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VOLUME 83

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CAPE TOWN

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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A NEW GENUS AND THREE NEW SPECIES OF THE FAMILY CONGROGADIDAE (PISCES, PERCIFORMES) FROM NATAL, SOUTH AFRICA

By

RICHARD WINTERBOTTOM

Cape Town Kaapstad

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A NEW GENUS AND THREE NEW SPECIES OF THE FAMILY CONGROGADIDAE (PISCES, PERCIFORMES) FROM NATAL, SOUTH AFRICA

By

RICHARD WINTERBOTTOM

Royal Ontario Museum, Toronto

(With 3 figures)

[*MS. accepted 12 June 1980*]

ABSTRACT

Examination of two lots and six specimens of a congrogadid from Natal which had been identified as *Halidesmus scapularis* Günther, 1871, has led to the proposal of a new genus, *Natalichthys*, with three new species, *N. leptus*, *N. ori* and *N. sam*. The range of *H. scapularis* is restricted to the coast between False Bay and the Umtata River mouth, Transkei.

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INTRODUCTION

Halidesmus scapularis is a well-known South African intertidal congrogadid, ranging from False Bay to Coffee Bay, Transkei. Günther (1871: 668, 669) described the genus and species based on two specimens from Port Elizabeth, adding in parentheses 'Port Natal'. A misinterpretation of Port Natal for Natal could explain why Gilchrist & Thompson (1917*a*: 220) placed *H. scapularis* in Part 1 of their 'A catalogue of sea fishes recorded from Natal', and why, in Part 2 (1917*b*: 416) they recorded it as being from '(Port Natal)'. Later, however, Barnard (1927: 871) gave the locality for this species as 'False Bay, Algoa Bay, Natal coast, down to 50 fathoms'. It was presumably this notation that was used by Smith (1961) and Smith & Smith (1966) to report the range of *H. scapularis* as being from False Bay to Natal, although Smith (1952: 100), in his earlier review of south and east African congrogadids, restricted the range from False Bay to East London. A list of the South African Museum's holdings of *H. scapularis* included two lots with a total of six specimens from off Natal. Extensive collecting by personnel from the J.L.B. Smith Institute of Ichthyology during the last decade in the area between Port Elizabeth and

Ann. S. Afr. Mus. **83** (1), 1980: 1–12, 3 figs.

Sodwana Bay, KwaZulu, failed to produce specimens of *H. scapularis* north of the Umtata River mouth, Transkei. Therefore, the two lots from Natal were of considerable interest, and were borrowed for examination. The six specimens proved to represent a new genus comprised of three new species.

METHODS

Counts and measurements are conventional (Hubbs & Lagler 1964) except that head length is measured from the tip of the snout to the tip of the opercular spine, and only the pored lateral-line scales are counted. Since the spine of the first dorsal fin is nearly or barely connected to the base of the first dorsal-fin ray, the condition is expressed by a slash between spine and ray counts (e.g. DI/42–43). The abbreviation SAM is an acronym for the South African Museum, Cape Town.

DESCRIPTIONS

Natalichthys gen. nov.

Type species

Natalichthys ori sp. nov.

Diagnosis

The new genus is placed in the family Congrogadidae because, among other reasons, it lacks anal spines, has a single dorsal spine not (or barely) attached to the base of the first dorsal-fin ray, lacks palatine teeth and has a single, spur-like opercular spine. *Natalichthys* primarily differs from other congrogadid genera in a combination of characters. The following three characters, taken together, will distinguish the genus from all other described congrogadids: pelvic fin of one spine and two rays (I,2), gill membranes united but free from isthmus, a single short lateral line.

Comparison

Only two other congrogadid genera possess a I,2 pelvic fin (*Blennodesmus* and *Halidesmus*, both monotypic). *Natalichthys* differs from the eastern Australian *Blennodesmus* in having the gill membranes free of the isthmus (v. fused), and in the presence of a supraotic sensory canal pore (v. absent). *Halidesmus* (which appears to be closely related to the monotypic *Pholioides* from Pakistan and India) possesses at least three complete lateral-lines (v. a single incomplete lateral-line), seven (v. six) preopercular sensory canal pores, and a sensory canal pore between the first suborbital and first preopercular sensory canal pores (v. absent). *Pholioides* agrees with *Halidesmus* in all these characters, but differs from that genus in lacking pelvic fins (v. present) and in having eight (v. 10) pectoral rays. Anatomical studies presently being undertaken will hopefully allow monophyletic supraspecific taxa to be proposed for the congrogadids, and this may result in some reduction of the number of genera (presently ten genera, seventeen species, including this study).

