedmann, 1962*a*: 176, pl. 14 (fig. 2), figs 37–38. Almela & Revilla, 1957: 20, pl. 4 (fig. 3). Murphy, 1967*a*: 23, pl. 2 (figs 1–4); figs 10–11. Renz, 1968: 19, pl. 1 (figs 6–7), figs 6d, 7a–b. Wiedmann & Dieni, 1968: 48, pl. 4 (fig. 4), pl. 5 (fig. 4). Wiedmann, 1973: 608, pl. 8 (figs 3–4).
? *Tetragonites brazoensis* Böse, 1927: 203, pl. 1 (figs 2–7).
Tetragonites jurinianus var. *angolana* Haas, 1942: 170, pl. 44 (fig. 3), pl. 45 (fig. 1).
Tetragonites timotheanus Matsumoto (*non* Mayor), 1959: 78, fig. 16.
Tetragonites jurinianus angolanus Haas, Wiedmann, 1973: 609.

Material

Ten specimens, USNMNH 236915, 236917–21, 236977–79, all with recrystallized shell preserved, and all from Porto Amboim.

Description

Shell inflated, involute, with a slightly depressed, trapezoidal whorl section in juveniles ($^{W}/_{H}$ = 1,00–1,29), the venter becoming rounded in maturity. Umbilicus narrow (16–30% of the diameter), deep, with almost vertical walls and evenly rounded umbilical shoulders. The flanks are flattened, with maximum width close to the umbilical shoulder, and converge towards the venter. Up to 25 mm diameter, the venter is flattened, very slightly convex, whereafter it becomes rounded and the ventrolateral angulations disappear. At this stage the whorl section is broadly ovate. Constrictions are lacking at all observed growth stages.

Measurements

No.	D	H	W	$^{W}/_{H}$	U
USNMNH 236915	52,5	25,5(49)	±28(53)	1,10	10(19)
USNMNH 236917	38,5	20(52)	±22(57)	1,10	±9(23)
,,	30	14,5(48)	16(53)	1,10	9(30)
USNMNH 236918	43	19(44)	22,3(52)	1,17	9,8(23)
USNMNH 236919	16	7,5(47)	8,5(53)	1,13	4(25)
USNMNH 236920	18	8(44)	10(55)	1,25	±4(22)
USNMNH 236921	21	10(48)	±10(48)	1,00	5(24)
USNMNH 236977	17,5	6,8(39)	8,5(49)	1,25	4,5(26)
USNMNH 236978	17	7(41)	9(53)	1,29	4,7(28)
T. jurinianus angolanus (holotype)	105	56(53)	51(48)	0,91	17(16)
,,	63	32(51)	34(54)	1,06	?

Intraspecific variation

The intraspecific variation seen in *Tetragonites jurinianus* shows features which have an important bearing on the classification of tetragonitids in general. The wide range of inflation within juveniles far exceeds the range of variation admitted by Wiedmann (1973) within the constricted tetragonitids as a whole, and population studies may show his subdivisions of the group to be utilitarian rather than biologically significant.

As can be seen from Figure 6, there is not only a distinct decrease in the umbilical ratio with growth, but there is also an ontogenetic increase in the height of the whorls, which become progressively less inflated.

Wiedmann (1973) maintained *T. jurinianus angolanus* as a separate subspecies by virtue of its narrower umbilicus (16% versus 23% of the diameter in *T. jurinianus jurinianus*), high-oval whorl section and large size. It appears, however, that these differences result from a comparison of different ontogenetic stages, and the authors include *T. jurinianus angolanus* in the synonymy of *T. jurinianus sensu stricto*.

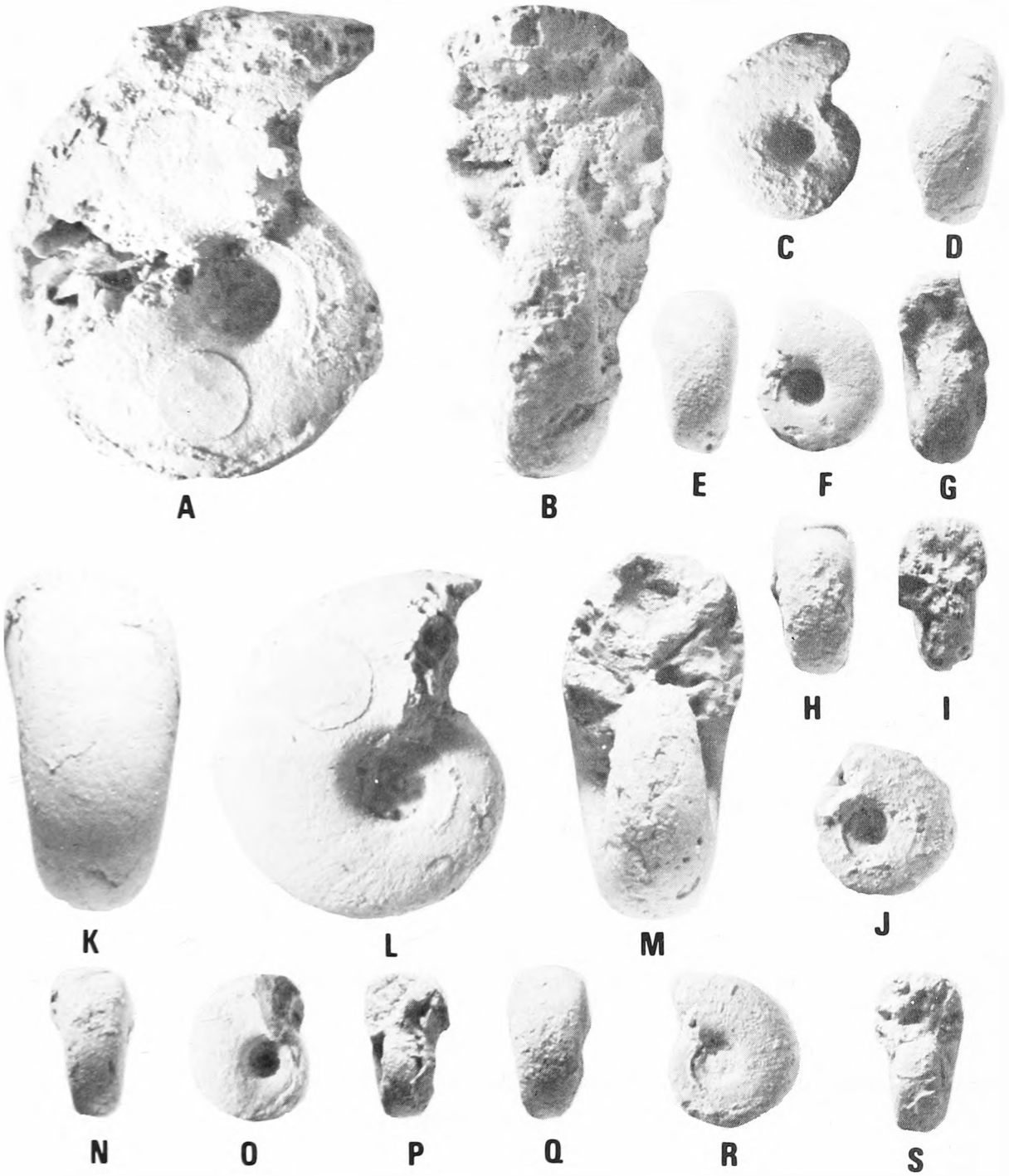

Fig. 5. *Tetragonites* (*Tetragonites*) *jurinianus* (Pictet). A–B. USNMNH 236918. C–D, G. USNMNH 236921. E–F. USNMNH 236978. H–J. USNMNH 236977. K–M. USNMNH 236917. N–P. USNMNH 236919. Q–S. USNMNH 236920. ×1.

Discussion

As diagnosed by Wiedmann (1973: 606), *Tetragonites nautiloides* (Pictet) does not have constrictions beyond 10 mm diameter and thus closely approaches *T. jurinianus*. Indeed, the present material all exceeds this diameter and could, therefore, equally well be assigned to *T. nautiloides*. However, Murphy (1967*a*) has noted that constrictions are present to 27 mm diameter in topotype material of *T. nautiloides* when there is considerable difficulty in distinguishing this

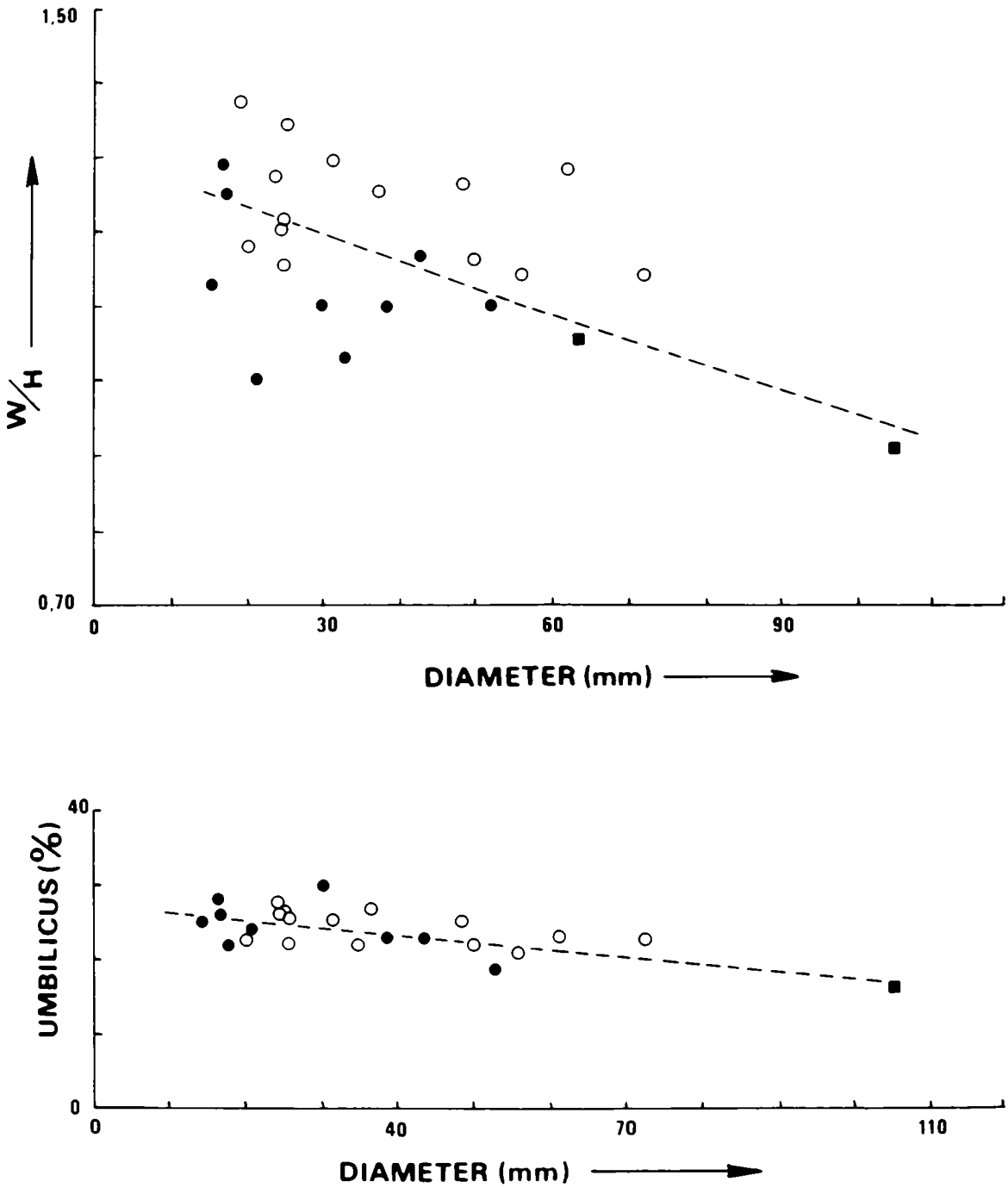

Fig. 6. Plot of inflation (whorl width/height ratio) and umbilical ratio against diameter for examples of *Tetragonites jurinianus* (Pictet). Dots = present Angolan material; squares = the holotype of *T. jurinianus angolanus* Haas; circles = material described by Wiedmann (1962, 1973), Murphy (1967*a*), Wiedmann & Dieni (1968).

species from some constricted tetragonitids, e.g. *T. rectangularis* Wiedmann. Wiedmann's (1973) diagnosis of *T. nautiloides* is difficult to support, since some of his figured specimens (pl. 8 (figs 2, 5)) clearly show weak constrictions at 22 and 27 mm diameter respectively, suggesting that this species may better be included in the *T. rectangularis* group.

Occurrence

Tetragonites jurinianus ranges from Middle Albian to Lower Cenomanian, and is recorded from Switzerland, France, Sardinia, Mallorca, Madagascar, Angola, Mexico, and California.

Family **Gaudryceratidae** Spath, 1927

Subfamily Gaudryceratinae Spath, 1927

Genus *Eogaudryceras* Spath, 1927

Type species *Ammonites numidus* Coquand, 1880

Discussion

Eotetragonites was originally separated (Breistroffer 1947) from *Eogaudryceras* by the possession of strong constrictions throughout ontogeny, and a suture with irregularly bifid saddles. However, Wiedmann (1962*b*: 35) has noted the occurrence of species which show combinations of these characters, consequently treating *Eotetragonites* as a subgenus of *Eogaudryceras*. As defined by him (1962*b*), *E.* (*Eogaudryceras*) has initially trapezoidal whorls which become rounded in maturity and are ornamented by fine, flexuous lirae, whereas *E.* (*Eotetragonites*) has quadrate juvenile whorls and lacks liration.

Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni, 1968
Figs 7–11

Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni, 1968: 34, pl. 1 (fig. 8), fig. 6.

Material

Ten specimens, USNMNH 236905–236914, all with recrystallized shell preserved, and all from Porto Amboim.

Description

Up to 23 mm diameter: shell evolute, compressed, with a wide, shallow umbilicus (30–41 % of the diameter) and steep umbilical walls which merge imperceptibly with the strongly convex flanks. The whorl section is oval, depressed ($^{W}/_{H}$ = 1,00–1,36), with a broadly rounded venter. The outer whorl conceals about 55 per cent of the preceding whorl. The earliest whorls are very finely lirate, almost smooth to the naked eye, with sporadic, rather distinct, prorsiradiate collars.

24–45 mm diameter: the shell form is much as at the earlier growth stages, except that the flanks flatten slightly and the whorl section changes from slightly depressed to almost quadrate. At this stage the lirae are visible to the naked eye; they arise at the umbilical seam and pass forwards (prorsiradiate) on the lower third of the flanks. Thereafter they recurve slightly, only to flex forwards again before crossing the venter. At intervals one or two adjacent lirae are strengthened, presumably corresponding to the collars of the earliest whorls. The lirae become flat-topped, band-like, much broader than the interspaces, and of variable thickness at this stage.

Greater than 46 mm diameter: in maturity the whorls become flat-sided and compressed ($^{W}/_{H}$ = 0,66–0,80), with an elliptical whorl section and narrowly rounded venter. The umbilicus is moderately wide (26–33% of the diameter), shallow, with steep umbilical walls and evenly rounded umbilical shoulders. Maximum width is at about mid-flank. At this growth stage the irregular band-like ribs are split by fine, threadlike grooves. In the largest specimen (still septate at 82 mm diameter) there are still occasional strengthened ribs, followed by a slightly deeper intercostal groove. These may correspond to the collars of the earliest whorls.

Fig. 7. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. Reconstruction of juvenile and adult shells. × 1.

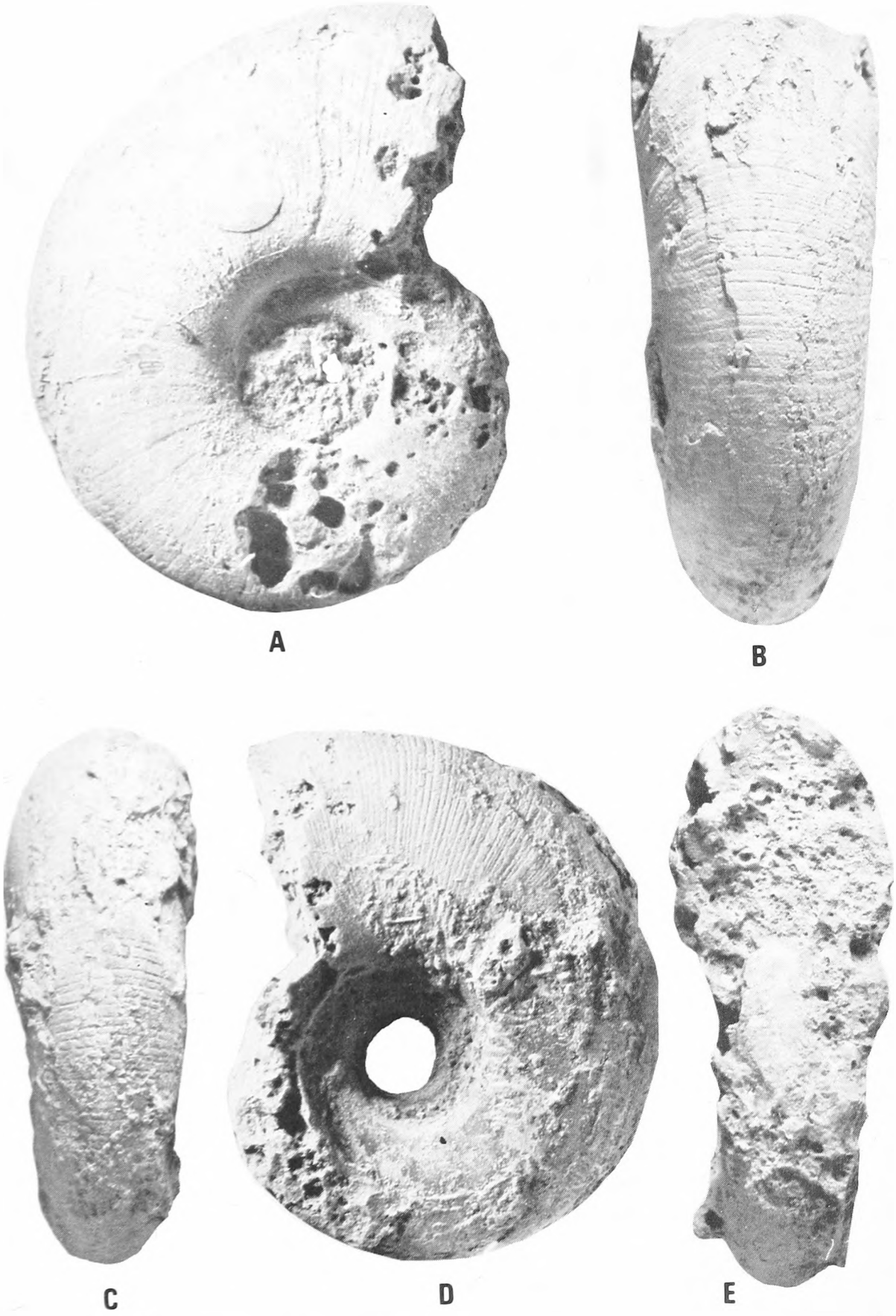

Fig. 8. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. A–B. USNMNH 236905. C–E. USNM 236908. ×1.

Measurements

No.	D	H	W	W/H	U
USNMNH 236905	81	37,5(46)	25(31)	0,66	21(26)
,,	56	25(45)	19,5(35)	0,78	17,5(31)
USNMNH 236906	34	13(38)	15,5(45)	1,19	±10(29)
USNMNH 236907	±47	±21(45)	±18(38)	0,86	15,5(33)
USNMNH 236908	71	33,5(47)	±27(38)	0,80	19(27)
USNMNH 236909	26	11(42)	11(42)	1,00	8(31)
,,	19,5	8(41)	8(41)	1,00	±5,5(28)
USNMNH 236910	24	9(38)	8(38)	1,00	8,5(35)
,,	18	6,5(36)	7(39)	1,08	7(39)
USNMNH 236911	15	5,5(37)	6(40)	1,09	5(30)
USNMNH 236912	22	8(36)	9(41)	1,13	8(36)
USNMNH 236913	17	5,5(32)	±7,5(44)	1,36	7(41)
USNMNH 236914	25	9(36)	±11(44)	1,22	±8,5(34)
*E. (E.)italicum**	±50	25(50)	19(38)	0,76	±14(28)
*E. (E.)aenigmum**	58,3	28,3(48,5)	24(41,5)	0,86	14(24)
*E. (E.)b. bourritianum**	33	14(42)	20(60)	1,43	10(30)
*E. (E.)b. hispanicum**	47	20(42)	22(47)	1,10	13(28)
Gaudryceras aff. *madraspatanum* Spath (*non* Stoliczka)	28	11,8(42)	11,8(42)	1,00	10(36)

* Asterisks mark holotypes or neotypes.

Intraspecific variation

The most noteworthy feature of the present material is the great change in whorl section with growth. The earliest whorls show a wide range in inflation ($^{W}/_{H}$ = 1,00–1,36) but, with continued growth, the shell becomes increasingly high-whorled and the whorl section becomes strongly compressed (Fig. 11). At the same time there is a slight, but distinct, tendency for the umbilical ratio to decrease (Fig. 11).

Discussion

E. (*Eogaudryceras*) *italicum* Wiedmann & Dieni is based upon a smooth, fragmentary internal mould from the Upper Albian of Sardinia. It agrees precisely with the present material in whorl section and relative proportions; lack of liration may simply be a reflection of different preservation.

Gaudryceras aff. *madraspatanum* (Stoliczka) (Spath 1923: 22, pl. 1 (fig. 4)) is based upon a smooth phosphatic internal mould from the Cambridge Greensand of southern England. In relative proportions it falls well within the range of variation of the present Angolan material, and the writers would tentatively refer it, therefore, to *E. italicum*.

Fig. 9. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni. A–C. USNMNH 236905. D–F. USNMNH 236906. G, K–L. USNMNH 236910. H–J. USNMNH 236909. M–O. USNMNH 236912. ×1.

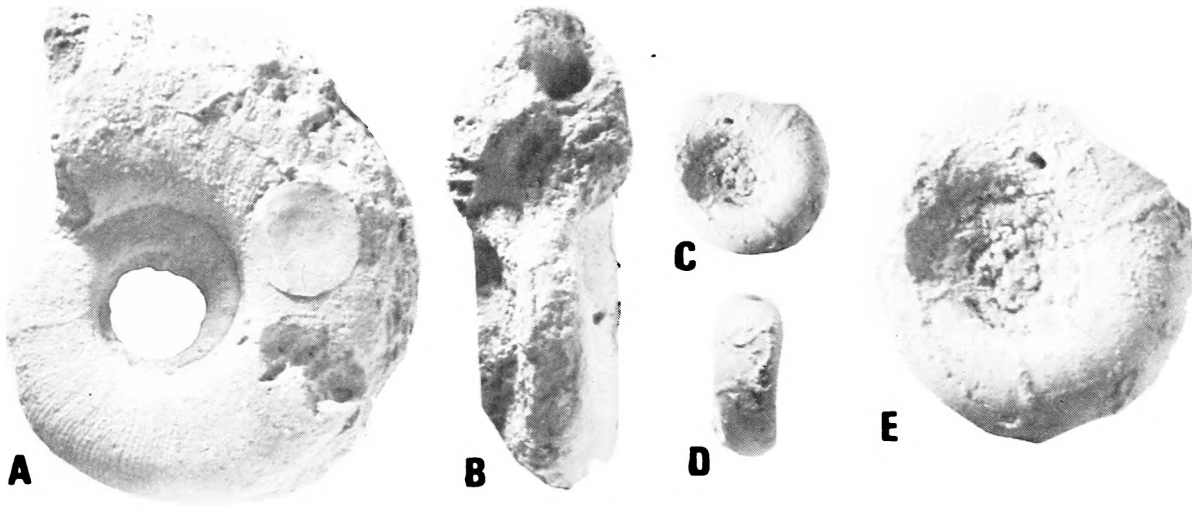

Fig. 10. *Eogaudryceras* (*Eogaudryceras*) *italicum* Wiedmann & Dieni.
A–B. USNMNH 236907. C–E. 236911. A–D ×1, E ×2.

The present sample is the largest single population of an *E.* (*Eogaudryceras*) species yet described, and shows a wide range of ontogenetic and intraspecific variation. In view of this wide range of variation, it seems probable that population studies will reduce in number the twelve species currently assigned to this subgenus, viz. *E.* (*E.*) *numidum* (Coquand), *E.* (*E.*) *intermedium* (Fallot), *E.* (*E.*) *vocontianum* (Fallot), *E.* (*E.*) *elegans* Basse, *E.* (*E.*) *shimizui* Breistroffer, *E.* (*E.*) *llosetae* Breistroffer, *E.* (*E.*) *turgidum* Breistroffer, *E.* (*E.*) *skoenbergense* Collignon, *E.* (*E.*) *bourritianum* (Pictet), *E.* (*E.*) *aenigmum* (Haas) and *E.* (*E.*) *muntaneri* Wiedmann.

Of other Upper Albian species of *Eogaudryceras* (*Eogaudryceras*), Wiedmann (1962*a*: 154) selected a neotype for *E.* (*E.*) *bourritianum* (Pictet) (*in* Pictet & Roux 1848: 298, pl. 4 (fig. 1)) and divided it into two chronological subspecies: *E.* (*Eogaudryceras*) *bourritianum bourritianum*, from the uppermost Albian (*dispar* zone) of south-west France is characterized by its strongly depressed whorl section ($^{W}/_{H}$ = 1,43), involute form (U = 30% of the diameter) and smooth whorls (the neotype is preserved as an internal mould and hence the lack of ornament may not be a diagnostic character). It differs from the Angolan material in its much more depressed whorl section and narrower umbilicus; *E.* (*Eogaudryceras*) *bourritianum hispanicum* Wiedmann (1962*a*: 155, pl. 12 (fig. 6), fig. 15) is a low Upper Albian form (associated with *Hysteroceras* and *Mortoniceras*) which was said to differ from the typical form in its less depressed, trapezoidal whorl section ($^{W}/_{H}$ = 1,10), flattened venter, and greater involution (U = 28% of the diameter). It differs from *E.* (*E.*) *italicum* in being more involute, having a slightly more depressed whorl section and a flattened venter.

E. (*Eogaudryceras*) *aenigmum* (Haas) (1942: 167, pl. 42 (fig. 3), pl. 44 (fig. 2), fig. 24) is from the Upper Albian of Angola. Crushed material assigned to this species, in the British Museum (Natural History), comes from Praia do Jombe

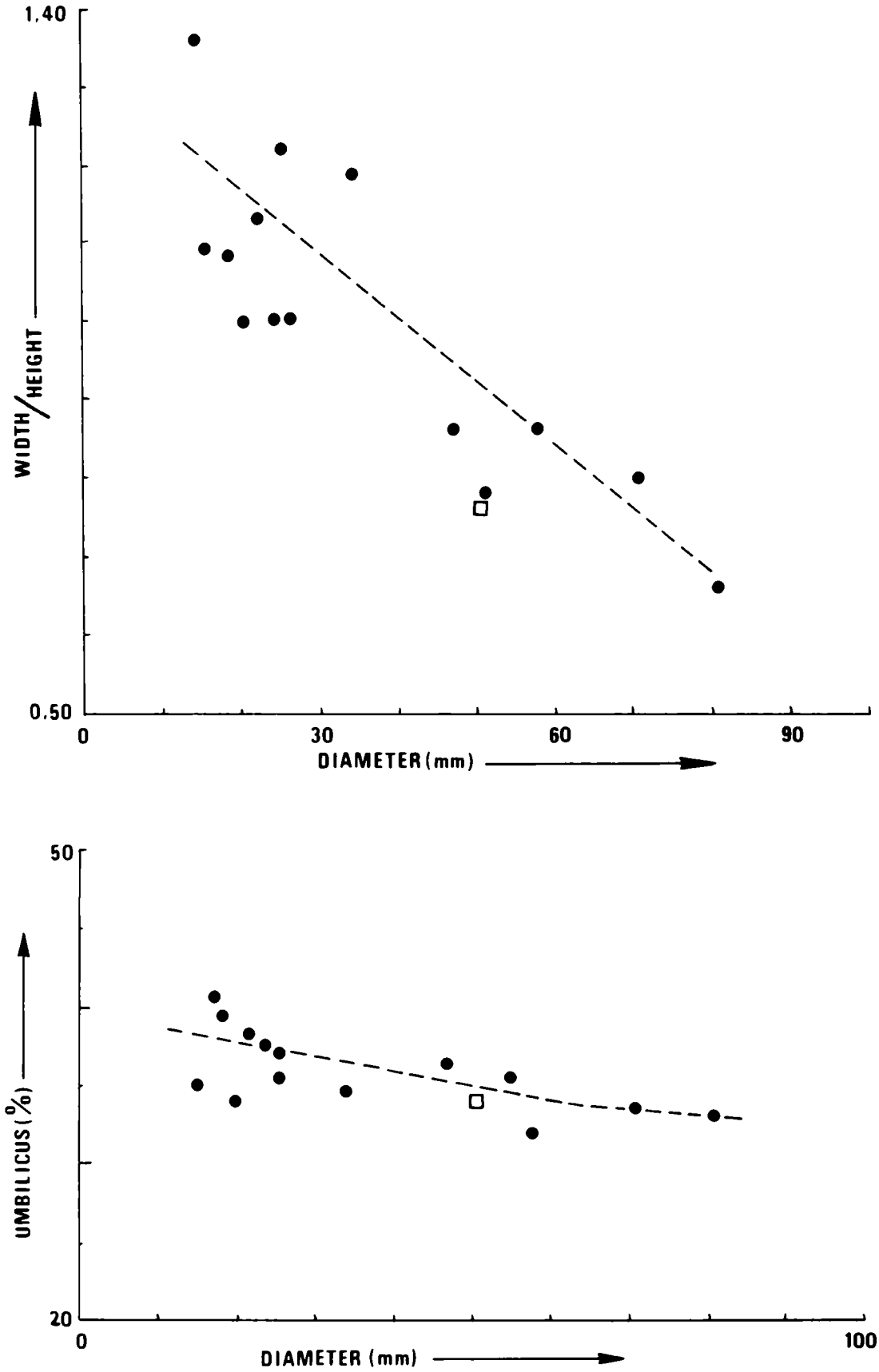

Fig. 11. Plot of inflation and umbilical ratio against diameter for *Eogaudryceras italicum* Wiedmann & Dieni. Dots = present Angolan material; square = holotype (after Wiedmann & Dieni 1968).

where it is associated with a low Upper Albian fauna which includes *Prohysteroceras wordiei* Spath, *Beudanticeras beudanti* (Brongniart) and *Mortoniceras* cf. *inflatum* (J. Sowerby). It is thus a contemporary of *E.* (*E.*) *bourritianum hispanicum*. The style of ornament is difficult to judge from Haas's (1942) illustration, although the specimen is clearly lirate (it has shell preserved). Although its whorl width/height ratio is closely comparable to *E. italicum* (? due to crushing), it is much more involute (U = 24% of the diameter). Haas's (1942) whorl section of the species shows inner whorls with a strongly fastigiate to keeled venter which suggest his material to be crushed. If true, this species may prove to have priority over *E.* (*E.*) *bourritianum hispanicum*.

Occurrence

E. (*Eogaudryceras*) *italicum* is currently known from the uppermost Albian of Sardinia, Angola, and possibly southern England.

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily ANCYLOCERATACEAE Meek, 1896

Family **Ancyloceratidae** Meek, 1876

Subfamily Anisoceratinae Hyatt, 1900

Genus *Anisoceras* Pictet, 1854

Type species *Hamites saussureanus* Pictet, 1847

Anisoceras (*Anisoceras*) *perarmatum* Pictet & Campiche, 1861
Figs 12A–H, 13C–D, 14A–C, 15C–F, 16B

Hamites armatus J. de C. Sowerby (*non* J. Sowerby), 1850: pl. 29 (fig. 13).
Anisoceras perarmatum Pictet & Campiche, 1861: 65, pl. 48 (figs 7–8), pl. 49 (figs 1–3, 5–7). Pictet, 1861: 21. Ooster, 1863: 19. Pictet & Renevier, 1866: 103. Jukes-Browne, 1875: 288. Barrois, 1878: 271. Renevier, 1890: 340. Boule, Lemoine & Thévenin, 1907: 35. Ganz, 1912: 121. Spath, 1921: 289. Böse, 1923: 144. Diener, 1925: 73. Spath, 1925*b*: 191. Barbu, 1932: 16. Roman, 1938: 52. Spath, 1939: 548, pl. 59 (figs 1–3), pl. 61 (figs 3–7), fig. 192. Breistroffer, 1947: 62. Reyment, 1955: 12, pl. 1 (fig. 1). Collignon, 1963: 50, pl. 259 (figs 1126–1127). Swensen, 1963: 67, pl. 4 (figs 1, 3, 7). Dieni & Massari, 1963: 798. Clark, 1965: 25, pl. 6 (figs 1, 3, 7). Wiedmann & Dieni, 1968: 65, pl. 6 (fig. 4), pl. 7 (fig. 9), figs 38–39. Renz, 1968: 74, pl. 13 (fig. 5a–c), pl. 14 (figs 1, 3, 5), figs 27a, 28g.
Hamites (*Anisoceras*) *perarmatus* (Pictet & Campiche) von Hauer, 1861: 644, pl. 2 (figs 2–4). Pervinquière, 1907: 85.
Hamites (*Anisoceras*) *saussureanus* von Hauer (*non* Pictet), 1861: 644, pl. 2 (fig. 1).
Anisoceras armatus Stoliczka (*non* J. Sowerby), 1866: 174, pl. 81 (figs 8–10), pl. 82 (fig. 1).
Hamites perarmatus (Pictet & Campiche) Neumayr, 1875*a*: 30; 1875*b*: 898.
? *Anisoceras vraconense* Renz, 1968: 75, pl. 16 (fig. 2), fig. 27b.
Anisoceras perarmatum simplex Renz, 1968: 75, pl. 13 (fig. 7), pl. 14 (fig. 4), fig. 27k.
? *Anisoceras pseudopunctatum* Pictet & Campiche, 1861: 74, pl. 52 (figs 1–3). Breistroffer, 1947: 62. Renz, 1968: 79, pl. 16 (figs 1, 3, 5). Wiedmann & Dieni, 1968: 72.

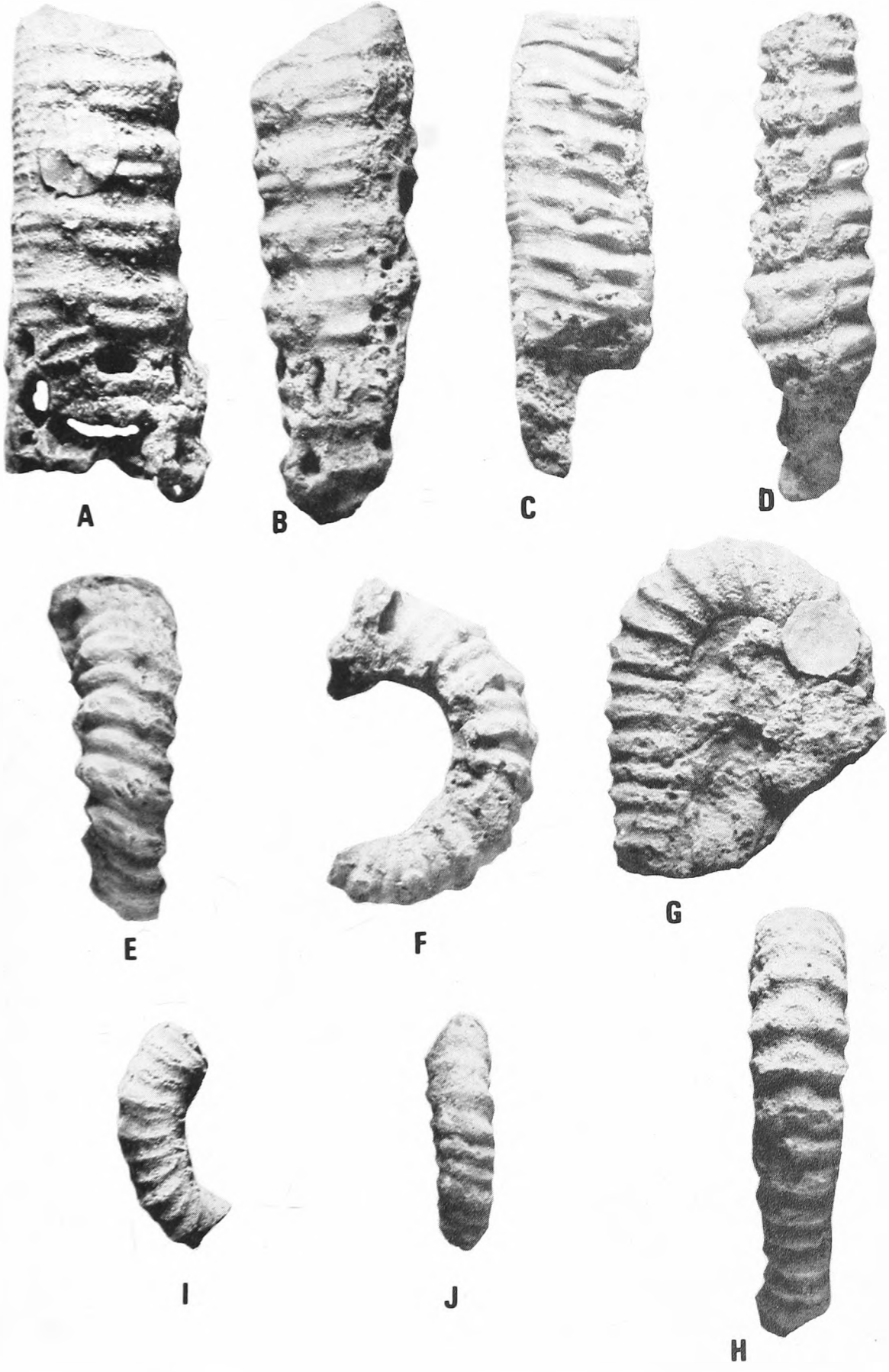

Fig. 12. A–H. *Anisoceras perarmatum* Pictet & Campiche. A–B. USNMNH 236928. C–D. USNMNH 236929. E–F. USNMNH 236944. G–H. USNMNH 236940. I–J. *Anisoceras* sp. juv., USNM 236745. ×1.

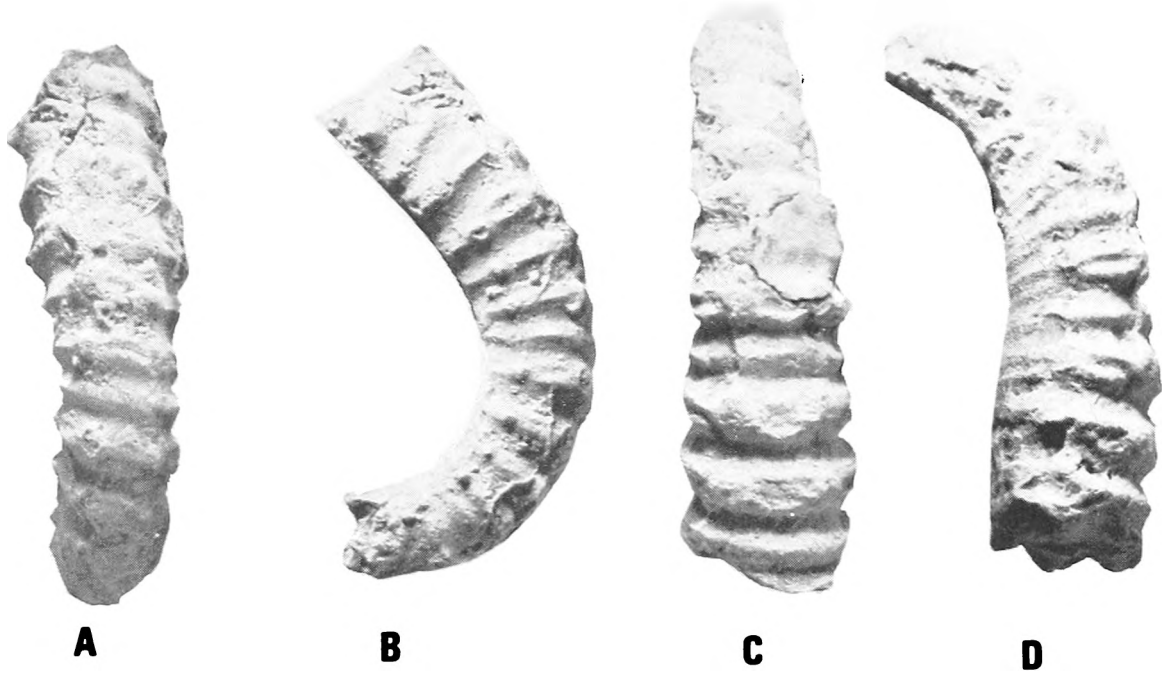

Fig. 13. A–B. *Anisoceras armatum* (J. Sowerby), USNMNH 236934. C–D. *Anisoceras perarmatum* Pictet & Campiche, USNMNH 236931. ×1.

Material

Twenty-seven specimens, SAM–PCA2940, 2950, 2956, 3115, 3122, 3143, 3148, 3152, 3193, 3214, 3243, 3283, 3285, 3299, 3339, 3352, 3355, 3358, 3361 and 3391, all from Egito, SAM–PCA4801, 4804 from Cabo Ledo and USNMNH 236928–29, 236931, 236933, 236940, and 236944 from Porto Amboim, either retaining recrystallized shell or preserved as composite internal moulds.

Description

Whorl section varies from almost circular in specimens replaced by calcite to slightly elliptical in those crushed individuals preserved as composite internal moulds.

Ornament comprises small dorsolateral to lateral tubercles and the septate bases of prominent ventrolateral spines, between which strong ribs are looped in pairs. There are sporadic non-tuberculate intercalatories between looped ribs. The main ribs are also looped across the venter, and split into fine riblets, thirteen per three dorsolateral tubercles, on the dorsum. On the body chamber there may be one to two simple ribs (SAM–PCA3143, 3148) between looped ribs, whilst on the final shaft of USNMNH 236940, the button-and-loop ribbing is lost, and all ribs become single.

Discussion

Amongst contemporaneous species of *Anisoceras*, only *A. saussureanum* and *A. armatum* closely approach this species. Differences are noted under the discussion of *A. armatum*.

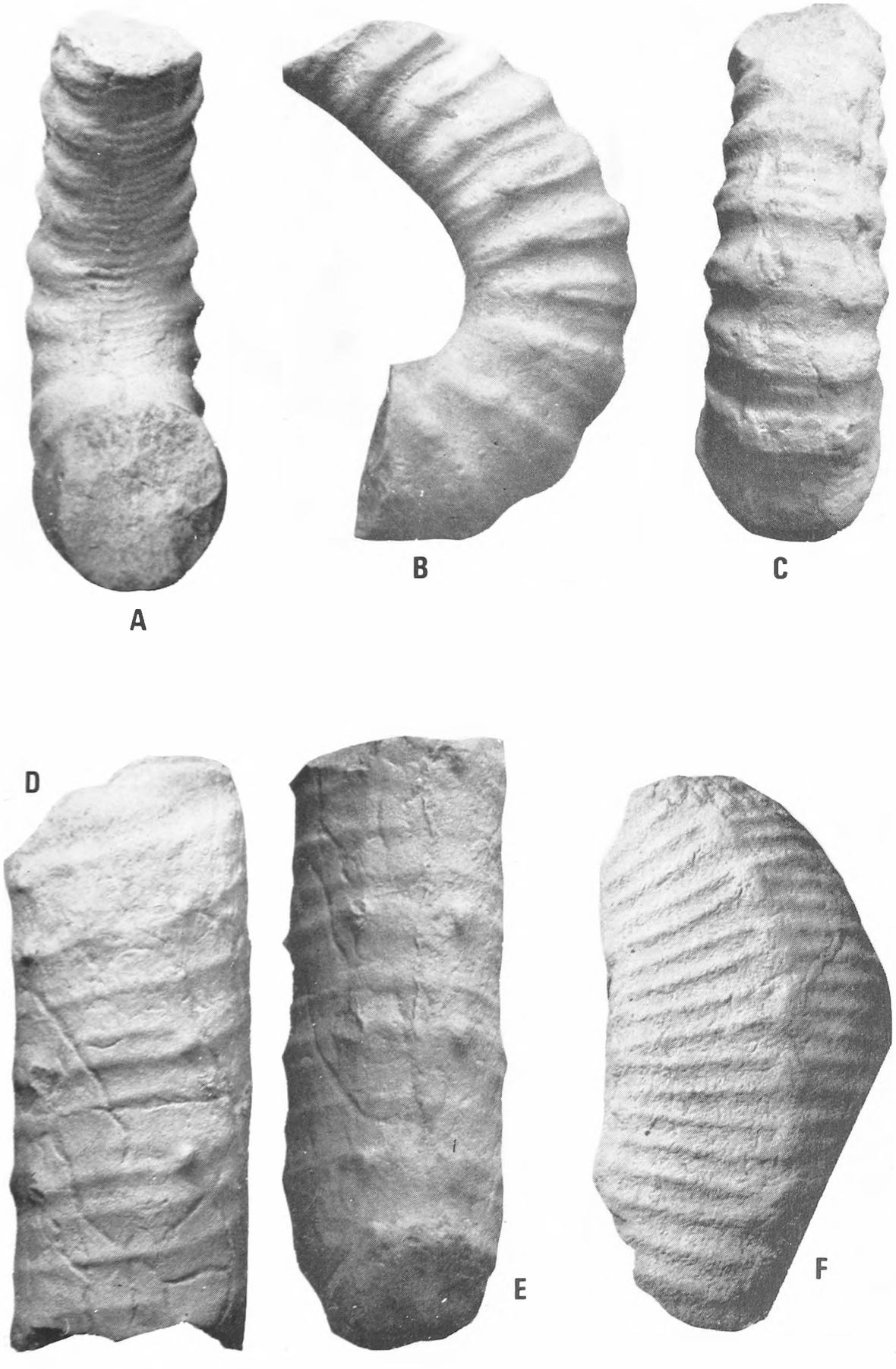

Fig. 14. A–C. *Anisoceras perarmatum* Pictet & Campiche. Dorsal, lateral and ventral views of SAM–PCA3115. D–E. *Anisoceras* cf. *armatum* (J. Sowerby). A fragment of a body chamber, SAM–PCA3287, which may belong here. F. *Anisoceras* sp. Oblique lateral view of SAM–PCA3220. ×0,75.

Anisoceras vraconense Renz (1968: 75, pl. 16 (fig. 2), fig. 27b) differs from *A. perarmatum* in having most ribs simple and much weaker dorsolateral tubercles. This species may be based upon a fragment of the final shaft of *A. perarmatum*, since the ribbing simplifies on the body chamber.

Anisoceras charlottense Anderson (1958: 209, pl. 11 (fig. 3)) has a circular whorl section and very prominent looped ribs separated by three to four simple, finer intercalatories. It may be conspecific with the low Upper Albian *A. salei* Clark (1958: 1079, pl. 140 (fig. 3)).

Anisoceras perarmatum simplex Renz (1968: 75, pl. 13 (fig. 7), pl. 14 (fig. 4), fig. 27k) is simply a variant based on a small body chamber fragment.

Anisoceras pseudopunctatum Pictet & Campiche (1861: 74, pl. 52 (figs 1–3)) is based on material which, like *A. perarmatum simplex*, has also lost button-and-loop ribbing, and may equally be an intraspecific variant.

Occurrence

Anisoceras perarmatum is a typical *dispar* Zone species known from England, France, Switzerland, Sardinia, Tunisia, Nigeria, Madagascar, southern India, Texas, and Angola.

Anisoceras (*Anisoceras*) *armatum* (J. Sowerby, 1817)

Figs 13A–B, 14D–E, 16A, C, E, I, 17–19

Hamites armatus J. Sowerby, 1817: 153, pl. 168. De Haan, 1825: 152, no. 2. Buckland, 1837: 65, pl. 44 (figs 9–10). Brown, 1837: 2, pl. 2 (fig. 6). Romer, 1840: 94, pl. 15 (fig. 2). D'Orbigny, 1842: 547, pl. 135.

Non Hamites armatus Mantell (*non* J. Sowerby), 1822: 121, pl. 23 (figs 3–4) (= *A. plicatile*).

Baculina armata (J. Sowerby) Fleming, 1828: 250.

? Hamites undulatus Brown (*non* Forbes), 1837: pl. 2 (fig. 11).

Non Hamites armatus J. de C. Sowerby (*non* J. Sowerby), 1850: pl. 29 (fig. 13) (= *A. perarmatum*).

? Hamites armatus J. Sowerby, Dixon, 1851: pl. 29 (fig. 13).

Anisoceras armatum (J. Sowerby) Pictet & Campiche, 1861: 62, pl. 48 (figs 1–2, 4, 6). Spath, 1939: 543, pl. 59 (fig. 6), pl. 60 (fig. 1), pl. 61 (?figs 9–11), pl. 62 (?fig. 5), fig. 191. Swensen, 1963: 66, pl. 3 (fig. 4), pl. 4 (?fig. 6). Clark, 1965: 25, pl. 5 (fig. 4), pl. 6 (?fig. 6), fig. 7a. Renz, 1968: 75, pl. 15 (figs 1, 3), figs 27d, 28a.

? Hamites (*Anisoceras*) *armatus* J. Sowerby, von Hauer, 1861: 644, pl. 1 (figs 9–10).

Non Anisoceras armatum Stoliczka (*non* J. Sowerby), 1866: 174, pl. 81 (figs 8–10), pl. 82 (fig. 1) (= *A. perarmatum*).

Hamites (*Anisoceras*) *armatus* J. Sowerby, Kossmat, 1895: 149.

? Anisoceras armatum (J. Sowerby) Choffat, 1905: 41, pl. 1 (fig. 6).

Non Hamites (*Anisoceras?*) *armatus* Pervinquière (*non* J. Sowerby), 1907: 84, pl. 4 (figs 2–3) (= *? A. exoticum*).

Anisoceras aff. *armatum* (J. Sowerby) Adkins, 1920: 69.

? Hamites cf. *armatus* J. Sowerby, Passendorfer, 1921: 237.

Anisoceras cf. *armatum* (J. Sowerby) Böse, 1923: 143, pl. 10 (figs 22–24). Haughton, 1924: 94. Clark, 1958: 1080, pl. 139 (fig. 2).

Non Anisoceras aff. *armatum* (J. Sowerby) Spath, 1925*b*: 190 (= *A. raynaudi*).

Anisoceras picteti Spath (*non* Matheron), 1926*a*: 432. Spath, 1939: 554, pl. 59 (fig. 4), pl. 61 (fig. 8), pl. 63 (figs 3, 8), fig. 194. Renz, 1968: 76, pl. 13 (figs 8–9), pl. 14 (figs 6–9), pl. 15 (fig. 4), figs 27c, 28f.