Etymology

Named for Natal, the province off which all specimens were collected, and *ichthys*, a fish. Gender: masculine.

KEY TO THE SPECIES OF *NATALICHTHYS*

1a. DI/42, A 32, P 10, two dorsal and a single ventral procurrent caudal-fin rays...... *N. sam*
1b. DI/48 or more, A 39 or more, P 9..2
2a. DI/52–53, A 42–43, two dorsal and two ventral procurrent caudal-fin rays, cheeks naked *N. ori*
2b. DI/48, A 39, a single dorsal and ventral procurrent caudal-fin ray, cheeks scaled *N. leptus*

Natalichthys ori sp. nov.

Fig. 1

Holotype

SAM–17340, 60,2 mm SL (67,8 mm TL), Umhlangakulu River, Natal, South Africa (30°04′10″S 30°21′47″E ?). No further data, but see discussion.

Paratype

SAM–28993, 53,7 mm SL (60 mm TL), collected with holotype.

Diagnosis

Differs from the other two species in the genus in the higher number of dorsal- and anal-fin rays (DI/52–53, A 42–43 v. DI/42 or 48, A 32 or 39). It can further be separated from *N. sam* in having one less pectoral-fin ray (nine v. ten), two ventral procurrent caudal-fin rays (v. one), more lower gill rakers (seven to eight v. five), and the absence of vomerine teeth (v. present). Additional characters separating *N. ori* from *N. leptus* include the first ray of the dorsal fin unbranched (v. branched), two dorsal and ventral procurrent caudal-fin rays (v. one each) and the absence of scales on the cheek (v. present).

Description

A small (60,2 mm maximum recorded SL) congrogadid known only from two specimens collected off Natal. The following counts and measurements are given for the holotype, with values for the paratype in parentheses where different. As per cent standard length: soft dorsal-fin base 77,2 (78,2); anal-fin base 59,6 (59,4); snout tip dorsal-fin spine origin 21,1 (20,9); snout tip to first dorsal-fin ray origin 23,6 (23,1); snout tip to first anal-fin ray origin 40,9 (39,5); head length 15,0 (15,6). As per cent head length: head depth at parietal commissure 51,1 (52,4), body depth at anal-fin origin 50,0 (51,2); eye diameter 25,6

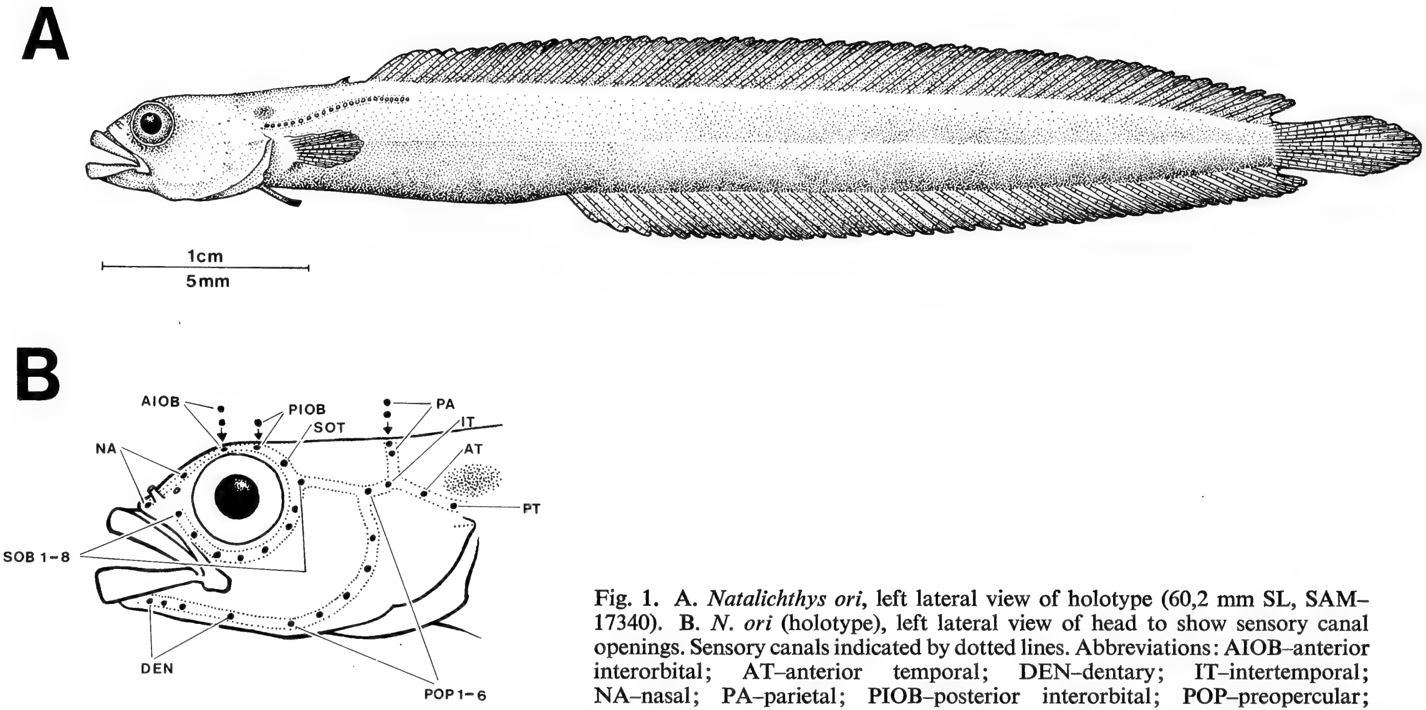

Fig. 1. A. *Natalichthys ori*, left lateral view of holotype (60,2 mm SL, SAM–17340). B. *N. ori* (holotype), left lateral view of head to show sensory canal openings. Sensory canals indicated by dotted lines. Abbreviations: AIOB–anterior interorbital; AT–anterior temporal; DEN–dentary; IT–intertemporal; NA–nasal; PA–parietal; PIOB–posterior interorbital; POP–preopercular; PT–posterior temporal; SOB–suborbital; SOT–supraotic. Drawn by A. Odum.

(26,2); snout length 22,2 (23,8); bony interorbital 7,7 (7,1); upper-jaw length 37,8 (38,1); lower-jaw length 54,4 (52,4); pectoral-fin length 44,4 (45,2); pelvic-fin length 23,3 (25,0); length of first dorsal-fin ray 24,4 (27,4); tenth 38,9 (44,0); twentieth 50,0 (46,4); thirtieth 48,9 (47,6); fortieth 47,8 (50,0); penultimate 47,8 (50,0); length of first anal-fin ray 22,2 (23,8); tenth 33,3 (35,7); twentieth 34,4 (36,9); thirtieth 35,6 (38,1); penultimate 38,9 (44,0).

Dorsal fin I/52–53, first five rays of holotype and first ray only of paratype unbranched; A 42–43, first ray of holotype and no rays of paratype unbranched; pectoral fin 9; pelvic fin I,2, spine rudimentary; caudal fin with two dorsal procurrent rays, the posteriormost ray with a few segmentations, five dorsal and five ventral principal rays (the dorsalmost and ventralmost unbranched in the holotype, branched in the paratype), two ventral procurrent rays, the posteriormost ray with a few segmentations in the paratype but not in the holotype. Caudal fin connected to dorsal and anal fins by a membrane which reaches about half-way along the length of the last dorsal- and anal-fin rays.

Sensory canal openings (Fig. 1B—all pores bilateral except where otherwise stated): nasal double, with one just posterior to upper lip and the other just behind posterior nostril; an anterior interorbital and a single, median posterior interorbital; a supraotic (absent on left side of paratype); eight suborbitals; six in preopercular canal; four in dentary. An intertemporal; anterior and posterior post-temporal; and two parietal pores.