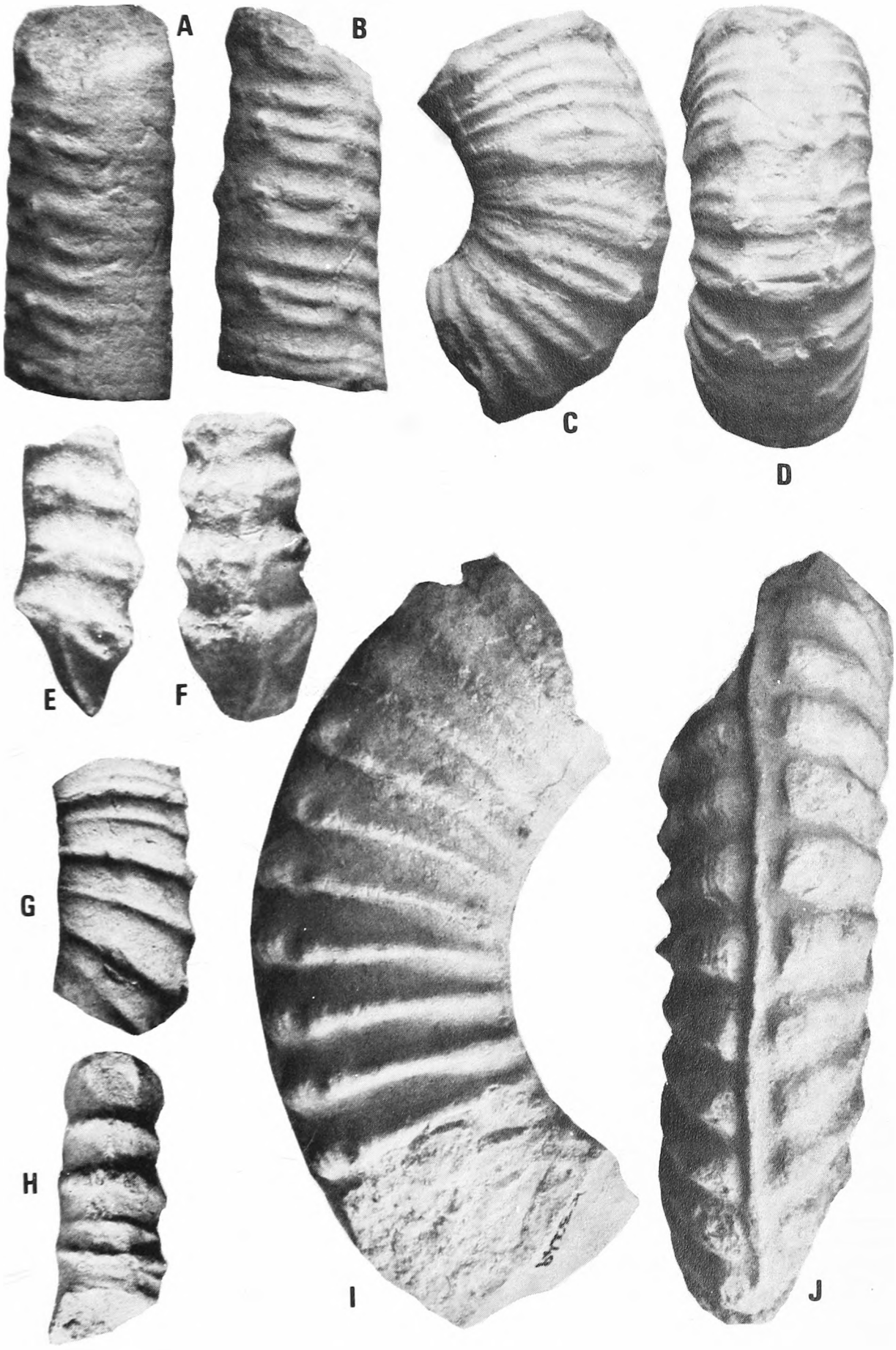

Fig. 15. A–B. *Anisoceras* sp. Oblique dorsolateral and lateral views of SAM–PCA3301 from Egito. C–F. *Anisoceras perarmatum* Pictet & Campiche. C–D. Ventral and lateral views of SAM–PCA3154. E–F. Lateral and ventral views of SAM–PCA4801. G–H. *Anisoceras* sp. An indeterminate body chamber fragment from Egito, SAM–PCA2942. I–J. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Lateral and ventral views of SAM–PCA3249. A–D, G–H ×0,75, E–F, I–J ×1.

? *Hamites* aff. *armatus* J. Sowerby, Scott, 1926: 80. Böse, 1928: 146. Adkins, 1928: 24.
? *Anisoceras* cf. *armatum* (J. Sowerby) Passendorfer, 1930: 667.
? *Non Hamites* (*Anisoceras*) *armatus* Collignon (*non* J. Sowerby), 1932: 20, pl. 4 (fig. 1).
Anisoceras saussureanum var. *spinosa* Haas, 1942: 192, pl. 46 (figs 1–3), fig. 30.
Non Anisoceras armatum Haas (*non* J. Sowerby), 1942: 189, fig. 29 (= *A. tropicale*).
Anisoceras jacobi Breistroffer, 1946: 310; 1947: 62. Wiedmann & Dieni, 1968: 67, pl. 6 (fig. 13), fig. 41.
? *Anisoceras* aff. *picteti* Spath, Kennedy, 1971: 13, pl. 3 (fig. 6), pl. 7 (fig. 10).
? *Non Anisoceras armatum* (J. Sowerby) Kennedy, 1971: 14, pl. 5 (fig. 11).

Material

Fourteen specimens, SAM–PCA2932, 2947, 2953, 3174, 3364, and 3398 from Egito, USNMNH 236930, 236934, 236936–37, 236939, and ?236952 from Porto Amboim, and SAM–PCA4606 and 4610 from Cabo Ledo.

Description

Shell form suggests initial coiling in an open planispiral, straightening in maturity. The whorl section is approximately circular.

The ornament is rather variable, comprising slightly rursiradiate to slightly prorsiradiate looped ribs, between which are generally one, sometimes two, simple intercalatories. Looped ribs are ornamented with small pointed dorsolateral tubercles and the septate bases of prominent ventrolateral spines. All ribs are of more or less equal strength. Across the dorsum the ribs divide into fine riblets and are accompanied by intercalatories.

In USNMNH 236939, which is taken to represent an early portion of the spire of the species, main ribs are weakly looped and are separated by two to three intercalatories. In USNMNH 236952, the largest specimen (which is, however, still septate), the whorl section is slightly compressed, oval, and there is generally only one intercalatory between looped ribs, although even these are sometimes absent.

Discussion

Anisoceras armatum is a widely-cited but poorly understood species, and in consequence the holotype is refigured here (Fig. 17). As noted by Spath (1939: 546), this is a crushed, composite internal mould which shows the following features: the penultimate shaft has distinct looped ribs separated by only one non-tuberculate intercalatory which is of approximately the same strength as the looped ribs. At this stage there are about five ribs in a distance equal to the whorl height (allowing for post mortem crushing). On the hook, the preservation is poor, but the looped ribs clearly break up so as all to become single on the final non-septate shaft. At this stage there are still only about five ribs in a distance equal to the whorl height, and most of the ribs are of approximately the same strength. The dorsolateral tubercles are still present in maturity, although weak and irregularly developed.

It is clear from the above description, and comparison with Sowerby's original illustration (cf. Spath 1939, fig. 191), that this species has been mis-

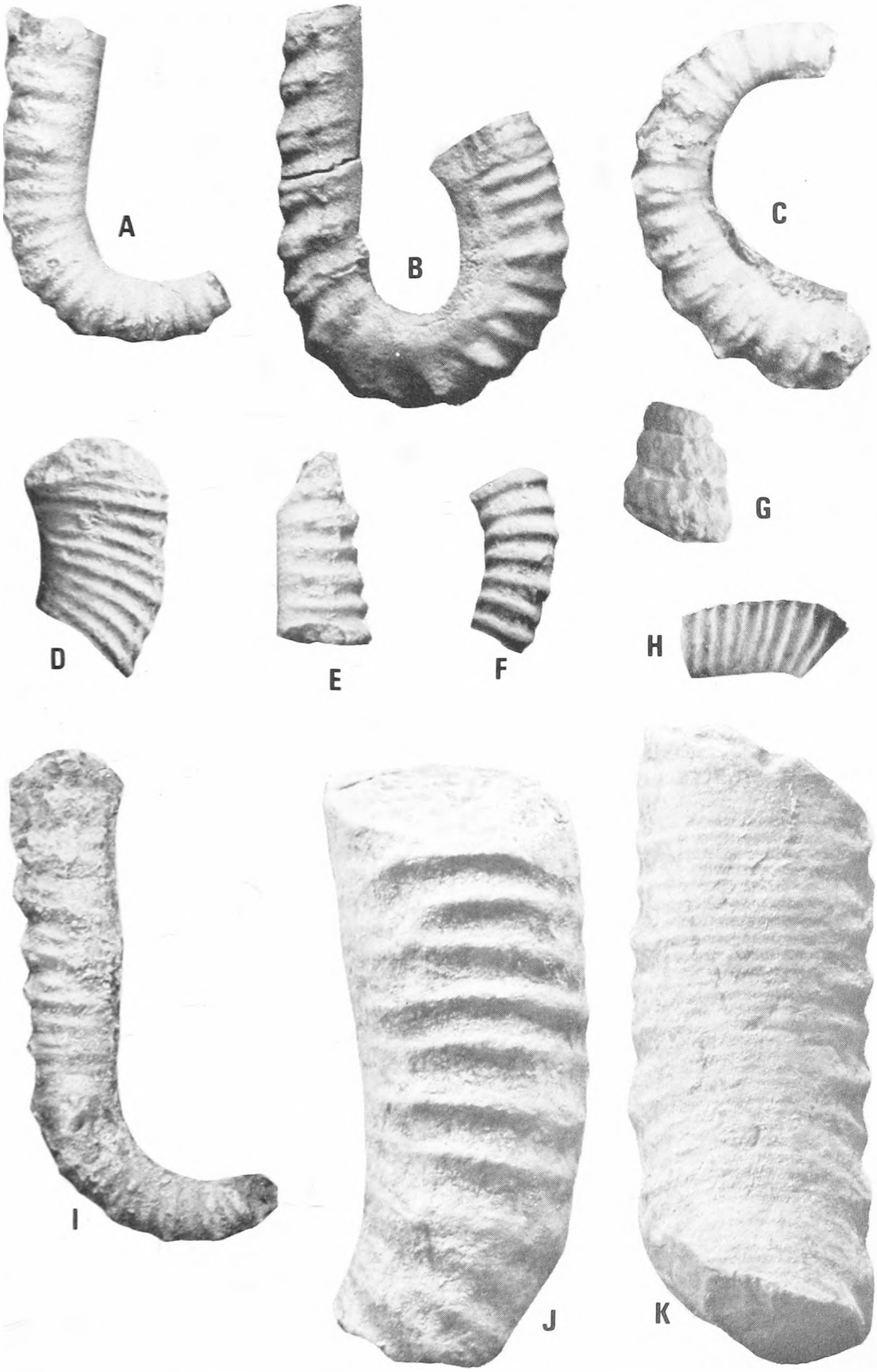

Fig. 16. A, C, E, I. *Anisoceras armatum* (J. Sowerby). A. SAM–PCA5470. C. SAM–PCA5471. E. SAM–PCA5473. I. SAM–PCA5472. B. *Anisoceras perarmatum* Pictet & Campiche. Lateral view of SAM–PCA3339, showing change of ornament on the body chamber. D. *Hamites duplicatus* Pictet & Campiche. Lateral view of SAM–PCA2955. F. *Hamites virgulatus* Brongniart. Lateral view of SAM–PCA3158, showing *venetzianus*-type ribbing. G. *Mariella* (*Mariella*) *gresslyi* (Pictet & Campiche). SAM–PCA3133. H. *Hamites virgulatus* Brongniart. Lateral view of SAM–PCA2959, showing rather dense *subvirgulatus*-type ribbing. J–K. *Anisoceras phillipsi* sp. nov. Lateral and dorsal views of SAM–PCA 4799. B ×0,75, other ×1.

interpreted. Indeed, Sowerby's figure bears no great resemblance to the original and shows too many intercalated ribs both on the penultimate and final shafts, while the differentiation of the ribs on the final shaft is less prominent than is shown in Sowerby's drawing.

Anisoceras jacobi Breistroffer (nom. nov. pro *Anisoceras picteti* Spath (*non* Matheron) 1939: 554, pl. 59 (fig. 4), pl. 61 (fig. 8), pl. 63 (figs 3, 8), fig. 194) was diagnosed as follows: 'Like *A. armatum*, but more coarsely ornamented, with

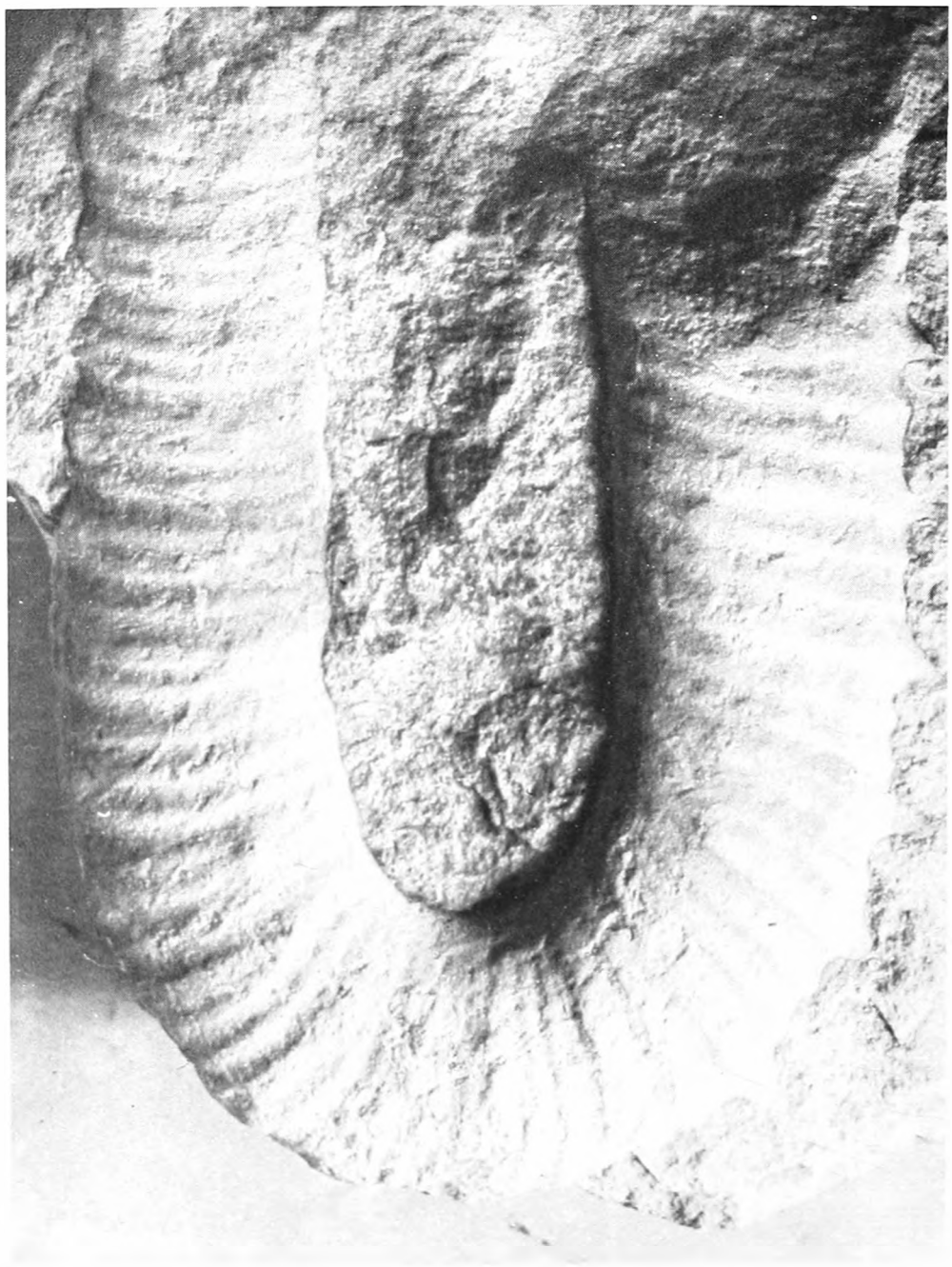

Fig. 17. *Anisoceras armatum* (J. Sowerby). Sowerby's (1817, pl. 178) original figured specimen from the Upper Greensand of Roak, near Benson, Oxfordshire. Oxford University Museum K675a. × 1.

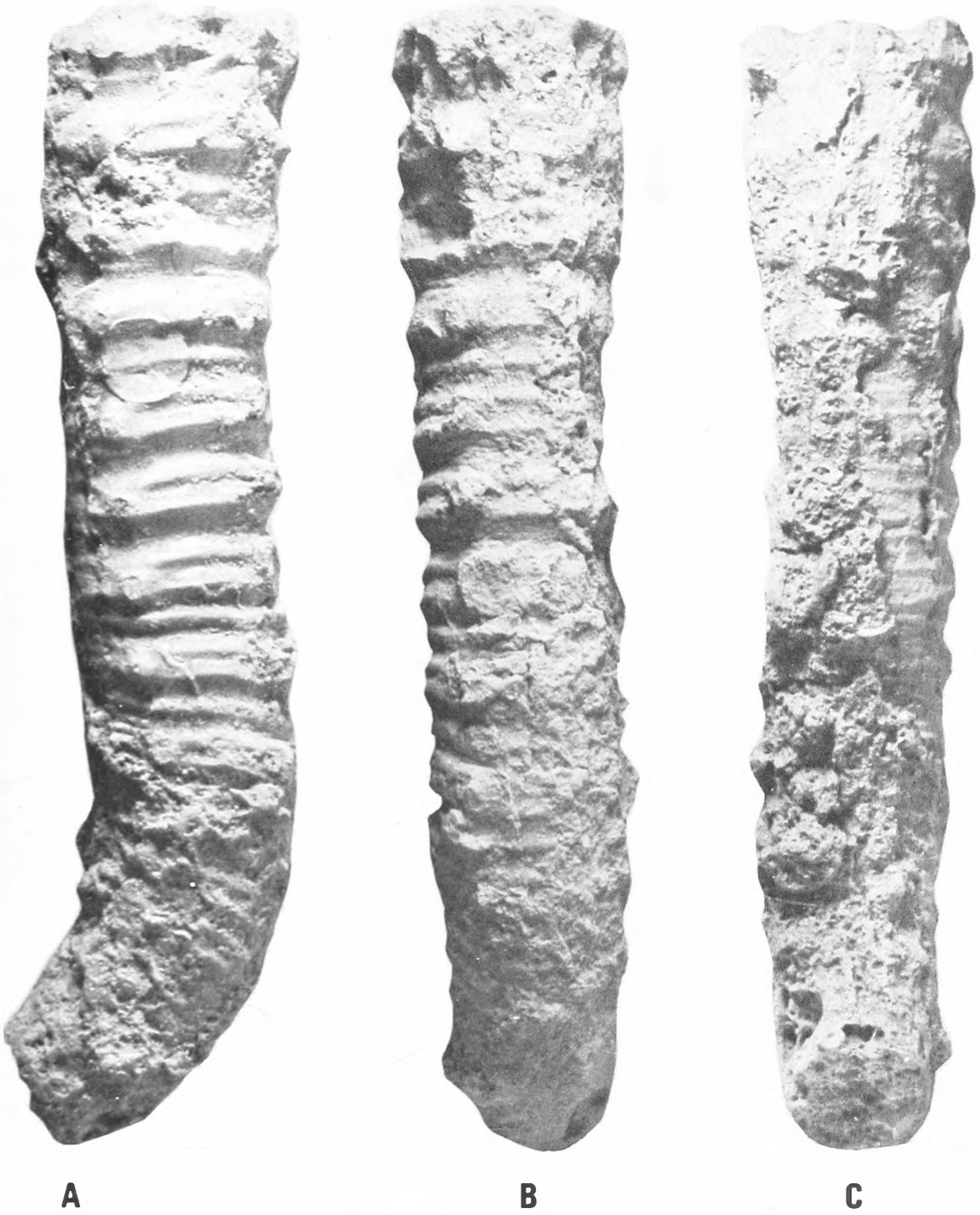

Fig. 18. A–C. *Anisoceras armatum* (J. Sowerby), USNMNH 236952. ×1.

the intermediate ribs (one, rarely two) as prominent as the main ribs that meet at the strong tupercles. Suture-line similar to that of *A. armatum*.'

These are the exact features which characterize the penultimate shaft of the holotype of the contemporaneous *A. armatum*, and the authors regard *A. jacobi* as a junior subjective synonym of *A. armatum*.

Anisoceras armatum and *A. perarmatum* are contemporaneous species which differ in that the latter generally lacks intercalatories between the

looped ribs in maturity, although there are intermediates between the two species, e.g. USNMNH 236952 (Fig. 18).

Spath (1939) noted the very close resemblance between *A. saussureanum* (Pictet) and *A. armatum* and considered immature growth stages indistinguishable. In maturity, *A. saussureanum* was said to differ by its distant tuberculation, with commonly two to three intercalatories between looped ribs, whilst coming from a lower level in the Albian. Spath (1939) appeared to place much weight, in his separation of the above two species, on the supposedly lower horizon of

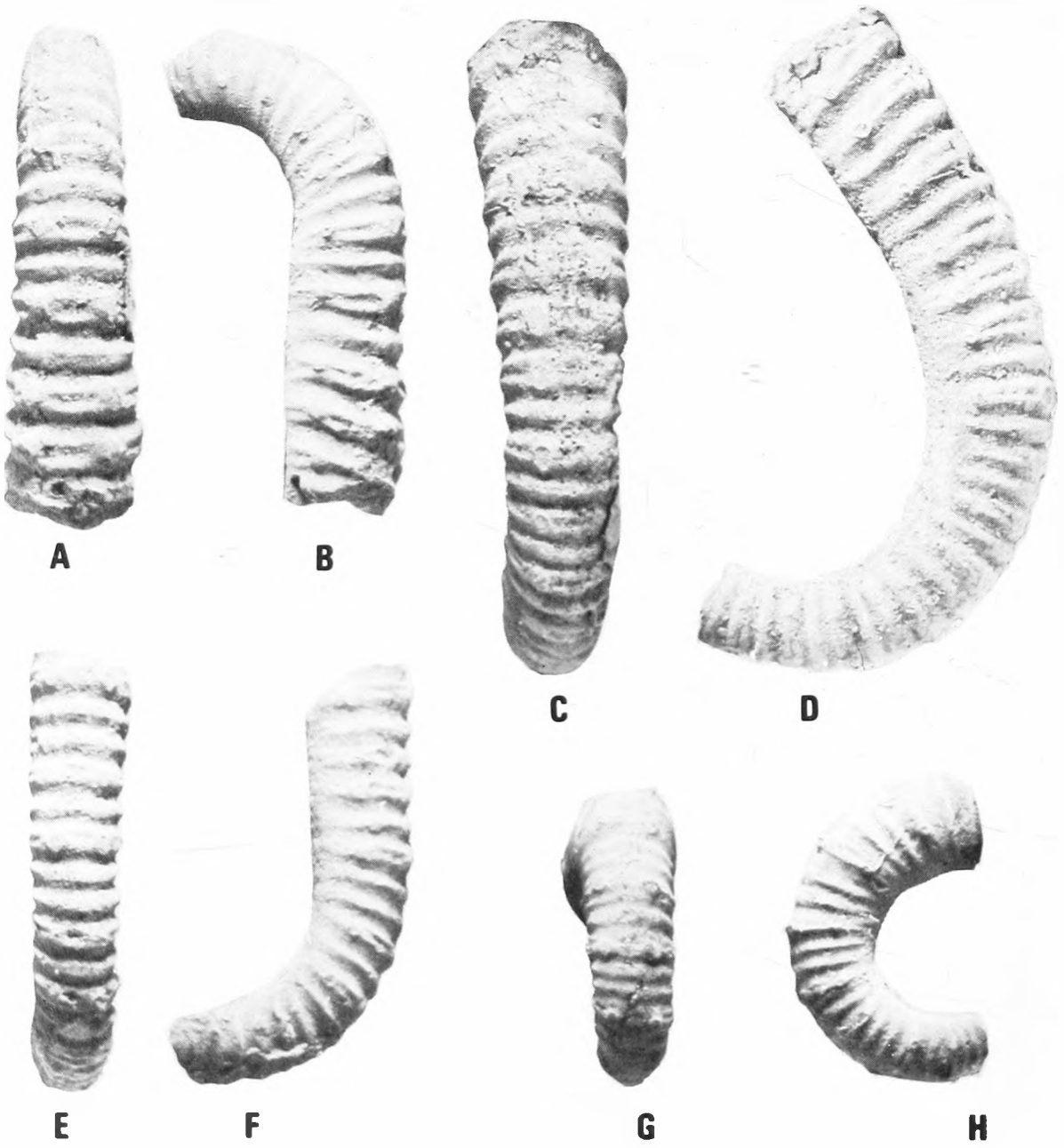

Fig. 19. *Anisoceras armatum* (J. Sowerby). A–B. USNMNH 236930. C–D. USNMNH 236936. E–F. USNMNH 236937. G–H. Doubtful juvenile, USNMNH 236939. ×1.

A. saussureanum, although Breistroffer (1940, 1947) and Renz (1968) record it from the uppermost Albian of France and Switzerland respectively. Moreover, *A. saussureanum spinosum* (Haas) is recorded from the uppermost Albian of Angola and Mexico (*fide* Haas 1942). The holotype of *A. saussureanum spinosum* comes from the same locality as the Washburn collection and the authors have no hesitation in regarding it as a junior subjective synonym of *A. armatum*. However, Haas's identification clearly focuses on the difficulties of separating *A. armatum* and *A. saussureanum* and, in view of the fact that they are contemporary species in the uppermost Albian, they probably do not bear specific separation. However, until the type and topotype material of *A. saussureanum* are restudied with regard to their intraspecific variation, it seems preferable to retain these two well-known species separate.

Anisoceras tropicale (Meunier) (1887: 62, pl. 1 (fig. 5)) is based upon a very poorly preserved internal mould which was tentatively referred to *A. armatum* by Choffat (1905: 41) and Haas (1942: 191), although Spath (1939: 558) considered it closer to *A. pseudoelegans*. Meunier's specimen shows three fine intercalatories between looped ribs and, judging from the locality, a valley to the north of Lobito, is somewhat older than *A. armatum*. This is supported by the example of *A. armatum* figured by Haas (1942, fig. 29), which the authors would assign to *A. tropicale*; it occurs on the reverse side of the holotype of *Mortoniceras vokesi* (Haas), topotype material of which comes from the mid-Upper Albian zone of *Elobiceras elobiense* (Cooper 1978) at Lobito, in association with *Puzosia cuvervillei* (Meunier).

Anisoceras exoticum Spath (1939: 555, pl. 59 (fig. 7), pl. 60 (fig. 4), pl. 63 (fig. 2), fig. 195) differs from *A. armatum* in having four to six intercalatories between main ribs, with very feebly-developed dorsolateral tubercles. The ribbing of this species is also attenuated across the siphonal line.

In *Anisoceras oldhamianum* (Stoliczka) (1865: 135, pl. 83 (figs 1–4), pl. 92 (fig. 1)) all the ribs of the early growth stages are tuberculate and presumably looped, whilst on the straight shaft there is a fine, non-tuberculate rib separating looped ribs. The early whorls are coiled in a shallow, open helix.

Occurrence

Anisoceras armatum is at present known with certainty only from the uppermost Albian of southern England, France, Switzerland, Sardinia, Angola, Texas, and Mexico.

Anisoceras haasi sp. nov.

Figs 20–22

Idiohamites (?) indet. sp., Haas, 1942: 195, pl. 45 (fig. 6).
Idiohamites spiniger Haas (*non* J. Sowerby), 1942: 195, pl. 46 (fig. 4), fig. 31a–b.
Idiohamites indet. sp., Haas, 1942: 197, pl. 45 (fig. 7), fig. 31c.
Idiohamites aff. *subspinigero* Haas (*non* Spath), 1942: 197, pl. 46 (fig. 5), fig. 31d–e.

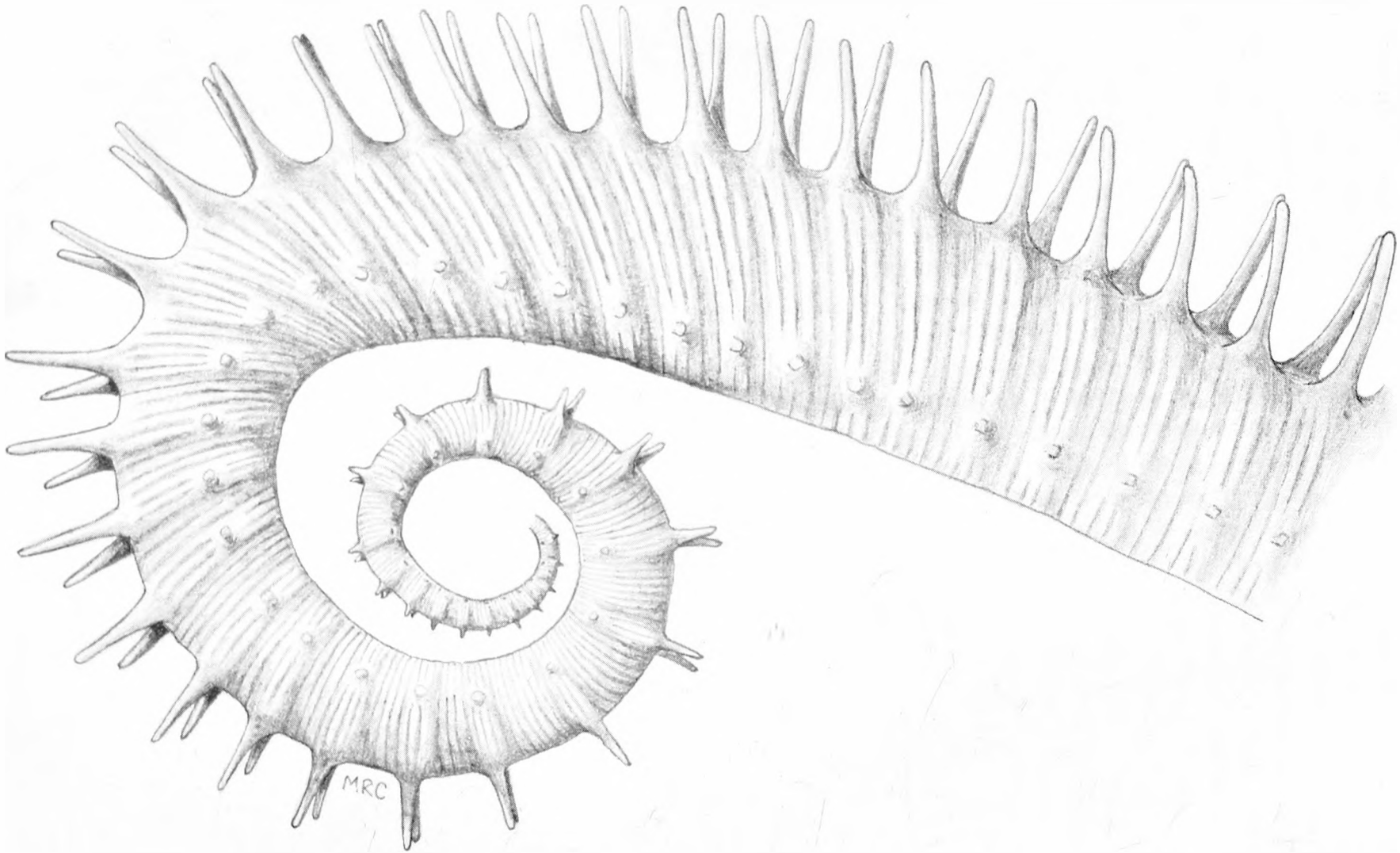

Fig. 20. *Anisoceras haasi* sp. nov. Reconstruction of early and middle growth stages. ×1.

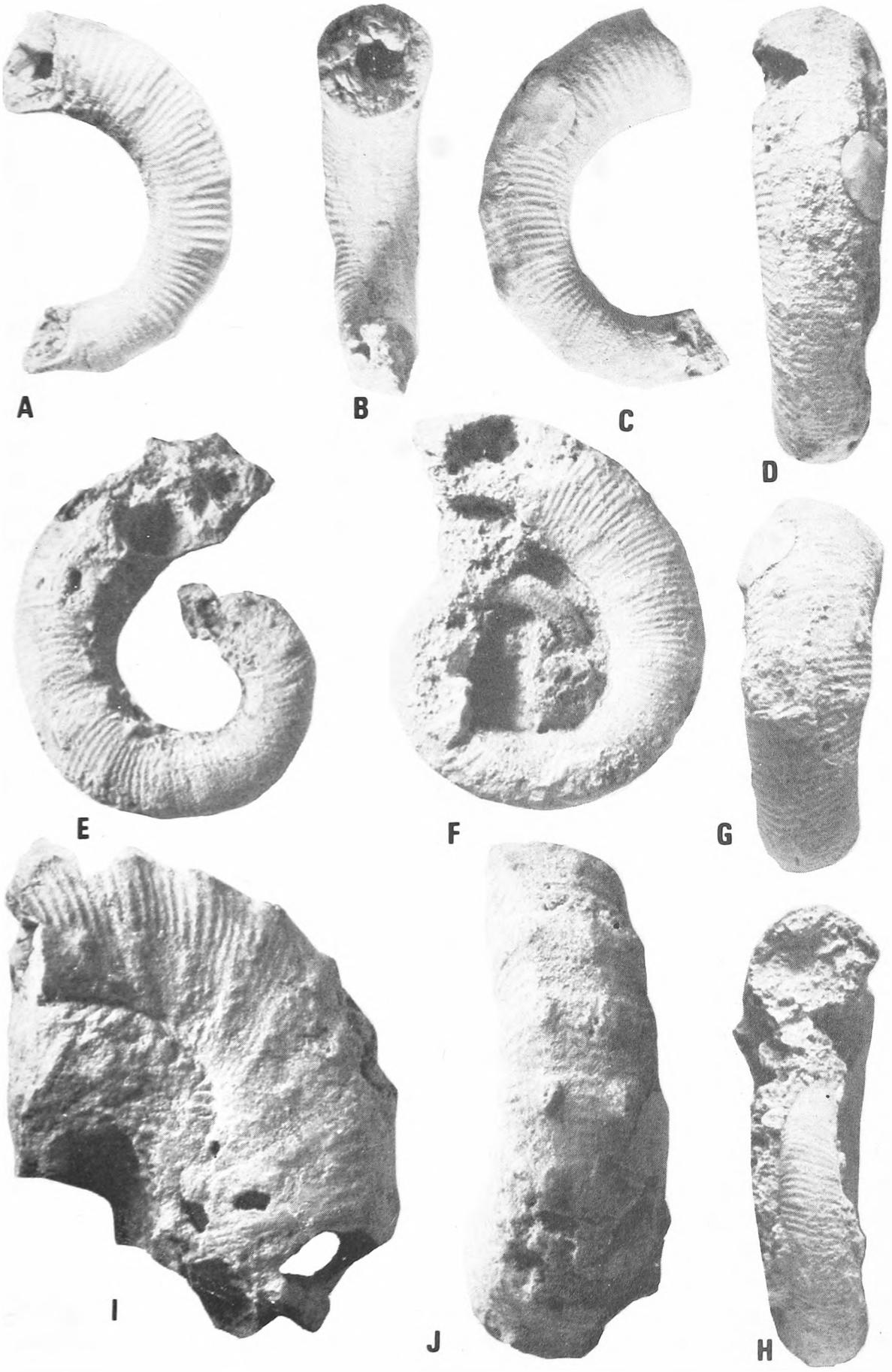

Fig. 21. *Anisoceras haasi* sp. nov. A–C. USNMNH 236923. D, F, H. USNMNH 236924. E, G. USNMNH 236922. I–J. USNMNH 236925. ×1.

Material

Seven specimens, USNMNH 236922–7, all retaining recrystallized shell and all from Porto Amboim, together with a single crushed internal mould, SAM–PCA2952 from Praia-Egito.

Type material

USNMNH 236922 is designated holotype; the remaining specimens from Porto Amboim are paratypes.

Etymology

Named for Otto Haas, pioneer of ammonite studies on the Angola Cretaceous.

Diagnosis

A densely ribbed species of *Anisoceras* with 8–15 ribs in a distance equal to the whorl height; 2 or 3 ribs are looped from small, acute dorsolateral tubercles to prominent rounded bases of septate ventrolateral spines, commonly with 3–4 looped between tubercles across the venter; there are between 2 and 9 fine intercalatories separating looped ribs. Whorl section circular to elliptical, compressed.

Description

Up to 13 mm whorl-width: at this stage, the shell is coiled in a loose planispire, and has a slightly depressed to circular cross-section. Ornament comprises fine, slightly rursiradiate ribs, about as wide as the interspaces and effaced across the dorsum. There are periodic broad bulges which follow the course of the ribbing and are ornamented with very weak, pointed dorsolateral tubercles and the septate bases of large, prominent, ventrolateral spines. The fine ribs commonly arise in pairs from the dorsolateral tubercles and are joined by a third rib to meet the ventrolateral spine-base. Three to four ribs are looped across the venter connecting the ventrolateral spines. There are four to nine fine intercalated ribs between adjacent bulges.

14–16 mm whorl-width: beyond 13 mm whorl width, the shell begins to uncoil, developing an almost straight shaft. At the same time, the whorl section becomes slightly compressed ($^{W}/_{H}$ = 0,83–0,86) and elliptical. The bulges become more regular with generally three in a distance equal to the whorl height, and commonly with two to three fine ribs separating adjacent bulges. Ribbing remains rursiradiate at this stage and the dorsolateral tubercles have migrated up flank to a low lateral position.

Discussion

The lectotype of *A. pseudoelegans* (Renz 1968, pl. 14 (fig. 12)) differs from the Angolan material in having a strongly compressed whorl section with flattened flanks and maximum width near the dorsolateral tubercles, whilst it is

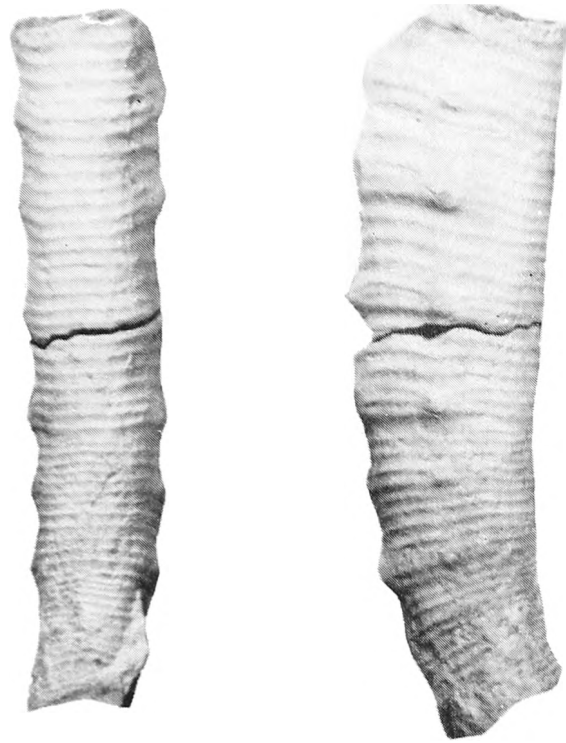

Fig. 22. *Anisoceras haasi* sp. nov. Dorsal and lateral views of a slightly crushed composite internal mould, SAM-PCA2952, from Egito. ×1.

more coarsely ribbed, with ribs arising in bundles from distinctly bullate dorsolateral tubercles. Juveniles of *A. pseudoelegans* also appear to be much more coarsely ribbed than the present material (compare Renz 1968, pl. 14 (figs 10–11)).

According to Kennedy (1971: 12, pl. 3 (figs 12–13), pl. 4 (figs 1–3)), *Anisoceras plicatile* is a Middle Cenomanian species with 12 fine ribs in a distance equal to the whorl height, and a circular whorl section. 2 or 3 ribs are looped between the midlateral and ventrolateral tubercles and are separated by 1–3 non-tuberculate intercalatories. *Anisoceras plicatile* differs from the present material, therefore, in having much more swollen main ribs and a much more prominent lateral tubercle which is at the middle of the flank, not dorsolateral as in *A. haasi*. The Angolan species also has more numerous, fine intercalatories, whilst the ribbing is not as coarse in maturity as it is in *A. plicatile* (compare Kennedy 1971, pl. 2 (fig. 12)).

Anisoceras bendirei (Adkins) (1920: 8, pl. 11 (fig. 1)) from the late Albian of Texas differs from the Angolan material in being much more coarsely ribbed, with the lateral tubercle higher on the flanks.

Anisoceras raynaudi (Boule, Lemoine & Thévenin 1907: 170, pl. 4 (figs 7–8), fig. 38) is a finely ribbed species in maturity, which differs from *A. haasi* in having fewer intercalatories (only 2–3) between looped ribs in the early growth stages, a more prominent dorsolateral tubercle and, judging from material from Catuane, southern Mozambique, in the South African Museum, Cape Town, in

having the early whorls coiled in an open helical spire up to 20 cm in height. It is also an earlier species (*orbignyi-varicosum* Subzones).

Anisoceras nanaense (von Hauer) (1861, pl. 1 (figs 11–12)) differs from the present species in lacking dorsolateral tubercles, and in having prorsiradiate ribs with only two to three intercalatories between tuberculate ribs.

Anisoceras arrogans (Giebel) (1852: 305) (nom. nov. pro *Hamites elegans* d'Orbigny (*non* Parkinson) 1842: 542, pl. 133 (figs 1–5)) can be distinguished from *A. haasi* in its lack of dorsolateral tubercles, with only two to four non-tuberculate intercalatories, and in the coarse, distant ribbing of the body chamber.

Occurrence

Anisoceras haasi sp. nov. is at present known only from the uppermost Albian of Angola.

Anisoceras phillipsi sp. nov.

Figs 16J–K, 23–24

Material

Eight fragments, SAM–PCA2974, 3179, 3183, 3211–3212, 3220 and 3222, all preserved as composite internal moulds, from Praia-Egito, and SAM–PCA4799 from the Quissama Ridge at Cabo Ledo.

Type material

The specimen illustrated as Figure 23, SAM–PCA3183 from Praia-Egito is designated as holotype. All other specimens cited above are paratypes.

Etymology

The species is named for Denis Phillips of the British Museum (Natural History) who, during many years, has given both authors invaluable assistance and advice in connection with their researches.

Diagnosis

A large species of *Anisoceras* with subrectangular, depressed to ovate whorl section in maturity. Prominent dorsolateral clavae give rise to two, occasionally only one, rursiradiate ribs which meet the well-developed ventrolateral clavae singly or in pairs. There are no intercalated ribs. Across the venter the ribs are looped or single.

Description

In the smallest example, SAM–PCA3179, the whorl section is elliptical, compressed, although it may have suffered lateral compaction. All the other larger fragments show a strongly depressed, subrectangular whorl section (Fig. 24) prior to the final hook, and an ovate whorl section afterwards.

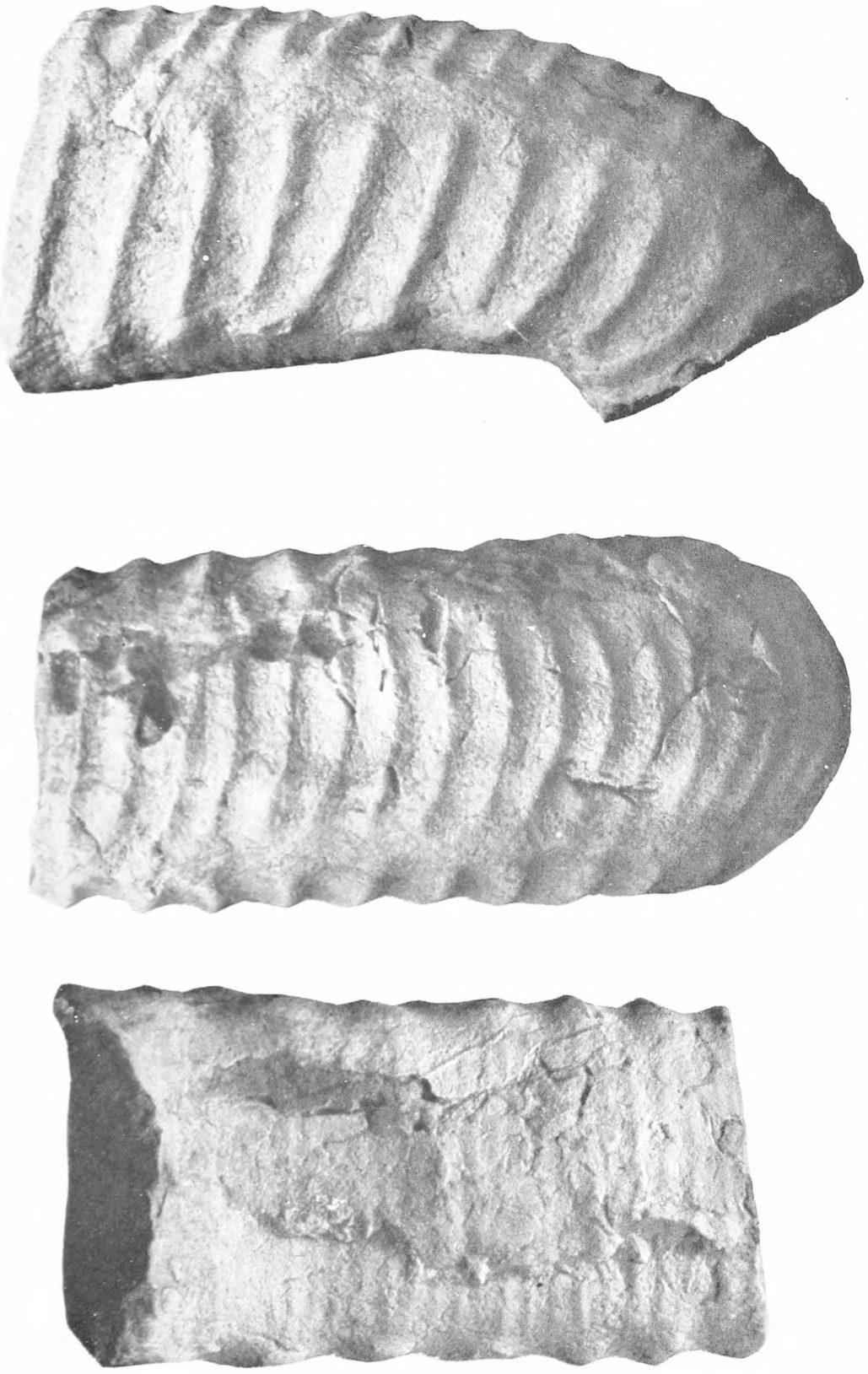

Fig. 23. *Anisoceras phillipsi* sp. nov. Dorsal, ventral and lateral views of the holotype, SAM–PCA3183, preserved as an internal mould. ×0,75.

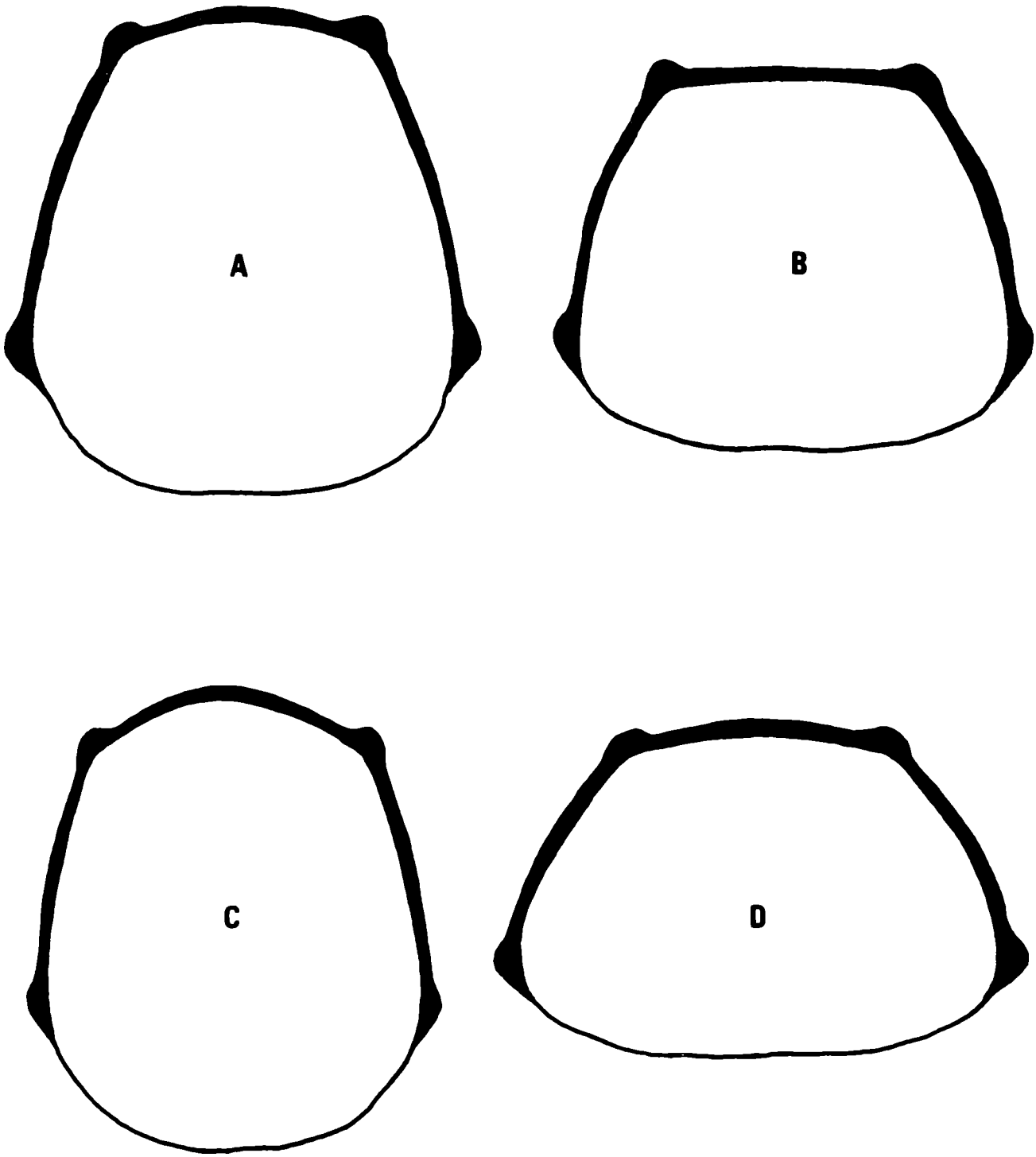

Fig. 24. *Anisoceras phillipsi* sp. nov. Whorl sections. A–B. SAM–PCA2974. C. SAM–PCA3183. D. SAM–PCA3222. ×1.