Gill membranes fused to each other in ventral midline, but free from isthmus. Six branchiostegal rays; gill rakers on first arch with two to three epibranchial, one in angle, and seven to eight ceratobranchial = (2—3) + 1 + (7—8). A single, short, incomplete lateral line ending beneath the third ray of soft dorsal fin, consisting of 22–23 pored scales. Olfactory capsule with two nostrils, anterior a short tube, posterior pore-like. Cheeks and opercles naked, body scaled almost to parietal commissure with small, elliptical, cycloid scales. Pseudobranch with five lobes.

Vomer and palate edentate. Jaw teeth conical, slightly recurved, decreasing in size posteriorly. A short inner row of about four teeth in upper jaw, two in lower jaw.

Colour pattern (alcohol-preserved specimens)—plain yellow-brown with a diffuse, somewhat elliptical dark blotch (about half eye diameter) on shoulder above opercle. The blotch was apparently unocellated—although the material appears faded.

Etymology

The specific name *ori* (treated as a noun in apposition) is the acronym of the Oceanographic Research Institute, Durban, whose Directors (Drs D. H. Davies and A. E. F. Heydorn) and staff have contributed greatly to the knowledge of South Africa's coastal marine fauna.

Natalichthys sam sp. nov.

Fig. 2

Holotype

SAM–21915, 42,7 mm SL (48,5 mm TL), Indian Ocean, off Port Shepstone, south coast of Natal, South Africa (30°47′06″S 30°29′06″E), 44 m, stony bottom. Collected by University of Cape Town (NAD 2x), 17 May 1958.

Paratype

SAM–28940, 40,3 mm SL (44,5 mm TL), collected with holotype.

Diagnosis

Differs from the other two species in the genus in the lower number of dorsal and anal-fin rays (DI/42, A 32 v. DI/48–53, A 39–43), one more pectoral-fin ray (10 v. 9), and four to six teeth on the vomer (v. two or none). It can be further separated from *N. ori* in having a single ventral procurrent caudal-fin ray (v. two), and fewer lower gill rakers on the first gill arch (five v. seven to eight). Additional characters separating *N. sam* from *N. leptus* include first ray of dorsal fin unbranched (v. branched), one more dorsal procurrent caudal-fin ray (two v. one) and naked cheeks (v. scaled cheeks).

Description

A short, small (42,7 mm maximum recorded SL) congrogadid known only from two specimens collected off Natal. The following counts and measurements are given for the holotype, with values for the paratype in parentheses where different. As per cent standard length: soft dorsal-fin base 73,1 (69,5); anal-fin base 55,3 (51,1); snout tip to dorsal-fin spine origin 23,4 (26,1); snout tip to first dorsal-fin ray origin 26,0 (27,8); snout tip to first anal-fin ray origin 44,5 (46,4); head length 18,3 (18,9). As per cent head length: head depth at parietal commissure 59,0 (56,6); body depth at anal-fin origin 57,7 (59,2); eye diameter 25,6 (25,0); snout length 21,8 (22,4); bony interorbital 7,7 (6,6); upper-jaw length 38,5 (34,2); lower-jaw length 51,3 (53,9); pectoral-fin length 53,8 (50,0); pelvic-fin length 24,4 (26,3); length of first dorsal ray 26,9 (26,3); tenth 44,9 (44,7); twentieth 47,4; thirtieth 51,3; penultimate 52,6; length of first anal-fin ray 26,9 (22,4); tenth 38,5 (36,8); twentieth 39,7 (39,5); penultimate 51,3 (42,1).

Dorsal fin I/42, only first ray unbranched; A 32, all rays branched; pectoral fin 10, pelvic fin I,2, spine rudimentary; caudal fin of two procurrent and five principal dorsal rays, and one procurrent and six principal ventral rays. The second (more posterior) dorsal procurrent ray has a few segmentations near its tip in the paratype, but is unsegmented in the holotype. Caudal fin connected to dorsal and anal fins by a membrane which reaches to about the midpoint of the length of the last dorsal- and anal-fin rays.