On the dorsolateral shoulder, prominent clavae give rise to commonly two, sometimes only one, coarse, rursiradiate flank ribs which, on curved fragments, are strongly convex adorally. The flank ribs meet the well-developed ventrolateral clavi either singly or in pairs, with six to eight ribs in a distance equal to the whorl height. Across the venter, ribs are single or looped.

Discussion

The only species with which the present form may usefully be compared is *Anisoceras arrogans* (Giebel) (= *Anisoceras campichei* Spath 1942: 559, pl. 63 (figs 6–7), fig. 197) which differs in lacking the dorsolateral clavae and in the regular nature of its ribbing across the venter.

Occurrence

Anisoceras phillipsi sp. nov. is known only from the uppermost Albian of Angola.

Anisoceras cf. *arrogans* (Giebel, 1852)

Figs 25–26

Compare

Hamites elegans d'Orbigny (*non* Parkinson), 1842: 542, pl. 133 (figs 1–5).
Hamites arrogans Giebel, 1852: 305.
Anisoceras pseudoelegans Pictet & Campiche, 1861: pl. 50 (figs 6–7 only).
Anisoceras campichei Spath, 1926: 432; 1939: 559, fig. 197 only.
Metahamites (?) *arrogans* (Giebel) Spath, 1939: 559.
Anisoceras aff. *campichei* Spath, 1939: pl. 63 (figs 6–7).
Anisoceras arrogans (Giebel) Wiedmann & Dieni, 1968: 69, pl. 7 (fig. 10), pl. 8 (figs 5, 7, 11), figs 46–50.

Description

This species is known only from large fragments. In SAM–PCA3205, the whorl section is slightly compressed, subquadrate, but the remaining material shows some variation in this character.

Ornament comprises prominent, single flank ribs arising from weak umbilical tubercles and passing slightly prorsiradiate across the flanks to the bases of large, septate ventrolateral spines. Ribs are either single or looped across the venter, and the rib pattern is shown in Figure 26. There are six to seven flank ribs in a distance equal to the whorl height. Across the dorsum, fine ribs are looped between the weak dorsolateral tubercles, with generally an intercalated rib between pairs, so that there are about fifteen ribs across the dorsum per five dorsolateral tubercles.

Discussion

The present specimen is closest to *Anisoceras arrogans* (Giebel) (= *A. campichei* Spath, 1939: 559, fig. 197 only) from which it differs in its subquadrate whorl section, slightly prorsiradiate flank ribs, and the fact that all

ribs across the venter arise from ventrolateral tubercles. *Anisoceras arrogans* also does not show the peculiar zigzagging of the ribs across the venter (see Fig. 26) seen in the Angolan material. However, since *A. arrogans* and the present material represent different ontogenetic stages, the differences may not be as great as they first appear, and consequently the present material is identified as *A.* cf. *arrogans* (Giebel).

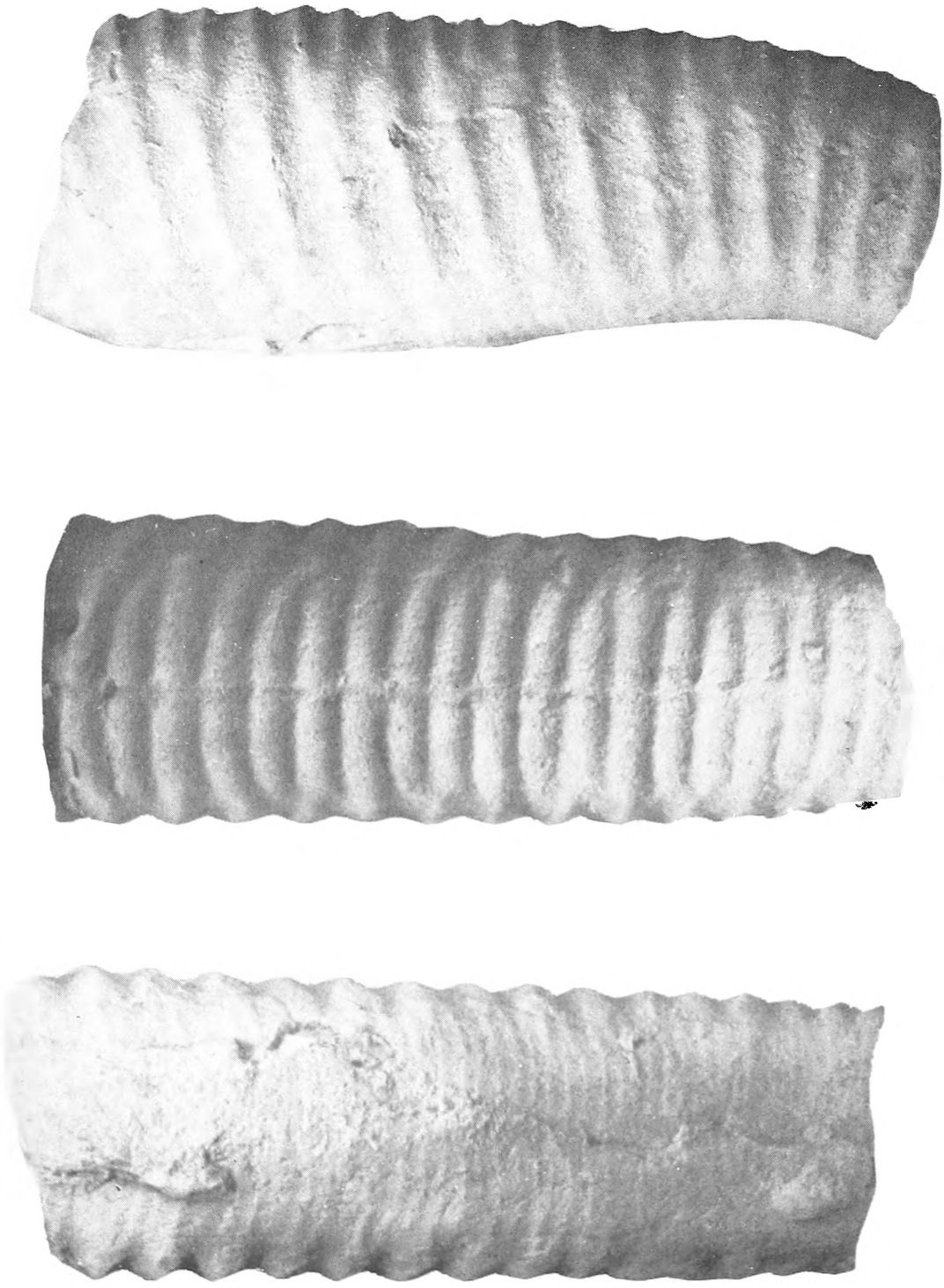

Fig. 25. *Anisoceras* cf. *arrogans* (Giebel). Dorsal, ventral and lateral views of SAM–PCA3205. ×0,75.

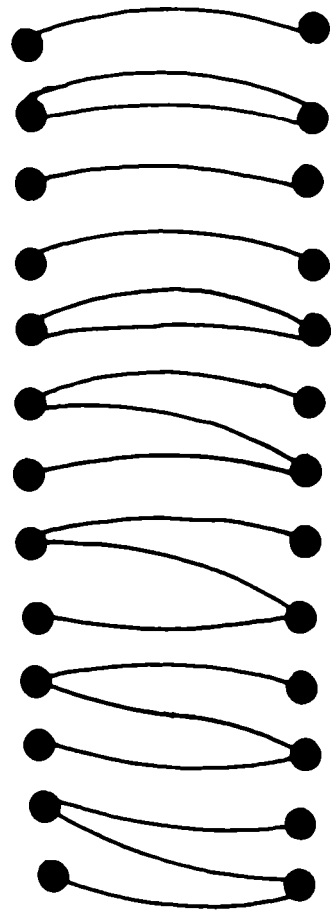

Fig. 26. *Anisoceras* cf. *arrogans* (Giebel). Schematic rib pattern across the venter of SAM–PCA3205. ×0,75.

Anisoceras phillipsi sp. nov. differs from the present material in the possession of distinctly clavate dorsolateral tubercles, from which ribs frequently arise in pairs.

Occurrence

Anisoceras arrogans is known from the uppermost Albian of Switzerland, France and Sardinia, and may also be present in southern England and Angola.

Anisoceras aff. *exoticum* Spath, 1939

Fig. 27

Compare

Anisoceras saussureanum Pictet & Campiche (*non* Pictet), 1861: 118, pl. 1 (fig. 2).
Anisoceras exoticum Spath, 1939: 555, pl. 59 (fig. 7), pl. 60 (fig. 4), pl. 63 (fig. 2), fig. 195.

Material

A single specimen, SAM–PCA3174, preserved as a composite internal mould, from Praia-Egito.

Description

The specimen represents a slightly crushed fragment of a straight shaft in which the whorl section was originally probably almost circular. Ornament comprises slightly rursiradiate main ribs between which are three to seven fine, secondary ribs, the density of which increases adorally. The fragment lacks obvious tuberculation.

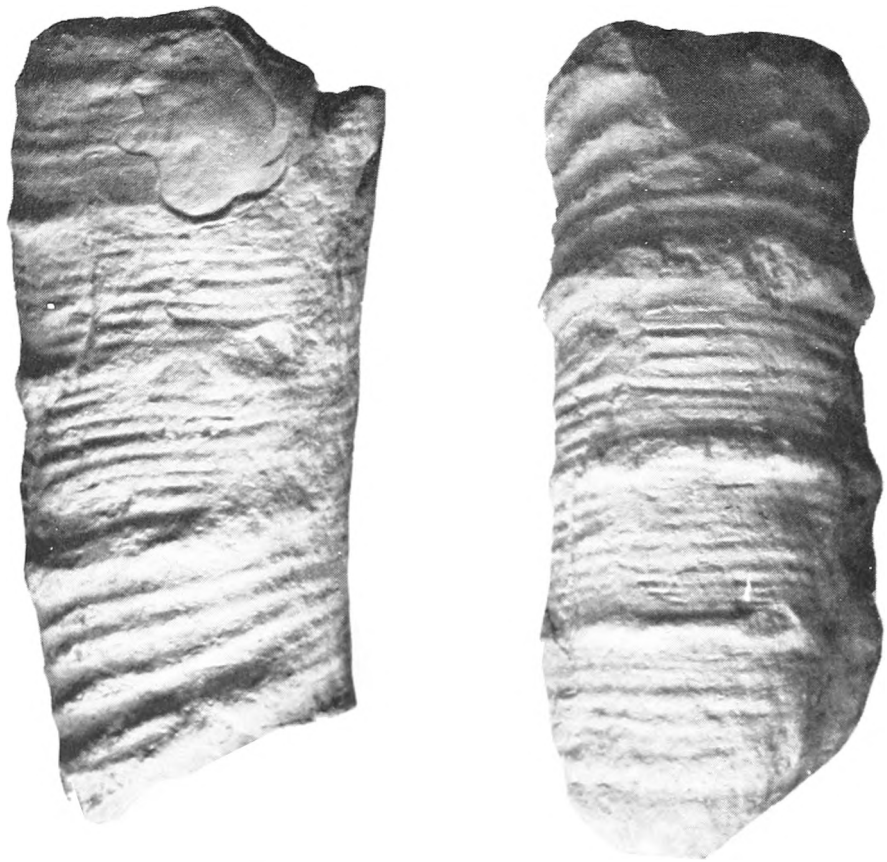

Fig. 27. *Anisoceras* aff. *exoticum* Spath. A body chamber fragment, SAM-PCA3174. ×0,75.

Discussion

The specimen is a body chamber fragment and, since ornament frequently changes drastically on the body chamber of *Anisoceras*, reference to Spath's species is somewhat tentative.

Occurrence

Anisoceras exoticum is known from England, Switzerland, Sardinia, and possibly Angola.

Anisoceras aff. *subarcuatum* Spath, 1939

Fig. 28

Compare

Anisoceras subarcuatum Spath, 1939: 560, pl. 65 (fig. 1), pl. 66 (fig. 1), fig. 198.

Material

A single specimen, SAM–PCA3143, from the *dispar* Zone at Praia-Egito.

Description

A short fragment shows affinities with Spath's species and may belong here. The whorl section is slightly compressed, oval. Ornament comprises slightly rursiradiate, strengthened, simple main ribs which bifurcate or trifurcate across the dorsum and are ornamented with dorsolateral and ventrolateral tubercles. Between main ribs are two to three, slightly weaker, somewhat irregular secondary ribs, which occasionally bifurcate across the venter. All the secondary ribs lack tubercles.

Discussion

Body chamber fragments of *Anisoceras* are notoriously difficult to identify and hence full determination of the present specimen must await further material.

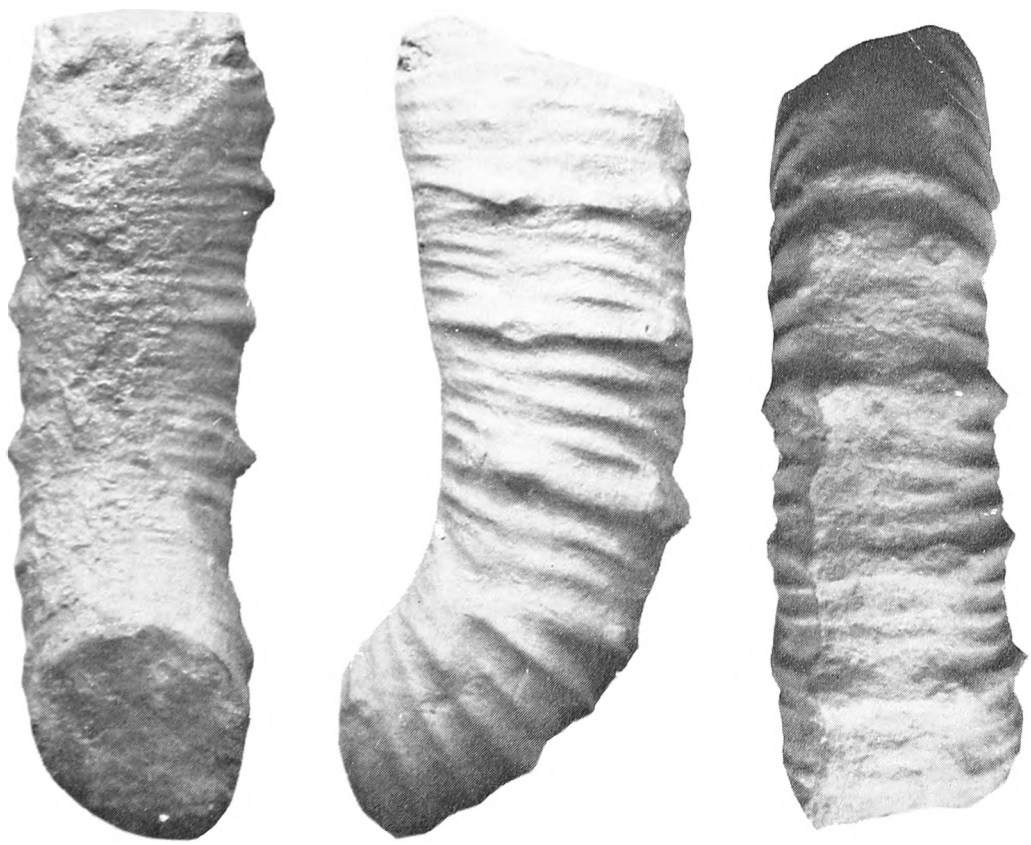

Fig. 28. *Anisoceras* aff. *subarcuatum* Spath. Ventral, lateral and dorsal views of SAM–PCA3143. ×0,75.

Occurrence

Anisoceras subarcuatum is known with certainty only from the low Upper Albian (*varicosum* and *auritus* subzones) of southern England, but may also be present in the uppermost Albian of Angola.

Anisoceras aff. *spathi* (Wiedmann, 1962)
Fig. 29

Compare
Anisoceras subarcuatum Spath, 1939: 560, pl. 63 (fig. 5 only).
Idiohamites spathi Wiedmann, 1962*a*: 188.

Material

A single fragment, SAM–PCA3223, from the upper part of the *dispar* Zone at Praia-Egito, preserved as a composite internal mould.

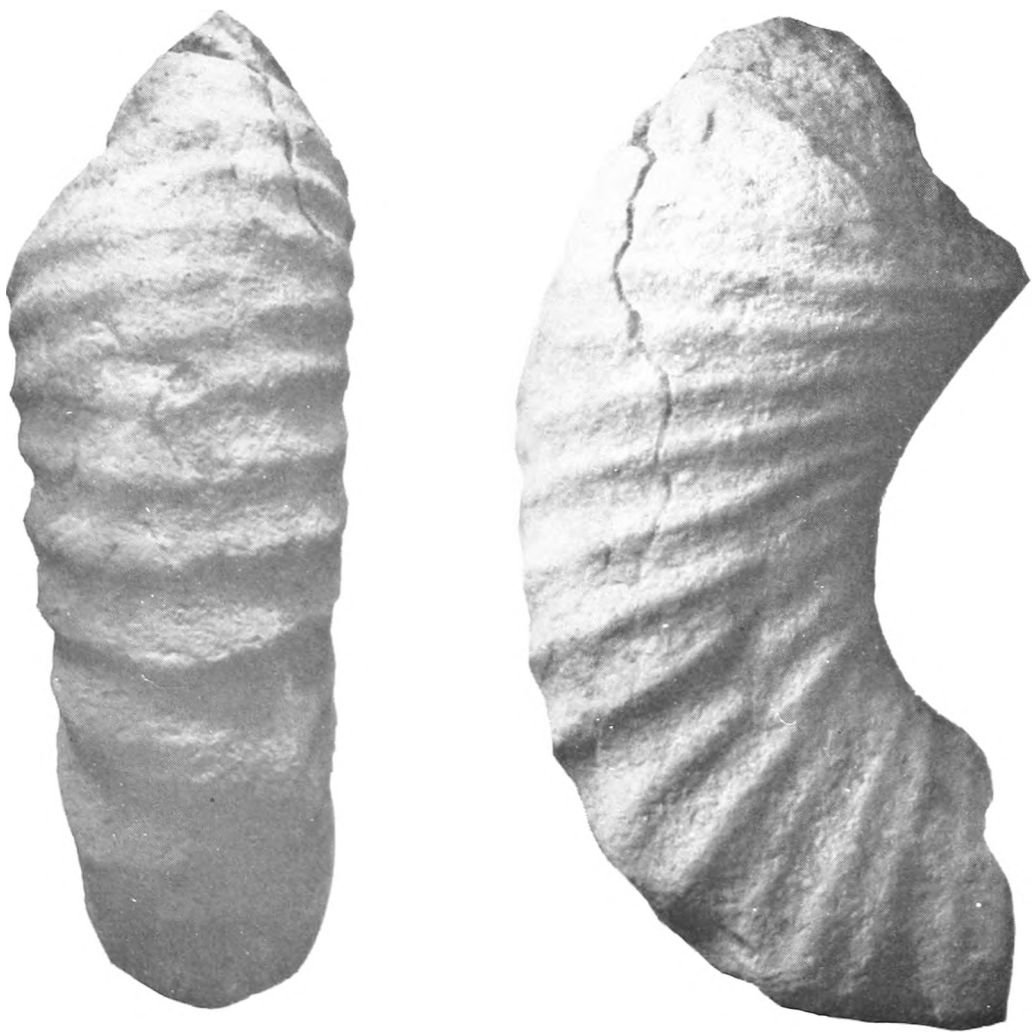

Fig. 29. *Anisoceras* aff. *spathi* (Wiedmann). Ventral and lateral views of SAM–PCA3223. ×0,75.

Description

The single fragment available represents part of the crozier. It has a compressed, elliptical whorl section with simple rursiradiate ribs. On the adoral portion of the fragment all ribs are relatively fine, of even strength, and lack tuberculation. On the adapical portion, every second rib is strengthened slightly and bears weak ventrolateral tubercles.

Discussion

The absence of lateral or dorsolateral tubercles led Wiedmann (1962*a*) to assign the present species to *Idiohamites*. However, the holotype is a body-chamber fragment which merely shows the radical change in ornament on the body chamber displayed by many *Anisoceras* species.

Occurrence

Anisoceras spathi is known from the low Upper Albian of southern England and Spain, and may be present in the *dispar* Zone of Angola.

Anisoceras sp. indet.

Fig. 14F

Material

A single, crushed fragment, SAM–PCA3220, from Praia-Egito, preserved as a composite internal mould.

Description

Only the greater part of one flank, one row of ventrolateral tubercles and much of the venter of the specimen concerned is preserved.

Rather fine (?looped) ribs on the flanks are slightly narrower than the interspaces, with at least 10 in a distance equal to the whorl height. The flank ribs join the ventrolateral clavi in pairs whereas, across the venter, the ventrolateral tubercles are connected by 2–3 ribs so that for 16 flank ribs, there are 20 ribs across the venter. The whorl section gives the appearance of having been strongly depressed.

Discussion

The specimen under discussion is too poorly preserved for specific identification, but may be regarded as belonging to the *plicatile-haasi* plexus.

Occurrence

Upper Albian, *dispar* Zone, Praia-Egito.

Genus *Idiohamites* Spath, 1925

Type species *Hamites tuberculatus* J. Sowerby, 1818

Discussion

Wiedmann (1962*a*) separated *Idiohamites* from *Anisoceras* because the former was considered to have the early whorls coiled in a helix, whereas in *Anisoceras* the juvenile whorls were considered to be planispirally coiled. The differences are not, however, so clear cut, since *Anisoceras* of the type referred to *A. raynaudi* (Boule, Lemoine & Thévenin) by Förster (1975) (= *Anisoceras saussureanum quadrifasciatum* Klinger) from the low Upper Albian of Catuane, Mozambique, and now in the South African Museum, show the early whorls to be coiled in an open helix up to 20 cm high. The straight final shafts of this species are figured by Förster (1975, pl. 4 (fig. 8)). Moreover, Matsumoto (1959, pl. 28 (fig. 1), pl. 29 (fig. 2)) has also figured an *Anisoceras* in which the early growth stages are helically coiled.

Nor is the presence or absence of lateral tubercles a diagnostic feature since some *Anisoceras*, e.g. *A. auberti* (Pervinquière) and *A. gracile* Renz, lack them. Moreover, Renz (1968) has recently figured a number of specimens which he considers transitional between *Idiohamites* and *Anisoceras* in this respect (cf. pl. 12 (figs 7–8), pl. 13 (figs 3, 6)). In addition both genera show a suture line with a fairly shallow, bifid external lobe (E), an asymmetrically bifid first lateral saddle (E/L), a bifid first lateral lobe (L) which is deeper than the external lobe, and a second lateral saddle (L/U) which is bifid, and a bifid second lateral lobe (U) which is almost as deep as the first. Clearly the two genera are very closely related although, at present, the typically smaller size, almost complete absence at any growth stage of looped flank ribs, and the helically coiled juvenile whorls, are considered to be sufficient for the generic separation of *Idiohamites* from *Anisoceras*.

Idiohamites dorsetensis Spath, 1926

Figs 30, 31G

Anisoceras alternatus Pictet & Campiche (*non* Mantell), 1861: 71, pl. 51 (figs 1, 3–4).
Idiohamites dorsetensis Spath, 1926*b*: 432; 1939: 596, pl. 62 (figs 2–3), pl. 63 (figs 1, 9, 15), pl. 65 (fig. 2), fig. 215. Renz, 1968: 70, pl. 11 (figs 39–40), pl. 12 (figs 3–4), figs 25a–d, f, 26a–d.
? *Idiohamites* aff. *turgidus robustus* Spath, Renz, 1968: 72, pl. 11 (figs 33–37), figs 25k–l, 26f–h.
? *Idiohamites elegantulus laticostatus* Renz, 1968: 73, pl. 11 (figs 38, 41–42), pl. 12 (figs 1–2), figs 25m, 26i–m.

Material

Three specimens in the South African Museum, SAM–PCA4803 and two unnumbered fragments, retaining recrystallized test, together with USNMNH 236951, preserved as a composite internal mould from Porto Amboim, and a single specimen from Cabo Ledo, SAM–PCA5469.

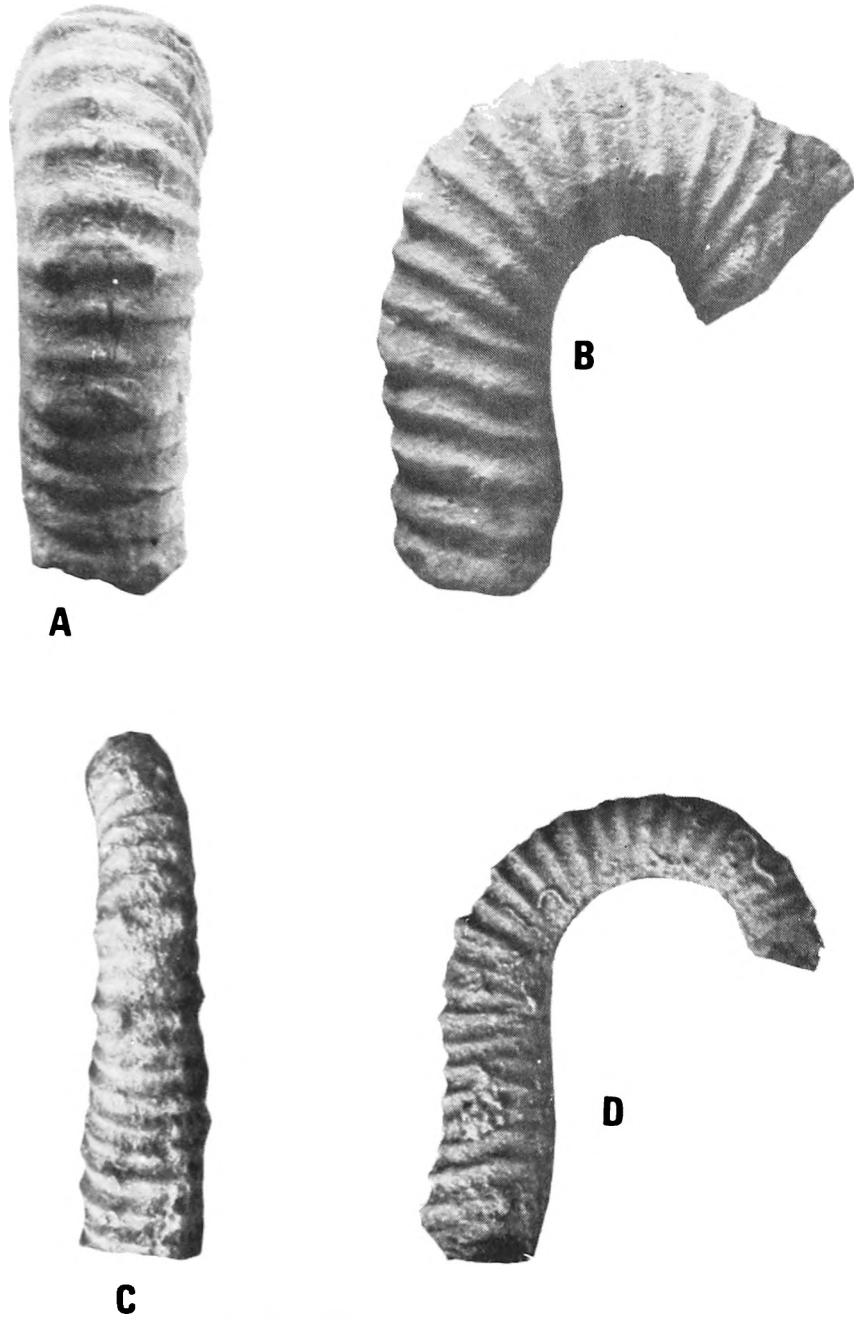

Fig. 30. A–D. *Idiohamites dorsetensis* Spath. A–B. Ventral and lateral views of SAM-PCA4803. C–D. Ventral and lateral views of SAM-PCA5469. ×1.

Description

All the fragments show the shell to be loosely coiled in a single plane, with an elliptical, compressed whorl section. Ornament comprises simple, strong, slightly prorsiradiate ribs, of which there are four to five in a distance equal to the whorl height. Every second or third (or occasionally adjacent) rib bears very small, sharp, pointed lateral tubercles and more prominent ventrolateral spines. At small growth stages, tubercles are connected across the venter by simple ribs but, on the mature body chamber, they may be weakly looped.

Discussion

Until populations of individuals are available for study, the differences between several named species of *Idiohamites* appear suspiciously small. The authors assign their material to *I. dorsetensis* because of the very close similarities to the types, and because it is the oldest available name for material of this age.

Occurrence

Idiohamites dorsetensis is known from the uppermost Albian of southern England, France, Switzerland and Angola.

Idiohamites cf. *elegantulus* Spath, 1939

Fig. 31A–D

Compare

Idiohamites elegantulus Spath, 1939: 599, fig. 216.

Material

One specimen, USNMNH 236950, a composite internal mould from Porto Amboim.

Discussion

The specimen consists of a body chamber hook with a maximum whorl height of 12 mm. There are six fine prorsiradiate ribs in a distance equal to the whorl height, the majority bearing ventral tubercles, suggesting reference to Spath's species.

Occurrence

Stoliczkaia dispar Zone of England, and possibly Angola.

Idiohamites pygmaeus sp. nov.

Fig. 31J–N

Material

Eight specimens, USNMNH 236942–49, all retaining recrystallized shell and all from Porto Amboim.

Type material

USNMNH 236942, a complete adult, is designated holotype; the remaining specimens are paratypes.

Etymology

From the Latin adjective *pygmaeus*, pygmy-like, dwarfish; derived from the Greek *pygmaios*. The *pygmaioi* were a fabulous dwarfish race of antiquity, especially in Africa; at war with the cranes, they were constantly defeated (Pliny).

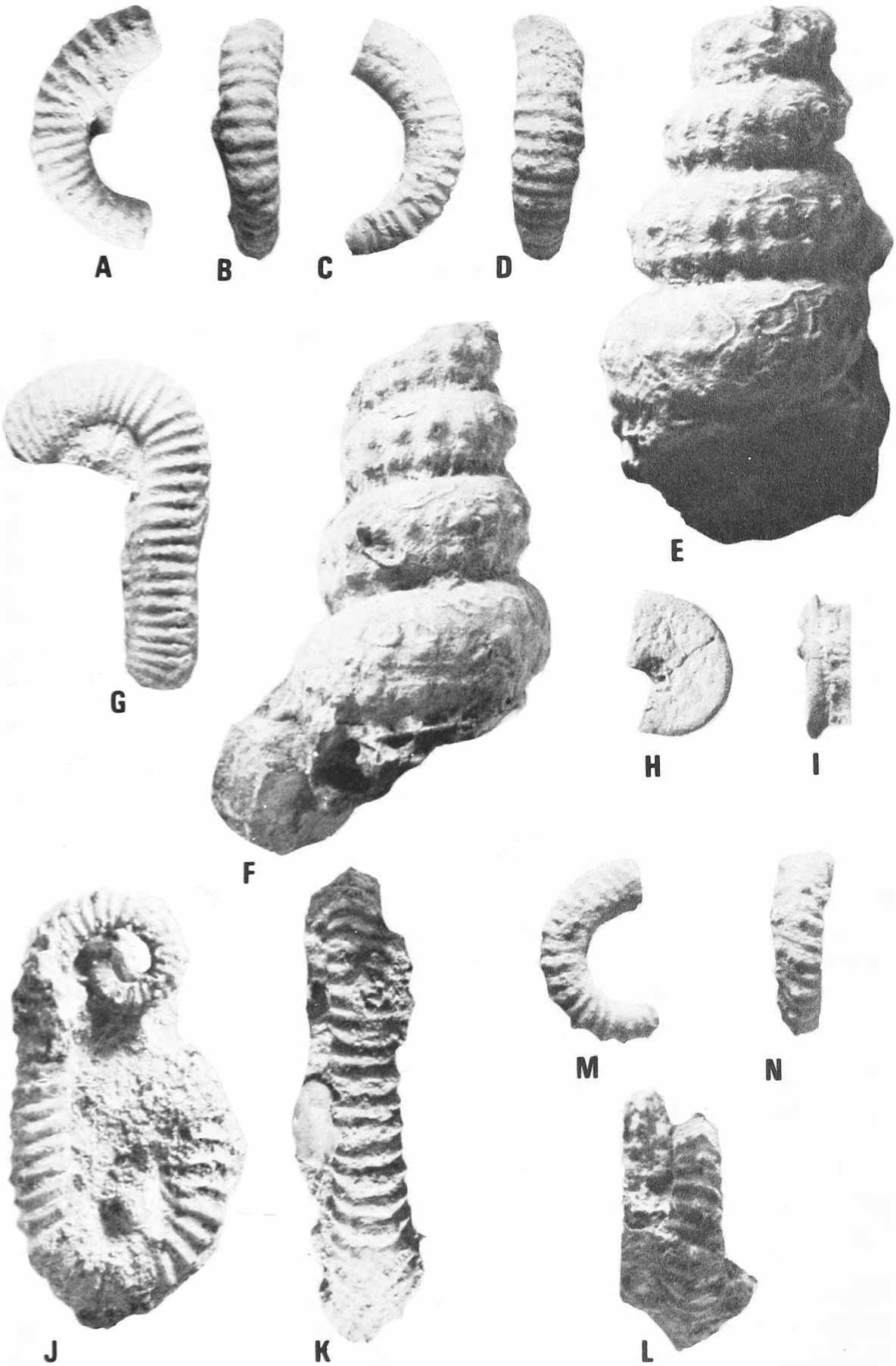

Fig. 31. A–D. *Idiohamites* cf. *elegantulus* Spath. A–B. USNMNH 236948. C–D. USNMNH 236938. E–F. *Mariella* (*Mariella*) *cirumtaeniatus* (Kossmat), USNMNH 236958. G. *Idiohamites* cf. *dorsetensis* Spath, USNMNH 236951. H–I. *Borissiakoceras* sp. nov.? aff. *reymenti* (Brunnschweiler), USNMNH 236980. J–N. *Idiohamites pygmaeus* sp. nov. J–L. USNMNH 236942. M–N. USNMNH 236943. ×1.

Diagnosis

A very small *Idiohamites* with a known maximum length of only 52 mm, characterized by helicoid early whorls with three quadrituberculate rursiradiate ribs in a distance equal to the whorl height, a straight shaft with four prorsiradiate ribs in a distance equal to the whorl height and ribbing tending to be rectiradiate at the aperture.

Description

Shell small, initially coiled in a low, open helical spire, straightening in maturity before recurving on the body chamber to form a crozier.

Earliest whorls ornamented with rather robust ribs, narrower than the interspaces and with three in a distance equal to the whorl height, which cross the venter obliquely so that the four rows of tubercles on the main ribs are asymmetrically arranged. There is a regular alternation of tuberculate and non-tuberculate ribs, which, at this stage, are slightly rursiradiate. On the first straight shaft, which commences at a whorl height of 6 mm, the ribbing becomes prorsiradiate, with still only three ribs in a distance equal to the intercostal whorl height. With the uncoiling of the shell, the tuberculation is no longer asymmetrical and main ribs are ornamented with small pointed dorsolateral and ventrolateral tubercles. The rib direction changes to rectiradiate on the final shaft. In maturity, the intercostal whorl section is oval, depressed, although it is almost circular at small diameters.

Discussion

This species is characterized by its small size at maturity. *Idiohamites dorsetensis* is adult at much larger diameters, with a slightly compressed whorl section, and closer ribbing (four to six in a distance equal to the whorl height). *Idiohamites elegantulus* is even more densely ribbed (seven in a distance equal to the whorl height), also with a compressed whorl section. *Idiohamites recticostatus* Renz is a much larger species with an almost circular whorl section and four rectiradiate ribs in a distance equal to the whorl height. It closely approaches the present material, but its very much larger size (septate at 23 mm whorl height) is distinctive.

Occurrence

Uppermost Albian of Angola only.

Family **Hamitidae** Hyatt, 1900

Genus *Hamites* Parkinson, 1811

Type species *Hamites attenuatus* J. Sowerby, 1814

Discussion

Recent discussions of the family are to be found in Wiedmann & Dieni (1968) and Klinger (1976), and further discussion on the material available here is unnecessary.

Hamites virgulatus Brongniart, 1822
Figs 16F, H, 32B–C

Hamites virgulatus Brongniart (*in* Cuvier & Brongniart), 1822: pl. 0 (fig. 6).
Hamites (*Stomohamites*) *virgulatus* (Brongniart?) Pictet & Campiche, Spath, 1941: 635, pl. 71 (figs 7–10), pl. 72 (fig. 11), fig. 230 (with synonymy). Renz, 1968: 65, pl. 11 (figs 9–11), fig. 23b–d (with synonymy).
Hamites (*Stomohamites*) *subvirgulatus* Spath, 1941: 645, fig. 234. Renz, 1968: 66, pl. 11 (figs 13–14), figs 23e, 24a (with synonymy).
Stomohamites brongniarti Breistroffer, 1947: 77.
Hamites (*Hamites*) *virgulatus* Brongniart, Wiedmann & Dieni, 1968: 53, pl. 5 (figs 1–2, 10), pl. 7 (figs 1–2), figs 21–27. Klinger, 1976: 60, pl. 23 (figs 4–5, 8), figs 8 l,n–o, 11i (with synonymy).
Hamites venetzianus Pictet (*in* Pictet & Roux), 1847: 134, pl. 14 (fig. 6).
Hamites (*Stomohamites*) *venetzianus* Pictet, Spath, 1941: 638, pl. 71 (figs 11–13), fig. 231. Renz, 1968: 67, pl. 11 (figs 15–16), figs 23f, 24b (with synonymy).

Material

Ten composite internal moulds, SAM–PCA2959, 2963–64, 2966, 2971, 3118, 3157–58, and 3371 from the upper part of the *dispar* Zone at Praia-Egito, three fragments retaining recrystallized tests from Porto Amboim, USNMNH 236955–7, and SAM–PCA4603 from Cabo Ledo.

Description

The whorl section is elliptical compressed, with three to six prorsiradiate ribs in a distance equal to the whorl height. The ribs are effaced across the dorsum.

Discussion

The writers follow Wiedmann & Dieni (1968) in regarding *H. brongniarti*, *H. venetzianus*, and *H. subvirgulatus* as synonyms of *H. virgulatus*, although there may be some justification for retaining *venetzianus* at the varietal level for those variants in which the ribs are as thick as, or thicker than, the interspaces.

Hamites duplicatus Pictet & Campiche, 1861
Figs 16D, 32A

Hamites virgulatus Pictet (*non* Brongniart) (*in* Pictet & Roux), 1847: 391, pl. 14 (figs 7, 9 only).
Hamites duplicatus Pictet & Campiche, 1861: 98.
Hamites (*Stomohamites*) *duplicatus* Pictet & Campiche, Spath, 1941: 640, pl. 72 (figs 12–16), fig. 232. Renz, 1968: 68, pl. 11 (figs 19–21), fig. 23h–k.

Material

A single composite internal mould from Praia-Egito, SAM–PCA2955.

Description

The whorl section is oval, compressed, with a somewhat flattened dorsum. Ornament comprises fine, rursiradiate ribs, seven in a distance equal to the whorl height, which are very weak across the dorsum.

Discussion

The writers are not convinced by Wiedmann & Dieni's (1968) argument for the inclusion of *H. duplicatus* in the synonymy of *H. virgulatus* and, for the present, maintain it as distinct.

Occurrence

Hamites duplicatus is known from the Upper Albian of England, France, Switzerland, and Angola.

Superfamily TURRILITACEAE Meek, 1876

Family **Turrilitidae** Meek, 1876

Subfamily Turrilitinae Meek, 1876

Genus *Mariella* Nowak, 1916

Type species *Turrilites bergeri* Brongniart, 1822

Discussion

Kennedy (1971) and Klinger & Kennedy (1978) have recently provided a comprehensive discussion of the taxonomic standing of *Mariella*, including in it three subgenera, viz. *M.* (*Mariella*), *M.* (*Plesioturrilites*) and *M.* (*Wintonia*).

As noted by Clark (1965: 49), however, *M.* (*Wintonia*) and *M.* (*Plesioturrilites*) differ only in that the former has an early, straight shaft which then passes into the helical coiling of *M.* (*Plesioturrilites*), although specimens of *M.* (*Wintonia*) *graysonensis* (Adkins), the only known species, cannot be distinguished from *M.* (*Plesioturrilites*) *bosquensis* (Adkins) in the absence of this straight shaft. Klinger & Kennedy (1978) suggest the 'shaft' is an artefact of preservation and treat *Plesioturrilites* as a synonym of *Wintonia*.

Mariella (*Mariella*) *circumtaeniatus* (Kossmat, 1895)

Figs 31E–F, 39H

Turrilites gresslyi Stoliczka (*non* Pictet & Campiche), 1865: 186, pl. 87 (figs 1–5, ? *non* 2).
Turrilites circumtaeniatus Kossmat, 1895: 141, pl. 18 (figs 4–5); Boule, Lemoine & Thévenin, 1907: 57, pl. 13 (fig. 4).
Non Turrilites circumtaeniatus Scott (*non* Kossmat), 1926: 145, pl. 1 (figs 10–11) (= *M. worthensis*).
Paraturrilites aff. *circumtaeniatus* (Kossmat) Collignon, 1963: 46, pl. 258 (fig. 1120).
Non Turrilites circumtaeniatus Kossmat, Woods, 1917: 11, pl. 5 (figs 2–3) (= *M. thomsoni* Henderson).

Material

A single specimen USNMNH 236958, with recrystallized shell preserved, from Porto Amboim.

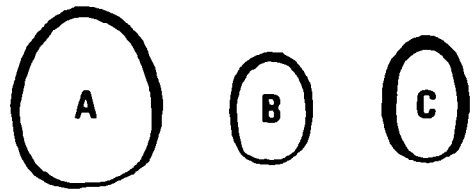

Fig. 32. A. *Hamites duplicatus* Pictet & Campiche. Whorl section of SAM–PCA2955. B–C. *Hamites virgulatus* Brongniart. Whorl sections. B. SAM–PCA2959. C. SAM–PCA3158. ×1.

Description

Coiling sinistral, with a very acute apical angle (approximately 20°). Flanks rounded intercostally, with two rows of prominent, rounded tubercles and a third hidden in the spiral seam. There are nine to eleven tubercles per half-whorl situated on very weak, slightly oblique ribs. The upper row of tubercles is situated slightly above mid-flank, and the central row midway between the upper row and the lower spiral suture. Ribbing is conspicuous only on the area between the upper row of tubercles and the upper spiral suture, where rather fine ribs commonly connect in pairs to the upper row of tubercles, frequently with an intercalated rib between tubercles.

Discussion

Amongst contemporaneous species of *Mariella*, *M.* (*M.*) *cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 181a–b, 182d–e) approaches the present species most closely. It differs in its much larger spiral angle (30° or more) and in lacking the fine looped ribs on the upper, outer face of the whorls.

M. (*Mariella*) *nobilis* (Jukes-Browne) (Spath 1937: 520, pl. 58 (figs 10–11), fig. 182) differs in having more prominent single ribs and subdued tuberculation.

M. (*Mariella*) *bergeri* (Brongniart) (1822: 395, pl. 7 (fig. 3)), of which *M.* (*M.*) *miliaris* (Pictet & Campiche) (1861: 136, pl. 51 (fig. 5)) may be only an extreme variant, has four rows of tubercles exposed on the outer face of the whorls.

M. (*Mariella*) *dubourdieui* (Collignon) (1963: 46, pl. 285 (fig. 1121)) resembles *M.* (*M.*) *circumtaeniatus* in the possession of looped ribs, but also has four rows of tubercles exposed on the outer face of the whorls.

M. (*Mariella*) *worthensis* (Adkins & Winton) (1920: 44, pl. 7 (figs 10–11, 13)) from the uppermost Albian Pawpaw Formation of Texas, closely resembles *M.* (*M.*) *circumtaeniatus*, but appears to lack the fine looped ribs of Kossmat's species, as does *M.* (*M.*) *hillyi* (Dubourdieu) (1953: 46, pl. 4 (figs 1–3)).

Occurrence

This species is known from the uppermost Albian of India, Madagascar, Zululand, Angola, and New Zealand.

Mariella (*Mariella*) *nobilis* (Jukes-Browne, 1877)
Fig. 33A–B

Turrilites intermedius Pictet & Campiche, 1861: 127, pl. 57 (fig. 15 only).
Turrilites escherianus Pictet & Campiche (*non* Pictet), 1861: 130, pl. 56 (figs 6–8 only).
Turrilites nobilis Jukes-Browne, 1877: 493, pl. 21 (fig. 1).
Mariella nobilis (Jukes-Browne) Breistroffer (*in* Besairie), 1936: 147. Spath, 1937: 520, pl. 58 (figs 10–11), fig. 182a–c. Breistroffer, 1940: 147. Clark, 1965: 40, pl. 10 (figs 2–4), pl. 11 (figs 4–5). Renz, 1968: 89, pl. 17 (figs 28, 40), figs 31l, 32k.
Mariella nobilis var. *cruciana* Breistroffer (*in* Besairie), 1936: 148. Spath, 1937: 521. Breistroffer, 1940: 148. Renz, 1968: 90, pl. 17 (fig. 34), figs 31b, 32d.
Mariella aff. nobilis (Jukes-Browne) Spath, 1937: 520, pl. 58 (fig. 21).
Paraturrilites nobilis (Jukes-Browne) Breistroffer, 1947: 60; 1953: 1350.
Paraturrilites nobilis var. *cruciana* (Breistroffer) Breistroffer, 1947: 60.
Paraturrilites nobilis var. *brownei* Breistroffer, 1947: 96.
Mariella nobilis brownei (Breistroffer) Renz, 1968: 90, pl. 17 (figs 35–36, 38–39), figs 31i, 32e.

Material

Two specimens, SAM–6531 (from an unknown location on the Angolan littoral), and a single fragment in the Washburn collection, USNMNH 237019 from Porto Amboim.

Description

These two fragments of *M.* (*Mariella*) bear prominent oblique ribs, narrower than the interspaces, estimated at totalling twenty-six per whorl. They are ornamented by three rows of weak tubercles; the tubercles of the adoral row are weakly clavate, whereas those of the other two rows are weakly rounded.

Discussion

M. (*Mariella*) *nobilis* var. *cruciana* Breistroffer (*in* Besairie 1936: 148) was separated from the typical form by its denser ribbing (30 ribs per whorl, as against 26–28) and more prominent tubercles. *M.* (*Mariella*) *nobilis* var. *brownei* Breistroffer (1947: 96) was distinguished by its sparser ribbing (24–26 per whorl) and weaker tuberculation.

As noted by Spath (1937: 521), *M.* (*Mariella*) *escheriana* (Pictet) (*in* Pictet & Roux 1847: 154, pl. 15 (fig. 11)) closely resembles the present species and there even appear to be intermediates. Pictet's species was distinguished by its denser ribbing (35–40 ribs per whorl), and flattened flanks with only two rows of tubercles.

The closest species to *M.* (*M.*) *nobilis* is *M.* (*M.*) *cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 181a–b, 182d–e) from the late Albian of western Europe. Not only are they strictly contemporaneous, but Spath (1937: 519) also admits to the presence of intermediates. Typically, however, it differs in its sparser ribbing and more prominent tubercles.

M. (*Mariella*) *worthensis* (Adkins & Winton) (1920: 44, pl. 7 (figs 10–11, 13)) is very close to *M.* (*M.*) *nobilis* but is generally more coarsely ribbed (14–28 ribs per whorl) with four rows of tubercles per whorl.

M. (*Mariella*) *gresslyi*, *M.* (*M.*) *cantabrigiensis*, *M.* (*M.*) *nobilis*, *M.* (*M.*) *escheriana*, *M.* (*M.*) *worthensis* and *M.* (*M.*) *hillyi* are a contemporaneous group of very closely allied species whose intraspecific variation clearly needs documenting before the true taxonomic status of the species involved can be resolved.

Occurrence

M. (*Mariella*) *nobilis* is known only from the upper Upper Albian of southern England, Texas, and Angola.

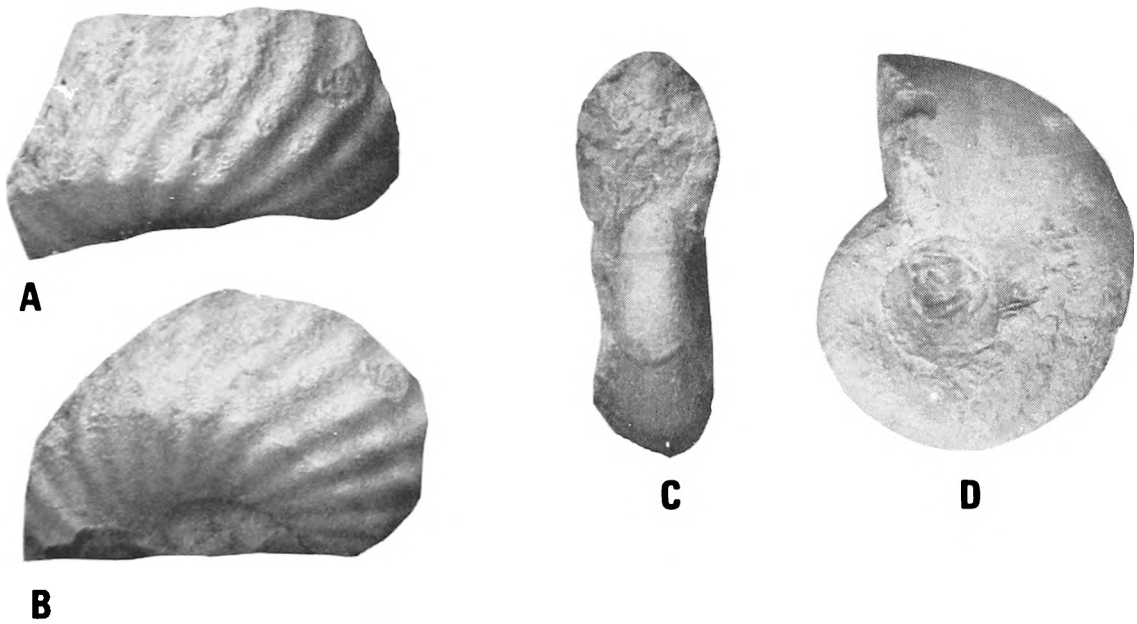

Fig. 33. A–B. *Mariella* (*Mariella*) *nobilis* (Jukes-Browne), SAM–6531. C–D. *Puzosia* (*Puzosia*) sp., SAM–6407. ×1.

Mariella gresslyi (Pictet & Campiche, 1861)

Fig. 16G

Turrilites gresslyi Pictet & Campiche, 1861: 132, pl. 57 (figs 11–13). Neumayr, 1875*a*: 901. Renevier, 1890: 339. Pervinquière, 1910: 54. Böse, 1923: 147. Diener, 1925: 83. Collignon, 1929: 65, pl. 1 (fig. 15).

Turrilitoides (?) *gresslyi* (Pictet & Campiche) Breistroffer, 1936: 65.

Mariella gresslyi (Pictet & Campiche) Spath, 1937: 516, pl. 58 (figs 3–4), fig. 180. Breistroffer, 1940: 149. Renz, 1968: 89, pl. 17 (figs 30a–b, 32–33), figs 31c, 32a–b.

Paraturrilites gresslyi (Pictet & Campiche) Breistroffer, 1947: 60. Collignon, 1963: 47, pl. 258 (fig. 1122).

? *Turrilites gresslyi* Pictet & Campiche, Boule, Lemoine & Thévenin, 1907: 39, pl. 6 (fig. 2).

Mariella gresslyi bifurcata Renz, 1968: 89, pl. 17 (fig. 42a–b), figs 31e, 32c.

? *Turrilites cantabrigiensis* Jukes-Browne, 1877: 493.

? *Mariella cantabrigiensis* (Jukes-Browne) Spath, 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 181a–b, 182d–e.

Material

A single specimen, SAM–PCA3133, from low down in the coastal cliffs immediately north of the estuary at Praia-Egito, and thus from a level below the main *Stoliczkaia* occurrence.

Description

The specimen is rather poorly preserved, but retains recrystallized test. The shell is sinistrally coiled, with a moderately large apical angle. The outer faces of the whorls are gently convex intercostally, and angular, polygonal costally. Three rows of tubercles are visible on rather oblique ribs. The upper row of tubercles are conical whereas the middle row is distinctly clavate. The nature of the tubercles of the lower row was difficult to discern, but they, too, appear to be clavate.

Discussion

The features of the present specimen are those of *M. gresslyi* and the authors have no hesitation in assigning the Angolan example to this species.

Mariella cantabrigiensis (Jukes-Browne) (Spath, 1937: 518, pl. 57 (fig. 36), pl. 58 (figs 1–2), figs 180h, 181a–b, 182d–e) closely approaches *M. gresslyi*, but was said to differ in having all tubercles rounded, whereas the lower two rows are clavate in *M. gresslyi*. However, the two species are strictly contemporaneous and occur side by side, whilst Spath (1937) admits to transitions between the two. Population studies may show *M. cantabrigiensis* to be an intraspecific variant of *M. gresslyi*.

Mariella gresslyi bifurcata Renz (1968: 89, pl. 17 (fig. 42), figs 31e, 32c) is based on a single specimen which shows the ribs on the base of the spire bifurcating from the lowest (adoral) row of tubercles.

Mariella nobilis (Jukes-Browne) (Spath 1937: 520, pl. 58 (figs 10–11), figs 181c, 182a–c) differs from the present species in having very subdued tubercles, with ribs dominant.

Occurrence

Mariella gresslyi is currently known from southern England, France, Switzerland, Algeria, Angola, Zululand, and Madagascar.

Mariella cf. *oehlerti* (Pervinquière, 1910)

Figs 3H, 34

Compare

Turrilites gresslyi Boule, Lemoine & Thévenin (*non* Pictet & Campiche), 1907: 57, pl. 13 (fig. 2). Collignon, 1929: 65, pl. 6 (fig. 15).

? Turrilites cf. *gresslyi* Spath (*non* Pictet & Campiche), 1921: 289.

Turrilites oehlerti Pervinquière, 1910: 53, pl. 5 (figs 14–17). Collignon, 1929: 65, pl. 6 (figs 16–17); 1964: 15, pl. 320 (figs 1398–1399).
? *Mariella malgachensis* Breistroffer, 1940: 79.
? *Turrilites bergeri* Choffat (*non* Brongniart), 1903: 15, pl. 1 (figs 4–6).
? *Mariella bergeri* var. *conduciensis* Breistroffer, 1940: 149.
Mariella (*Mariella*) *oehlerti* (Pervinquière), Förster 1975: 190, pl. 7 (figs 7–8), fig. 52. Klinger & Kennedy 1978: 31, pl. 3 (fig. E), pl. 4 (fig. E), pl. 6 (figs H, N), pl. 7 (fig. G), pl. 8 (figs G–H), figs 1a–b, 7b, d, 8g.

Material

A single composite internal mould, SAM–PCA4798, from the Quissama Ridge at Cabo Ledo.

Fig. 34. *Mariella* (*Mariella*) cf. *oehlerti* (Pervinquière), SAM–PCA4798. ×1.

Description

The shell is a high-spired, sinistrally-coiled turriliticone, with a spiral angle of about 22°. The whorls are just touching with the outer face gently convex, and somewhat flattened. The adapical shoulder is abrupt and subangular (Fig. 3H) whilst the adoral shoulder is evenly rounded. The outer face is ornamented with

four rows of prominent tubercles arranged on weak, oblique ribs, of which there are about thirty per whorl. The upper row of tubercles is the most prominent, and they are slightly bullate and situated slightly above mid-whorl. The tubercles of the two middle rows are conical and are separated by a weak spiral groove. The tubercles of the lower row are the smallest and are situated in the whorl seam. On the adoral face of the final whorl there are prominent ribs. The spacing of the tubercles is subequal on the penultimate whorl of the present specimen, but on the final whorl the middle two rows are distinctly closer together than the others.

Discussion

At present the species *M. gresslyi*—*M. cantabrigiensis*—*M. oehlerti*—*M. circumtaeniatus* are not well differentiated.

Mariella gresslyi (Pictet & Campiche) (1861: 132, pl. 57 (figs 11–13)) is typically an uppermost Albian species which differs from the present form and *M. oehlerti* in that the rows of tubercles are typically clavate. However, Spath (1937: 519) records passage form between *M. gresslyi* and the contemporaneous *M. cantabrigiensis* (Jukes-Browne) (Spath 1937: 518, pl. 51 (fig. 36), pl. 58 (figs 1–2)), the latter distinguished from Pictet & Campiche's species in having rounded tubercles of equal size, and thus very close to *M. oehlerti* and the Angolan material. Since, however, the present specimen is much larger than known material of *M. gresslyi* and *M. cantabrigiensis*, differences may be due to a comparison of different ontogenetic stages. Clearly, however, this problem cannot be resolved in the present paper.

Mariella circumtaeniatus has only three rows of tubercles, generally with conspicuous looping of the ribs on the adapical shoulder of the whorls.

Mariella dorsetensis (Spath) (= *Turrilites bergeri* Sharpe (*non* Brongniart) 1857: 65, pl. 26 (fig. 11 only)) differs from the present material in having fewer ribs per whorl and in having the third and fourth (adoral) rows of tubercles approximated, whilst ribs are absent on the base of the spire.

Mariella gallienii (Boule, Lemoine & Thévenin) (1906: 60, pl. 14 (figs 5–6)) differs from the present specimen in that the tubercles of the four rows are distinctly bullate.

Occurrence

Mariella oehlerti is known from the Lower Cenomanian of Algeria, Madagascar, Mozambique, Zululand, and possibly Japan, and possibly the uppermost Albian of Angola and Switzerland.

Suborder AMMONITINA Hyatt, 1889

Superfamily HOPLITACEAE Douvillé, 1890

Family **Desmoceratidae** Zittel, 1895

Subfamily Puzosiinae Spath, 1922

Genus *Puzosia* Bayle, 1878

Subgenus *Puzosia* Bayle, 1878

Type species *Ammonites planulatus* J. de C. Sowerby, 1827

Puzosia (*Puzosia*) sp.
Fig. 33C–D

Material

A single crushed specimen, SAM–6407, retaining recrystallized shell, from Porto Amboim.

Description

The shell is compressed, moderately involute, with about 60 per cent of the preceding whorl covered by the outer whorl. The umbilicus is moderately narrow (22% of the diameter), with steep umbilical walls and evenly rounded umbilical shoulders. The whorl section is oval, compressed ($^{W}/_{H}$ = 0,83) with an evenly rounded venter. There are an estimated five constrictions per half-whorl, preceded by a strong ventral rib. Flank and venter also bear faint, ill-preserved, fine ribs.

Measurements

No.	D	H	W	$^{W}/_{H}$	U
SAM–6407	37	18(49)	15(41)	0,83	±8(22)

Discussion

The specimen cannot be usefully compared with the large number of late Albian puzosiids known, although if the estimated number of constrictions is correct, it must approach forms such as *P. crebrisulcata* Kossmat (1898: 116, pl. 17 (fig. 4), pl. 18 (fig. 2) and *P. malandiandrensis* Collignon (1963: 66, pl. 265 (fig. 1156)).

Puzosia (*Puzosia*) cf. *sharpei* Spath, 1923
Fig. 35

Compare

Ammonites planulatus Sharpe (*non* Sowerby), 1854: 29, pl. 12 (fig. 4 only).

Puzosia sharpei Spath, 1923: 46, pl. 1 (figs 11–12), fig. 11b. Renz, 1968: 21, pl. 1 (figs 4, 8), figs 6b, 7e (with synonymy).

Material

A single fragment, SAM–PCA3141, preserved as an internal mould, from the *dispar* Zone of Praia-Egito.

Description

The single specimen is a fragment of about one-quarter whorl. The shell was moderately evolute, with a fairly wide, shallow umbilicus and evenly rounded umbilical shoulders. The flanks are broad, subparallel and only slightly convex, with a broadly rounded venter. There are two deep constrictions on the fragment, separated along the venter by a distance slightly greater than the whorl height. The constrictions are initially prorsiradiate, but soon recurve before flexing strongly forwards to form a chevron across the venter.

Discussion

The Angolan material differs from *P. sharpei* in that the constrictions do not show as strong a geniculation, and are therefore not as strongly falcate.

Wiedmann & Dieni (1968) included this species in the synonymy of *Puzosia provincialis* (Parona & Bonarelli), a lower Middle Albian species. The material figured by these authors (1968) as *P. provincialis* shows relict lappet structures and are, therefore, microconchs. The holotype of *P. sharpei*, on the other hand, is still septate at 83 mm diameter and appears to be a macroconch. Consequently, the authors regard the inclusion of *P. sharpei* into the synonymy of *P. provincialis* as premature, and prefer to maintain Spath's species as distinct, for the time being.

Occurrence

Puzosia sharpei is known with certainty only from southern England, France, Switzerland, and possibly Angola, where it is typical of the *dispar* Zone.

Fig. 35. *Puzosia* (*Puzosia*) cf. *sharpei* Spath. Lateral and ventral views of SAM–PCA3141. ×1.

Fig. 36. *Desmoceras* (*Desmoceras*) *latidorsatum* (D'Orbigny). The original of D'Orbigny's (1841, pl. 80 (fig. 5)) figured specimen from the Middle Albian of France, in the D'Orbigny collection, Natural History Museum, Paris. ×1.

Subfamily Desmoceratinae Zittel, 1895

Genus *Desmoceras* Zittel, 1884

Subgenus *Desmoceras* Zittel, 1884

Type species *Ammonites latidorsatus* Michelin, 1838

Desmoceras* (*Desmoceras*) *latidorsatum perinflatum subsp. nov.

Figs 37–38, 39D–F

Desmoceras latidorsatum var. *inflata* Breistroffer, Haas, 1952: 2, figs 1, 3–10.
Desmoceras reynesianum Haas, 1952: 4, figs 2, 11–13.

Material

Twenty-one specimens, SAM–6414, SAM–PCA2931, 2934, 2968, 3170 and 3172 from Egito, preserved as composite internal moulds, and USNMNH 236961–75 from Porto Amboim with recrystallized shell generally preserved.

Type material

USNMNH 236970 from Porto Amboim is designated holotype; the remaining specimens are paratypes.

Etymology

From the Latin, *per*—exceedingly, very much, *inflatus*—swollen; applying to the strongly inflated shell form.

Diagnosis

A rather small, late Albian (*dispar* Zone) subspecies of *D. latidorsatum* in which the majority of the population comprises strongly inflated individuals ($^{W}/_{H}$ = 1,10–1,50) which correspond to the *D. latidorsatum* var. *inflatum* of previous workers.

Description

Very involute, cadicone, with a narrow, crater-like umbilicus (16–20% of diameter). Umbilical walls steep, with gently rounded shoulders. Flanks flattened (USNMNH 236972) to strongly convex (USNMNH 236964), with maximum width just below mid-flank. Venter broadly rounded. Shell smooth,

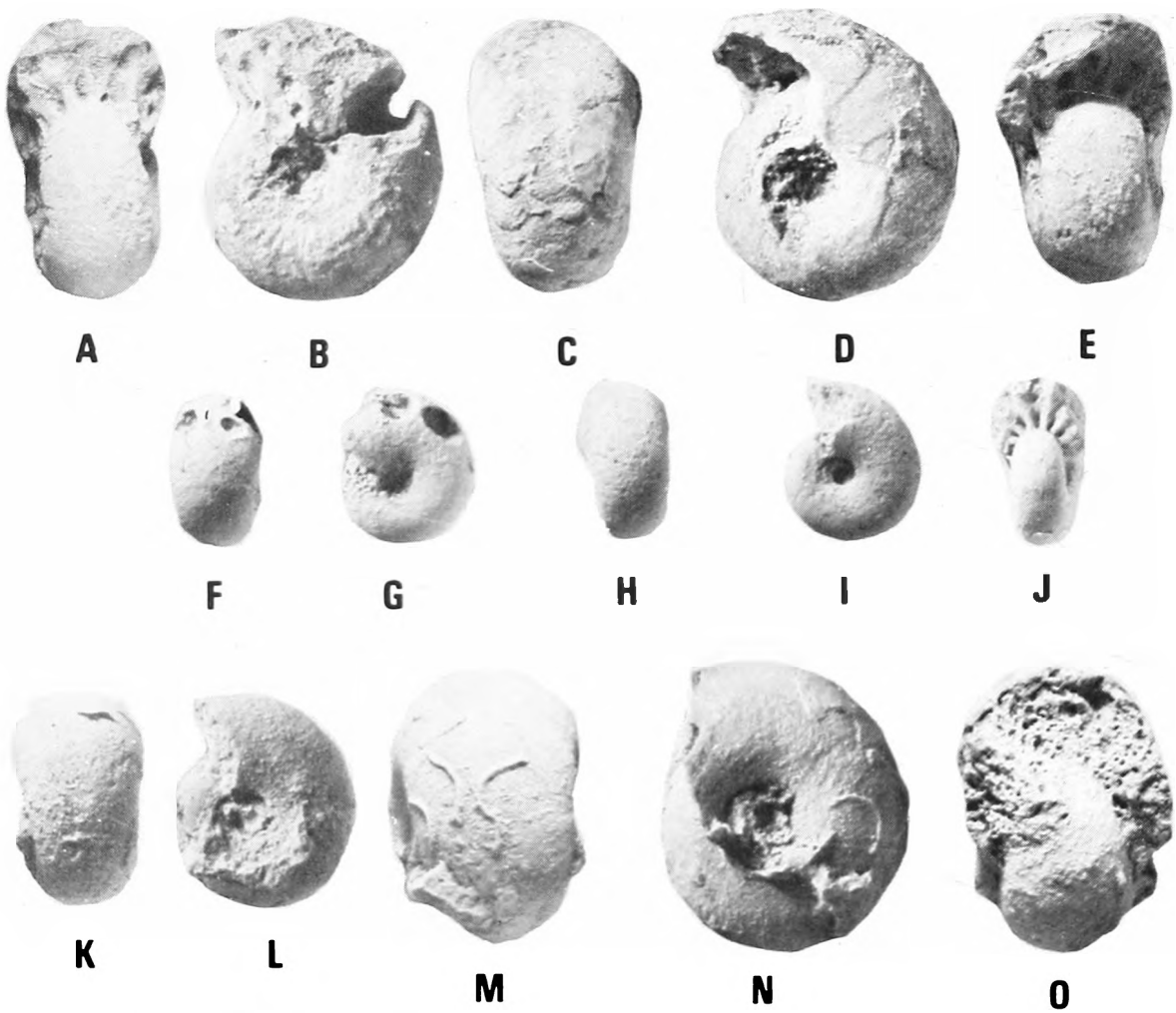

Fig. 37. *Desmoceras* (*Desmoceras*) *latidorsatum perinflatum* subsp. nov. A–B. USNMNH 236966. C–E. The holotype USNMNH 236970. F–G. USNMNH 236973. H–J. USNMNH 236768. K–L. USNMNH 236967. M–O. USNMNH 236964. ×1.

except for weak constrictions on some specimens (USNMNH 236970). Where present, constrictions begin at the umbilical seam and pass strongly forwards to the umbilical shoulder where they recurve strongly, flexing forwards again just above mid-flank to form a prominent U-shaped tongue across the venter.

Measurements

No.	D	H	W	W/H	U
USNMNH 236961	21	±9(43)	±12(57)	1,33	±4(19)
USNMNH 236962	14	7(50)	8,5(61)	1,21	2,3(16)
USNMNH 236964	27	13(48)	18,3(68)	1,41	±5(18)
USNMNH 236965	21	11,5(55)	14(67)	1,22	?
USNMNH 236966	23	9,5(41)	13(56)	1,37	±4,5(20)
USNMNH 236967	20	10,2(51)	12(60)	1,18	±4(20)
USNMNH 236968	12,3	6,2(50)	8,3(67)	1,34	±2(16)
USNMNH 236969	42	22(52)	±24(57)	1,09	±8(9)
USNMNH 236970	24	11(46)	15(63)	1,36	4,5(19)
USNMNH 236971	14,6	7,5(51)	9(62)	1,20	?
USNMNH 236972	15	6(40)	8,5(57)	1,42	2,7(18)
,,	10,5	5(48)	6,5(62)	1,30	2,0(19)
USNMNH 236973	13	±6(46)	8,1(62)	1,35	?
USNMNH 236975	±14	6,5(46)	8,2(59)	1,26	2,2(16)

Intraspecific variation

The wide range of intraspecific variation shown by *D.* (*Desmoceras*) *latidorsatum* has long been recognized (D'Orbigny 1941, Pictet (*in* Pictet & Roux) 1848, Kossmat 1897, Jacob 1908, Fallot 1910, Spath 1923, Wiedmann & Dieni 1968) and it would appear that species separation is possible only at the population level since gross intraspecific variation exceeds subtle differences between successive faunas. Consequently, the following names, which are used both at the varietal and subspecific levels by various authors, are based merely upon individuals within these populations and are of no taxonomic value: *media* (Jacob), *complanata* (Jacob), *inflata* (Breistroffer), *obesa* (Reynès), *petkovici* Breistroffer, *longesulcata* (Collignon) and *angusteumbilicata* Haas.

Jacob (1908) studied the intraspecific variation within *Desmoceras latidorsatum* from the Balme de Rencurel, a fauna contemporaneous with D'Orbigny's (1841) material (Fig. 36) from the 'Argile à *Hoplites dentatus* Sow.' of Aube, and of early Middle Albian age. Within this assemblage, Jacob (1908) recognized the typical form, as well as his varieties *media* and *complanata* which are more compressed than typical *D. latidorsatum*. In contrast, the present collection, together with that described by Haas (1952) shows that inflated variants, normally assigned to the variety *inflata* Breistroffer, form the vast majority of the populations from the *S. dispar* Zone of Angola (Fig. 38), whereas compressed

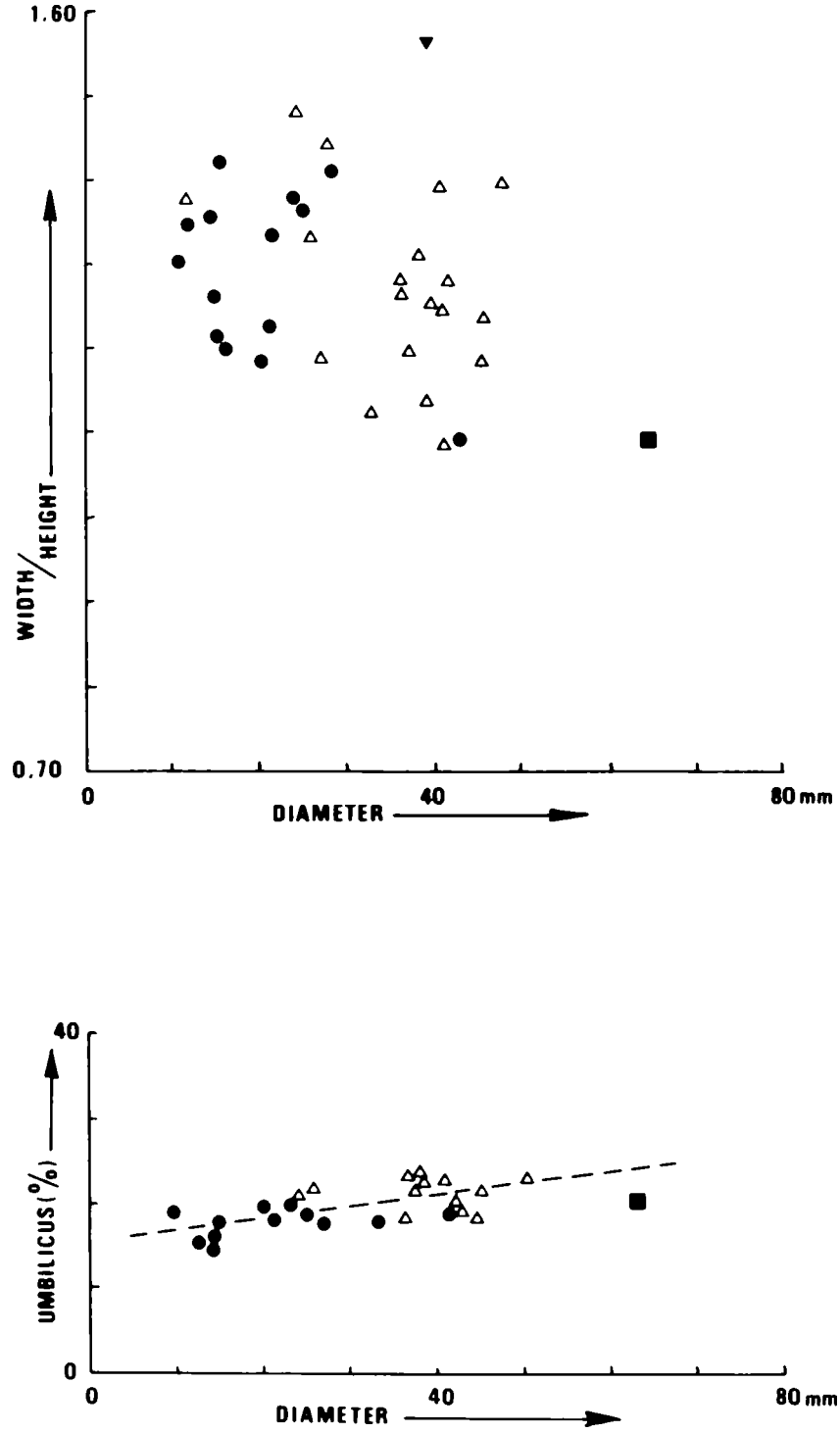

Fig. 38. Plot of inflation and umbilical ratio against diameter for *Desmoceras latidorsatum perinflatum* subsp. nov. Dots = present Angolan material; open triangles = material described by Haas (1952), and Wiedmann & Dieni (1968); black triangle = *Desmoceras reynesianum* (after Haas 1952); square = *Desmoceras latidorsatum latidorsatum* (Michelin), (after D'Orbigny 1841).

forms are entirely absent. It would seem, therefore, that there has been a genuine shift within the population structure of *D. latidorsatum* through time, from predominantly compressed individuals in the Middle Albian to predominantly inflated variants in the uppermost Albian. The observation that certain individuals throughout this range can be assigned to *Desmoceras latidorsatum* s.s. suggests that the differences are not of specific importance. Since the Angolan population comprises mainly strongly inflated individuals ($^{W}/_{H}$ = 1,10–1,50), the differences are sufficient for subspecific separation and the *entire* Angolan population (it is the *characters of the population* which define the subspecies) is assigned to *D. latidorsatum perinflatum* subsp. nov.

Desmoceras reynesianum Haas (1952: 4, figs 2, 11–13) was proposed to replace *Ammonites obesus* Reynès (*non* Stoliczka) and is characterized by its extreme inflation. The Angolan material assigned to this species, however, differs in being of uppermost Albian age and, as can be seen from Figure 38, merely represents extreme variants within the present population, and consequently Haas's (1952) material is included in the synonymy of *D. latidorsatum perinflatum* subsp. nov.

Discussion

Population studies will probably show that *D. collignoni* Breistroffer (*in* Besairie 1936: 170, pl. 16 (fig. 2), fig. 10d), *D. inane* (Stoliczka) (1865: 121, pl. 59 (figs 13–14)) and *D. chirichense* (Pervinquière) (1907: 152, pl. 6 (figs 17–20)) do not bear separation from *D. latidorsatum*. *Desmoceras barryae* Anderson (1958: 214, pl. 12 (fig. 2)) and *D. merriami* Anderson (1902: 103, pl. 6 (figs 135–138)), which was treated as a variety of *D. latidorsatum* by Breistroffer (1947: 61), are probably better referred to the subgenus *Pseudouhligella*.

Occurrence

Desmoceras latidorsatum perinflatum subsp. nov. is currently known with certainty only from Angola.

Superfamily ACANTHOCERATACEAE Hyatt, 1900

Family **Lyelliceratidae** Spath, 1921

Discussion

Wright (*in* Arkell *et al.* 1957) included the following genera within the Lyelliceratidae—*Prolyelliceras*, *Lyelliceras*, *Tegoceras*, *Neophlycticeras*, *Stoliczkaia* (with *Faraudiella* as a subgenus), *Budaiceras* and *Salaziceras*. More recently, Casey (1965) introduced the subgenus *Stoliczkaia* (*Villoutreysia*), and proposed the new genus *Paradolphia* for forms from the *S. dispar* Zone of southern England said to be transitional between *Stoliczkaia* and *Forbesiceras*. Matsumoto & Inoma (1975: 277) have also introduced the subgenus *Stoliczkaia* (*Shumarinaia*).

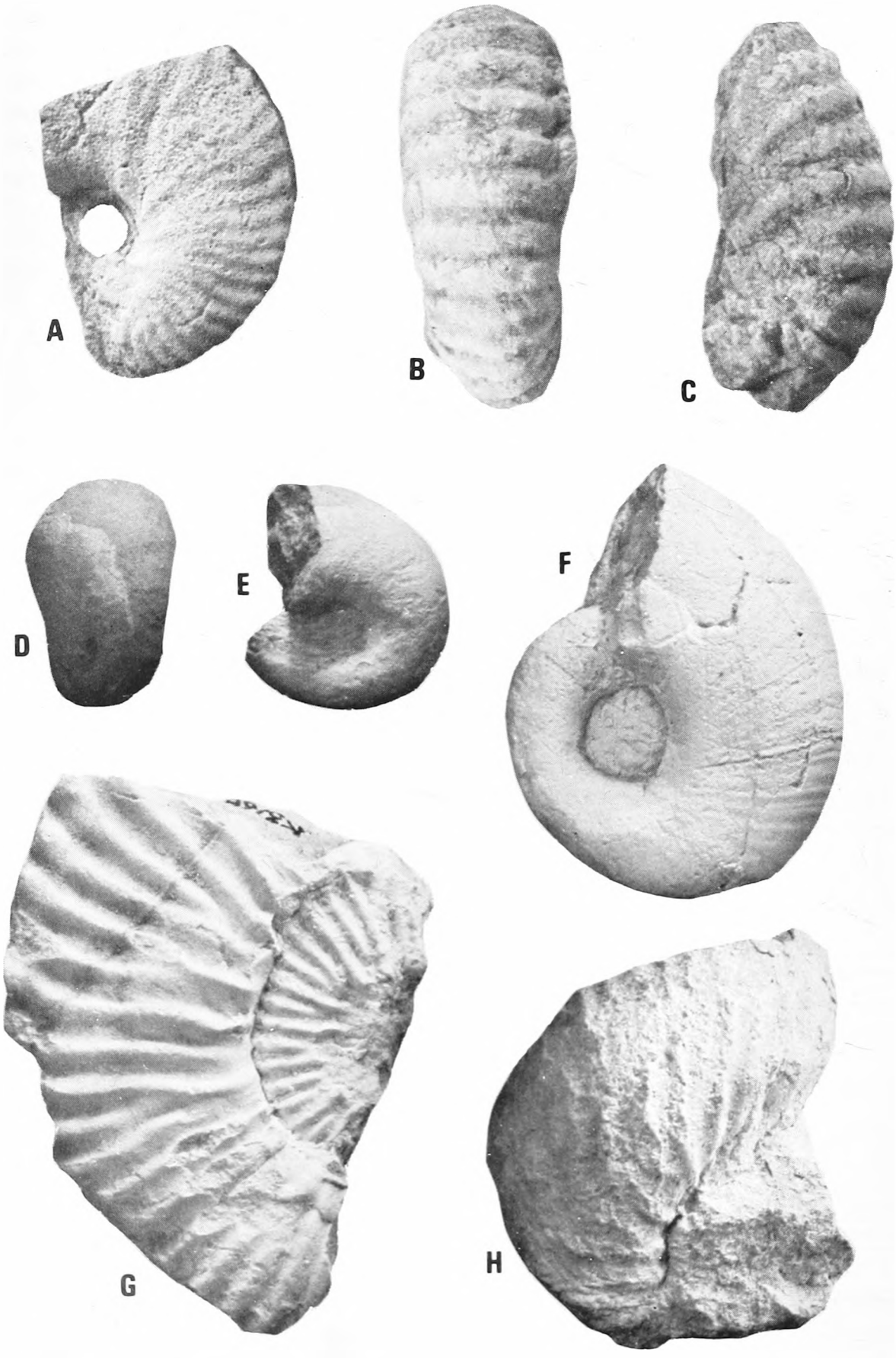

Fig. 39. A. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. Lateral view of SAM–PCA5478. B–C. *Stoliczkaia* (*Stoliczkaia*) sp. A fragmentary internal mould, SAM–PCA4805, from Cabo Ledo. D–F. *Desmoceras latidorsatum perinflatum* subsp. nov. D–E. Ventral and lateral views of SAM–PCA2934. F. Lateral view of SAM–PCA2931. G. *Mortoniceras* (*Angolaites*) *gregoryi* (Spath). Lateral view of a crushed fragment, SAM–PCA3168. H. *Mariella* aff. *circumtaeniatus* (Kossmat). SAM–PCA3130, from low in the sea cliffs (lower part of *dispar* Zone) at Praia-Egito. ×1.

Amedro (1976) has recently suggested that *Paradolphia* is better regarded as a subgenus of *Neophylicticeras* (along with *Protissotia* and *Eotropitoides*), whilst there is a case for regarding both *Paracalycoceras* and *Cottreauites*, both of which derive from *Stoliczkaia*, as Lyelliceratidae rather than Acanthoceratidae.

The collection of *Stoliczkaia* to be discussed below shows a remarkable similarity to the earliest *Forbesiceras*, i.e. the *beaumontianum–largilliertianum* group (compare Juignet & Kennedy 1977, pl. 6 (fig. 1)), and both from a stratigraphic and morphological point of view is most likely to have provided the ancestor to *Forbesiceras*. The close similarity between *Forbesiceras* and *Stoliczkaia* of the *dispar–clavigera* group suggests that the monogeneric subfamily Forbesiceratinae is superfluous, and that *Forbesiceras* should be transferred to the Lyelliceratidae. A study of the early ontogenetic stages of *Forbesiceras* has led Casey (1965) to suggest that *Neopulchellia* (Collignon 1929) was based upon pyritic nuclei of *Forbesiceras*.

Genus *Stoliczkaia* Neumayr, 1875

Type species *Ammonites dispar* d'Orbigny, 1841

Discussion

Stoliczkaia occupies a key position in the evolution of the mid-Cretaceous Acanthocerataceae, as it appears to be the origin of both the Mantelliceratinae and Acanthoceratinae which in turn gave rise to the remaining Upper Cretaceous acanthoceratids.

More than a score of specific names have been applied to the genus, but there has been no sound account of intraspecific variation, nor of the apparent dimorphism present, some subgenera and species reaching a large size and becoming feebly ribbed at maturity (e.g. *S.* (*S.*) *dispar*), others remaining small with strong ribs throughout (*S.* (*Shumarinaia*)). Furthermore, because of their transitional position between Lyelliceratidae, Acanthoceratinae and Mantelliceratinae, there are a number of forms whose position is equivocal. Indeed, the authors find themselves in disagreement over the precise position of some of these passage forms.

The subgenera of *Stoliczkaia* are as follows:

1. *Stoliczkaia* (*Stoliczkaia*) (type species *Ammonites dispar* d'Orbigny). Typically rather involute, compressed ammonites with straight or slightly curved primary ribs, with shorter intercalated ribs between. Primary ribs may be weakly bullate, and during early growth stages bear ventrolateral tubercles or clavi, whilst the venter may be flat or slightly raised. In middle growth tuberculation disappears and ribs extend across a rounded venter; at maturity ribs broaden, become irregular, and may become effaced on the adult body chamber. Typical representatives of the type species *S.* (*S.*) *dispar* are shown as Figures 40 and 41.

2. *Stoliczkaia* (*Faraudiella*) (type species *Ammonites blancheti* Pictet & Campiche). Small *Stoliczkaia* in which distinct siphonal, and sometimes ventro-

Fig. 40. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). The holotype, Renaux collection, Faculté des Sciences, Montpellier, from the Upper Albian of Ventoux, Vauceuse, France. Slightly reduced.

lateral tubercles persist on to the body chamber. Typical representatives are shown in Figure 42.

3. *Stoliczkaia* (*Shumarinaia*) (type species *S.* (*Shumarinaia*) *hashimotoi* Matsumoto & Inoma). Small, with simple suture line and coarse ribbing throughout.

A fourth subgenus, *Villoutreysia* was proposed by Casey (1965: 435, fig. 161; type species *S.* (*V.*) *villoutreysi* Casey) (Fig. 43) for what he described as *Hypacanthoplites* homoeomorphs diagnosed as '*Stoliczkaia* with broad, square venter and strong persistent ribbing, differing from *Mantelliceras* in much

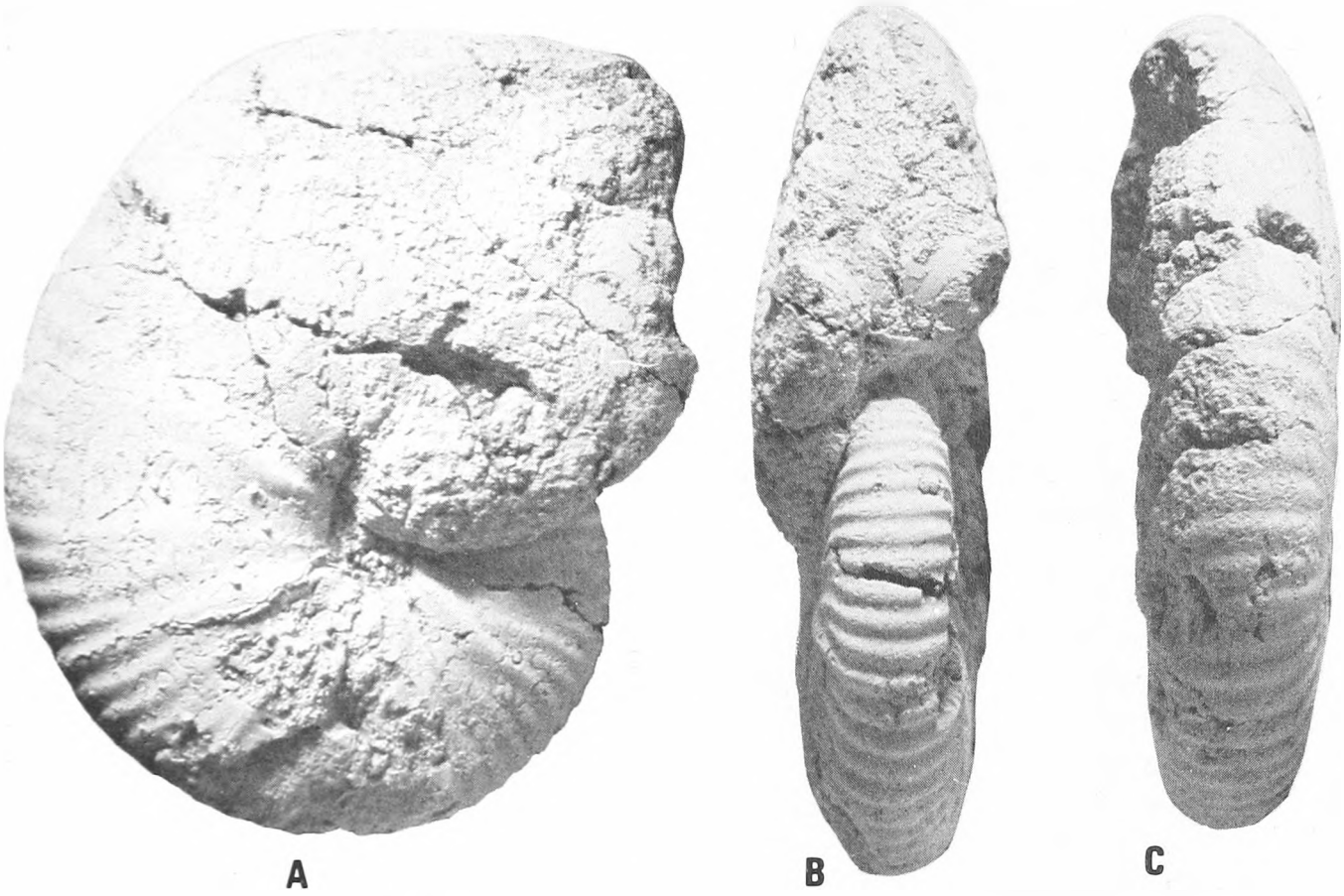

Fig. 41. *Stoliczkaia* (*Stoliczkaia*) *dispar* (d'Orbigny). Juvenile specimen in C. W. Wright collection WW 72344, from the *dispar* Zone Ammonite Bed of the Dorset Coast. ×1.

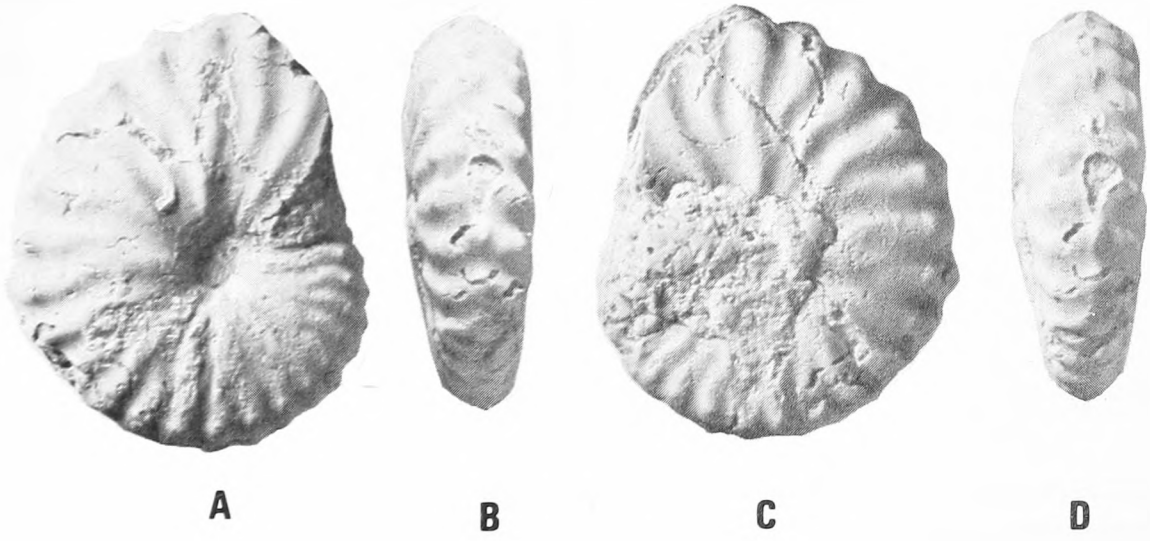

Fig. 42. *Stoliczkaia* (*Faraudiella*) *sexangulata* (Seeley). Seeley's original specimen, Sedgwick Museum, Cambridge, B53, from the Cambridge Greensand, Cambridge. ×1.

earlier loss of ventral tubercles, squarer whorls and, generally, narrow and shallower umbilicus'. The holotype of *S.* (*V.*) *villoutreysi* is illustrated here as Figure 43; after an examination of the large collections of *Stoliczkaia* in the Paris Museums the authors have concluded that it is not separable subgenerically from *Stoliczkaia sensu stricto.*

The genus *Paradolphia* Casey was proposed (Casey 1965: 461, pl. 77 (figs 5–6)) for the type species *P. prisca* Casey (illustrated here as Fig. 44) for intermediates between *Stoliczkaia* and *Forbesiceras* but, as noted above, is possibly a subgenus of *Neophlycticeras.*

Paracalycoceras (type species *Ammonites wiestii* Sharpe 1857: 47, pl. 21 (fig. 3)) is an enigmatic genus from the Lower Cenomanian of southern England, known with certainty only from two specimens—the lost holotype (*fide* Kennedy 1971) and an extant specimen in the collections of C. W. and E. V. Wright (Fig. 45). Kennedy (1971: 79) diagnosed the genus as follows: 'Medium-sized, somewhat involute ammonites. Inner whorls slightly compressed, with long ribs bearing umbilical bullae, and lower and upper ventrolateral tubercles separated by 1, 2, or sometimes more shorter ribs. There is a distinctly raised siphonal area, and an incipient siphonal tubercle on all ribs. Outer whorl with a broad venter, and broad, distant, flexuous rursiradiate ribs, irregularly long and short.'

Both morphologically and in the observed ontogenetic changes, *Paracaly-*

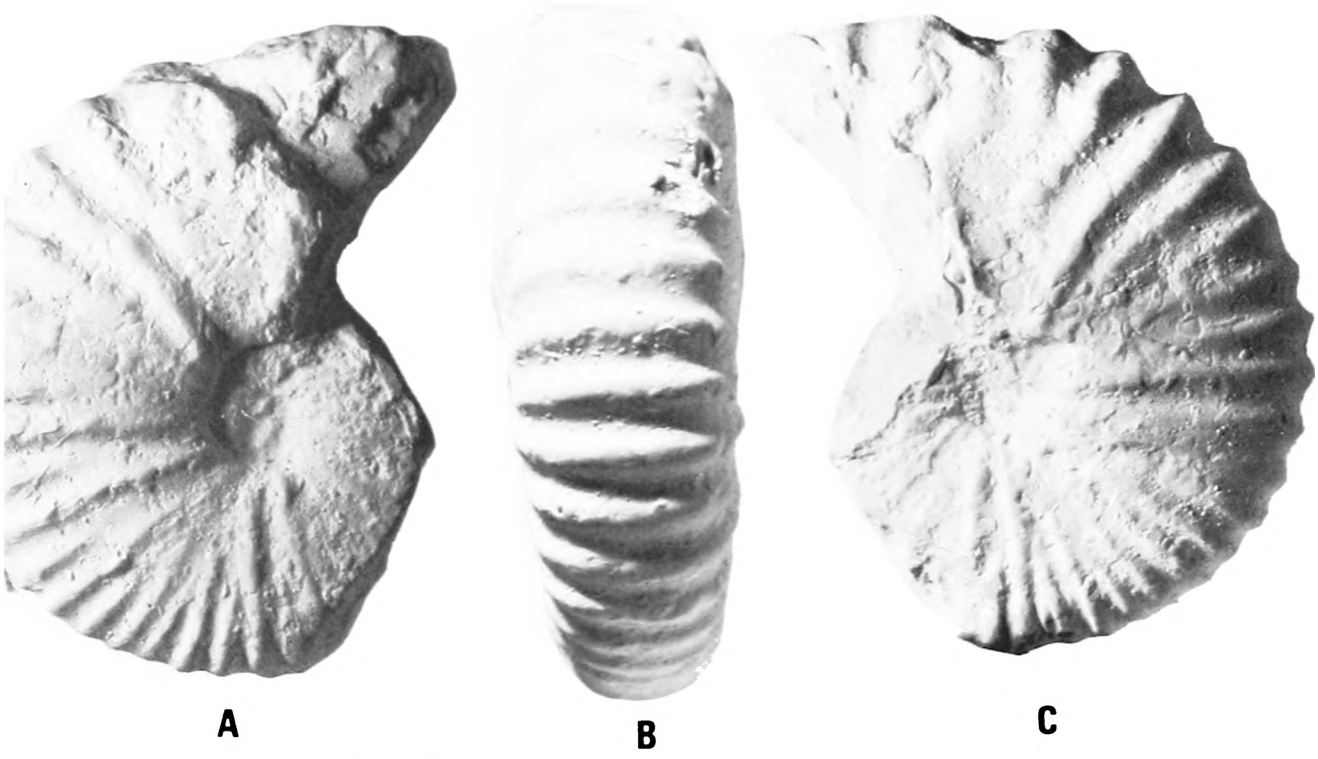

Fig. 43. *Stoliczkaia* (*Stoliczkaia*) *villoutreysi* Casey. Holotype, O. de Villoutreys collection, Uppermost Albian, Monte Carlo Tunnel, Monte Carlo. ×1.

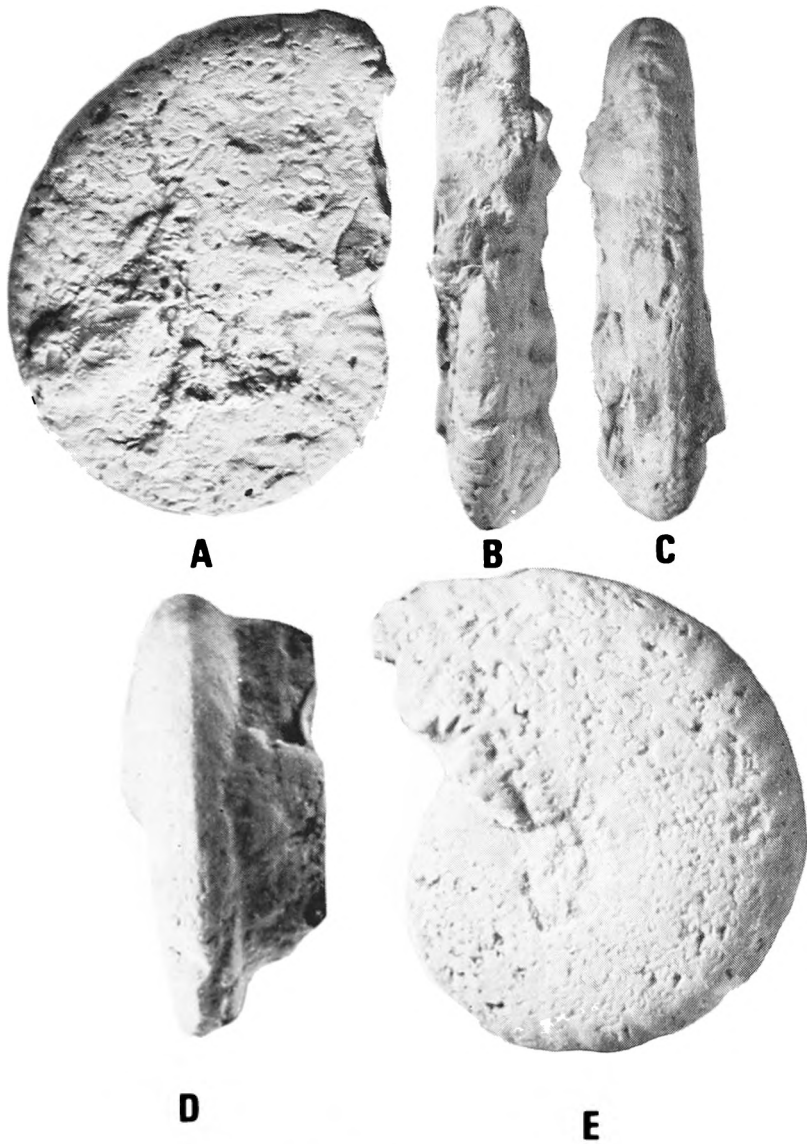

Fig. 44. *Neophylicticeras* (*Paradolphia*) *prisca* (Casey). A–C. Holotype, Norwich Castle Museum 61.18(1679). D–E. Paratype, Sedgwick Museum, Cambridge, B93303. Both from the Cambridge Greensand, Cambridge. A–C ×1, D–E ×2.

coceras is virtually indistinguishable from certain species of *Stoliczkaia*, from which it is obviously descended. Little more can be said until topotype material is studied, but it may prove more satisfactory to regard it as a subgenus of *Stoliczkaia*.

Kennedy (1971: 80) considered that the genus *Cottreauites* (Collignon 1929), based upon pyritic nuclei, 'may be wholly or partly a synonym of *Paracalycoceras*'. Again, this question cannot be resolved until *Paracalycoceras* is better known or mature *Cottreauites* are described. It seems very likely, however, that some *Cottreauites* are juveniles of either *Stoliczkaia* or *Paracalycoceras*, and that it should be considered a *nomen dubium*.

Fig. 45. *Stoliczkaia* (*Paracalycoceras*) *wiestii* (Sharpe). C. W. Wright collection 3556, Lower Cenomanian, Cenomanian Limestone, Bed A2, White Cliff, Seaton, Devon. ×1.

Subgenus *Stoliczkaia* (*Stoliczkaia*) Neumayr, 1875

Renz (1968: 46) recognized four species groups within *Stoliczkaia sensu stricto*:

1. The group of *S. dispar* with ventrolateral tubercles only on the inner whorls and weak ribbing on the body chamber, comprising *S. dispar* (d'Orbigny), *S. dorsetensis* Spath and *S. tenuis* Renz.

2. The group of *S. africana* which retains ventrolateral tubercles on to the body chamber, with well-developed, broad, falcate ribs, and includes *S. africana* (Pervinquière) and *S. flexicostata* Breistroffer. Matsumoto & Inoma (1975) have proposed the subgenus *Shumarinaia* for this group.

3. The group of *S. notha*, which lacks ventrolateral tubercles whilst retaining strong ribbing on to the body chamber, and comprises *S. notha* (Seeley) and *S. clavigera* Neumayr.

4. The group of *S. levis* which lacks ventrolateral tubercles and is virtually without ornament. Only *S. levis* Renz, based on a unique holotype, is assigned to this group.

Stoliczkaia (*Stoliczkaia*) *tenuis* Renz, 1968

Figs 46–53, 54A–F, 55, 68E

Stoliczkaia tenuis Renz 1968: 48, pl. 6 (figs 6, 12), fig. 16b, f.

Material

37 specimens, USNMNH 236981–237012a–b, 237014–5, together with 3 specimens in the collections of the South African Museum, SAM–PCA5477–78 and 6811, all retaining part or all of their recrystallized shell, from Porto Amboim, and 7 specimens, SAM–PCA2938–39, 2944, 3169, 3373 and 5475–5476, preserved as composite internal moulds from Egito.

Description

Up to 20 mm diameter: shell compressed ($^{W}/_{H}$ = 0,50–0,63), very involute with a deep, narrow umbilicus (11–17% of diameter). Umbilical walls steep, almost vertical, with evenly rounded umbilical shoulders. Flanks broad, slightly convex to flat, with maximum width below mid-flank, converging towards the narrow venter. Venter slightly convex to almost tabulate, and weakly raised along the siphonal line. Ornament comprises thirteen to sixteen prorsiradiate ribs per half-whorl, generally alternating long and short. The ribs are more or less strongly flexed and bear distinct ventrolateral tubercles. The latter are joined across the venter by convex ribs.

Up to a diameter of 12 mm in USNMNH 237005 (10 mm in USNMNH 237012) ribs appear to be absent, although there are weak tubercles possibly marking their position along the ventrolateral shoulders. In USNMNH 237010, the main ribs are ornamented by rather distinct umbilical bullae.

21–40 mm diameter: shell compressed ($^{W}/_{H}$ = 0,53–0,68), very involute (umbilicus 15–17% of diameter), with a high rectangular whorl section. Ribbing denser (twenty to twenty-four ribs per half-whorl), not infrequently with two intercalatories between main ribs. The ventrolateral tubercles are generally still prominent at this stage.

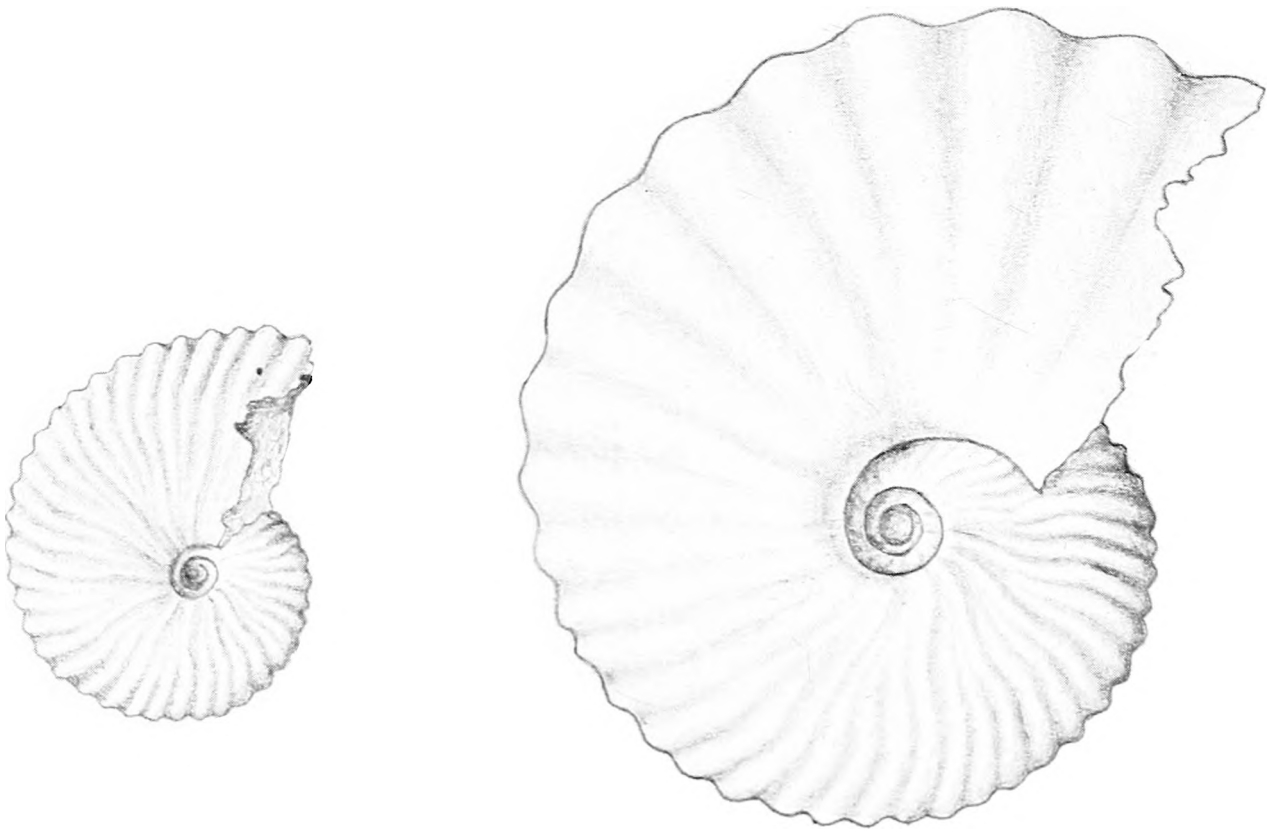

Fig. 46. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. Reconstructed juvenile and middle growth stages. ×1.

41–70 mm diameter: the ventrolateral tubercles are commonly lost between 40–45 mm diameter (37 mm in USNMNH 236996) and the ribs pass uninterruped across the venter, sometimes with a slight thickening in the ventrolateral position. The shell becomes slightly more inflated ($^{W}/_{H}$ = 0,58–0,69), with distinctly convex flanks and a rounded venter. The flank ribs coarsen considerably and there are commonly one or two intercalatories between long ribs, although in USNMNH 236994 and USNMNH 236987 there are probably more long ribs than intercalatories. Where there are two intercalatories between long ribs they may be of markedly different lengths (USNMNH 236984). Immediately prior to the aperture, all ornament is lost and the body chamber becomes smooth (USNMNH 236981).

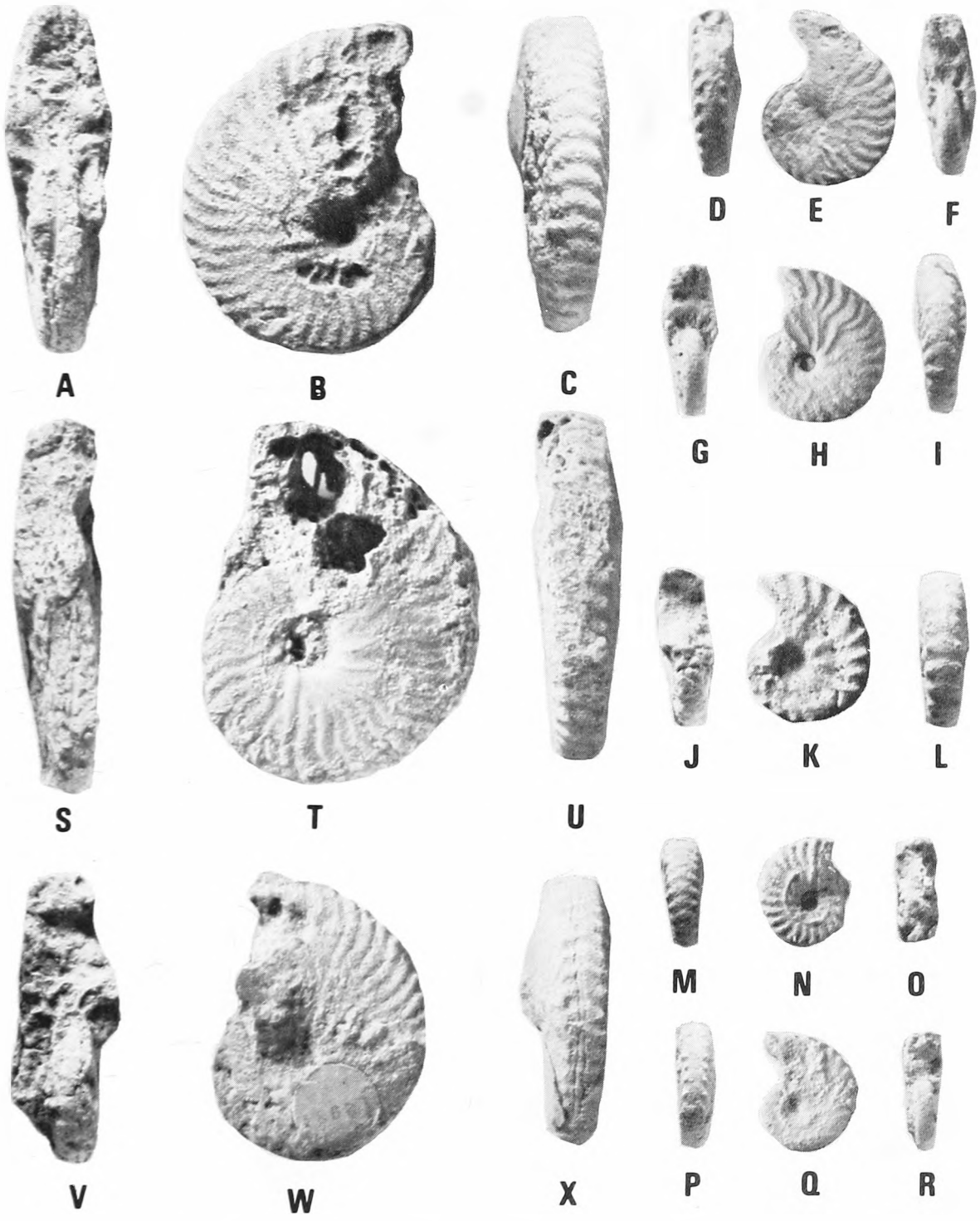

Fig. 47. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–C. USNMNH 236999. D–F. USNMNH 237009. G–I. USNMNH 237006. J–L. USNMNH 237010. M–O. USNMNH 237015. P–R. USNMNH 237014. S–U. 236997. V–X. USNMNH 237003. ×1.

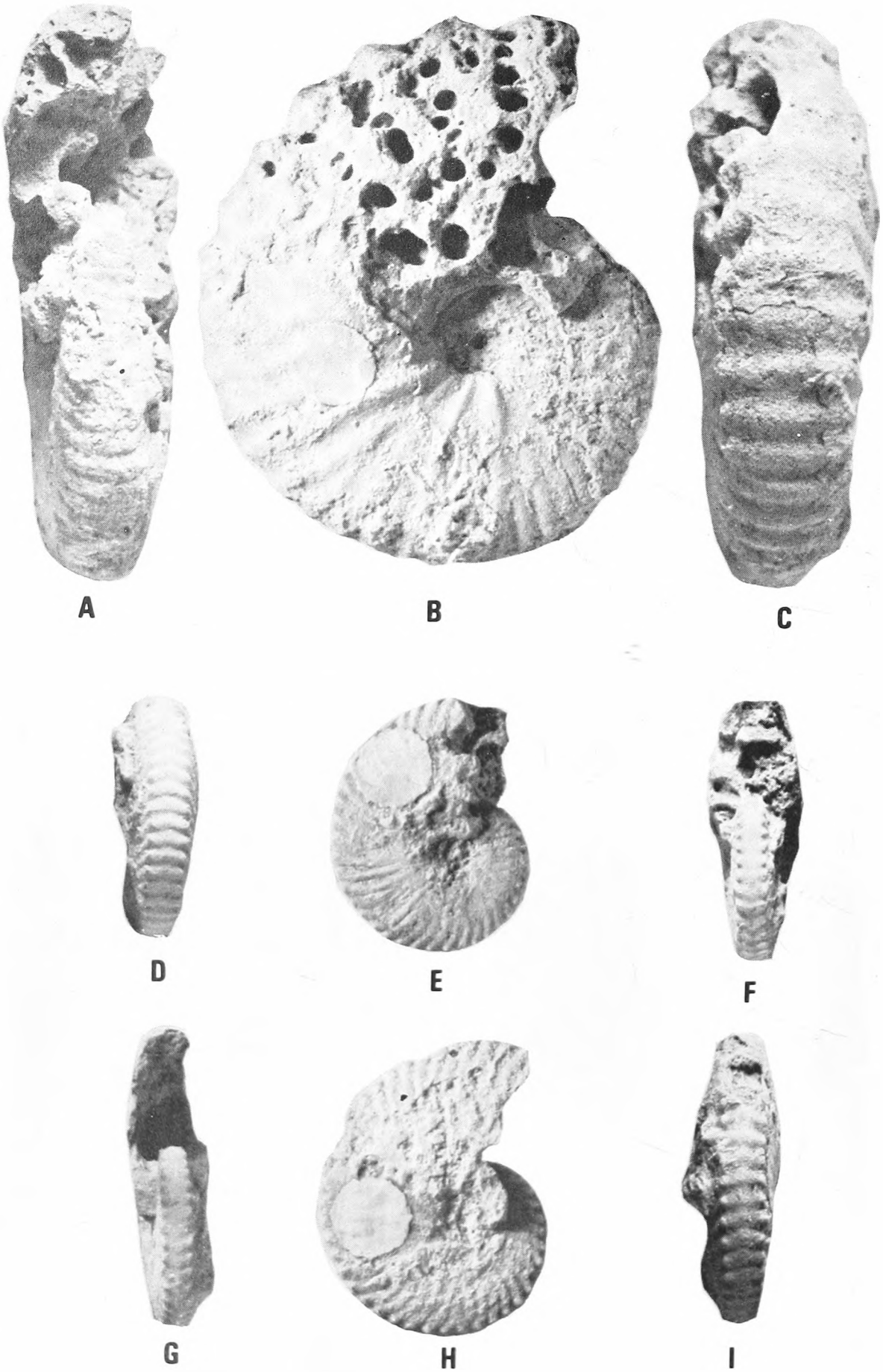

Fig. 48. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–C. USNMNH 236988. D–F. USNMNH 237003. G–I. USNMNH 236990. ×1.

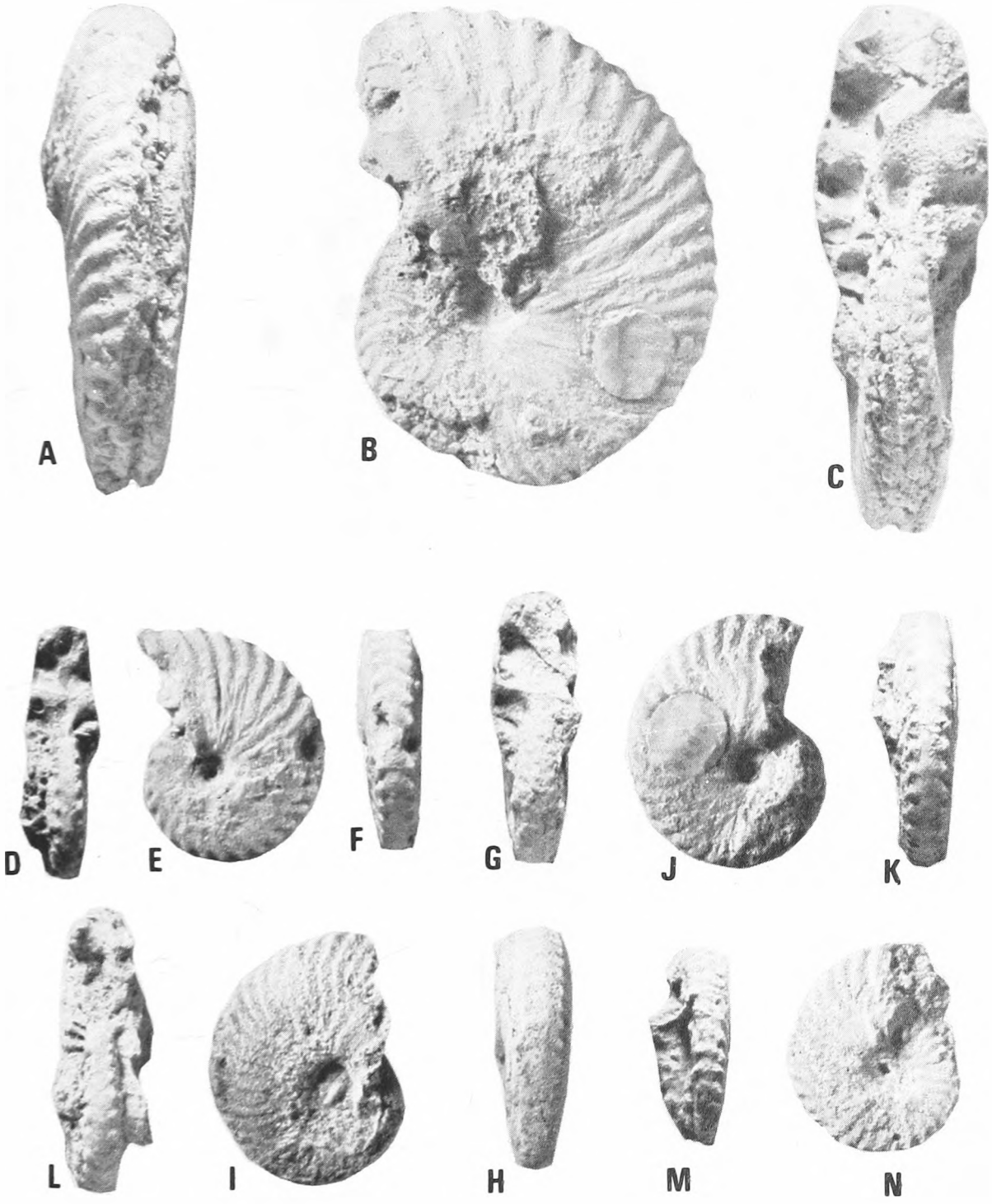

Fig. 49. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–C. USNMNH 236945. D–F. USNMNH 237004. G–I. USNMNH 237000. J–L. USNMNH 237001. M–N. USNMNH 237007. ×1.

Fig. 50. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–C. USNMNH 236985. D–F. USNMNH 236984. ×1.

Measurements

No.	D	H	W	W/H	U
USNMNH 236983	66	32(48)	±22(33)	0,69	10(15)
USNMNH 236985	65	36(55)	26(40)	0,72	±13(20)
USNMNH 236986	±56	29(52)	17,6(31)	0,61	±9(16)
USNMNH 236987	67	35(52)	±23,5(35)	0,67	±9,7(14)
USNMNH 236988	68	33(48)	?	?	11,1(16)
,,	50	26(52)	18(36)	0,69	±9(18)
USNMNH 236989	55,5	27,5(50)	±19(34)	0,69	±10(18)
USNMNH 236990	26	13,5(52)	7,2(28)	0,53	?
USNMNH 236992	38	±19(50)	±10(26)	0,53	?
USNMNH 236994	50	26(52)	15,2(30)	0,58	7,7(15)
USNMNH 236995	55	30(54)	18,7(34)	0,62	7,9(14)
USNMNH 236996	37	17,5(47)	±12(32)	0,68	?
USNMNH 236997	35	18(54)	9(26)	0,50	6(17)
USNMNH 236998	34	19(56)	±10(29)	0,52	5,5(16)
USNMNH 236999	34	19(56)	11(32)	0,58	5(15)
,,	26	14(54)	7,5(29)	0,54	?
USNMNH 237000	30	15(50)	9(30)	0,60	?
USNMNH 237001	30	15,7(52)	8,3(28)	0,53	4,7(16)
,,	20,5	10,8(53)	5,5(27)	0,51	2,5(12)
USNMNH 237002	30	±16,5(55)	8,5(28)	0,51	?
USNMNH 237003	31,3	17(54)	10(32)	0,59	±4,5(14)
USNMNH 237004	28	15(54)	8(29)	0,53	4(14)
,,	17,5	9,5(54)	6(34)	0,63	2,7(15)
USNMNH 237005	17,3	9(52)	±4,5(26)	0,50	±3(17)
USNMNH 237006	17,7	9(51)	5(28)	0,56	2(11)
,,	12,3	6(49)	3,4(28)	0,57	?
USNMNH 237008	21	11(52)	6(29)	0,54	3(14)
,,	15	7(47)	4(27)	0,57	2,2(15)
USNMNH 237010	17	8(47)	4,5(26)	0,56	2,5(15)
USNMNH 237012	9,5	4(42)	3(32)	0,75	±1,5(16)

Intraspecific variation

The large number of well-preserved specimens available to the authors permits a better understanding of the intraspecific and ontogenetic variation in this species. The marked ontogenetic change in ornament shown by this species has been outlined above. However, Figure 55 also shows that there is considerable variation in the degree of inflation of the whorls ($^{W}/_{H}$ = 0,50–0,72), with a distinct tendency for the whorls to become more inflated at large diameters. Futhermore, Figure 55 shows that not only is there some variation in the width of the umbilicus, but there is also a slight tendency for the shell to become more evolute with growth.

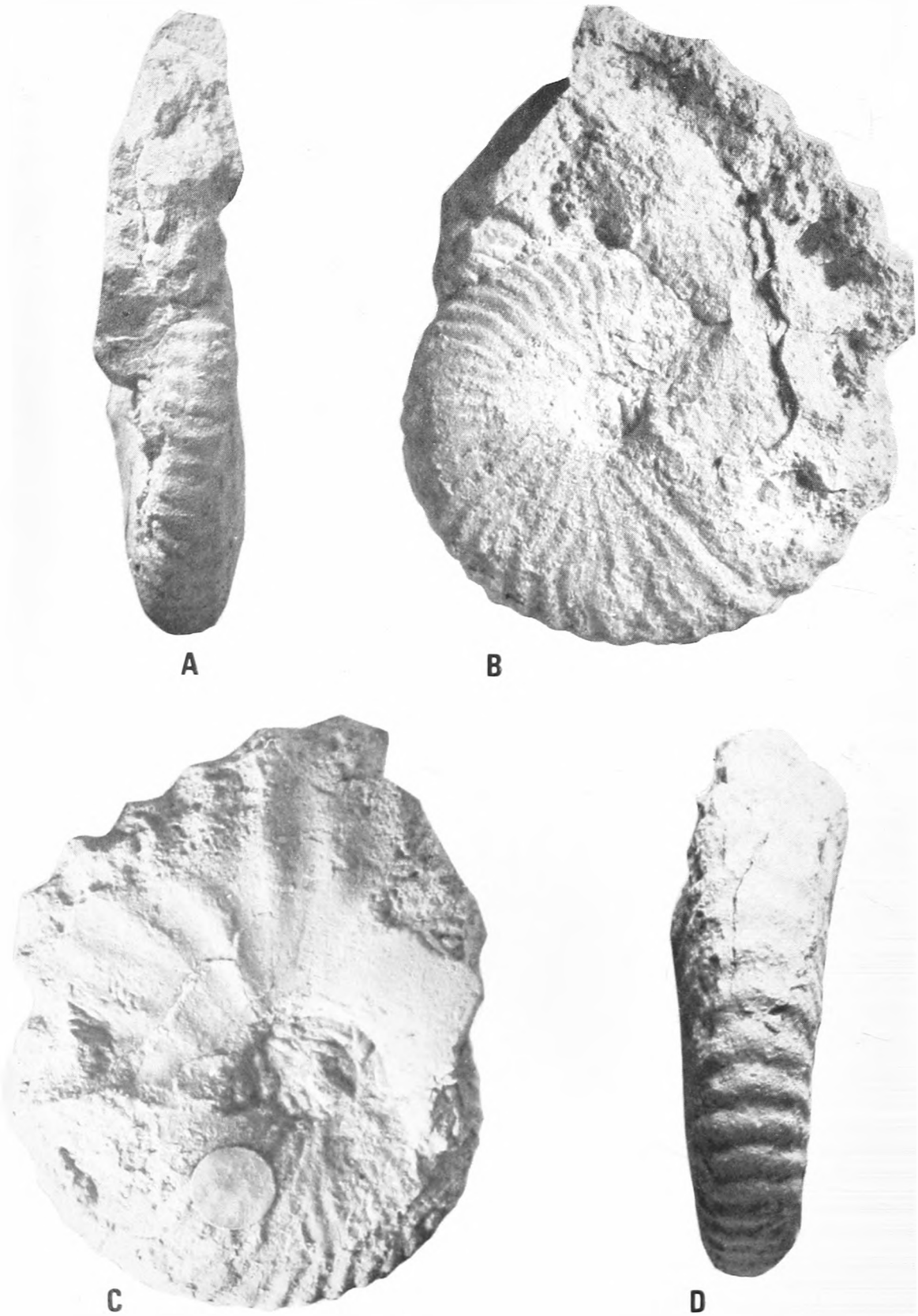

Fig. 51. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–D. USNMNH 236994. ×1.

Discussion

As shown above, the present material is rather variable, and the type of *S.* (*S.*) *tenuis* and the specimen referred to as *S.* (*S.*) aff. *tenuis* by Renz (1968, pl. 6 (fig. 12)) fall within this range.

When mature, *S. tenuis* closely resembles *S.* (*S.*) *clavigera* Neumayr (= *Ammonites dispar* Stoliczka (*non* d'Orbigny) 1865: 45, pl. 85 (figs 1–3 only)) (see Fig. 56), from which it appears to differ only in being consistently more compressed. Further work may show that the two merit only subspecific separation.

S. (*Stoliczkaia*) *dispar* (d'Orbigny) (1841: 143, pl. 45 (figs 1–2)) is a widely-cited but much misinterpreted species. Consequently, the holotype is here photographically figured for the first time (Fig. 40), as well as a typical specimen from the *dispar* Zone of Dorsetshire, England (Fig. 41). *S.* (*Stoliczkaia*) *dispar* differs from the present species in having far more (up to nine) intercalatories between long ribs, whilst the latter are ornamented with weak umbilical bullae. The venter loses its ventrolateral tubercles and becomes rounded at smaller diameters and the body chamber ornament is also different; in *S.* (*S.*) *dispar*, ribbing rapidly weakens in maturity (at least on the internal mould) and all that

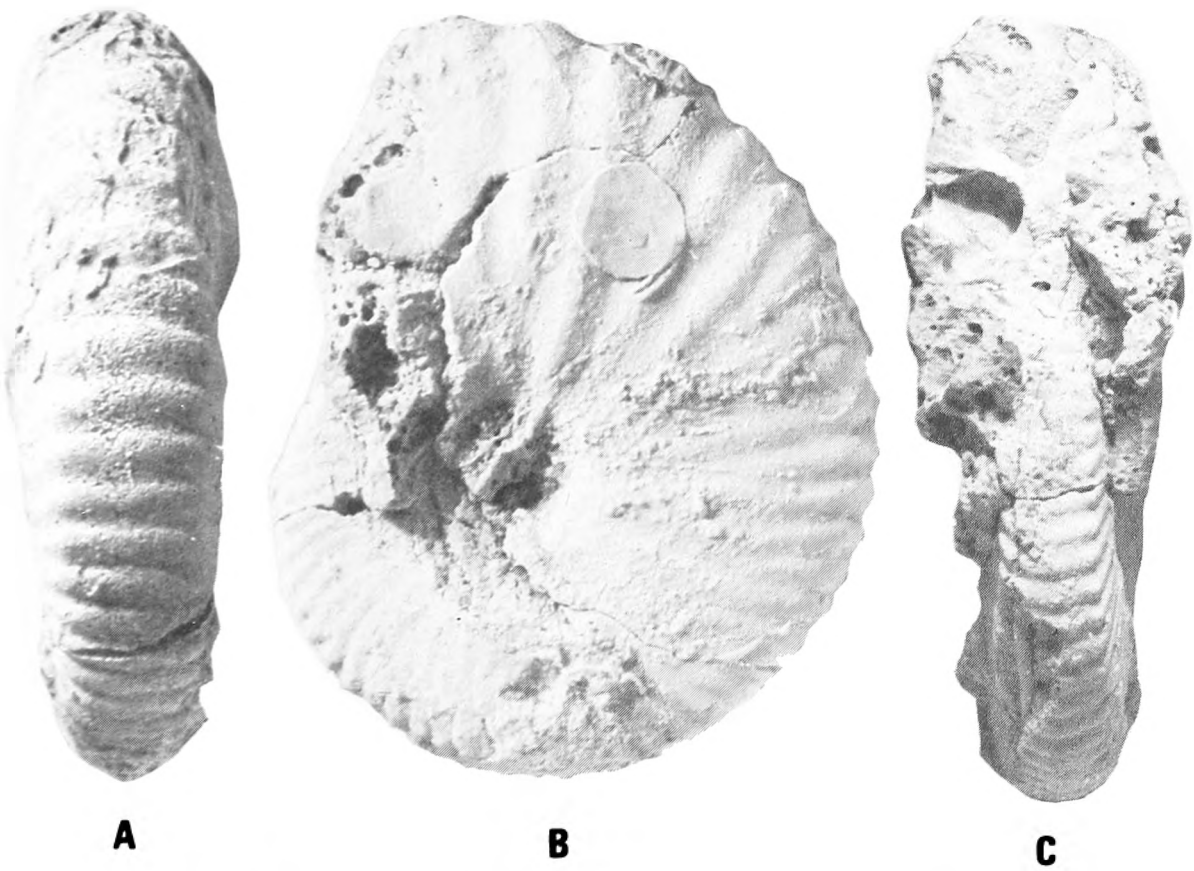

Fig. 52. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–C. USNMNH 236987. ×1.

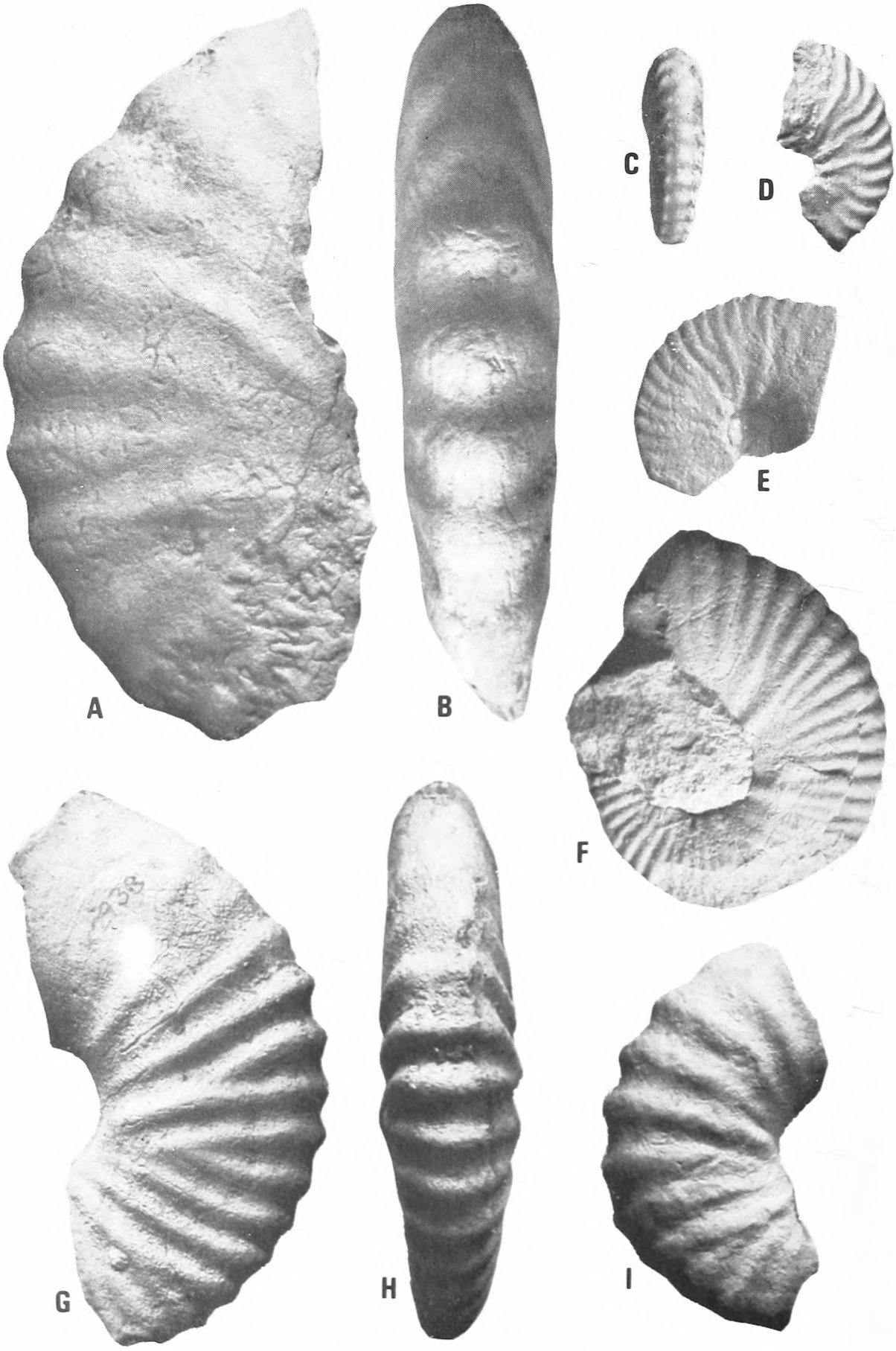

Fig. 53. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–B. Lateral and ventral views of SAM–PCA3169. C–D. Ventral and lateral views of SAM–PCA5475. E. Lateral view of SAM–PCA5476. F. Lateral view of SAM–PCA2939. G–H. Lateral and ventral views of SAM–PCA2938. I. Lateral view of SAM–PCA3373. A–B, I ×0,75, C–H ×1.

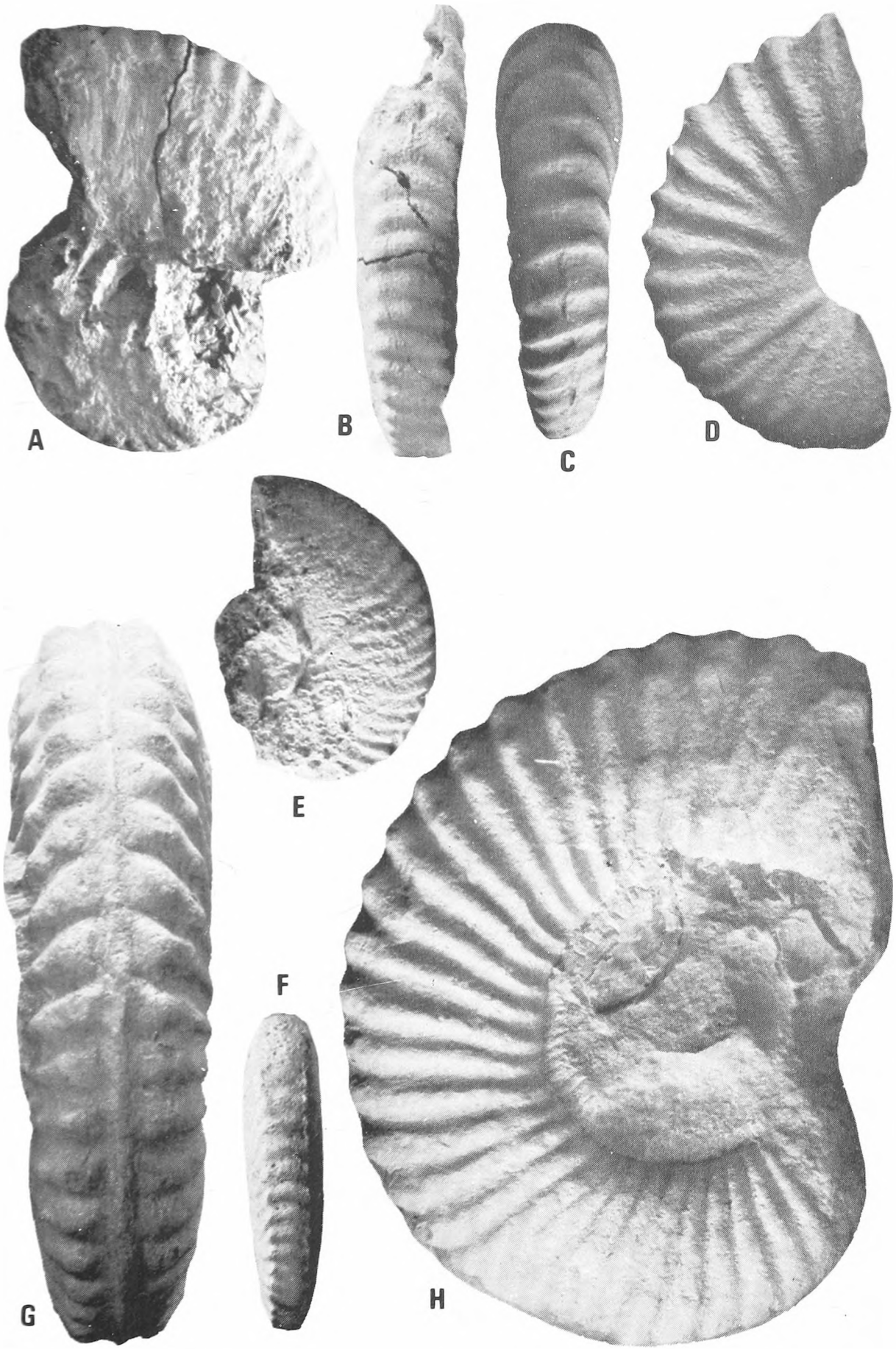

Fig. 54. A–F. *Stoliczkaia* (*Stoliczkaia*) *tenuis* Renz. A–B. Lateral and ventral views of SAM–PCA6811. C–D. Ventral and lateral views of SAM–PCA2944. E. Lateral view of SAM–PCA5477. F. Ventral view of SAM–PCA5478. G–H. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Ventral and lateral views of SAM–PCA3107. A–B, E–H ×1, C–D ×0,75.

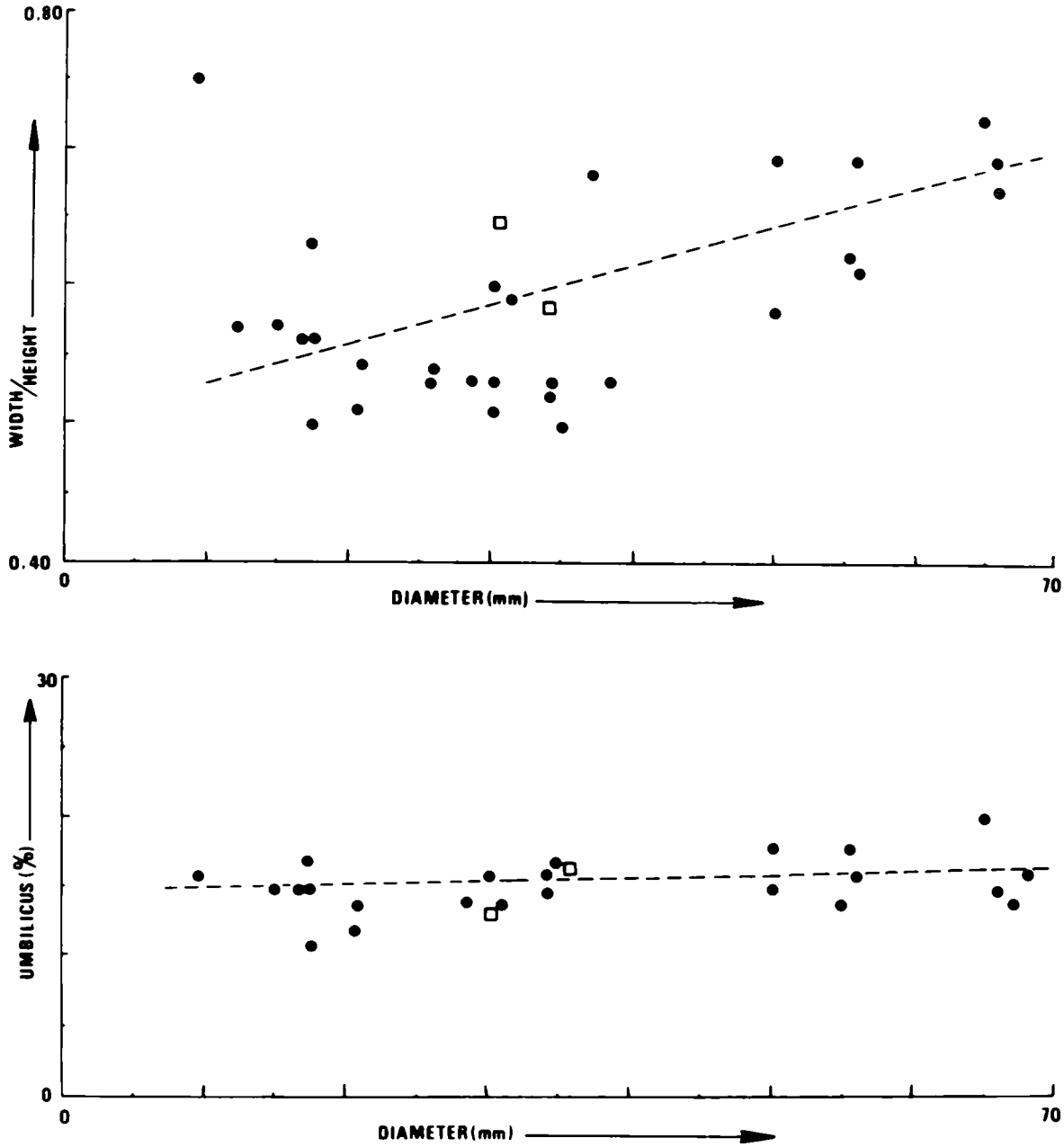

Fig. 55. Plots of inflation and umbilical ratio against diameter for *S. tenuis*. Dots = present material; squares = holotype and paratype (after Renz 1968).

remains are the weak umbilical bulges of the long ribs. Furthermore, the upper half of the flanks are concave, forming a broad, spiral depression.

S. (*Stoliczkaia*) *notha* (Seeley) (1865: 232: Spath 1929: 335, fig. 110) (Fig. 57) differs from *S. tenuis* in having a rounded venter at all growth stages. *Stoliczkaia dorsetensis* Spath (1929: 337, pl. 31 (fig. 2), pl. 33 (fig. 1)) is more inflated and more densely ribbed than the Angolan material, as well as having more (three to nine) intercalatories between long ribs on the inner whorls. *S.* (*Stoliczkaia*) *villoutreysi* Casey (Fig. 43) has more intercalatories between long ribs (up to seven), whilst the venter is tabulate in maturity, when it homoeomorphs *Hypacanthoplites*.

S. (*Stoliczkaia*) *argonautiformis* (Stoliczka) (1864: 87, pl. 46 (figs 1–2)) has strongly converging flanks, subdued ribbing and a more narrowly arched venter than the present species. *Stoliczkaia tetragona* Neumayr (nom. nov. pro *Ammonites dispar* Stoliczka (*non* d'Orbigny), 1864: 85, pl. 45 (fig. 2)) (Fig. 58) differs from the Angolan material in being much more inflated, although the style of ornament is similar in adults.

Stoliczkaia grandidieri Boule, Lemoine & Thévenin (1907: 34, pl. 8 (fig. 8)), *S. gardonica* (Herbert & Meunier-Chalmas) (1875: 116, pl. 4 (figs 1–2)); *S. rhamnonota* (Seeley) (1865: 233, pl. 11 (fig. 7); Spath 1929: 333, fig. 109)) and *S. blancheti* (Pictet & Campiche) (1859: 188, pl. 23 (figs 2, 6); Renz 1968: 46, pl. 5 (fig. 21)) are all referable to the subgenus *Faraudiella*, whilst *S. africana* Pervinquière (1907: 388, pl. 12 (fig. 10)), *S. flexicostata* Breistroffer (nom. nov. pro *A. dispar* Pictet & Campiche (*non* d'Orbigny) 1860: 264, pl. 38 (fig. 4); Renz 1968: 49, pl. 6 (fig. 9)), *S. hashimotoi* Matsumoto & Inoma, and *S. asiatica* Matsumoto & Inoma (1975) are all *Shumarinaia*.

As suggested by Matsumoto & Inoma (1975), *Stoliczkaia uddeni* Böse (1927: 211, pl. 4 (figs 12–15)), is probably a synonym of *S. texana* Cragin (1893: 235, pl. 44 (fig. 1)) which itself is a close relative of *S. crotaloides* (Stoliczka) (1864: 88, pl. 46 (fig. 3)) (Fig. 59). The latter species differs from the Angolan material in maintaining single prorsiradiate ribs to the peristome, with only rare intercalatories, and in the flattened venter of the inner whorls; they may represent a distinct Cenomanian offshoot.

'*Stoliczkaia*' *razafimbeloi* Collignon (1968: 29, pl. 6 (fig. 7), pl. 7 (fig. 4)) and '*S.*' *vendegiesi* Collignon (1968: 31, pl. 7 (fig. 5)) both differ from the present material in the development of distinct upper and lower ventrolateral tubercles on the body chamber and are thus transitional to *Graysonites*. They do not appear to be referable to the genus *Stoliczkaia*.

Stoliczkaia patagonica Stoyanow (1949: 128, pl. 26 (figs 3–4)), *S. excentrumbilicata* Stoyanow (1949: 129, pl. 26 (figs 5–6)) and *S. scotti* Stoyanow (1949: 129, pl. 26 (figs 7–8)) are all from the same stratigraphic level and locality and it is doubtful whether more than one species is represented. In this material, flexuous main ribs are ornamented with umbilical bullae and separated by two to four intercalatories. The ribs pass strongly across the venter and appear to lack ventrolateral tubercles. These 'species' are very close to *S. dorsetensis* Spath.

Stoliczkaia adkinsi Böse (1927: 193, pl. 18 (figs 9–17)) differs from the present material in having more strongly differentiated long and short ribs, the former with distinct umbilical tubercles.

'*Submantelliceras*' *worthense* (Adkins) (1920: 93, pl. 1 (figs 11–13)) from the Pawpaw Formation of Tarrant County, Texas, may be based upon juveniles of *Stoliczkaia*. It differs from the present material in the possession of umbilical tubercles and in the (?) earlier loss of ventrolateral tubercles.

Some of the *Mantelliceras* (*Submantelliceras*) *saxbii* (Sharpe) figured by Thomel (1972: 16–17, pl. 1 (figs 8–12 only)) are clearly based upon *Stoliczkaia*

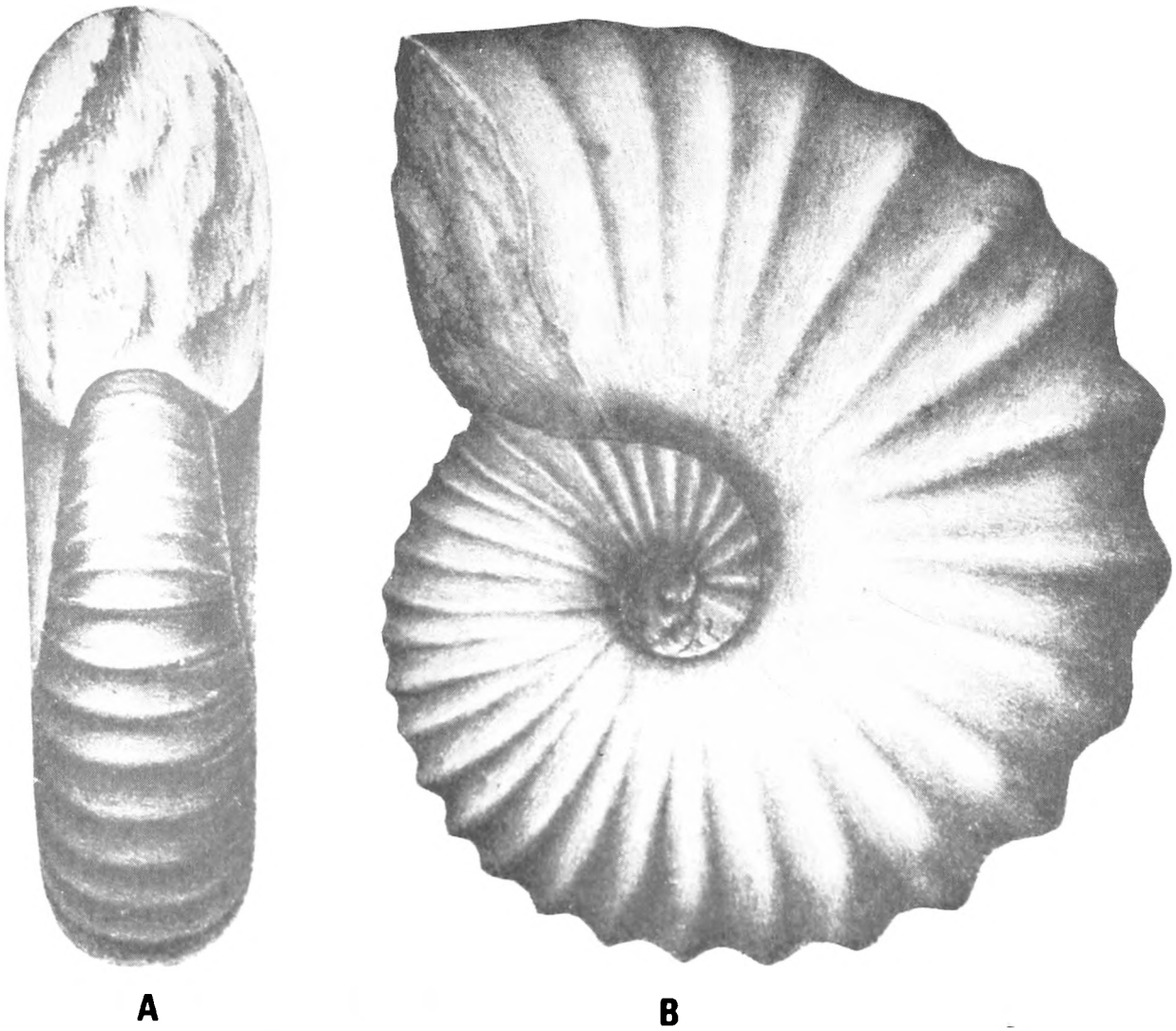

Fig. 56. *Stoliczkaia* (*Stoliczkaia*) *clavigera* Neumayr. Copy of Stoliczka 1864, pl. 45 (fig. 1–1a). ×1.

of the *dispar–dorsetensis* group and differ from the Angolan material in having more intercalatories between long ribs.

Stoliczkaia praecursor Anderson (1958: 246, pl. 12 (fig. 1)) is too poorly figured and described for proper comment, but appears to differ from the present species in being more inflated, more coarsely ribbed, and in the presence of umbilical bullae at large diameters. It seems to be allied to *S. tetragona* Neumayr.

In his original account of this species, Renz compared *S. tenuis* with *Mantelliceras martimpreyi* (Coquand), and, indeed, as demonstrated by the present population *S.* (*S.*) *tenuis* confirms that some *Stoliczkaia* have submantellicerine nuclei, as suggested by Kennedy (1971). In particular, the authors are impressed by their close similarity to pyritic nuclei such as those figured by Collignon (1929, pl. 3 (figs 4–5)) from Diego-Suarez, Madagascar, as *Acanthoceras* (*Mantelliceras*) *martimpreyi* Coquand. The latter differ only in having

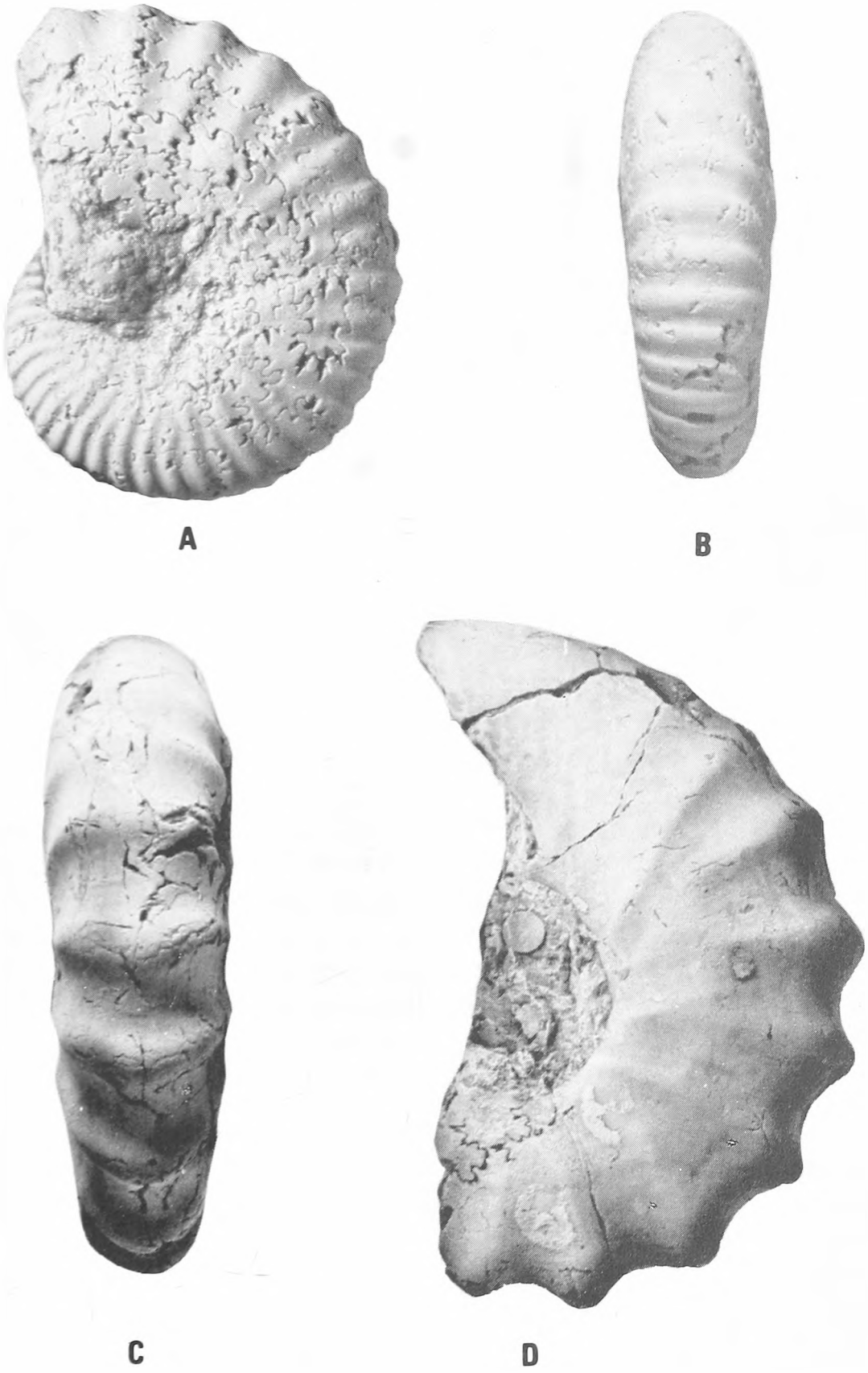

Fig. 57. *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley). A–B. Holotype, Sedgwick Museum, Cambridge, B40. C–D. BMNH C4811, type of the variety *ultima* Spath. Both from the Cambridge Greensand, Cambridge. ×1.

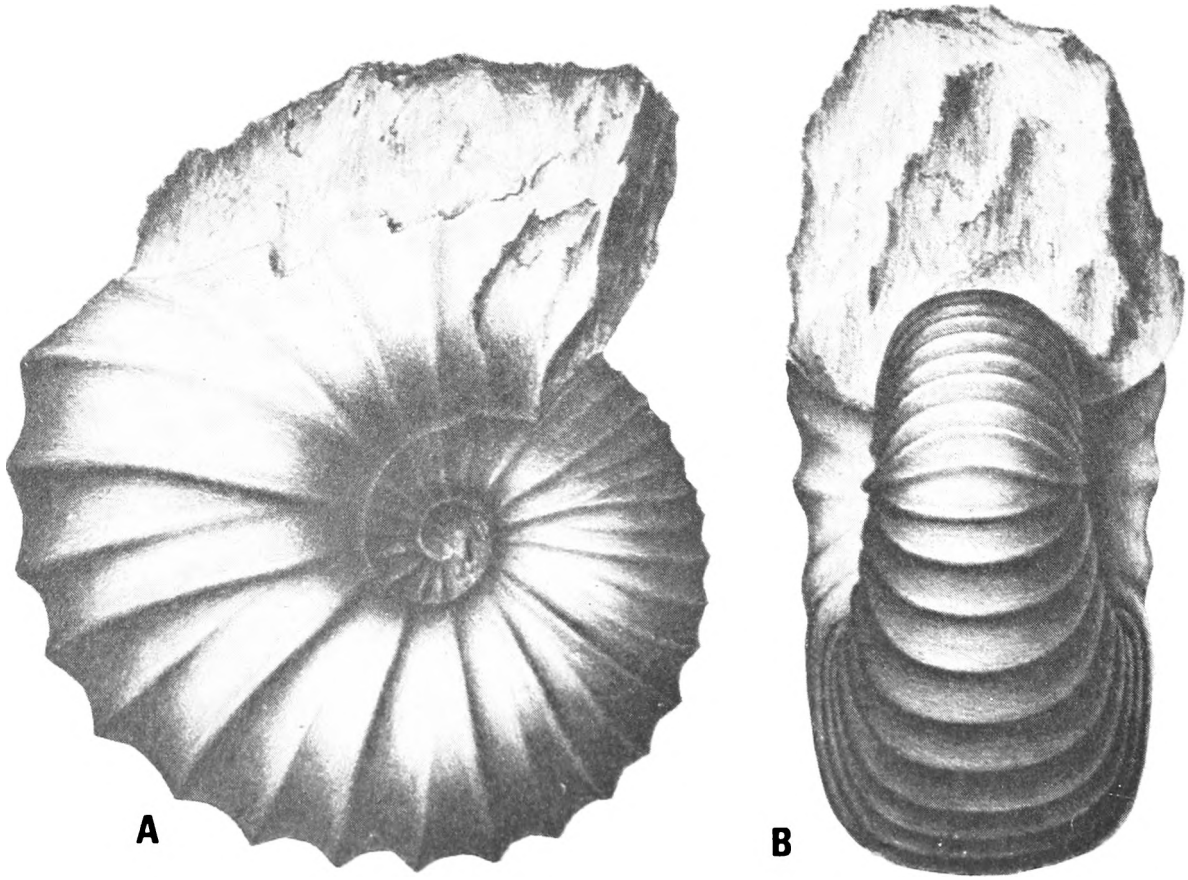

Fig. 58. *Stoliczkaia tetragona* Neumayr. Copy of Stoliczkaia 1864, pl. 45 (fig. 2–2a). ×1.

distinctly differentiated lower ventrolateral tubercles. However, there can be little doubt that records of *Mantelliceras* (Thomel 1972) and *Submantelliceras* (Adkins 1920) from the Upper Albian are based upon juveniles of *Stoliczkaia*. Kennedy & Hancock (1971) have shown *Submantelliceras martimpreyi* (Coquand) to be a junior subjective synonym of *M. saxbii* (Sharpe), from which the authors' material differs in being more compressed, lacking distinct lower ventrolateral tubercles and in showing a marked, and characteristic, change of ornament on the body chamber. However, the fact that Thomel (1972) assigned late Albian species of *Stoliczkaia* to *M. saxbii* merely serves to emphasize the close relationship between these two genera and suggests that the origin of (at least) compressed *Mantelliceras* and *Utaturiceras* lies close to *Stoliczkaia* of *tenuis* type. The writers would also point to the close similarity of compressed variants to juvenile *Forbesiceras* (see Juignet & Kennedy 1977), generally described as *Neopulchellia* (a subjective synonym), and evidence for the descent of *Forbesiceras* from the *S.* (*S.*) *tenuis* group is to be published elsewhere.

Occurrence

S. (*Stoliczkaia*) *tenuis* is so far known only from the Upper Albian of Switzerland and Angola.

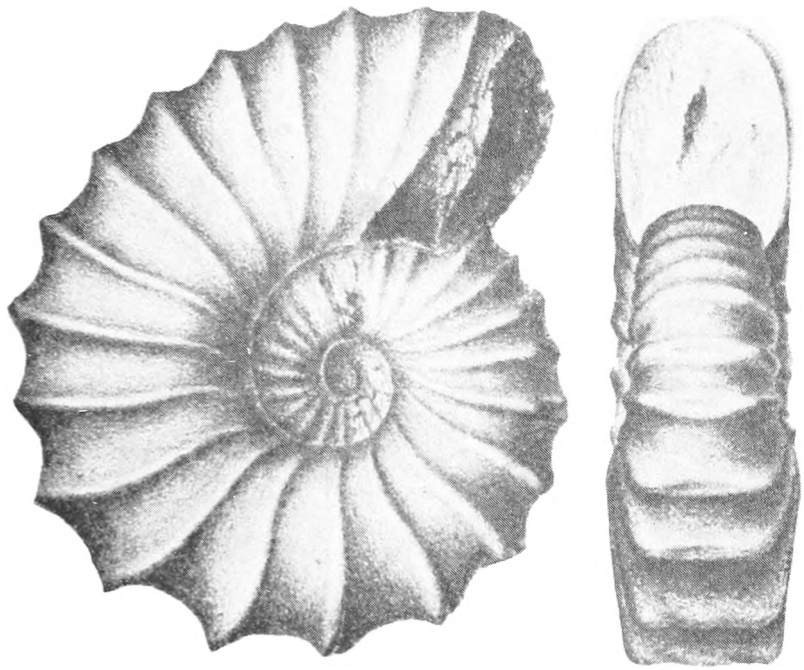

Fig. 59. *Stoliczkaia crotaloides* (Stoliczka). Copy of Stoliczka 1864, pl. 46 (fig. 3–3a). ×1.

Family **Brancoceratidae** Spath, 1934

Subfamily Brancoceratinae Spath, 1934

Genus *Hysteroceras* Hyatt, 1900

Type species *Ammonites varicosus* J. de C. Sowerby, 1824

Discussion

Hysteroceras is typically a low Upper Albian micromorph genus, clearly descended from the earlier *Brancoceras*, and has generally been regarded as characteristic of, and largely confined to, the *Mortoniceras inflatum* Zone. However, micromorph brancoceratids persist into the highest levels of Albian where they have generally been referred to as *Spathiceras* or *Mortoniceras* (*Cantabrigites*).

Whitehouse (1927: 110) introduced *Spathiceras* without formal diagnosis, merely naming as type of the genus *Hystrichoceras antipodeum* Etheridge (1902: 47, pl. 7 (figs 6–7)). The holotype of *S. antipodeum* is from the Upper Albian of Point Charles, near Darwin, Northern Australia, where it occurs associated with *Desmoceras latidorsatum* (Michelin) (= *D. carolensis* Etheridge 1902, pl. 7 (figs 2–5)), *Idiohamites* cf. *spinulosus* (J. Sowerby) (= *Ancyloceras* (?) sp. ind., Etheridge 1902, pl. 7 (figs 14–15)), *Scaphites eruciformis* Etheridge (very close to *S. simplex* Jukes-Browne), *Hamites* cf. *virgulatus* (Brongniart) (= *Hamites* (?) sp. ind., Etheridge 1902, pl. 7 (figs 12–13)), *Aucellina gryphaeoides* (J. de C. Sowerby) (= *A. incurva* Etheridge), together with the genera *Beudanticeras*, *Labeceras*, *Myloceras*, *Anisoceras* and *Ptychoceras* (Whitehouse 1928). Because

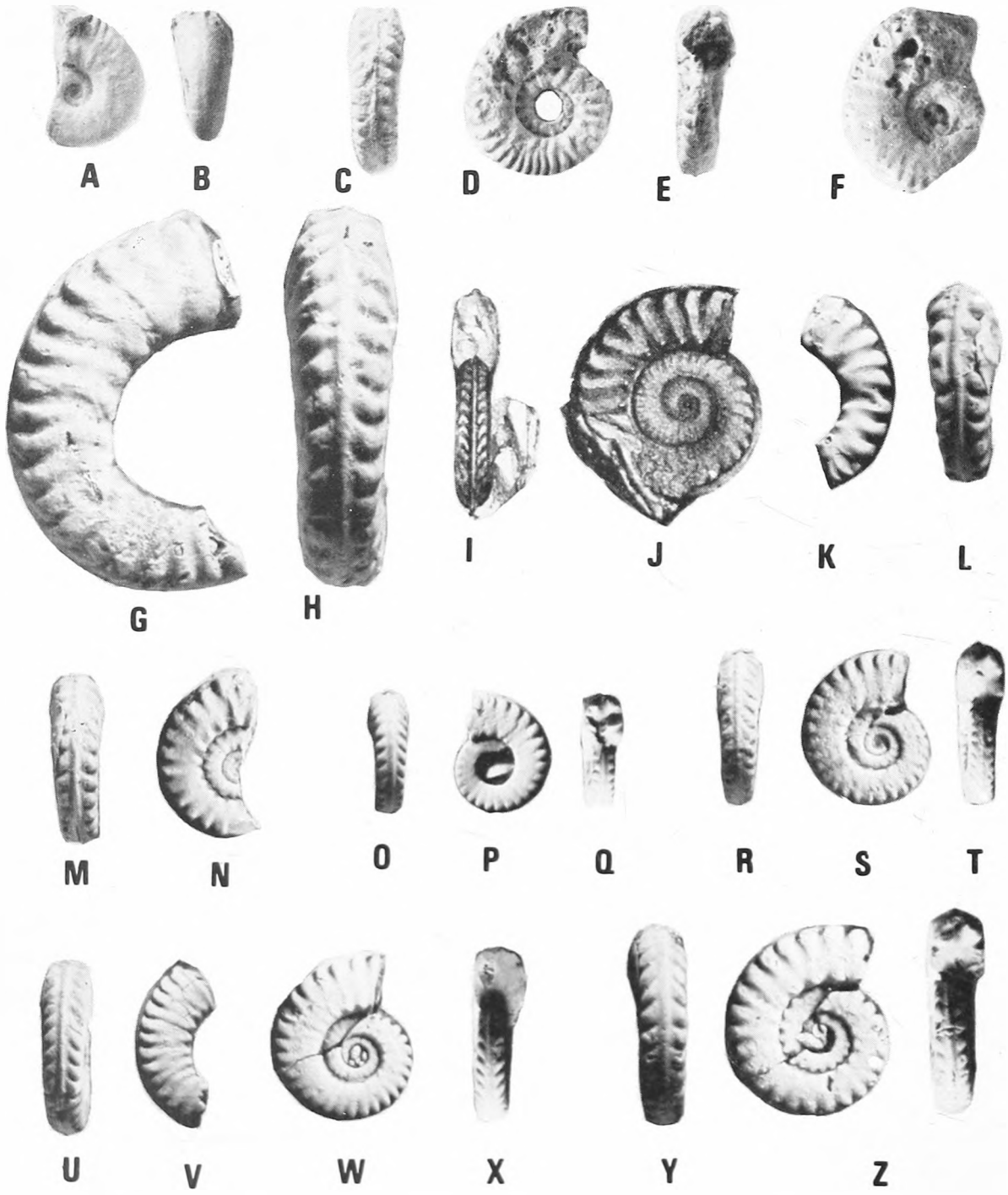

Fig. 60. *Hysteroceras?* spp. juv. A–B. USNMNH 237018. C–E. USNMNH 237017. F. *Hysteroceras?* cf. *ootatoorense* (Stoliczka), USNMNN 237016. G–H, K–Z. *Hysteroceras antipodeum* (Etheridge), a series of limonitic specimens from northern Australia. G–H. BMNH C26539. K–L. BMNH C26551. M–N. BMNH C26523. O–Q. BMNH C26552. R–T. BMNH C26548. U–V. BMNH C26518. W–X. BMNH C26546. Y–Z. BMNH C35269. I–J. *Hysteroceras? ootatoorense* (Stoliczka). Copy of Stoliczka 1865, pl. 32 (fig. 2). All ×1.

Whitehouse (1928: 279) considered the fauna to be '. . . typical of the *substuderi* Zone of the Upper Albian', the name *Spathiceras* has been applied to all flat-sided, weakly tuberculate micromorph mortoniceratinids of uppermost Albian age. However, the genera *Labeceras*, *Myloceras* and *Beudanticeras* are nowhere known to range above the *Mortoniceras inflatum* Zone, and the faunas recorded by Etheridge (1902) and Whitehouse (1927) seem to be typical low Upper Albian (approximately *varicosum* Subzone) assemblages. It is, perhaps, not coincidental, therefore, that *S. antipodeum* (Fig. 60K–Z) bears a remarkable resemblance to *Hysteroceras* of the *binum-subbinum* group, from which it differs only in being consistently more evolute (umbilicus 40–45 % of the diameter). The differences are not sufficient for generic separation, and *Spathiceras* is considered a junior subjective synonym of *Hysteroceras*. There is no good evidence for Cenomanian occurrences of the genus.

We are left, therefore, only with *Hysteroceras* for those uppermost Albian mortoniceratinid micromorphs with an evolute shell, and undivided ventrolateral tubercles. Either these represent a continuation of the *Hysteroceras* stock, or they represent an unnamed homoeomorphic development. Until better and larger collections are known, the authors prefer to follow Renz (1968) and refer their material to *Hysteroceras*.

Hysteroceras? cf. *ootaturense* (Stoliczka, 1865)

Fig. 60E–F, I–J

Compare

Ammonites ootaturensis Stoliczka, 1865: 56, pl. 32 (fig. 2).

Mortoniceras ootaturense (Stoliczka) Pervinquière, 1910: 64, pl. 6 (figs 2–5).

Spathiceras ootaturense (Stoliczka) Spath, 1934: 444, 445, fig. 160h. Breistroffer, 1940: 75.

? Pervinquieria (?) sp. nov. Breistroffer, 1940: 75.

Material

A single specimen, USNMNH 237016, with recrystallized shell preserved, although somewhat corroded, from Porto Amboim.

Description

Shell small, evolute, with a wide, shallow umbilicus, steep umbilical walls and evenly rounded umbilical shoulder. The whorl section is subquadrate, compressed with flattened flanks. Ribbing is very weak on the inner flank, but strengthens markedly over the ventrolateral shoulder, whilst there is a prominent keel.

Discussion

Stoliczka's (1865) type (Fig. 60I–J) comes from a locality 'near Odium', from where he also records other typical uppermost Albian species such as *M.* (*Mariella*) *bergeri* (Brongniart), *M.* (*M.*) *circumtaeniatus* (Kossmat),

Anisoceras perarmatum Pictet & Campiche, *D.* (*Desmoceras*) *latidorsatum* (Michelin), and *Lechites gaudini* (Pictet). *Ammonites ootaturense* is probably, therefore, of latest Albian age, although Stoliczka's record of *Turrilites costatus* Lamarck and *Neoptychites xetra* (Stoliczka) from the same locality suggests the presence of beds as high as the Lower Turonian in the vicinity.

Hysteroceras antipodeum (Etheridge) (Fig. 60G–H, K–Z) differs from the Angolan specimen in being somewhat older, with a wider umbilicus, flatter flanks and more prominent umbilical tubercles. The specimen of *Schloenbachia rostratus* var. *antipodeus* (Etheridge) figured by Etheridge (1909, pl. 67 (figs 3–4)) (*non* Etheridge 1902) was referred to *Dipoloceras bouchardianum* (d'Orbigny) by Stieler (1920), but was renamed *Prohysteroceras richardsi* var. *nitidum* by Whitehouse (1926). However, Etheridge's specimen appears indistinguishable from *Dipoloceras quadratum* Spath (1921: 278, pl. 25 (fig. 3)).

Hysteroceras? nanum Renz (1968: 63, pl. 11 (fig. 4), fig. 22c–d) differs from *H? ootaturense* in having prominent umbilical tubercles at an early stage. The specimen of *H. semileve* Haas recorded by Renz (1968: 63, pl. 11 (fig. 6), fig. 22g–h) from the 'Unteren Vraconnien' appears to be based upon a larger fragment of his *H.? nanum*.

Hysteroceras? tunisiense (Spath) (nom. nov. pro *Mortoniceras inflatum* var. *orientalis* (?) Pervinquière (*non* Kossmat) 1907: 229, pl. 11 (fig. 2)) differs from *H? ootaturense* and the present specimen in having sharp, flexuous prorsiradiate ribs which bifurcate from distinct umbilical bullae at only 17 mm diameter.

Hysteroceras? wenoense (Adkins) (1928: 229, pl. 20 (fig. 13)) differs from the authors' material in its sharp ribbing and distinct umbilical tubercles. The specimen figured by Renz (1968: 62, pl. 11 (fig. 5)) as *Hysteroceras* cf. *subbinum* Spath may possibly belong here.

'*Algericeras*' *boghariense* (Coquand) (Pervinquière 1907: 240, pl. 11 (fig. 16)) differs from the present specimen in having a quadrate whorl section ($^{W}/_{H}$ = 1,00) with dense, fine, straight ribs, about thirty-two per half whorl, which arise in pairs from umbilical bullae and terminate in ventrolateral tubercles. It is said to be of Cenomanian age but appears merely to be based upon pyritic nuclei of *Mortoniceras*.

Occurrence

Hysteroceras? ootaturense is known from the Upper (? uppermost) Albian of southern India, and possibly the uppermost Albian of France, Algeria and Angola.

Subfamily Mortoniceratinae Spath, 1925

Genus *Mortoniceras* Meek, 1876

Subgenus *Durnovarites* Spath, 1932

Type species *Subschloenbachia perinflata* Spath, 1921

Discussion

Wiedmann & Dieni (1968: 142) have divided the subgenus *Durnovarites* into two species groups:

1. The group of *M.* (*D.*) *subquadratum*, characterized by four rows of tubercles on the ribs. To this group may be assigned *M.* (*D.*) *subquadratum* Spath, *M.* (*D.*) *quadratum* Spath, *M.* (*D.*) *perinflatum* (Spath), *M.* (*D.*) *postinflatum* Spath, *M.* (*D.*) *depressum* (Spath), *M.* (*D.*) *adkinsi* (Young), *M.* (*D.*) *vraconense* Renz, *M.* (*D.*) *spinosum* (van Hoepen *non* Pervinquière), *M.* (*D.*) *subnanum* (Breistroffer), *M.* (*D.*) *ishiguaense* Reyment, *M.* (*D.*) *levecostatum* Reyment, *M.* (*?D.*) *crassicornutum* (Reyment), *M.* (*D.*) *lowrii* McLearn, *M.* (*D.*) *downii* McLearn, *M.* (*D.*) *rerati* Collignon and *M.* (*D.*) *haueri* Collignon.
2. The group of *M.* (*D.*) *spinosum*, with only three rows of tubercles and subordinate ribbing (appears merely to be based upon juveniles which have still to develop the fourth row of tubercles). To this group belong *M.* (*D.*) *spinosum* (Pervinquière), *M.* (*D.*) *kentronotum* Spath, *M.* (*D.*) *lemoinei* (Spath), *M.* (*D.*) *neokentroides* Wiedmann & Dieni and *M.* (*D.*) *aubersonense* Renz.

Mortoniceras (*Durnovarites*) *perinflatum* (Spath, 1922)
Figs 3G, 61, 62D–I, 63–64

Ammonites inflatus Pictet & Campiche (*non* J. Sowerby), 1860: 178, pl. 21 (fig. 5), pl. 22 (fig. 3).
Inflaticeras ('*Subschloenbachia*') *perinflatum* Spath, 1922: 113.
? Inflaticeras (*Subschloenbachia*) *depressum* Spath, 1922: 114, figs B, 2a–d.
Inflaticeras (*Subschloenbachia*) *quadratum* Spath, 1922: 115.
Pervinquieria quadrata (Spath) Spath, 1926*b*: 423.
? Pervinquieria depressa (Spath) Spath, 1928: 51.
Mortoniceras (*Durnovarites*) *perinflatum* (Spath) Spath, 1933: 430, pl. 40 (fig. 2), fig. 150. Wiedmann & Dieni, 1968: 143, pl. 14 (figs 3–4), fig. 92. Renz, 1968: 51, pl. 8 (figs 3, 5, 8), pl. 9 (figs 1–2), figs 17a, 18c, 19c, f. Marcinowski & Naidin, 1976: 109, pl. 6 (figs 1–2).
Mortoniceras (*Durnovarites*) *quadratum* (Spath) Spath, 1933: 432, pl. 45 (fig. 3), pl. 46 (fig. 6), pl. 49 (fig. 12). Reyment, 1955: 38, pl. 6 (figs 4–5), pl. 7 (fig. 3), fig. 15. Wiedmann & Dieni, 1968: 145, fig. 93.
Mortoniceras (*Durnovarites*) *postinflatum* Spath, 1933: 433, pl. 40 (figs 3–5), pl. 46 (figs 3, 7), pl. 47 (fig. 6). Renz, 1968: 53, pl. 8 (figs 1–2, 6), figs 17b, d, 18b, 19a–b, d. Marcinowski & Naidin, 1976: 109, pl. 7 (fig. 1), pl. 8 (fig. 1).
? Mortoniceras (*Durnovarites*) *depressum* (Spath) Collignon (*in* Besairie), 1936: 195. Reyment, 1955: 37, pl. 7 (fig. 4), fig. 14.
Durnovarites adkinsi Young, 1957: 6, pl. 1 (figs 3, 6).
Mortoniceras (*Durnovarites*) *vraconense* Renz, 1968: 54, pl. 7 (figs 6–7, 11), fig. 19e. Marcinowski & Naidin, 1976: 111, pl. 9 (fig. 1).

Material

Two specimens, USNMNH 237021–22, both with recrystallized shell preserved from Porto Amboim, together with three specimens, SAM–PCA4802, 4576 and 4587, from Cabo Ledo.

Fig. 61. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). The holotype, Pictet collection, Natural History Museum, Geneva. From the Upper Albian of Vraconne, Switzerland. ×1.

Description

The shell is moderately inflated and rather evolute (umbilicus 32–36% of the diameter), with a wide, shallow umbilicus and steep umbilical walls. The whorl section is almost quadrate ($^{W}/_{H}$ = 0,93–1,05), with subparallel flanks. The umbilical shoulder is evenly rounded intercostally. Ribs begin at the umbilical seam and are rectiradiate to the umbilical shoulder where they terminate in weak bullae. The latter give rise to 1–2 prorsiradiate flank ribs, 38–43 per whorl and broader than the interspaces. All ribs are ornamented by a midlateral tubercle and closely spaced upper and lower ventrolateral tubercles. On the venter, the ribs pass forwards, finally becoming effaced in the sulci bordering the siphonal keel. The ribs show spiral ornament which is especially prominent on the ventrolateral tubercles.

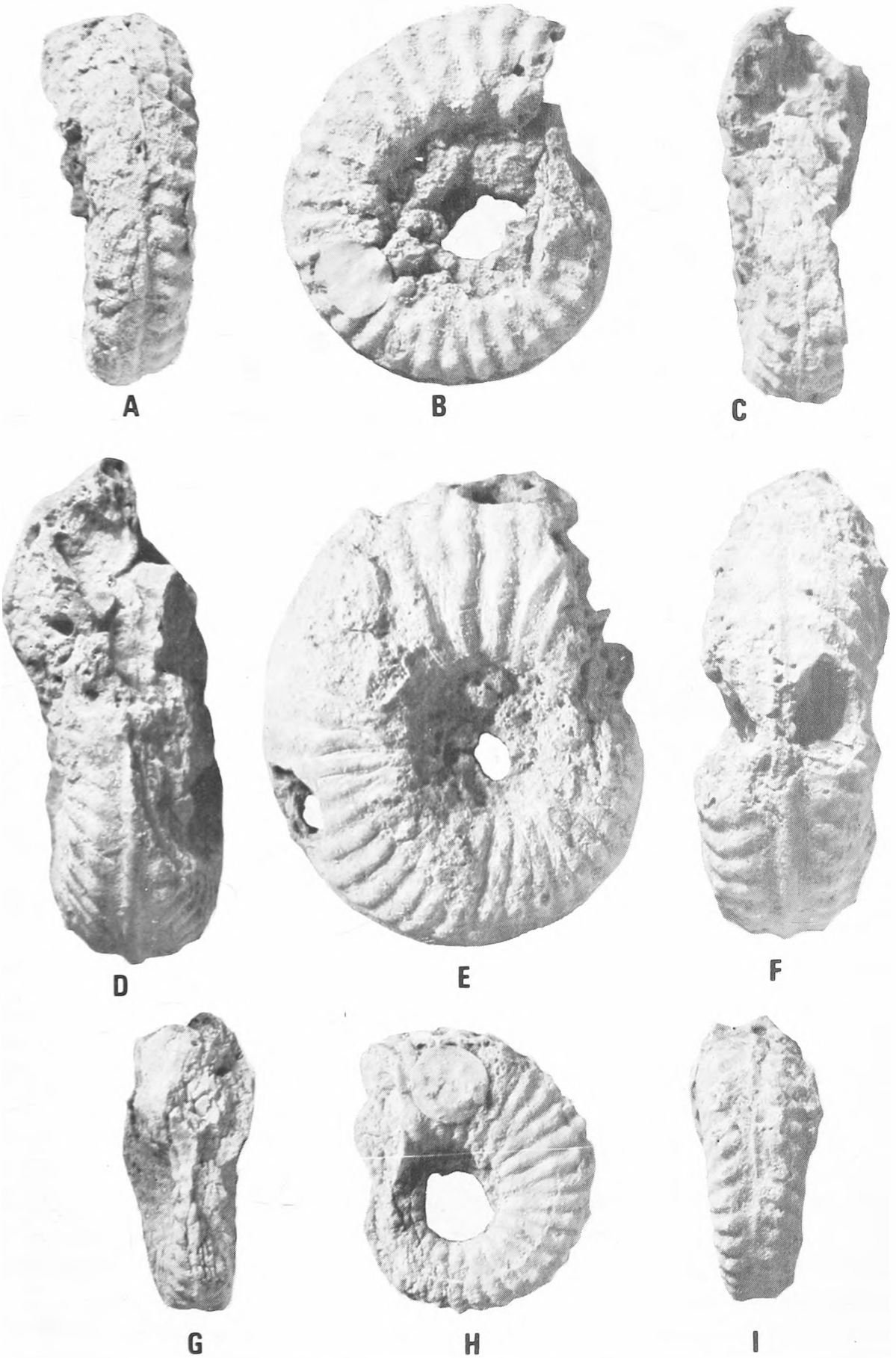

Fig. 62. A–C. *Mortoniceras* (*Durnovarites*) *subquadratum* Spath, USNMNH 237023. D–I. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). D–F. USNMNH 237021. G–I. USNMNH 237022. ×1.

Fig. 63. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). Ventral and lateral views of SAM-PCA4802. ×1.

Measurements

No.	D	H	W	W/H	U
USNMNH 237021	53	22,5(42)	?	?	17(32)
,,	44	±19(43)	±20(45)	1,05	?
USNMNH 237022	35	±16(46)	±15(43)	0,93	12,5(36)

Discussion

Renz (1968) showed *M.* (*D.*) *quadratum* to be based upon juveniles of *M.* (*D.*) *perinflatum*, whilst *M.* (*D.*) *vraconense* appears to comprise hyponodose adults which the authors do not consider to bear specific separation from *M.* (*D.*) *perinflatum*.

Similarly, *M.* (*D.*) *postinflatum* differs from the strictly contemporaneous *M.* (*D.*) *perinflatum* only by its more prominent ventrolateral tubercles and more inflated whorls ($^{W}/_{H}$ = 1,20–1,65). The authors do not regard the differences as sufficient for specific separation and place *M.* (*D.*) *postinflatum* within the synonomy of *M.* (*D.*) *perinflatum*, although the name might usefully be retained at the varietal level.

Durnovarites adkinsi Young was separated from *M.* (*D.*) *perinflatum* on the basis of its slightly rounder ribs, less tumid flanks, and denser-ribbed inner

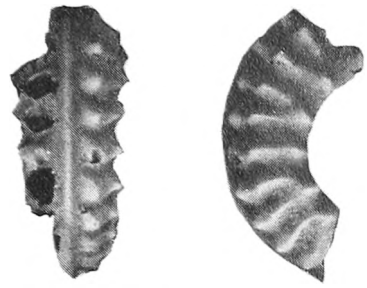

Fig. 64. *Mortoniceras* (*Durnovarites*) *perinflatum* (Spath). The holotype of *Durnovarites spinosus* van Hoepen, SAM–D3154, from the Upper Albian of the Mzinene Formation, Zululand. ×1.

whorls. The differences appear to be those between individuals, and the Texas species is considered to be referable to *M.* (*D.*) *perinflatum*.

Mortoniceras (*Durnovarites*) *depressum* (Spath) was said to differ from *M.* (*D.*) *quadratum* in its far more depressed whorl section, with rounded instead of parallel flanks. It closely approaches *M.* (*D.*) *postinflatum* and may, therefore, be no more than an extreme variant of *M.* (*D.*) *perinflatum*.

Occurrence

Mortoniceras (*Durnovarites*) *perinflatum* is known from the uppermost Albian of Switzerland, Poland, southern England, Sardinia, Texas, Nigeria and Angola. The authors have also seen comparable material from Zululand.

Mortoniceras (*Durnovarites*) *subquadratum* Spath, 1933
Figs 62A–C, 65C–D

? Subschloenbachia meunieri Spath, 1922: 115.
? Mortoniceras (*Durnovarites*) *meunieri* (Spath), Spath 1932: 399.
Mortoniceras (*Durnovarites*) *subquadratum* Spath, 1933: 435, pl. 42 (fig. 5), pl. 43 (fig. 1), pl. 44 (fig. 6), pl. 45 (fig. 5), pl. 47 (figs 2–4), pl. 48 (fig. 2). Reyment, 1955: 38. Dieni & Massari, 1963: 798. Wiedmann & Dieni, 1968: 142, pl. 13 (fig. 9), fig. 90. Renz, 1968: 55, pl. 7 (figs 8, 10), pl. 10 (figs 1–4, 7–8), fig. 17f_1–f_2. Marcinowski & Naidin, 1976: 110, pl. 6 (fig. 3).
Mortoniceras (*Durnovarites*) *subquadratum* var. *tumida* Spath, 1933: 435, pl. 48 (fig. 4). Wiedmann & Dieni, 1968: 143, pl. 13 (fig. 10), fig. 91.
Mortoniceras (*Durnovarites*) *subquadratum* var. *crassicostata* Spath, 1933: 432, pl. 42 (fig. 9).
? Mortoniceras (*Pervinquieria*) sp. juv., Spath, 1933: 412, pl. 41 (fig. 7).
? Pervinquieria (*Cantabrigites ?*) *subnana* Breistroffer, 1947: 91.
Pervinquieria (*Durnovarites*) *subquadrata* (Spath) Breistroffer, 1947: 61.
Durnovarites spinosum van Hoepen, 1951: 324, figs 380–383.
? Mortoniceras (*Durnovarites*) *levecostatum* Reyment, 1955: 38, pl. 7 (fig. 2).
? Mortoniceras (*Durnovarites*) *subnanum* (Breistroffer) Renz, 1968: 56, pl. 10 (figs 5–6), fig. 17g.

Material

A single specimen, USNMNH 237023, with recrystallized shell preserved from Porto Amboim, and one, SAM–PCA3235, from Praia-Egito, preserved as an internal mould.

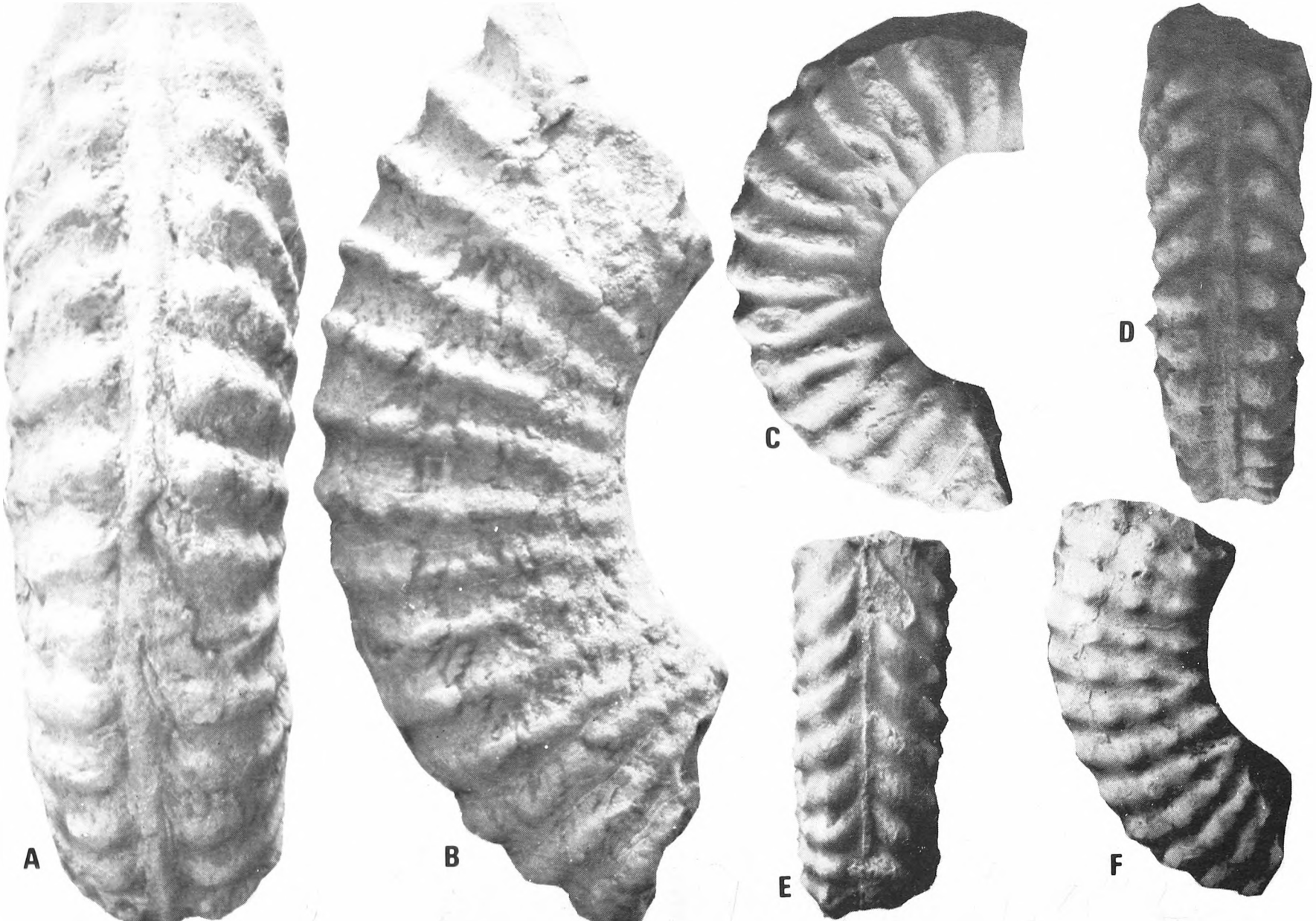

Fig. 65. A–B. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Ventral and lateral views of SAM–PCA3150. C–D. *Mortoniceras* (*Durnovarites*) *subquadratum* Spath. Lateral and ventral views of SAM–PCA3235. E–F. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. Ventral and lateral views of a paratype, SAM–PCA3309. ×1.

Description

The shell is very evolute (umbilicus 50% of diameter), compressed, with a slightly depressed, subquadrate whorl section ($^{W}/_{H}$ = 1,11). The umbilicus is wide, shallow, with steeply inclined walls and evenly rounded umbilical shoulders. The flanks are flattened, with maximum width close to the umbilical shoulder, and converge slightly to the broad venter.

There are 10 prominent, somewhat bullate umbilical tubercles per half-whorl, from which arise 1–2 rectiradiate to slightly rursiradiate ribs. Where single there is frequently an adjacent intercalated rib, so that there are 19 ribs per half-whorl. The ribs are thick, robust, about as wide as the interspaces, and are ornamented by closely spaced double ventrolateral tubercles. The lower ventrolateral tubercle is sharp and prominent, whereas the upper ventrolateral tubercle is more weakly developed and clavate. On the final third of the outer whorl (which is entirely septate), there is a weakly developed midlateral tubercle. The well-developed siphonal keel is separated from the upper ventrolateral clavi by prominent sulci. The ribs on the adoral portion of the outer whorl show weakly developed spiral ornament.

Measurements

No.	D	H	W	$^{W}/_{H}$	U
USNMNH 237023	46	13,5(29)	±15(33)	1,11	23(50)

Discussion

Mortoniceras (*Durnovarites*) *meunieri* (Spath) (1922: 115; 1932: 399) (nom. nov. pro *Ammonites inflatus* Meunier (*non* J. Sowerby) 1887: 61, pl. 1 (fig. 2)) is an evolute species with about 30 coarse, rectiradiate to slightly rursiradiate ribs arising singly or in pairs from umbilical tubercles, each ornamented with a prominent midlateral tubercle and a (?) double ventrolateral tubercle. Meunier (1888) figured his specimen only in lateral view, without description, and hence comparison is difficult. If it is, indeed, a *M.* (*Durnovarites*), then not only might it be a synonym of *M.* (*D.*) *subquadratum*, but it also has priority over that name.

This species differs from *M.* (*D.*) *perinflatum* (Spath) in its much wider umbilicus (43–50% as against 28–36%) and its typically less depressed whorl section ($^{W}/_{H}$ = 1,03–1,16). However, adults of *M.* (*D.*) *subquadratum* are unknown and until population studies are undertaken it is not known whether the differences are truly of specific importance.

Renz (1968) included *Durnovarites spinosum* van Hoepen (*non* Pervinquière) in the synonomy of *M.* (*D.*) *subquadratum*, an assignment with which the authors concur; the type is re-illustrated here as Figure 64.

Mortoniceras (*Durnovarites*) *ishiaguense* Reyment (1955: 38, pl. 7 (fig. 1)) is very close to *M.* (*D.*) *subquadratum* but is apparently much more densely ribbed. Since the Nigerian species is based upon a mature individual, it is not

directly comparable with *M.* (*D.*) *subquadratum* at the present time. *Mortoniceras* (*Durnovarites*) *levecostatum* Reyment (1955: 38, pl. 7 (fig. 2)) is based upon a somewhat distorted composite internal mould showing about twenty-six coarse, robust ribs per whorl and with a wide umbilicus. Judging from Reyment's (1955) description, it may not bear separation from *M.* (*D.*) *subquadratum.*

Occurrence

Mortoniceras (*Durnovarites*) *subquadratum* is known from southern England, Poland, Switzerland, Sardinia, Zululand, and Angola.

Mortoniceras* (*Durnovarites*) *collignoni sp. nov.

Figs 65E–F, 66–67, 68B–D, 69

Material

About a hundred specimens, in the South African Museum, Cape Town, from Praia-Egito. All are preserved as composite internal moulds.

Type material

SAM–PCA3227 is designated as holotype; paratypes are SAM–PCA2975, 3189, 3199, 3202, 3217, 3259, 3277, 3294, 3309, 3317 and 3407.

Etymology

For the late General Maurice Collignon who contributed so much to our knowledge of ammonite systematics, and who helped the authors with their studies in many ways.

Diagnosis

A densely ribbed species of *M.* (*Durnovarites*) characterized by a dramatic change in shell morphology on the adult body chamber. The phragmocone has a subrectangular, compressed whorl section and is ornamented with 36–42 rectiradiate to prorsiradiate ribs per whorl which frequently bifurcate from umbilical bullae and are all ornamented with midlateral and double ventrolateral tubercles. On the adult body chamber, however, all tuberculation is rapidly lost and the simple ribs develop a strong convex-adoral curvature, while the whorl section now becomes strongly compressed and lanceolate.

Description

Almost all the material has been crushed to varying degrees.

The coiling is evolute (umbilicus about 24–30% of diameter), with a more or less compressed whorl section from an early growth stage (Fig. 69). Up to the body chamber, the intercostal whorl section is generally subrectangular, compressed. On the body chamber, the flanks become strongly convergent and the whorl section eventually becomes lanceolate. The umbilicus is wide, shallow, with a steep umbilical wall on the inner whorls, and an evenly rounded umbilical shoulder. On the outer whorl, the umbilical wall becomes sloping and the umbilical shoulder is gently rounded.

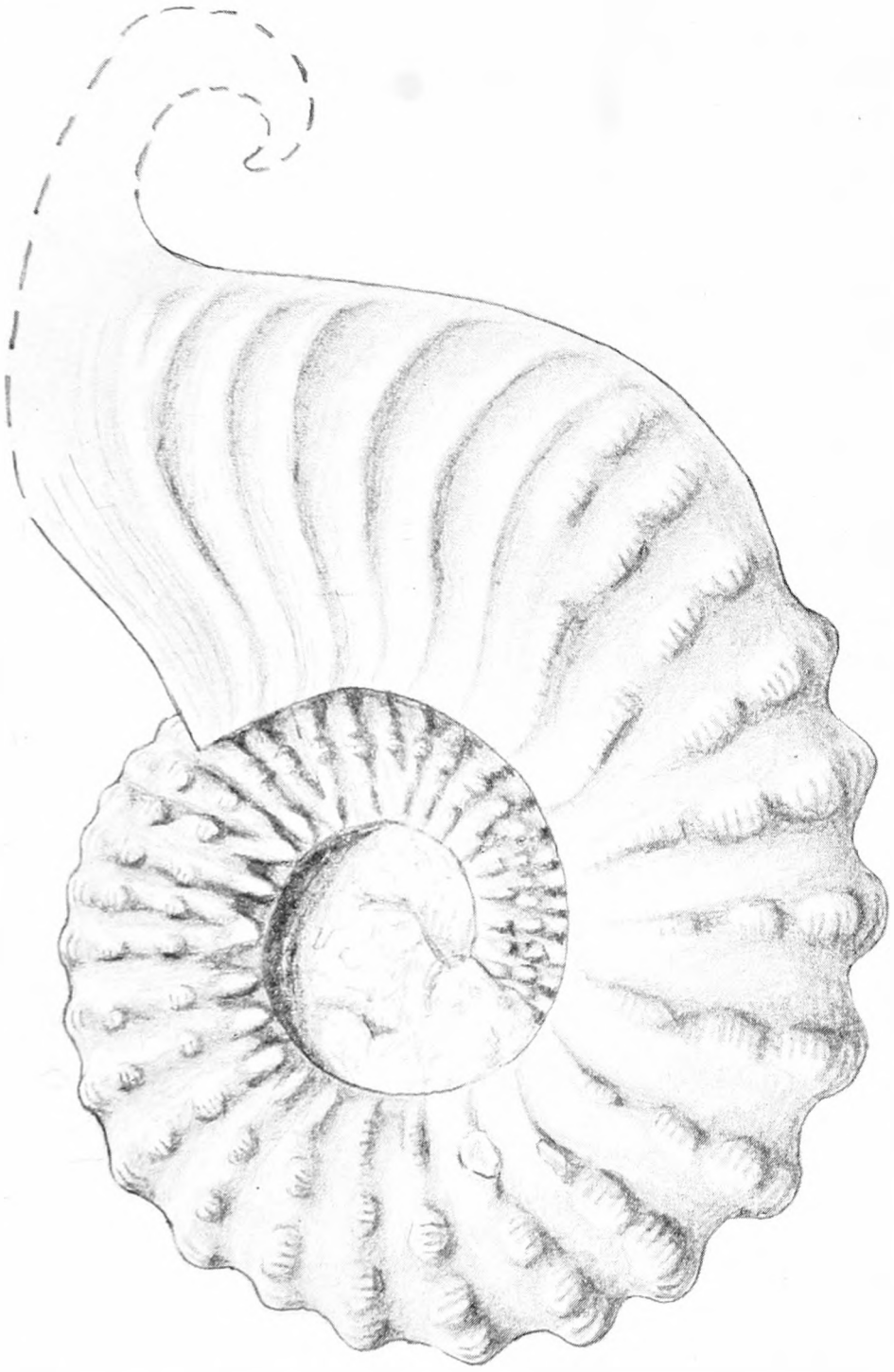

Fig. 66. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. A reconstruction based on the holotype and paratype material. ×0,66.

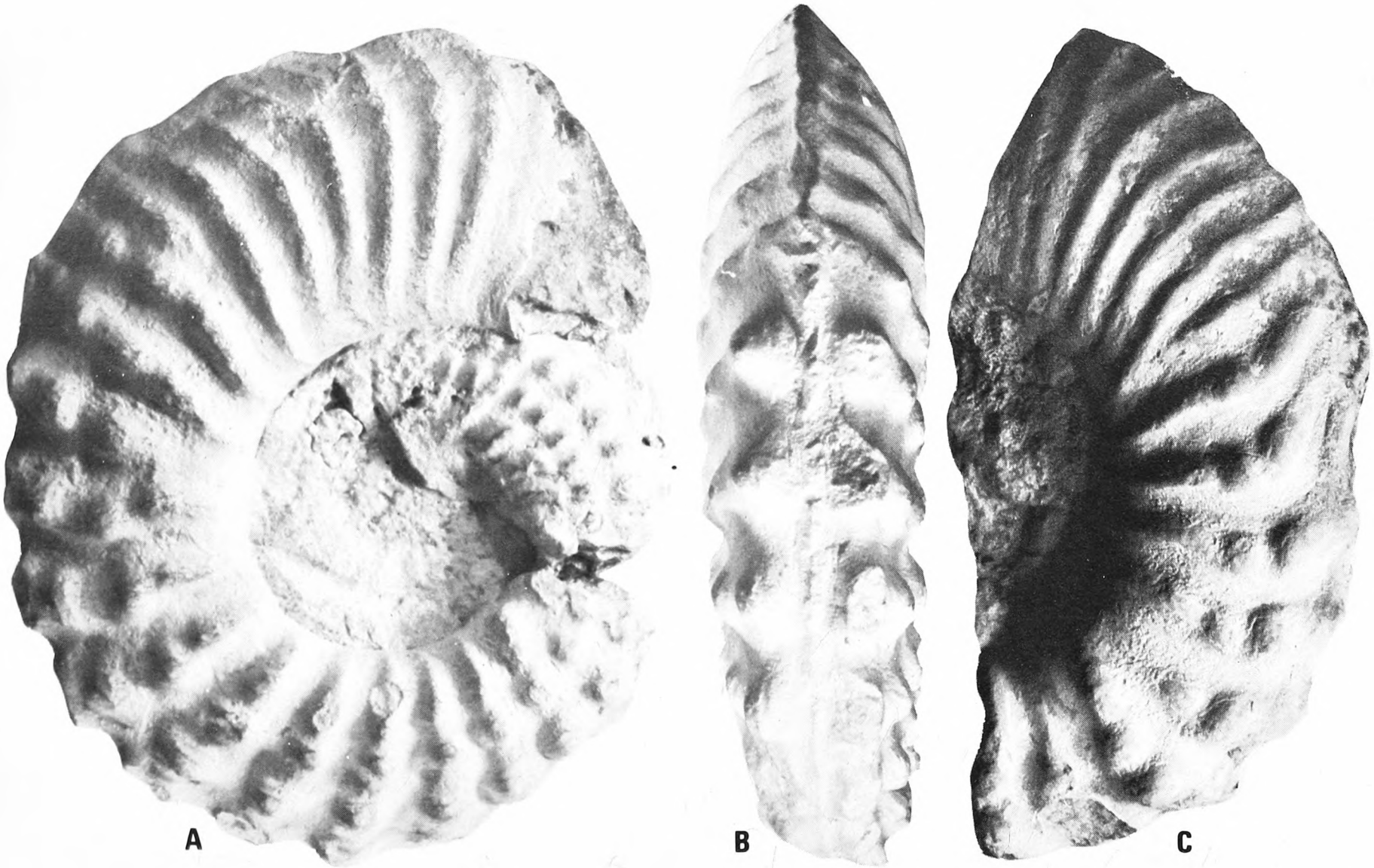

Fig. 67. A–C. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. A–B. Lateral and ventral views of the holotype, SAM–PCA3227, C. Lateral view of a paratype, SAM–PCA3278. A–B ×0,66, C ×1.

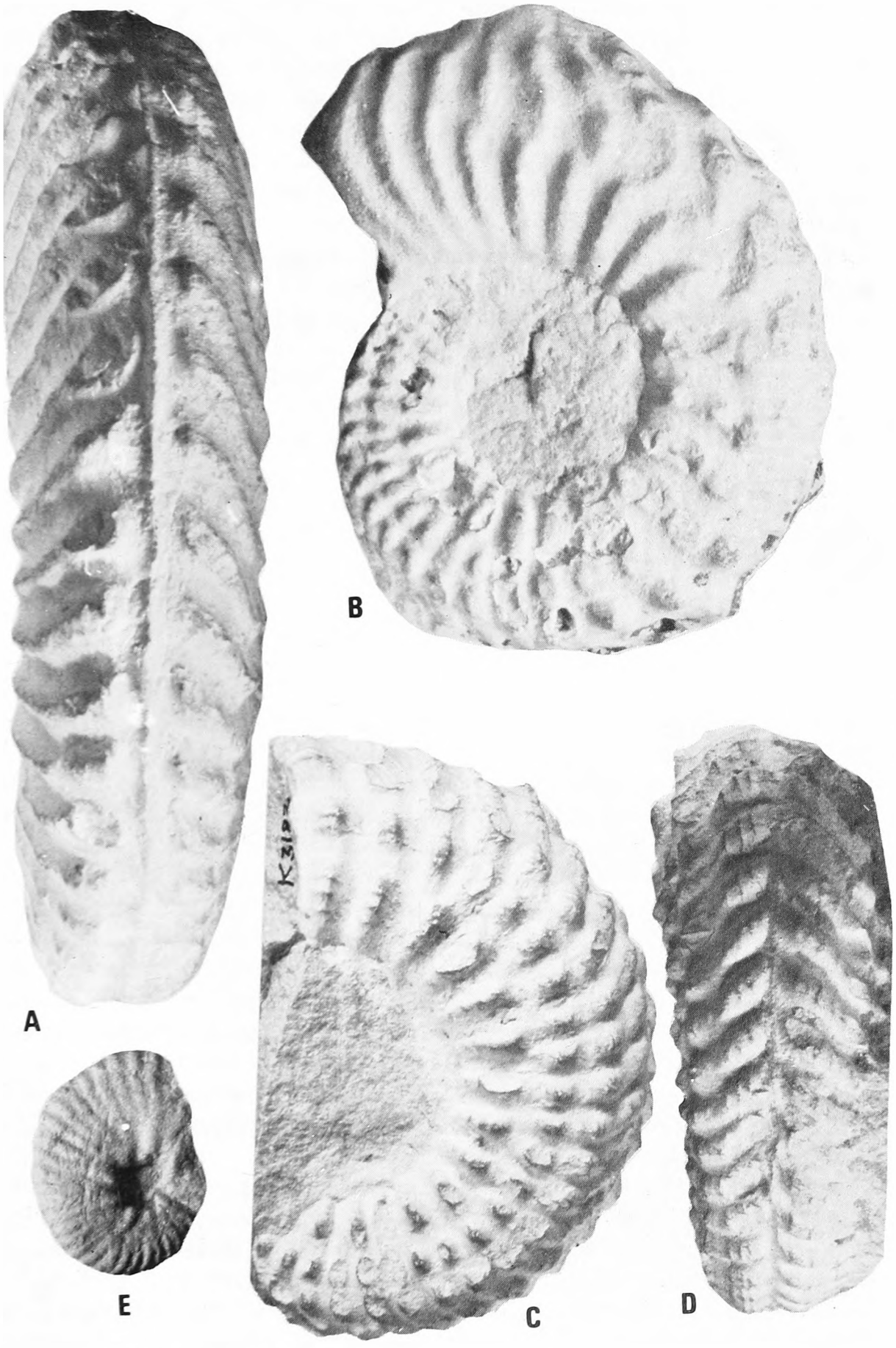

Fig. 68. A. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Ventral view of SAM–PCA3142. B–D. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. B. Lateral view of a paratype, SAM–PCA3269. C–D. Lateral and ventral views of a paratype, SAM–PCA3182. E. *Stoliczkaia tenuis* Renz. Lateral view of SAM–PCA3313. A–B ×0,66, C–E ×1.

In the earliest observed growth stages, the ribbing is generally simple, slightly prorsiradiate, with frequent intercalatories. All ribs are ornamented by distinct lateral and upper and lower ventrolateral tubercles, while long ribs arise from fairly prominent bullae. Even at this stage, spiral notching is evident on the tubercles. In the middle growth stages, the connections between the intercalated ribs and the umbilical bullae strengthen, and many ribs are seen to bifurcate from the latter, while the lateral and upper and lower ventrolateral tubercles become more swollen. At large growth stages, the ribbing again becomes simple but very subordinate to the now very swollen and prominent lateral and ventrolateral tubercles. At this stage, the lower lateral tubercle is somewhat clavate and the upper lateral and ventrolateral tubercles strongly so. The ventrolateral tubercles are now prominently raised above the narrow, sunken, keeled venter. On the last portion of the body chamber there is a great change in ornament. The whorl section changes from subrectangular to lanceolate, with the disappearance of all tubercles, and the ribs become strongly convex.

There are generally 36–42 ribs per whorl in the middle growth stages, about as wide as the interspaces, with somewhat fewer in juveniles and on the outer whorl.

Discussion

The body chamber ornament of this species is characteristic.

Mortoniceras (*Durnovarites*) *perinflatum* (Spath) (Renz 1968: 51, pl. 9 (fig. 1)) differs from *M.* (*D.*) *collignoni* sp. nov. in having a strongly depressed whorl section in maturity, whilst *M.* (*D.*) *subquadratum* Spath (1933: 435, pl. 37 (fig. 6)) differs from the Angolan species in being more evolute (umbilicus 40–48 % of the diameter) and in apparently lacking the dramatic change in body chamber ornament shown by *M.* (*D.*) *collignoni*.

Mortoniceras rostratum (J. Sowerby) (Fig. 70) differs from the present species in having sparser, more distant ribbing, whilst the ribs of the body chamber retain four rows of tubercles almost to the peristome.

Mortoniceras (*Durnovarites*) *ishiaguense* Reyment (1955: 38, pl. 7 (fig. 1)) differs from the present species in being more evolute, with less compressed whorls, and in apparently lacking the characteristic change in the body ornament seen in *M.* (*D.*) *collignoni*. *Mortoniceras levecostatum* Reyment (1955: 38, pl. 7 (fig. 2)) is from the same locality and horizon as *M.* (*S.*) *ishiaguense* but was said to differ in being more distantly ribbed, with more irregular ornament. The differences may not be of specific significance.

Howarth (1965) considered *Neokentroceras curvicornu crassicornutum* Reyment (1955: 41, pl. 4 (figs 7–8)) a species of *Durnovarites*, but Reyment (1955) records this form in association with a typical *N. curvicornu* Spath, and hence it is much older than typical *M.* (*Durnovarites*).

Mortoniceras (*Styphloceras*) *lowrii* McLearn (1972: 72, pl. 30 (figs 1–3), pl. 39 (figs 3–4)) and *M.* (*S.*) *downii* McLearn (1972: 73, pl. 31 (figs 1–3)) are

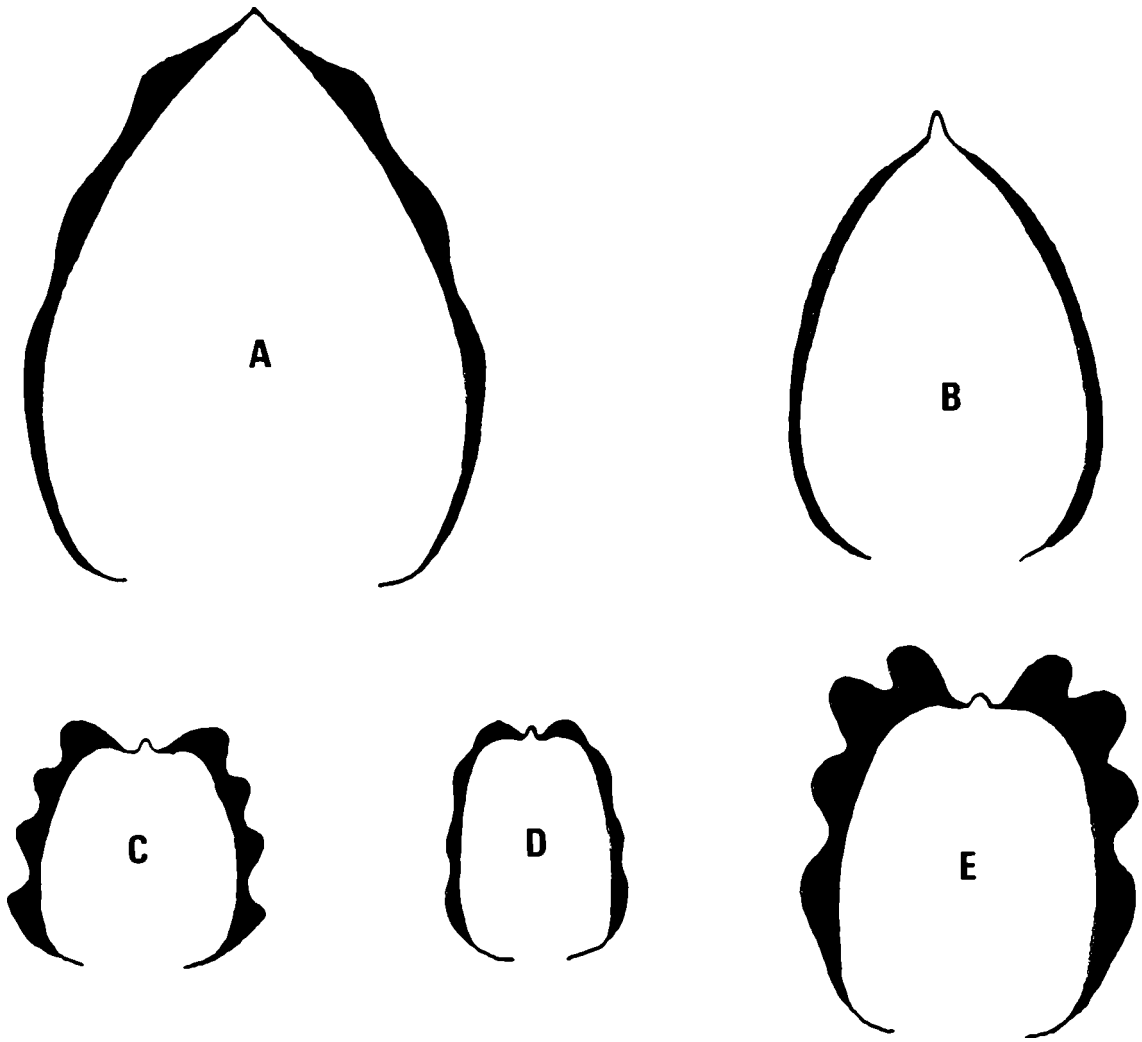

Fig. 69. *Mortoniceras* (*Durnovarites*) *collignoni* sp. nov. Whorl sections. A. SAM–PCA3202. B. SAM–PCA3309. C. SAM–PCA3278. D. SAM–PCA3257. E. SAM–PCA3309. ×1.

both species of *Durnovarites*, thus indicating the presence of uppermost Albian strata at the Skidegate Inlet, British Columbia. *Mortoniceras* (*Durnovarites*) *lowrii* differs from the present species in having very depressed inner whorls, somewhat more distant ribbing, and in lacking the modifications of the body chamber ornament seen in the Angolan species. *Mortoniceras* (*Durnovarites*) *downii* is based upon body chamber fragments. In its swollen, clavate tuberculation it approaches *M.* (*D.*) *collignoni*, but it appears to be more inflated, and shows no sign of the body chamber becoming lanceolate.

Mortoniceras (*Durnovarites*) *depressum* (Spath) (1922: 114, figs B, 2a–d) is based upon a body chamber fragment of a specimen about 50 mm in diameter. At this stage, the whorls are very depressed ($^{W}/_{H}$ = 1,41) and the fragment appears to have been very evolute. Slightly prorsiradiate ribs arise from prominent umbilical bullae and are indistinctly bifurcating, so as to appear alternating long and short. There are four rows of tubercles, with maximum width at mid-flank. This species would seem to be closely allied to *M.* (*D.*) *subquadratum* var. *tumidum* Spath; it differs from the Angolan material in being

Fig. 70. The holotype of J. Sowerby's *Ammonites rostratus*, from the Upper Greensand of Roak, near Benson, Oxfordshire. Oxford University Museum K835. ×0,75.

more coarsely ribbed and (?) more evolute, with a strongly depressed whorl section.

Mortoniceras (*Durnovarites*) *baueri* Collignon (1963: 159, pl. 305 (fig. 1311)) differs from *M.* (*D.*) *collignoni* sp. nov. in its coarse ribbing, depressed whorls, wide umbilicus and prominent umbilical tubercles. Its body chamber ornament is not known. *Mortoniceras* (*Durnovarites*) *rerati* Collignon (1963: 162, pl. 307 (figs 1312–1313)) differs from the Angolan material in much the same respects, but does not have the swollen umbilical tubercles of *M.* (*D.*) *baueri*. It very closely approaches *M.* (*D.*) *ishiaguense*.

Mortoniceras (*Durnovarites*) *subdepressum* Collignon (*in* Besairie 1936: 196, pl. 21 (figs 4–5)) is based upon a unique fragment with a very depressed whorl section. It was said to differ from *M.* (*D.*) *depressum* in having straighter ribs which are not projected forwards on the venter. It is more coarsely ribbed with a more depressed whorl section than *M.* (*D.*) *collignoni*.

Occurrence

Mortoniceras (*Durnovarites*) *collignoni* is known only from the uppermost Albian of Angola.

Subgenus *Angolaites* Spath, 1932
Type species *Subschloenbachia gregoryi* Spath, 1922

Discussion

Angolaites was separated as a subgenus of *Mortoniceras* (Spath 1932: 380) for '. . . serpenticones, with single costation from a very early stage, and two peripheral tubercles, close together'. The characters of the subgenus are consistent, making it an easily recognized and useful taxon.

Amongst mortoniceratinids, only *Drakeoceras* Young, 1957, and *Cantabrigites* Spath, 1933, have the same closely spaced ventrolateral tubercles whilst also lacking flank tubercles. *Drakeoceras* appears, however, to be a *Goodhallites* derivative characterized by its much narrower umbilicus and high whorls. The micromorph *Cantabrigites* is a contemporaneous form, abundant in western Europe where *Angolaites* is unknown, while the extreme rarity of *Cantabrigites* in Angola makes it unlikely that they represent sexual dimorphs.

Mortoniceras (*Angolaites*) *gregoryi* (Spath, 1922)
Figs 39G, 71, 72C, 73D

Subschloenbachia gregoryi Spath, 1922: 127, pl. 3 (fig. 1).
Mortoniceras (*Angolaites*) *gregoryi* (Spath) Reyment, 1955: 37, pl. 4 (fig. 13), pl. 6 (fig. 3).

Material

Three specimens, SAM–PCA3110, 3145 and 3235, from Praia-Egito, together with seven specimens from the Quissama Ridge of Cabo Ledo, SAM–PCA4601, 4608, 4611, 4626, 4685, 4712, and 4813, all preserved as composite internal moulds.

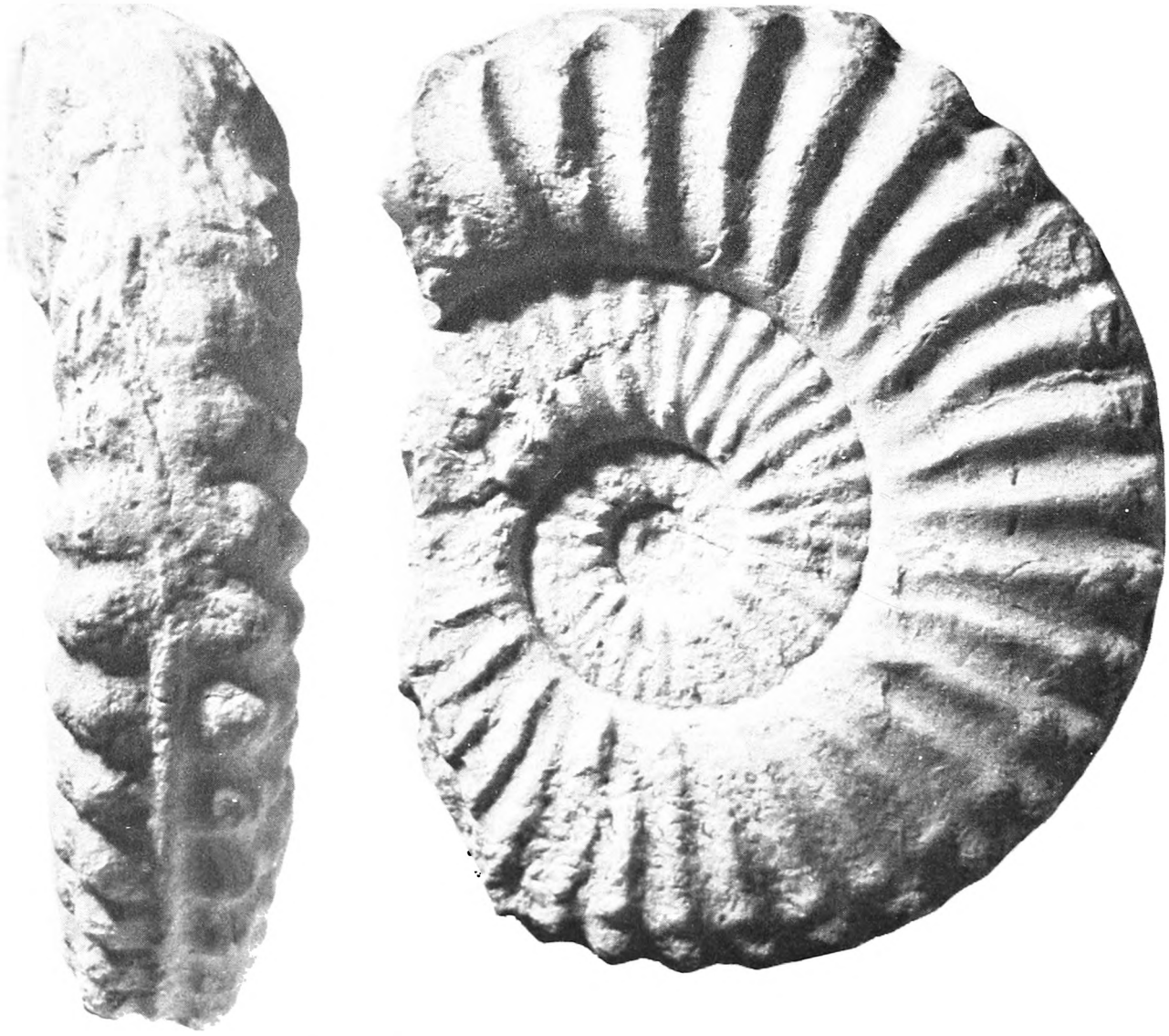

Fig. 71. *Mortoniceras* (*Angolaites*) *gregoryi* (Spath). The holotype, from the uppermost Albian at Catumbella, BMNH C20066. ×1.

Description

The shell is very evolute, compressed, with a wide, shallow umbilicus (42–47% of the diameter). The umbilical walls are gently rounded and the flanks are slightly convex intercostally, converging somewhat towards the venter, with greatest width slightly above the umbilical shoulder.

Ribs begin very weakly on the umbilical wall and pass radially outwards to the umbilical shoulder where they terminate in fairly prominent bullae, about seventeen per whorl. Each bulla gives rise to one to two flank ribs, with frequent intercalatories which become more abundant in maturity. Across the flanks the ribs are prorsiradiate and all are ornamented with closely spaced double ventrolateral tubercles. There are thirty-nine ventrolateral tubercles on the outer whorl, and the upper ventrolateral tubercles are spirally notched. The venter is moderately narrow, with shallow sulci on either side of the siphonal keel.

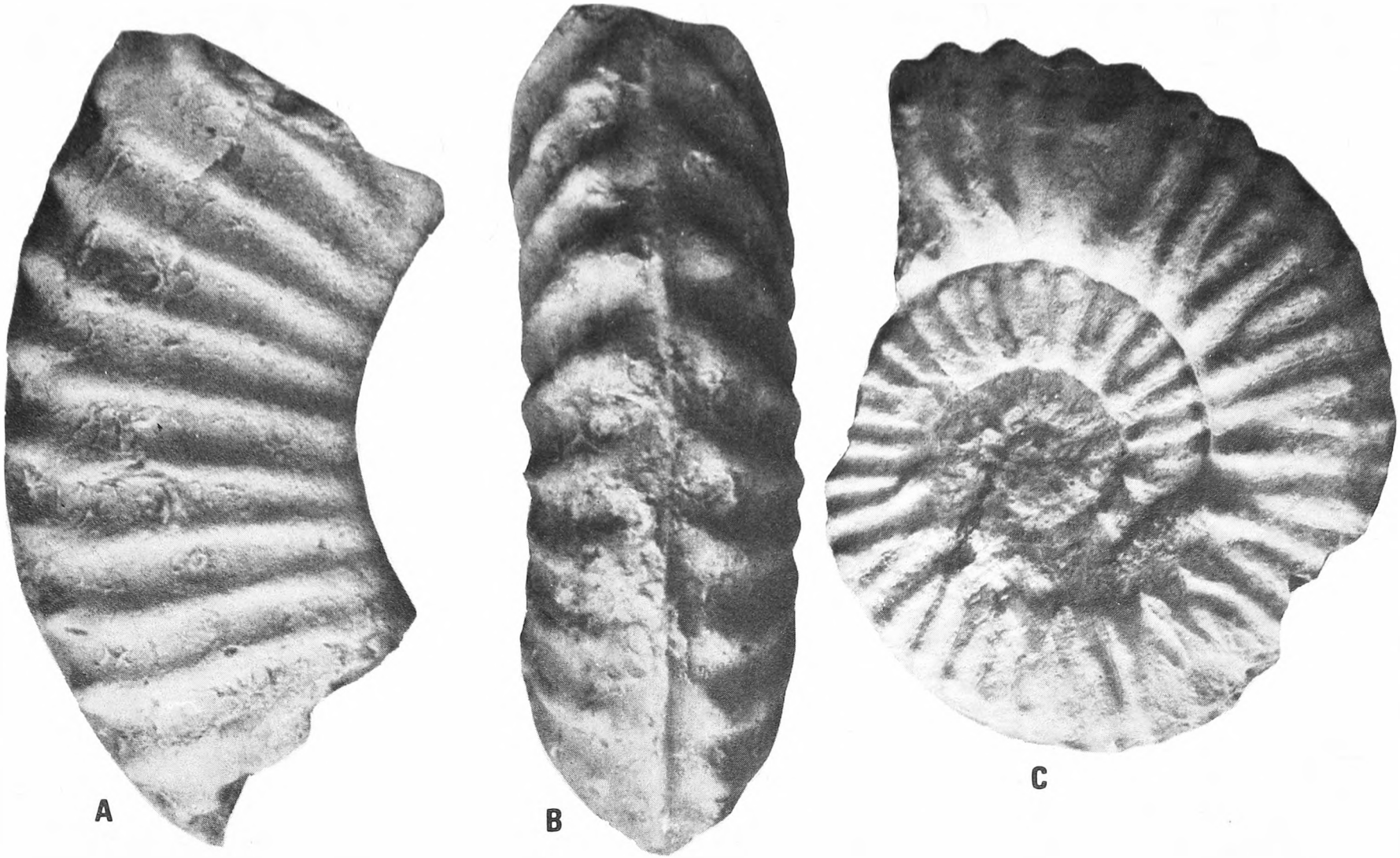

Fig. 72. A–B. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Lateral and ventral views of SAM–PCA3200. C. *Mortoniceras* (*Angolaites*) *gregoryi* (Spath). Lateral view of SAM–PCA3145. ×1.

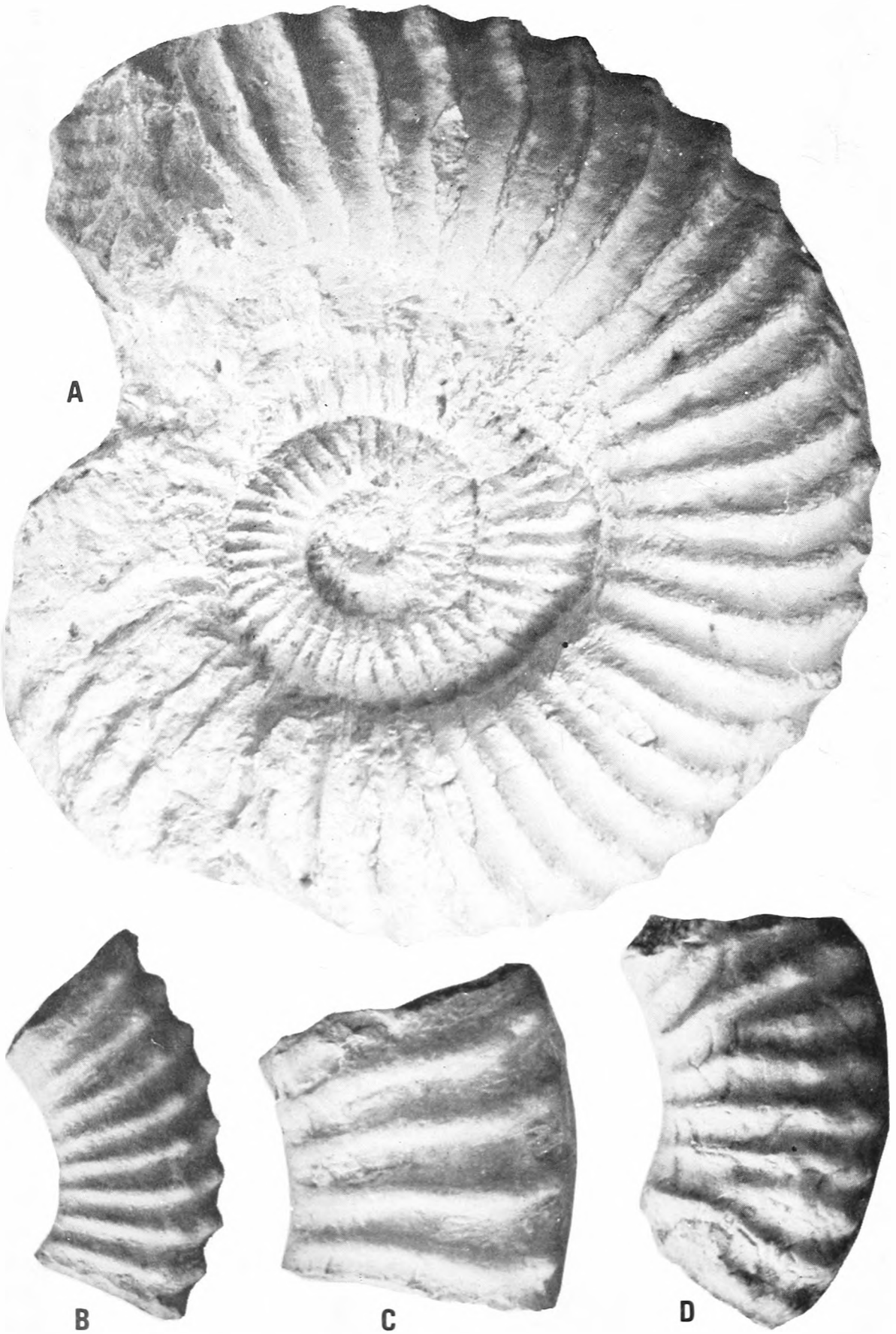

Fig. 73. A–C. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). A. Lateral view of SAM–PCA3142. B. Lateral view of SAM–PCA3153. C. Lateral view of SAM–PCA3114. D. *Mortoniceras* (*Angolaites*) *gregoryi* (Spath). Lateral view of SAM–PCA3147. A ×0,66, B–D ×1.

Measurements

No.	D	H	W	W/H	U
SAM–PCA3145	85	25(29)	20(24)	0,8	40(47)
,,	58	18(31)	—(—)	—	27(47)
SAM–PCA3235	67	22(32)	20(30)	0,9	28(42)

Discussion

Mortoniceras (*Angolaites*) *gregoryi* differs from *M.* (*A.*) *simplex* (Choffat) and *M.* (*A.*) *vicina* (Haas) in the common occurrence of bifurcating and intercalated ribs, and in having far fewer umbilical bullae.

Occurrence

Mortoniceras (*Angolaites*) *gregoryi* is known with certainty only from the Upper Albian of Angola and Nigeria.

Mortoniceras (*Angolaites*) *simplex* (Choffat, 1905)

Figs 3A–D, 54G–H, 72A–B, 73A–C, 74–77

Schloenbachia simplex Choffat, 1905: 35, pl. 4 (fig. 3).
Pervinquieria simplex var. *tenuis* Haas, 1942: 81, pl. 16 (fig. 1), figs 7e, 8a.
Inflaticeras sp. n. aff. *gregoryi* Spath, 1922: 127, pl. 3 (fig. 2).
Pervinquieria vicina Haas, 1942: 82, pl. 16 (fig. 2), fig. 8b.
Pervinquieria vicina var. *evoluta* Haas, 1942: 83, pl. 16 (fig. 3), fig. 8c.

Material

9 specimens, SAM–PCA3107, 3116, 3142, 3146, 3150, 3153, 3166, 3200 and 3249, from Praia-Egito, together with 30 specimens from the Quissama Ridge at Cabo Ledo, SAM–PCA4575, 4578–79, 4581–82, 4584–85, 4588, 4590, 4593–94, 4596, 4605, 4609, 4613, 4615–16, 4618, 4628, 4631, 4640, 4718, 4756, 4770, 4774, 4863, 4867–69, and 4874, all preserved as composite internal moulds.

Description

This species is abundant at Egito, with adult specimens attaining a diameter of 170 mm (SAM–PCA3142).

The shell is evolute, compressed, with the outer whorls only covering the preceding whorls to the top of the lower ventrolateral tubercles. The umbilicus is shallow and wide (41–47% of the diameter), with steep umbilical walls and well-rounded umbilical shoulders.

Ribbing begins at the umbilical seam, is rather faint at first, strengthening as it passes radially outwards to the umbilical shoulder. The ribs may strengthen slightly on the umbilical shoulder, but true umbilical tubercles are absent. In the immature growth stages, the flank ribs are slightly sinuous but on the final whorl they become adorally concave. Rare intercalated ribs occur only during the very early ontogenetic stages, and there are about twenty ribs per whorl. Lateral tubercles are lacking, but all ribs are ornamented with closely spaced double

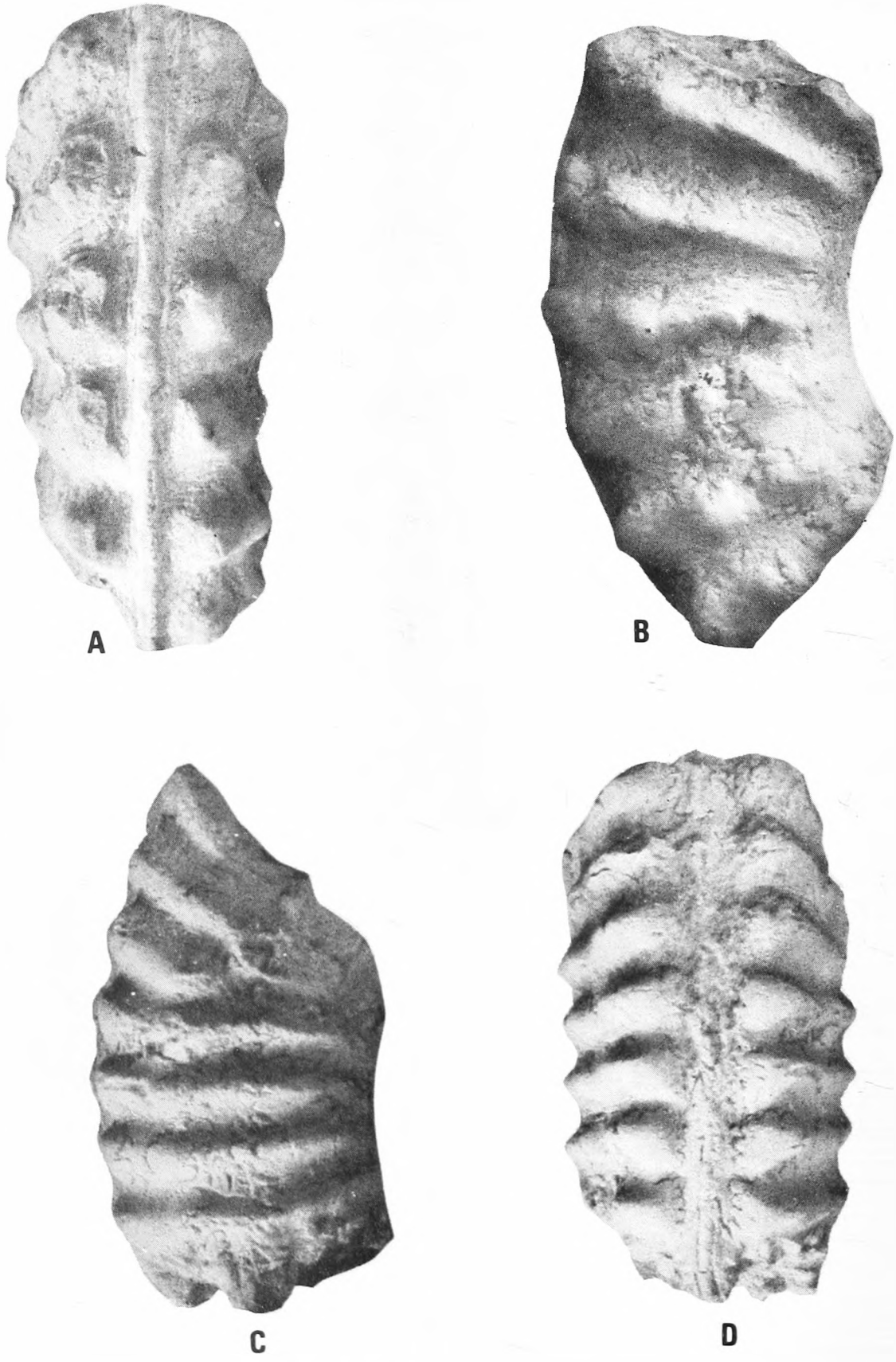

Fig. 74. A–B. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Ventral and lateral views of SAM–PCA3116. C–D. *Mortoniceras* (*Angolaites*) cf. *simplex* (Choffat). Lateral and ventral views of SAM–PCA3179. ×1.

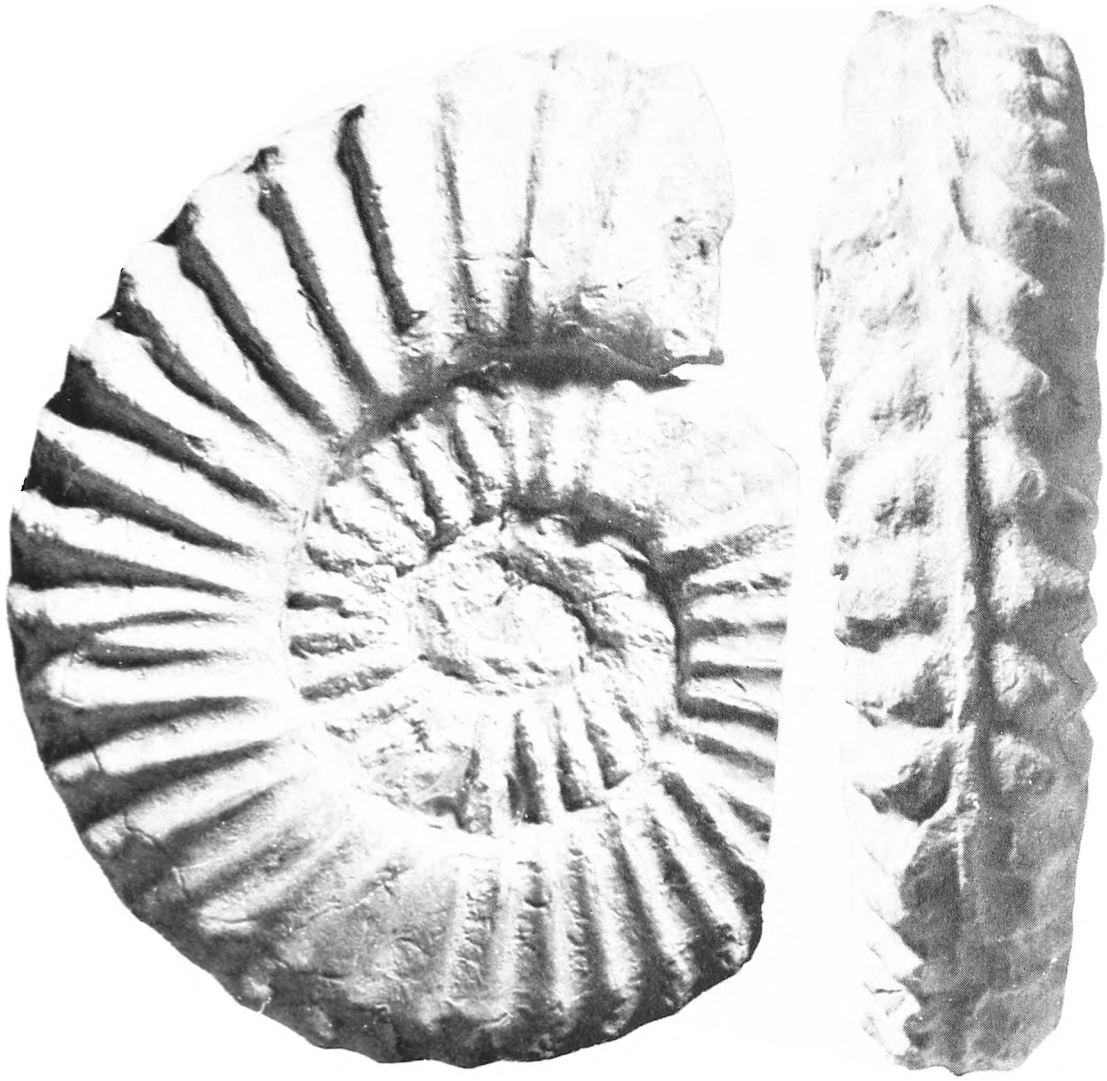

Fig. 75. *Mortoniceras* (*Angolaites*) *vicina* (Haas). The holotype BMNH–C20067. ×1.

ventrolateral tubercles which are spirally notched, especially the upper ventrolateral tubercle. The narrow, rounded venter is keeled, with smooth sulci on either side. At large growth stages, the ventrolateral tubercles stand somewhat above the level of the keel.

Measurements

No.	D	H	W	W/H	U
SAM–PCA3142	173	48(28)	41(24)	0,85	81(47)
,,	135	45(33)	35(26)	0,77	56(41)
SAM–PCA3107	91	31(34)	24(26)	0,77	37(41)
SAM–PCA3200	—	43(—)	33(—)	0,76	—
SAM–PCA3249	—	33(—)	26(—)	0,78	—
SAM–PCA3150	—	39(—)	35(—)	0,89	—
SAM–PCA3153	—	22(—)	19(—)	0,86	—
SAM–PCA3146	—	31(—)	26(—)	0,84	—

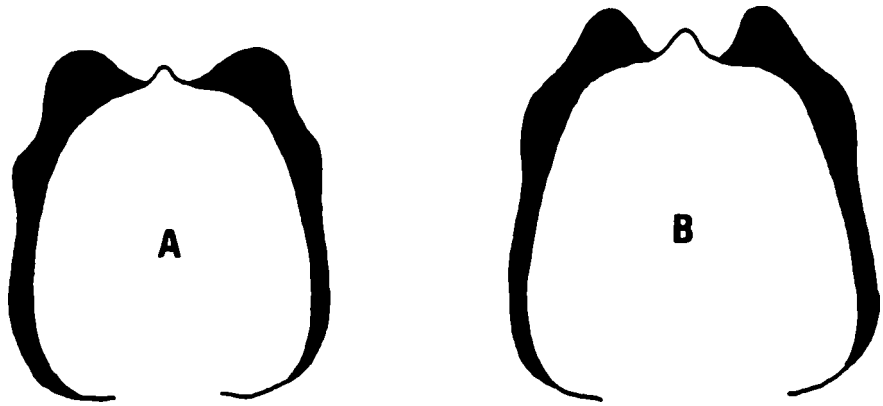

Fig. 76. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Whorl sections. A. SAM–PCA3166. B. SAM–PCA3116. ×1.

Discussion

Spath (1922) briefly discussed and figured a specimen which he considered to differ from *M. gregoryi* in having coarser, more distantly ribbed inner whorls (Fig. 75). This specimen was renamed *Pervinquieria vicina* by Haas (1942); it is in the British Museum (BMNH C20067) and, so far as the writers are able to judge, differs from *M.* (*A.*) *simplex* only in its coarser, more distant ribbing with five ribs in a distance equal to the whorl height, whereas in *M.* (*A.*) *simplex* there are eight to nine. The differences are slight, and within the range of variation seen in *M.* (*A.*) *simplex* from Egito; they are not regarded as of specific significance.

Occurrence

Mortoniceras (*Angolaites*) *simplex* is known only from Angola.

Genus *Cantabrigites* Spath, 1933

Type species *Mortoniceras* (*Cantabrigites*) *cantabrigense* Spath; by original designation

Discussion

The first appearance of the name *Cantabrigites* Spath (1932: 380) was as a *nomen nudum*, the diagnosis and description of the type species appearing only a year later (Spath 1933: 436). Consequently, the valid date of introduction for *Cantabrigites* is 1933.

Spath (1933) proposed *Cantabrigites* as a subgenus of *Mortoniceras* for 'dwarf-forms with reduced, generally single and almost untuberculate costation and greatly simplified suture-line'. In maturity, many typical *Mortoniceras* commonly exceed 200–300 mm in diameter, whereas *Cantabrigites* is mature at diameters of less than 80 mm. It would appear, therefore, to be a genuine micromorph taxon. The fact that *Cantabrigites* is restricted to one level in the Upper Albian, viz. the *dispar* Zone, suggests that it is not the microconch of *Mortoniceras*. *Cantabrigites* differs so greatly from *Mortoniceras vespertinum* (Morton), the type of the genus, that the authors consider the differences sufficient for generic separation.

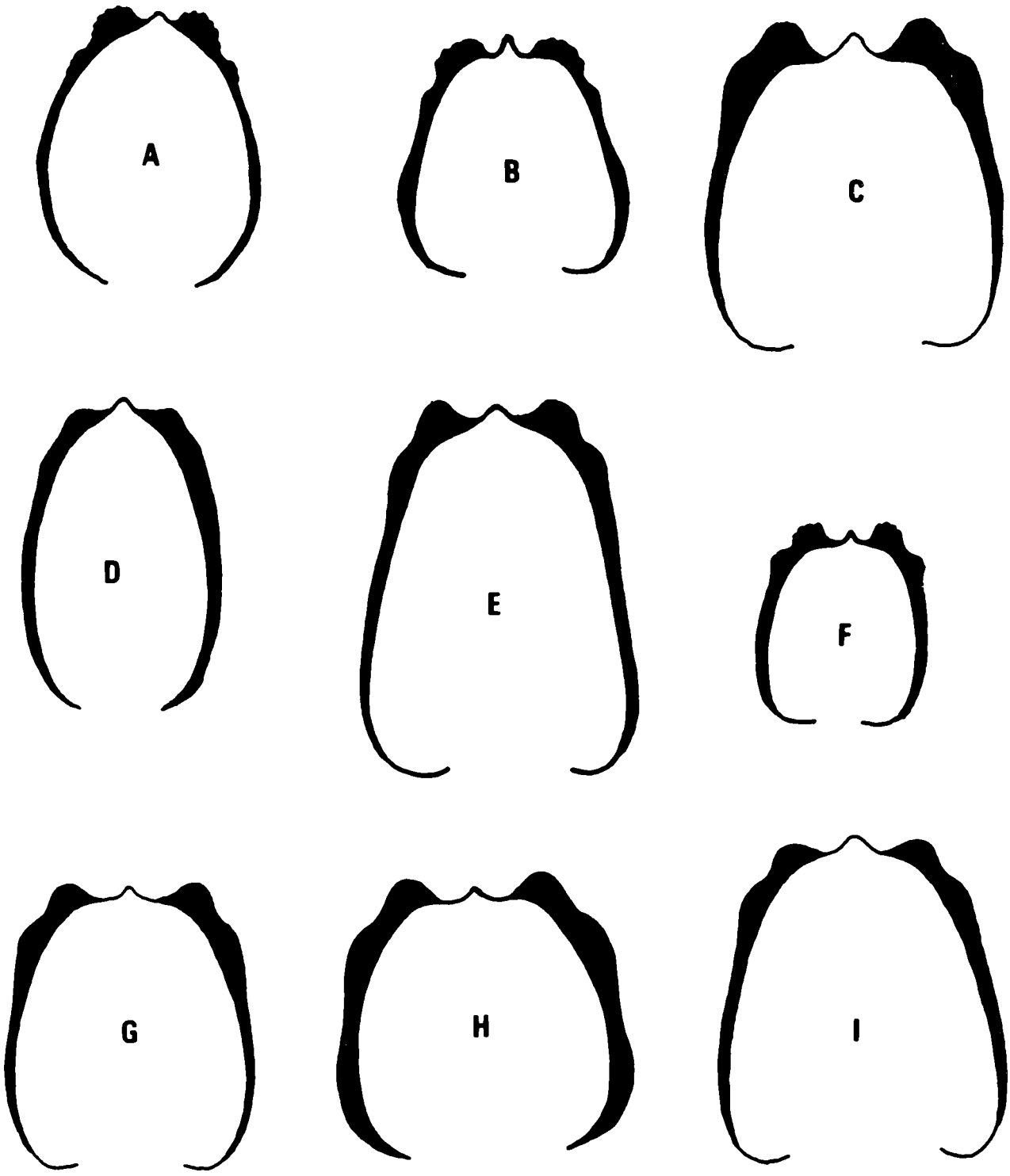

Fig. 77. *Mortoniceras* (*Angolaites*) *simplex* (Choffat). Whorl sections. A. SAM-PCA3249. B. SAM-PCA3147. C. SAM-PCA3150. D. SAM-PCA3144. E. SAM-PCA3200. F. SAM-PCA3153. G. SAM-PCA3111. H. SAM-PCA3179. I. SAM-PCA3200. ×1.

Cantabrigites? curvatum Renz, 1968
Figs 78–79

Cantabrigites curvatum Renz, 1968: 61, pl. 11 (figs 1a–b, 2a–c), figs 20g, 21f.

Material

A single specimen, SAM–PCA3177, from a horizon some way below the main occurrence of *Stoliczkaia* at Egito, in road gravels.

Description

The shell is evolute, with a wide, moderately deep umbilicus and a slightly compressed, subquadrate intercostal whorl section. The umbilical shoulders are well rounded and the flanks convex, with maximum width at about midflank. Ribs begin at the umbilical seam and pass radially outwards to small, but distinct, bullae on the umbilical shoulder. The ribs are rather thick, robust, and vary from slightly rursiradiate to slightly prorsiradiate across the flanks. Where no umbilical bullae are present, some ribs are intercalated at the level of the umbilical shoulder, so that there are eleven ribs per half whorl, of which six arise from umbilical bullae. Each rib is ornamented with a prominent, obliquely clavate, ventrolateral horn which projects backwards. There appears to be the faintest swelling just below the ventrolateral horns which may represent a very weakly developed lower ventrolateral tubercle. There is a distinct siphonal keel.

Measurements

No.	D	H	W	W/H	U
SAM–PCA3177	29	11(38)	9(31)	0,82	13(41)

Discussion

The Angolan specimen is indistinguishable from the holotype from Ste Croix, Switzerland, although the writers are in some doubt as to the generic identity of this species, since it closely resembles some of the earlier *Neokentroceras* spp. known from Angola. As, however, this species is known only from three small specimens and *Neokentroceras* is typical of the low Upper Albian of Angola and Nigeria, tentative assignment to *Cantabrigites* seems preferable, it being an homoeomorphous development only.

Fig. 78. *Cantabrigites? curvatum* Renz. Lateral and ventral views of SAM–PCA3177. ×1.

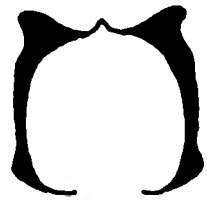

Fig. 79. *Cantabrigites? curvatum* Renz. Whorl section of SAM–PCA3177. ×2.

Mortoniceras (*Durnovarites*) *neokentroides* Wiedmann & Dieni (1968: 146, pl. 13 (fig. 5)) was, as its specific name implies, considered to resemble *Neokentroceras*. It differs from the present species in having well-developed upper and lower ventrolateral tubercles which are elongated at right angles to the keel.

Mortoniceras? nanum Spath (1933: 411, pl. 43 (fig. 6), pl. 46 (figs 4–5), fig. 141) (Fig. 80) resembles the present species, but has double ventrolateral tubercles and lacks the posteriorly directed horns of *C? curvatum*.

Occurrence

Cantabrigites? curvatum Renz is known only from Switzerland and Angola.

Fig. 80. *Mortoniceras? nanum* Spath. The holotype, BMNH–C72726, from the Cambridge Greensand. ×1.

Genus *Drakeoceras* Young, 1957

Type species *Drakeoceras drakei* Young, 1957

Discussion

Young (1957) erected the new genus *Drakeoceras* for *Goodhallites*-like forms in which the ventrolateral tubercles are doubled. As such, therefore, *Drakeoceras* bears the same relationship to *Goodhallites* that *Angolaites* does to

Mortoniceras, and further work may show that it is best treated as a subgenus of *Goodhallites*. *Drakeoceras* differs from *M.* (*Angolaites*) in being higher whorled, with *Goodhallites*-like inner whorls and a more quadrate whorl section in maturity, as well as retaining prominent umbilical bullae and bifurcating ribs onto the body chamber.

Drakeoceras cf. *dellense* Young, 1957

Figs 3E–F, 81–82

Compare

Drakeoceras dellense Young 1957: 25, pl. 7 (fig. 1), pl. 10 (figs 4–5, 8–10), figs 2j, 3a, h–j.

Material

Six specimens, SAM–PCA4662, 4673, 4705, 4733, 4786, and 4800, from the Quissama Ridge at Cabo Ledo, all poorly preserved limestone steinkerns, appear to belong here.

Description

The shell is strongly compressed and moderately involute (umbilicus 23–25% of the diameter). The umbilicus is fairly narrow and shallow, with steep umbilical walls and evenly rounded umbilical shoulder. The broad flanks are slightly convex and converge towards the narrowly arched venter. The whorl section is compressed, elliptical ($^{W}/_{H}$ = 0,70–0,94).

Fig. 81. *Drakeoceras* cf. *dellense* Young. Ventral and lateral views of SAM–PCA4800. ×1.

Ornament comprises about twelve weak umbilical bullae per half-whorl, from which ribs commonly arise in pairs, or singly with an intercalated rib between long ribs. The ribs are initially strongly prorsiradiate, but recurve just below midflank. The ribs are broader than the interspaces and there are about twenty-four per half-whorl at the venter. All ribs are ornamented with very weak (? due to abrasion) lower and distinct upper ventrolateral tubercles. There is a prominent siphonal keel.

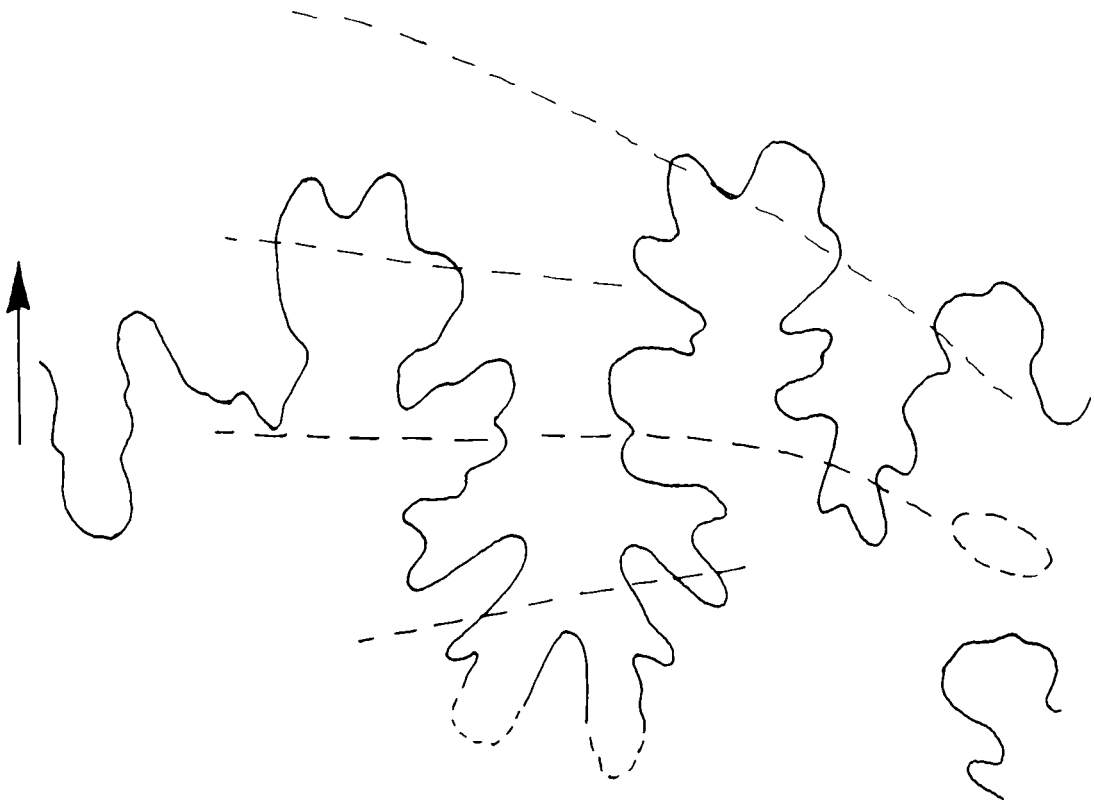

Fig. 82. *Drakeoceras* cf. *dellense* Young. Eroded suture at 65 mm diameter. Approx. ×3.

Discussion

The Angolan specimen is closest to *D. dellense* from which it differs only in being somewhat more involute. It is significant that in Texas *D. dellense* is associated with *M.* (*Durnovarites*) *perinflatum* (Spath) (= *D. adkinsi* Young) and is probably, therefore, strictly contemporaneous with the Angolan specimens. Differences from other species of *Drakeoceras* are noted by Young (1957).

Occurrence

Drakeoceras dellense is currently known only from the *dispar* Zone of Texas and probably Angola.

Family **Binneyitidae** Reeside, 1927

Genus *Borissiakoceras* Arkhangel'skii, 1916

Type species *Borissiakoceras mirabile* Arkhangel'skii, 1916

Discussion

As currently diagnosed (Wright *in* Arkell *et al.*, 1957), the Binneyitidae is a family of micromorph ammonites characterized by their compressed, flat-sided form, narrow umbilicus and greatly simplified suture. Considered to be descended from the typically Middle Albian *Falciferella*, the earliest recorded binneyitids are from the Middle Cenomanian of the Western Interior (Cobban 1961), although we know of specimens of comparable age from western Europe (Kennedy & Juignet 1973) and Zululand. The time separating the last appearance of *Falciferella* and the first appearance of *Borissiakoceras* has been something of a problem in this phylogenetic scheme. However, Brunnschweiler (1959) has recorded species of '*Falciferella*' from the late Albian of Australia which appear to bridge this gap. Our present record of *Borissiakoceras* from the uppermost Albian of Angola closes the gap even further, and, by extending the record of *Borissiakoceras* as far back as the late Albian, provides a direct morphological, chronological and phylogenetic link with the Middle Albian *Falciferella*. Cobban (1961: 747) diagnosed *Borissiakoceras* as follows: 'This genus is characterized by the small size of the conchs which are ordinarily compressed and moderately evolute to somewhat involute. The venter is rounded to flat. Most shells are smooth but a few have raised falcoid growth lines or faint closely spaced falcoid ribs. Nodes, when present, are on the ventrolateral shoulder. The suture has a broad ventral lobe indented by a broad, shallow ventral saddle. The first lateral saddle is bifid and as wide as the ventral lobe. The first lateral lobe is narrow, bifid, and about half as wide as the ventral lobe. The second lateral saddle is trifid and higher and broader than the first. The second lateral lobe is about half as large as the first and tends to be bifid. The auxiliaries, which are small and shallow, may be divided into bifid lobes and saddles.'

Casey (1954: 27) introduced *Falciferella* (type species: *F. milbournei* Casey, 1954: 274, pl. 7 (figs 1–5), fig. 3) as follows: 'Micromorph platycones with narrow, sharp-rimmed umbilicus and tabulate venter, feebly carinate in early youth. Test with strongly falcoid lineation or sub-costation, and a faint spiral groove at the middle of the sides. Mouth border plain. Suture-line of simplified *Aconeceras* pattern, with reduced auxiliary elements.'

In southern England, *Falciferella* is known only from the Middle Albian *Euhoplites loricatus* Zone (*intermedius* and *niobe* Subzones) (Owen 1971), although Brunnschweiler (1959) has recorded two species from the Upper Albian of Australia. *Falciferella breadeni* Brunnschweiler (1959: 15, pl. 1 (figs 5–6)) is associated with *Labeceras* and *Myloceras* and is thus of early late Albian age. In this species, the earliest whorls are smooth, but strong falcate ribs develop in maturity and form weak folds across the tabulate venter. The suture-line of

F. breadeni is simpler than in *F. milbournei*, in which respect it is closer to *Borissiakoceras*. It differs, however, in the trifid nature of the first lateral lobe, but there is a tendency towards trifurcation of this sutural element in *B. orbiculatum* Stephenson (cf. Cobban 1961, fig. 5a, f). Although a trifid first lateral lobe is known in *Falciferella*, the characters of *F. breadeni* are largely those of *Borissiakoceras*, and it is to the latter genus that we refer '*F.*' *breadeni* and '*F.*' *reymenti*.

Borissiakoceras sp. nov. ? aff. *reymenti* (Brunnschweiler, 1959)
Fig. 31H–I

Compare
Falciferella reymenti Brunnschweiler 1959: 15, pl. 1 (figs 5–6).

Material

A single specimen, USNMNH 236980, with recrystallized shell preserved from Porto Amboim.

Description

Shell small, compressed (in part due to post-mortem deformation), with broad, flat flanks and a narrowly rounded venter. In places the venter appears to be fastigiate, but this is probably due to secondary crushing. The umbilicus is narrow (23% of the diameter) and the shell smooth.

Measurements

No.	D	H	W	W/H	U
USNMNH 236980	17	±7,3(43)	±3(18)	0,41	4(23)

Discussion

The only other species of *Borissiakoceras* yet known from late Albian strata are *B. breadeni* (Brunnschweiler) (1959: 15, pl. 1 (figs 5–6)) and *B. reymenti* (Brunnschweiler) (1959: 16, pl. 1 (figs 7–8)) from the Oodnadatta region of South Australia. Both these species differ from the Angolan specimen in their much narrower umbilicus (13–14% of diameter) and in possessing rather prominent falcate ribs. Cobban (1961) has shown, however, that the latter feature is not consistently developed, even within a single *Borissiakoceras* population, with both ribbed and smooth variants occurring side by side. Consequently differences in ornament of this type may not be of specific importance.

Smooth variants of *Borissiakoceras orbiculatum* Stephenson (1955: 64, pl. 6 (figs 1–4)) closely resemble the present specimen, but are much younger (Middle Cenomanian). *Borissiakoceras compressum* Cobban (1961: 747, pl. 87 (figs 19–33), pl. 89 (figs 1–9), fig. 4a–k) also resembles the present species, but is of Middle Cenomanian age and has a narrower umbilicus (14–17% of the diameter). *Borissiakoceras mirabile* Arkhangel'skii (1916: 55, pl. 8 (figs 2–3))

differs from the Angolan example in its much wider umbilicus (37% of the diameter) as well as being a Lower Turonian species. *Borissiakoceras reesidei* Morrow (1935: 463, pl. 49 (fig. 7), pl. 50 (fig. 5), fig. 8) is an Upper Cenomanian species which, like *B. orbiculatum*, cannot be separated from the unique Angolan example without knowledge of the suture-line characteristics of the latter.

Occurrence

Upper Albian of Angola; species with which the specimen is compared came from the Upper Albian of Australia.

AGE OF THE FAUNA

At present there are certain problems concerning the scope and nomenclature of the *Stoliczkaia dispar* Zone and its subzones. The divisions of the Albian Stage in England were erected by Spath on the basis of his understanding of the successions at Folkestone and elsewhere in England, and are based on firm stratigraphic principles. Spath (1943) gave the following zonation through the Upper Albian of southern England:

Stoliczkaia dispar Zone	*Stoliczkaia dispar/Durnovarites perinflatum* Subzone *Arrhaphoceras substuderi* Subzone
Mortoniceras inflatum Zone	*Mortoniceras aequatoriale* Subzone *Callihoplites auritus* Subzone *Hysteroceras varicosum* Subzone *Hysteroceras orbignyi* Subzone

Whilst accepting Spath's subdivision of the *S. dispar* Zone, Breistroffer (1940) showed that *Arrhaphoceras substuderi* (Spath) was common to both the *perinflatum/dispar* and *substuderi* Subzones and was, therefore, unsuitable for use as a subzonal index. Instead, he recognized a lower subzone of *S.* (*Faraudiella*) *gardonica*—*S.* (*F.*) *rhamnonota*—*Mariella gresslyi*—*Turrilitoides toucasi*. By 1947, however, Breistroffer had realized that *S.* (*F.*) *gardonica* and *S.* (*F.*) *rhamnonota* were synonyms of *S.* (*F.*) *blancheti* (Pictet & Campiche) and consequently renamed Spath's *A. substuderi* Subzone the 'Zone á *Paraturrilites Gresslyi*, *Turrilitoides Hugardianus* et *Stoliczkaia* (*Faraudiella*) *Blancheti*'. The upper horizon (Spath's *dispar/perinflatum* Subzone) was referred to a 'Zone á *Pervinquieria* (*Durnovarites*) *perinflata*, *P.* (*Subschloenbachia*) *rostrata*, *Paraturrilites Bergeri* et *Stoliczkaia dispar*'.

On the basis of newly exposed sections, however, Owen (1976) has recently shown that Spath's *aequatoriale* Subzone is a remanié assemblage which cannot be distinguished from the underlying subzone of *Callihoplites auritus* and he has, therefore, proposed its abandonment. In addition, Owen (1976) recalled Breistroffer's (1940) observation that *Arrhaphoceras substuderi* was unsuitable for use as a subzonal index in the *S. dispar* Zone and, because Owen (1976: 492) quite inexplicably considered *S.* (*F.*) *blancheti* '. . . is not sufficiently distinct to

be used as a subzonal index', he proposed to replace this subzonal index with *Mortoniceras rostratum* (J. Sowerby). This, however, is a very unfortunate suggestion because *M. rostratum* was for many years (because of misidentification) the index species for the earlier zone now called after *M. inflatum*. In addition, Breistroffer (1947) has subsequently used it as one of the subzonal indices for Spath's *dispar/perinflatum* Subzone. Moreover, it is abundantly clear that the true characters of *M. rostratum* are not known since all the material assigned by Spath (1932, pl. 38 (fig. 4), pl. 39 (fig. 4), pl. 40 (figs 1, 7), pl. 41 (fig. 7)) to this species was renamed *Pervinquieria fallax* by Breistroffer (1940: 67). Thus, only Sowerby's holotype (Fig. 70), now in the Oxford University Museum, is without doubt assignable to this species. The authors' have had the opportunity of studying the holotype of *M. rostratum*. Its inner whorls are obscured by matrix whilst the ribs of the body chamber bear four rows of tubercles. Although a number of species of *Mortoniceras* s.s. have four rows of tubercles on the inner whorls, the upper and lower ventrolateral tubercles coalesce on the body chamber of *M.* (*Mortoniceras*) to produce ventrolateral horns and thus only three rows of tubercles remain on the body chamber. In the writers' opinion, therefore, *M. rostratum* is a species of *Durnovarites*, a subgenus so far recorded only from Spath's *dispar/perinflatum* Subzone, and is unsuited, therefore, for use as the subzonal index of the lower part of the *S. dispar* Zone. Moreover, since Owen (1976) does not state what he takes to represent *M. rostratum*, the species to which he is referring is totally unrecognizable. For this reason, the writers would propose a simple return to Breistroffer's (1947) subdivision of the *S. dispar* Zone into a lower subzone of *S.* (*F.*) *blancheti*, immediately overlying the *Callihoplites auritus* Subzone, and an upper subzone of *M.* (*Durnovarites*) *perinflatum*.

With the possible exception of the lower horizon at Egito, the present faunas can be referred with confidence to the *M.* (*D.*) *perinflatum* Subzone on the basis of the presence of *S.* (*Stoliczkaia*), *M.* (*Durnovarites*) and the heteromorphs present. There does, however, seem to be some compositional difference in the faunas. Thus, at Praia-Egito the fauna comprises:*

Anisoceras perarmatum Pictet & Campiche
A. armatum (J. Sowerby)
A. haasi sp. nov.
A. phillipsi sp. nov.
A. cf. *arrogans* (Giebel)
A. aff. *exoticum* Spath
A. aff. *subarcuatum* Spath
A. aff. *spathi* (Wiedmann)
Hamites virgulatus Brongniart
H. duplicatus Pictet & Campiche
Puzosia cf. *sharpei* Spath
Desmoceras latidorsatum perinflatum subsp. nov.

* These lists on pp. 299–301 follow the order in the text. Ed.

Stoliczkaia tenuis Renz
Mortoniceras (*Durnovarites*) *collignoni* sp. nov.
M. (*Angolaites*) *simplex* (Choffat)
M. (*A.*) *gregoryi* (Spath)

A somewhat lower level at this locality has yielded:

Tetragonites kitchini (Krenkel)
Mariella gresslyi (Pictet & Campiche)
Cantabrigites? curvatum Renz

The fauna from Cabo Ledo includes the following species:

Anisoceras perarmatum Pictet & Campiche
A. armatum (J. Sowerby)
A. phillipsi sp. nov.
Idiohamites dorsetensis Spath
Hamites virgulatus Brongniart
Mariella cf. *oehlerti* (Pervinquière)
Stoliczkaia sp.
Mortoniceras (*Durnovarites*) *perinflatum* (Spath)
M. (*Angolaites*) *simplex* (Choffat)
M. (*Angolaites*) *gregoryi* (Spath)
M. (*Mortoniceras*) spp.
Drakeoceras cf. *dellense* Young

This fauna differs from the higher horizon at Praia-Egito in that *M.* (*Mortoniceras*) is still fairly abundant whilst *M.* (*Durnovarites*) is rather rare. This suggests that the Cabo Ledo fauna may be somewhat older than the upper horizon at Praia-Egito, although the possibility of mixing of different horizons cannot be wholly dismissed.

The fauna from Porto Amboim comprises:

Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière
Tetragonites collignoni Breistroffer
T. jurinianus (Pictet)
Eogaudryceras italicum Wiedmann & Dieni
Anisoceras perarmatum Pictet & Campiche
A. armatum (J. Sowerby)
A. haasi sp. nov.
Idiohamites dorsetensis Spath
I. cf. *elegantulus* Spath
I. pygmaeus sp. nov.
Hamites virgulatus Brongniart
Mariella circumtaeniatus (Kossmat)
Desmoceras latidorsatum perinflatum subsp. nov.
Stoliczkaia tenuis Renz

Mortoniceras (*Durnovarites*) *perinflatum* (Spath)
M. (*D.*) *subquadratum* Spath
M. (*Angolaites*) *simplex* (Choffat)
Hysteroceras? cf. *ootaturense* (Stoliczka)
Borissiakoceras sp. nov? aff. *reymenti* (Brunnschweiler)

The abundance of very compressed *Stoliczkaia* at Porto Amboim, together with the relative rarity of mortoniceratinids, suggests that this fauna may be somewhat younger than the upper horizon at Praia-Egito, although stratigraphic evidence for this is lacking. None the less, the *Stoliczkaia* fauna from here bears a very close resemblance to the '*Submantelliceras*'—*Utaturiceras* assemblages that characterize the basal Cenomanian of many regions, although the persistence of *Mortoniceras* at this level suggests that it is still best regarded as uppermost Albian.

When the composition of the Angolan faunas is considered, there are marked differences from the faunas of the European *perinflatum* subzone in addition to the obvious absence of hoplitids. Noticeable in the Angolan assemblage is the complete absence of the widely distributed *Mariella* of the *bergeri-miliaris* group, *Lechites*, *Stoliczkaia* (*Faraudiella*), *Turrilitoides*, *Scaphites*, *Ostlingoceras* and nautiloids, together with the rarity of *Hamites* and *Cantabrigites*. Moreover, *Stoliczkaia tenuis* is rather different from the *S. dorsetensis*—*notha*—*dispar* plexus which characterizes the uppermost Albian of western Europe.

Although some differences may be ecological (in particular with respect to the heteromorphs and the absence of hoplitinids), it seems possible that two slightly different levels in the uppermost Albian are represented. It is perhaps noteworthy, therefore, that in Texas, *M.* (*D.*) *perinflatum* is known only from the Pawpaw Formation (Young 1957), some way below the basal Cenomanian faunas of the uppermost Main Street and Grayson/Del Rio sequences. It also occurs below the main level of *Stoliczkaia* in Poland (Marcinowski & Naidin 1976).

Notwithstanding these differences, the abundance of *Stoliczkaia*, together with *M.* (*Durnovarites*) *perinflatum* and *Anisoceras* of the *perarmatum* group, is sufficient to date the Porto Amboim fauna at *M.* (*D.*) *perinflatum* Subzone of the *S. dispar* Zone, and to point to the possibility of even further subzonal refinement of this critical interval.

SUMMARY

The Angolan littoral has yielded rich ammonite faunas referable to the uppermost Albian zone of *Stoliczkaia dispar*, and mainly to the upper subzone of *Mortoniceras* (*Durnovarites*) *perinflatum*. The following species are described:

Phylloceras (*Hypophylloceras*) *seresitense* Pervinquière
Tetragonites (*Tetragonites*) *collignoni* Breistroffer
Tetragonites (*Tetragonites*) *kitchini* (Krenkel)

Tetragonites (*Tetragonites*) *jurinianus* (Pictet)
Eogaudryceras (*Eogaudryceras*) *italicum* Wiedmann & Dieni
Anisoceras (*Anisoceras*) *perarmatum* Pictet & Campiche
Anisoceras (*Anisoceras*) *armatum* (J. Sowerby)
Anisoceras (*Anisoceras*) *haasi* sp. nov.
Anisoceras (*Anisoceras*) *phillipsi* sp. nov.
Anisoceras (*Anisoceras*) cf. *arrogans* (Giebel)
Anisoceras (*Anisoceras*) aff. *subarcuatum* Spath
Anisoceras (*Anisoceras*) aff. *exoticum* Spath
Anisoceras (*Anisoceras*) cf. *spathi* (Wiedmann)
Idiohamites dorsetensis Spath
Idiohamites cf. *elegantulus* Spath
Idiohamites pygmaeus sp. nov.
Hamites virgulatus Brongniart
Hamites duplicatus Pictet & Campiche
Mariella (*Mariella*) *circumtaeniatus* (Kossmat)
Mariella (*Mariella*) *gresslyi* (Pictet & Campiche)
Mariella (*Mariella*) cf. *oehlerti* (Pervinquière)
Mariella (*Mariella*) *nobilis* (Jukes-Browne)
Puzosia (*Puzosia*) cf. *sharpei* Spath
Desmoceras (*Desmoceras*) *latidorsatum perinflatum* subsp. nov.
Stoliczkaia (*Stoliczkaia*) *tenuis* Renz
Hysteroceras? cf. *ootaturense* (Stoliczka)
Mortoniceras (*Durnovarites*) *perinflatum* (Spath)
Mortoniceras (*Durnovarites*) *subquadratum* Spath
Mortoniceras (*Durnovarites*) *collignoni* sp. nov.
Mortoniceras (*Angolaites*) *simplex* (Choffat)
Mortoniceras (*Angolaites*) *gregoryi* (Spath)
Drakeoceras cf. *dellense* Young
Cantabrigites? curvatum Renz
Borissiakoceras sp. nov. ? aff. *reymenti* (Brunnschweiler)

The majority of these species have not previously been described from Angola; although precisely correlated with the *perinflatum* Subzone, there are differences in composition when compared with European faunas. In part these reflect differences between biogeographic provinces (e.g. the sparsity or absence of some heteromorphs). Other differences suggest that it may be possible to further subdivide the *dispar* Zone and the fauna also permits discussion of recent reviews of Upper Albian zonation, especially by Owen (1976). A return to a twofold division of the *dispar* Zone into *Stoliczkaia* (*Faraudiella*) *blancheti* and *Mortoniceras* (*Durnovarites*) *perinflatum* Subzones is suggested.

The chief systematic conclusions from the paper are discussions of intra-specific variation in *Phylloceras* (*Hypophylloceras*), *T.* (*Tetragonites*), *D.* (*Desmoceras*), *E.* (*Eogaudryceras*) and *S.* (*Stoliczkaia*) species.

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REFERENCES

ADKINS, W. S. 1920. The Weno and Pawpaw Formations of the Texas Comanchean. *Bull. Univ. Tex. econ. Geol. Tech.* **1856**: 1–172.

ADKINS, W. S. 1928. Handbook of Texas Cretaceous fossils. *Bull. Univ. Tex. econ. Geol. Tech.* **2838**: 1–385.

ADKINS, W. S. & WINTON, W. M. 1920. Palaeontological correlation of the Fredricksburg and Washita Formations in North Texas. *Bull. Univ. Tex. econ. Geol. Tech.* **1945**: 1–128.

ALMELA, A. & REVILLA, J. DE LA. 1957. Fósiles piritosos del cretáceo de la Sierre de Ricote (Murcia). *Bol. Inst. geol. Min. Espãna* **68**: 45–83.

AMEDRO, F. 1976. Une nouvelle espèce d'Ammonite: *Neophlycticeras* (*Eotropitoides*) *destombesi* nov. sp. (Lyelliceratidae) de l'Albien de Wissant (Boulonnais). *Annls Soc. géol. Nord* **96**: 107–111.

ANDERSON, F. M. 1902. Cretaceous deposits of the Pacific coast. *Proc. Calif. Acad. Sci.* (4) **23**: 1–34.

ANDERSON, F. M. 1958. Upper Cretaceous of the Pacific coast. *Mem. geol. Soc. Am.* **71**: 1–378.

ARKELL, W. J., *et al.* 1957. *Treatise on Invertebrate Palaeontology* Part L, 4. New York: University of Kansas Press and Geological Society of America.

ARKHANGEL'SKII, A. D. 1916. Les mollusques du crétacé supérieur du Turkestan. *Com. géol. Mém.* n.s. **152**: 1–57.

BARBU, I. Z. 1932. Catalogul cephalopodelor fosile din Romania. *Acad. Rom., Mem. Sect. Stiint.* (3) **8** (8): 1–35.

BARROIS, C. 1878. Mémoire sur le terrain crétacé des Ardennes et des régions voisines. *Annls Soc. géol. Nord.* **5**: 227–487.

BESAIRIE, H. 1936. Recherches géologiques à Madagascar. Premiere suite. La géologie du nord-ouest. *Mém. Acad. Malgache* **21**: 1–259.

BÖSE, E. 1923. Algunas faunas crétacicas de Zacatecas, Durango y Guerrero. *Bol. Inst. geol. Mexico* **42**: 1–219.

BÖSE, E. 1928. Cretaceous ammonites from Texas and northern Mexico. *Bull. Univ. Tex. econ. Geol. Tech.* **2748**: 143–357.

BOULE, M., LEMOINE, P. & THÉVENIN, A. 1906–1907. Céphalopodes crétacés des environs de Diego-Suarez. Paléontologie de Madagascar. *Annls Paléont.* **1** (4): 173–192 (1906); **2** (1): 1–56 (1907).

BREISTROFFER M. 1936. Les subdivisions du Vraconien dans le sud-est de la France. *Bull. Soc. géol. Fr.* (5) **6**: 63–68.

BREISTROFFER, M. 1940. Revision des ammonites du Vraconien de Salazac (Gard) et considerations générales sur ce sous-étage Albien. *Trav. Lab. géol. Grenoble* **22**: 1–101.

BREISTROFFER, M. 1946. Sur l'age exact des grès verts de Cambridge (Angleterre). *C. R. somm. séanc. Soc. géol. France* **1946**: 309–312.

BREISTROFFER, M. 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Trav. Lab. géol. Univ. Grenoble* **26**: 1–88.

BREISTROFFER, M. 1953. L'evolution des turrilitides albiens et cenomaniens. *C. R. hebd. Seanc. Acad. Sci., Paris* **327**: 1349–1351.

BRONGNIART, A. 1822. *In:* CUVIER, G. & BRONGNIART, A. *Description géologique des environs de Paris.* Paris: E. d'Ocagne.

BROWN, T. 1837–1840. *Illustrations of the Fossil Conchology of Great Britain and Ireland.* London: Swan Sonnenschein.

BRUNNSCHWEILER, R. O. 1959. New Aconeceratinae (Ammonoidea) from the Albian and Aptian of Australia. *Bull. Bur. Miner Resour. Geol. Geophys. Aust.* **54**: 5–19.

BUCKLAND, W. 1837. *Geology and Mineralogy considered with reference to Natural Theology.* Bridgewater Treatise, 2 vols. London: William Pickering.

CASEY, R. 1954. *Falciferella*, a new genus of Gault ammonites, with a review of the family Aconeceratidae in the British Cretaceous. *Proc. Geol. Ass.* **65**: 262–277.

CASEY, R. 1965. A monograph of the Ammonoidea of the Lower Greensand. *Palaeontogr. Soc. (Monogr.)* part **3**: 119–216.

CHOFFAT, P. 1903. Contribution à la connaissance géologique des colonies Portugaises d'Afrique. 1. Le Crétacique de Conducia. *Mém. Commn Servs. géol. Port.* **1903**: 1–29.

CHOFFAT, P. 1905. Nouvelles données sur la zone littorale d'Angola. *Comunções Servs geol. Port.* **1905**: 31–78.

CHOFFAT, P. & LORIOL, P. DE. 1888. Máteriaux pour l'étude stratigraphique et paléontologique de la province d'Angola. *Mém. Soc. Phys. Genève* **30**: 1–116.

CIESLINSKI, S. 1959. The Albian and Cenomanian in the northern periphery of the Swíety Kryz Mountains. *Inst. geol. Prace* **28**: 1–95 (in Polish).

CLARK, D. L. 1958. *Anisoceras* and *Ancyloceras* from the Texas Cretaceous. *J. Paleont.* **32**: 1076–1081.

CLARK, D. L. 1965. Heteromorph ammonoids from the Albian and Cenomanian of Texas and adjacent areas. *Mem. geol. Soc. Am.* **95**: 1–99.

COBBAN, W. A. 1961. The ammonite family Binneyitidae Reeside in the Western Interior of the United States. *J. Paleont.* **35**: 737–758.

COLLIGNON, M. 1928. Paléontologie de Madagascar. XV. Les céphalopodes du Cénomanien pyriteux de Diego-Suarez. *Annls Paléont.* **17**: 139–160.

COLLIGNON, M. 1929. Paléontologie de Madagascar. XV. Les céphalopodes du Cénomanien pyriteux de Diego-Suarez. *Annls Paléont.* **18**: 1–56.

COLLIGNON, M. 1932. Les ammonites pyriteuses de l'Albien supériéur du Mont Raynaud, Madagascar. *Annls géol. Serv. Mines Madagascar* **2**: 5–36.

COLLIGNON, M. 1950. Recherches sur les faunes albiennes de Madagascar. L'Albien de Mokaraha. *Annls géol. Serv. Mines Madagascar* **17**: 54–85.

COLLIGNON, M. 1956. Ammonites néocrétacées du Menabe (Madagascar). IV. Les Phylloceratidae; V. Les Gaudryceratidae; VI. Les Tetragonitidae. *Annls géol. Serv. Mines Madagascar* **23**: 1–106.

COLLIGNON, M. 1962. *Atlas de fossiles caractéristiques de Madagascar (Ammonites).* **X.** Aptien. Tananarive: Service géologique.

COLLIGNON, M. 1963. *Atlas des fossiles caractéristiques de Madagascar (Ammonites).* **IX.** Albien. Tananarive: Service géologique.

COLLIGNON, M. 1964. *Atlas des fossiles caractéristiques de Madagascar (Ammonites).* **XI.** Cenomanien. Tananarive: Service géologique.

COLLIGNON, M. 1968. Une remarque fauna à *Stoliczkaia* de la région d'Analalava (Madagasikara). *C. R. Sem. géol. Madag.* **1968**: 27–32.

COOPER, M. R. 1978. The mid-Cretaceous (Aptian-Turonian) stratigraphy of Angola. *Annls Mus. Hist. Nat. Nice.* (In press.)

CRAGIN, F. W. 1893. A contribution to the invertebrate palaeontology of the Texas Cretaceous. *Geol. Survey Texas 4th Ann. Rep.* **1893**: 141–294.

CRICK, G. C. 1907. Cretaceous fossils of Natal. Part III. *Rep. geol. Surv. Natal Zululand* **3**: 161–250.

DIENER, C. 1925. *Fossilium catalogus* **1**. *Animalia*; **29**. *Ammonoidea neocretacea.* Berlin: Junk.

DIENI, J. & MASSARI, F. 1963. Le Crétacé inférieur d'Orosei (Sardaigne) et les analogies avec celui du sud-est de la France. *Bur. Rech. géol. min.* **34**: 795–799.

DIXON, F. 1851. *The geology and fossils of the Cretaceous and Tertiary formations of Sussex* 1st ed. London: R. & J. Taylor.

DUBOURDIEU, G. 1953. Ammonites nouvelles des Monts du Mellègue. *Bull. Serv. Carte géol. Algér.* (1) Paléontologie **16**: 1–76.

ETHERIDGE, R. 1902. The Cretaceous Mollusca of South Australia and the Northern Territory. *Mem. R. Soc. S. Aust.* **2**: 1–54.

ETHERIDGE, R. 1909. Lower Cretaceous fossils from the sources of the Barcoo, Ward and Nive Rivers, south central Queensland. Part II. Cephalopoda. *Rec. Aust. Mus.* **7**: 135–165, 235–240.

FABRE, S. 1940. Le Crétacé supérieur de la Basse-Provence occidentale. I. Cénomanien et Turonien. *Annls Fac. Sci. Marseille* (2) **14**: 1–355.

FALLOT, P. 1910. Sur quelques fossiles pyriteux du Gault des Baléares. *Annls Univ. Grenoble* **22** (3): 495–523.

FLEMING, J. 1828. *A history of British animals.* London: Duncan & Malcolm.

FÖRSTER, R. 1975. Die geologische Entwicklung von sud-Mozambique seit der Unterkreide und die Ammoniten-Fauna von Unterkreide und Cenoman. *Geol. Jb.* **B12**: 3–324.

GANZ, E. 1912. Stratigraphie der Mittleren Kreide (Gargasien und Albien) der oberen helvetischen Decken in den nordlichen Schweizeralpen. *Neue Denkschr. schweiz. naturf. Ges. Abh.* **1**: i–vii, 1–148.

GIEBEL, C. G. 1852. *Die Fauna der Vorwelt mit steter Berücksichtigung der lebende Thiere* **3**. Mollusken (i): 1–856. Leipzig: Brockhaus.

HAAN, G. DE 1825. *Monographiae Ammoniteorum et Goniatiteorum.* Lugduni Batavorum.

HAAS, O. 1942. The Vernay Collection of Cretaceous (Albian) ammonites from Angola. *Bull. Am. Mus. nat. Hist.* **81**: 1–224.

HAAS, O. 1952. Some Albian desmoceratid and lytoceratid ammonites from Angola. *Am. Mus. Novit.* **1561**: 1–17.

HAUER, F. VON. 1861. Über die Petrefacten der Kreideformation des Bakonyer Waldes. *Sber. Akad. Wiss. Wien* **44**: 631–659.

HAUGHTON, S. H. 1924. Notes sur quelques fossiles crétacés de l'Angola (céphalopodes et echinides). *Comunções Servs. geol. Port.* **15**: 79–106.

HAUGHTON, S. H. 1925. Note on some Cretaceous fossils from Angola (Cephalopoda and Echinoidea). *Ann. S. Afr. Mus.* **22**: 263–288.

HEBERT, E. & MUNIER-CHALMAS, E. C. P. A. 1875. Description du terrain Crétacé supérieur du Bassin d'Uchaux. Appendice paléontologique. *Ann. Sci. Géol.* **6**: 113–122.

HOWARTH, M. K. 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. nat. Hist.* Geol. **10**: 335–412.

JACOB, C. 1908. Étude sur quelques ammonites du Crétacé moyen. *Mem. Soc. géol. Fr.* **15** (38): 1–64.

JUIGNET, P. & KENNEDY, W. J. 1977. Faunes d'ammonites et biostratigraphie comparée du Cénomanien du nord-ouest de la France (Normandie) et du sud de l'Angleterre. *Bull. Soc. Géol. Normandie* **63**: 1–192.

JUKES-BROWNE, A. J. 1875. On the relations of the Cambridge Gault and Greensand. *Q. Jl. geol. Soc. Lond.* **31**: 256–314.

JUKES-BROWNE, A. J. 1877. Supplementary notes on the fauna of the Cambridge Greensand. *Q. Jl. geol. Soc. Lond.* **33**: 485–504.

KENNEDY, W. J. 1971. Cenomanian ammonites from southern England. *Spec. Pap. Palaeont.* **8**: 1–133.

KENNEDY, W. J. & HANCOCK, J. M. 1971. *Mantelliceras saxbii* (Sharpe) and the horizon of the Martimpreyi Zone in the Cenomanian of England. *Palaeontology* **14**: 437–454.

KENNEDY, W. J. & JUIGNET, P. 1973. First record of the ammonite family Binneyitidae Reeside 1927 in western Europe. *J. Paleont.* **47**: 900–902.

KENNEDY, W. J. & KLINGER, H. C. 1977*a*. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Phylloceratidae. *Bull. Br. Mus. nat. Hist.* (Geol.) **27** (5): 347–380.

KENNEDY, W. J. & KLINGER, H. C. 1977*b*. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Tetragonitidae. *Ann. S. Afr. Mus.* **73**: 149–197.

KLINGER, H. C. 1976. Cretaceous heteromorph ammonites from Zululand. *Mem. geol. Surv. S. Afr.* **69**: 1–142.

KLINGER, H. C. & KENNEDY, W. J. 1978. Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. *J. Moll. Stud.* **44**: 1–48.

KOSSMAT, F. 1895–1898. Untersuchungen uber die südindische Kreideformation. *Beitr. Paläont. Geol. Öst-Ung.* **9**: 97–203 (1895); **11**: 1–46 (1897); **11**: 89–152 (1898).

KRENKEL, E. 1910. Die untere Kreide von Deutsch-Östafrika. *Beitr. Paläont. Geol. Öst-Ung.* **23**: 201–250.

MANTELL, G. A. 1822. *The fossils of the South Downs.* London.

MARCINOWSKI, R. & NAIDIN, D. P. 1976. An Upper Albian ammonite fauna from Crimea. *Acta geol. Polon.* **26**: 83–118.

MATSUMOTO, T. 1942. A short note on the Japanese Cretaceous Phylloceratidae. *Proc. imp. Acad. Japan* **18**: 674–676.

MATSUMOTO, T. 1959. Cretaceous ammonites from the Upper Chitina Valley, Alaska. *Mem. Fac. Sci. Kyushu Univ.* (D) Geol. **8**: 49–90.

MATSUMOTO, T. & INOMA, I. 1975. Mid-Cretaceous ammonites from the Shumarinai-Soeushinai area, Hokkaido. *Mem. Fac. Sci. Kyushu Univ.* (D) Geol. **23**: 263–293.

MCLEARN, F. H. 1972. Ammonoids of the Lower Cretaceous sandstone member of the Haida Formation, Skidegate Inlet, Queen Charlotte Islands, western British Columbia. *Bull. geol. Surv. Can.* **188**: 1–78.

MEUNIER, S. 1888. Contribution à la géologie de l'Afrique occidentale. *Bull. Soc. géol. Fr.* **16**: 61–68.

MORROW, A. L. 1935. Cephalopods from the Upper Cretaceous of Kansas. *J. Paleont.* **9** (6): 463–473.

MOUTA, F. 1937. Notice géologique sur l'Angola (Afrique Occidentale Portugaise). *Comunções Servs geol. Port* **20**: 19–37.

MOUTA, F. 1954. *Noticia explicativa do esboco geologico de Angola.* Lisboa.

MOUTA, F. 1956. *Lexique stratigraphique internationale* **4**. *Afrique, part 7b, Angola.* Paris: Centre National de la Recherché Scientifique.

MOUTA, F. & BORGES, A. 1926. Sur le crétacé du littoral de l'Angola (districts de Benguela et Mossamedes). *Bolm Ag. ger. Colón. Ultramar* **14**: 30–55.

MOUTA, V. I. S. T. & BORGES, A. 1928. Sur le Crétacé du littoral de l'Angola, (districts de Benguela et de Mossamedes). *Congr. Géol. Intern., C. R. XIVe Session* **3**: 911–928.

MOUTA, F. & O'DONNELL, H. 1933. *Carte géologique de l'Angola.* Lisbon: Ministério das Colónias.

MURPHY, M. A. 1967*a*. The Aptian—Cenomanian members of the ammonite genus *Tetragonites. Univ. Calif. Publs Bull. Dep. Geol.* **69**: 1–78.

MURPHY, M. A. 1967*b*. Aptian and Albian Tetragonitidae (Ammonoidea) from northern California. *Univ. Calif. Publs Bull. Dep. Geol.* **70**: 1–32.

NAKAI, I. & MATSUMOTO, T. 1968. On some ammonites from the Cretaceous Fujikawa Formation of Shikoku. *J. Sci. Hiroshima Univ.* (C) **6**: 1–15.

NEUMAYR, M. 1875*a*. Die Ammoniten der Kreide und die systematik der Ammonitiden. *Z. dt. geol. Ges.* **27**: 854–942.

NEUMAYR, M. 1875*b*. Über Kreide Ammonitiden. *Sber. Akad. Wiss. Wien* **71**: 639–693.

OOSTER, W. A. 1857–63. *Petrifactions rémarquables des Alpes Suisses. Catalogue des céphalopodes fossiles des Alpes Suisses.* Geneva: H. Georg.

ORBIGNY, A. D'. 1840–1842. *Paléontologie française. Terrains crétacés.* **1**. *Céphalopodes:* 1–120 (1840), 121–430 (1841), 431–662 (1842). Paris: Masson.

ORBIGNY, A. D'. 1850. *Prodrome de paléontologie stratigraphique universelle.* Paris: Masson.

OWEN, H. G. 1971. Middle Albian stratigraphy in the Anglo-Paris Basin. *Bull. Br. Mus. nat. Hist.* (Geol.) Supplement **8**: 1–164

OWEN, H. G. 1976. The stratigraphy of the Gault and Upper Greensand of the Weald. *Proc. Geol. Ass.* **86**: 475–498.

PARONA, C. F. & BONARELLI, G. 1897. Fossili albiani d'Escragnolles, del Nizzardo e della Liguria occidentale. *Palaeontogr. ital.* **2**: 53–112.

PASSENDORFER, E. 1921. Sur le Crétacé hauttatrique de la Tatra. *Bull. Soc. géol. Pologne* **1**: 217–250.

PASSENDORFER, E. 1930. Étude stratigraphique et paléontologique du Crétacé de la serie hauttatrique dans les Tatras. *Trav. Serv. géol. Pologne* **2** (4): 511–676.

PERVINQUIÈRE, L. 1907. *Études de paléontologie tunisienne. I. Céphalopodes des terrains secondaires.* (Regence de Tunis . . . Carte géologique de la Tunisie.) Paris: De Rudeval.

PERVINQUIÈRE, L. 1910. Sur quelques ammonites du Crétace Algérien. *Mem. Soc. géol. Fr.* Paléont. (17) **42**: 1–86.

PETKOVIC, V. K. 1913. Gault in Serbia. *Glas srp. Kralj. Akad.* 89 Prvi Razred **37**: 33–142. (In Serbian.)

PICTET, F. J. 1861. Note sur la succession des mollusques céphalopodes pendant l'époque crétacée dans la region des Alpes Suisse et du Jura. *Archs Sci. Bibl. Univ. Nouv. Per.* **10**: 1–28.

PICTET, F. J. & CAMPICHE, G. 1858–64. Matériaux pour la paléontologie Suisse. Description des fossiles du terrain Crétacé des environs de Ste Croix. *Mat. pal. Suisse* **1**: 1–380 (1858–60); **2**: 1–752 (1861–64).

PICTET, F. J. & RENEVIER, E. 1866. Céphalopodes de Chéville. *Bull. Soc. vaud. Sci. nat.* **9**: 93–114.

PICTET, F. J. & ROUX, W. 1847–53. Description des mollusques fossiles qui se trouvent dans les grès verts des environs de Genève. *Mem. Soc. phys. hist. nat. Genève* **11**: 257–412 (1847); **12**: 157–287 (1849); **13**: 73–173, 489–558 (1854).

RENEVIER, E. 1890. Monographie des Hautes-Alpes Vaudoises. *Beitr. geol. Karte Schweiz* **16**: 1–563.

RENZ, O. 1968. Die Ammonoides im Stratotyp des Vraconnien bei Sainte-Croix (Kanton Waadt). *Schweiz. Pal. Abh.* **87**: 1–99.

REYMENT, R. A. 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria* **25**: 1–112.

ROMAN, F. 1938. *Les ammonites Jurassiques et Crétacés.* Paris: Masson.

RÖMER, F. A. 1840–1841. *Die Verstienerungen des Norddeutschen Kreidegebirges.* Hannover: Hahn'schen Hofbuchhandlung.

SCOTT, G. 1926. *Études stratigraphiques et paléontologiques sur les terrains Crétacés du Texas.* Thèse, Faculté des Sciences, Grenoble.

SEELEY, H. G. 1865. Ammonites of the Cambridge Greensand in the Woodwardian Museum, Cambridge. *Ann. Mag. Nat. Hist.* **16**: 225–247.

SHARPE, D. 1853–1857. Description of the fossil remains of Mollusca found in the Chalk of England. I. Cephalopoda. *Palaeontogr. Soc.* (*Monogr.*): 1–26 (1853); 27–36 (1855); 37–68 (1857).

SILVA, G. H. DA. 1962. Ammonites do Cretácico inferior do rio Maputo (Catuane-Moçambique). *Bolm Servs geol. Minas Lourenço Marques* **29**: 7–32.

SOWERBY, J. 1812–22. *The mineral conchology of Great Britain.* London: B. Meredith.

SOWERBY, J. DE C. 1823–1846. *The mineral conchology of Great Britain.* London: B. Meredith.

SOWERBY, J. DE C. 1850. *In* DIXON, F. *The geology and fossils of the Cretaceous and Tertiary formations of Sussex.* 1st ed. London: R. & J. Taylor.

SPATH, L. F. 1921. On Cretaceous Cephalopoda from Zululand. *Ann. S. Afr. Mus.* **12**: 217–321.

SPATH, L. F. 1922. On Cretaceous Ammonoidea from Angola collected by Professor J. W. Gregory, DSc., F.R.S. *Trans. R. Soc. Edinb.* **53**: 91–160.

SPATH, L. F. 1923–43. A monograph of the Ammonoidea of the Gault. *Palaeontogr. Soc.* (*Monogr.*): 1–787.

SPATH, L. F. 1925*b*. On Upper Albian Ammonoidea from Portuguese East Africa. With an appendix on Upper Cretaceous ammonites from Maputoland. *Ann. Transv. Mus.* **11**: 179–200.

SPATH, L. F. 1926*b*. On the zones of the Cenomanian and the uppermost Albian. *Proc. Geol. Ass.* **37**: 420–432.

STEPHENSON, L. W. 1955. Basal Eagle Ford fauna (Cenomanian) in Johnson and Tarrant Counties, Texas. *Prof. Pap. U.S. geol. Surv.* **274–C**: 53–67.

STIELER, C. 1920. Über sogenannte Mortoniceraten des Gault. *Zentbl. Miner. Geol. Paläont.* **1920**: 345–352, 392–400.

STOLICZKA, F. 1863–1866. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India Palaeont. indica* (3) **1–13**: 41–216.

STOYANOW, A. 1949. Lower Cretaceous stratigraphy in southeastern Arizona. *Mem. geol. Soc. Am.* **95**: 1–99.

SWENSEN, A. J. 1963. Anisoceratidae and Hamitidae (Ammonoidea) from the Cretaceous of Texas and Utah. *Brigham Young Univ. Geol. Stud.* **9** (2): 53–82.

SZAJNOCHA, L. 1884. Zur Kenntnis der mittelcretacischen Cephalopoden-Fauna der Inseln Elobi an der westkuste Afrikas. *Denkschr. Akad. Wiss. Wien* **49**: 231–238.

THOMEL, G. 1972. Les Acanthoceratidae de châines subalpines méridionales. *Mem. Soc. géol. Fr.* **116**: 1–204.

VAN HOEPEN, E. C. N. 1951. Die gekielde ammoniete die Suid-Afrikaanse Gault. VII Pervinquieridae, Arestoceratidae, Cainoceratidae. *Paleont. Navors. nas. Mus. Bloemfontein* **1**:1–38.

VENZO, S. 1936. Cefalopodi del Cretacea medio-superiore dello Zululand. *Palaeontogr. ital.* **36**: 59–133.

WHITEAVES, J. F. 1876. Invertebrates from the coalbearing rocks of the Queen Charlotte Islands. *Mesozoic Fossils* **1**: 1–92.

WHITEHOUSE, F. W. 1926. The Cretaceous Ammonoidea of Eastern Australia. *Mem. Queensl. Mus.* **8**: 195–242.

WHITEHOUSE, F. W. 1927. Additions to the Cretaceous ammonite fauna of Eastern Australia. *Mem. Queensl. Mus.* **9**: 109–119; 200–206.

WHITEHOUSE, F. W. 1928. The correlation of the marine Cretaceous deposits of Australia. *Rep. 18th Meeting Austr. Assoc. Advanc. Sci., 1926*: 275–280.

WIEDMANN, J. 1962*a*. Ammoniten aus der vascogotischen Kreide (Nordspanien). I. Phylloceratina, Lytoceratina. *Palaeontographica* **A118**: 119–237.

WIEDMANN, J. 1962*b*. Unterkreide-Ammoniten von Mallorca. I. Lfrg: Lytoceratina, Aptychi. *Abh. math -naturw. Kl. Akad. Wiss. Mainz* **1962**: 1–148.

WIEDMANN, J. 1964. Unterkreide-Ammoniten von Mallorca. 2. Lfrg: Phylloceratina. *Abh. math. -naturw. Kl. Akad. Wiss. Mainz* **1963**: 155–264.

WIEDMANN, J. 1973. The Albian and Cenomanian Tetragonitidae (Cretaceous Ammonoidea), with special reference to the circum-Indic species. *Eclog. geol. Helv.* **66**: 585–616.

WIEDMANN, J. & DIENI, I. 1968. Die Kreide Sardiniens und ihre Cephalopoden. *Palaeontogr. ital.* **64**: 1–171.

WOODS, H. 1917. The Cretaceous faunas of the north-eastern part of the South Island of New Zealand. *Bull. geol. Surv. N.Z. Palaeontology* **4**: 1–41.

WRIGHT, C. W. & WRIGHT, E. V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. *Palaeont. Soc. (Monogr.)*: 1–40.

YOUNG, K. 1957. Upper Albian (Cretaceous) Ammonoidea from Texas. *J. Paleont.* **31**: 1–33.

ZWIERZYCKI, J. 1913. Zur Frage der Unteren Kreide in Portugiesisch-Mozambique. *Sber. Ges. naturf. Freunde Berl.* **7**: 319–326.