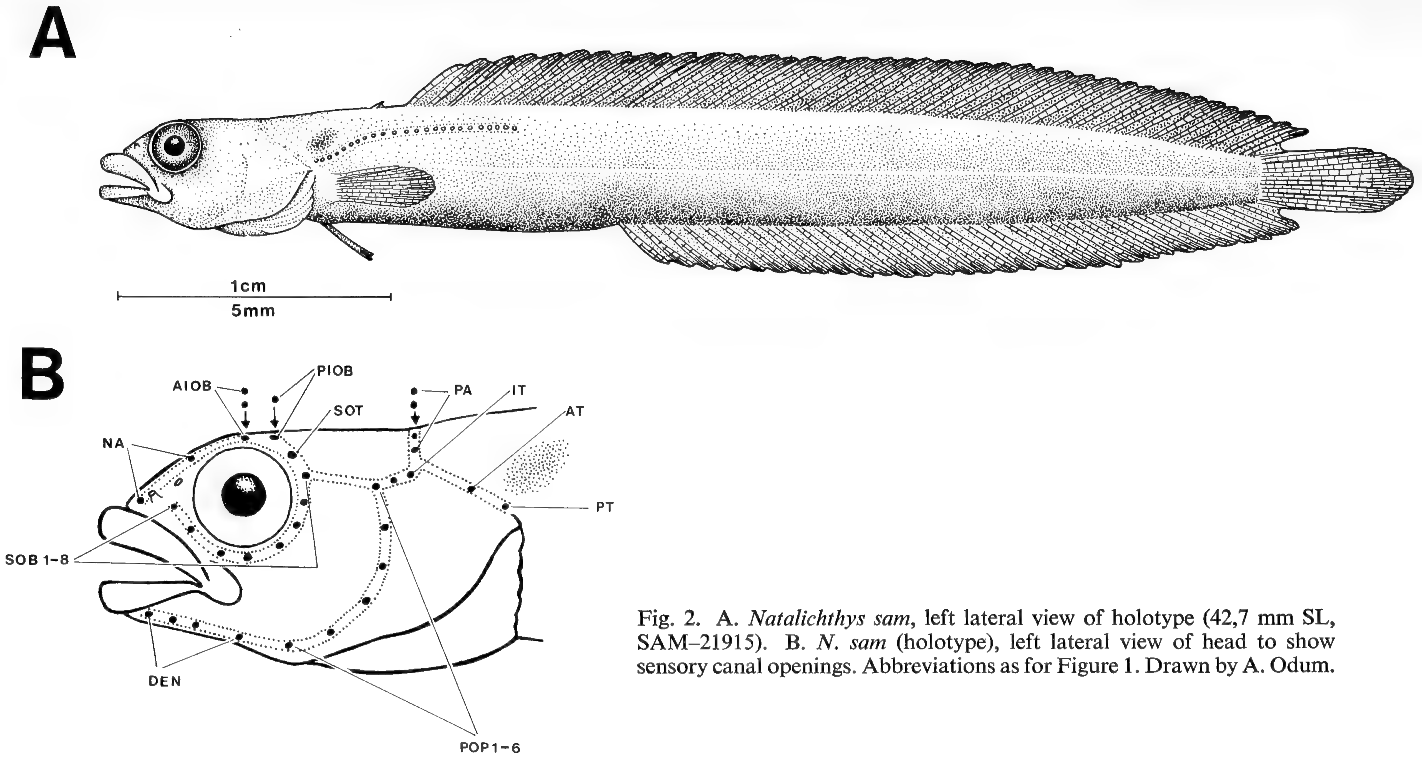

Fig. 2. A. *Natalichthys sam*, left lateral view of holotype (42,7 mm SL, SAM–21915). B. *N. sam* (holotype), left lateral view of head to show sensory canal openings. Abbreviations as for Figure 1. Drawn by A. Odum.

Sensory canal openings (Fig. 2B—all pores bilateral except where stated otherwise): nasal double, with one just posterior to the upper lip and the other just behind the posterior nostril; an anterior interorbital and a single, median posterior interorbital; a supraotic; eight suborbitals; six in preopercular canal; four in dentary. An intertemporal; anterior and posterior posttemporal; and two parietal pores. In addition, an extra pore between the dorsalmost preopercular pore and the intertemporal pore is present on the left, but not the right, sides of both specmens.

Gill membranes fused to each other in ventral midline, but free from isthmus. Six branchiostegal rays; gill rakers on first arch with two epibranchial, one in angle and five ceratobranchial $= 2 + 1 + 5$. A single, short, incomplete, lateral line ending beneath the sixth dorsal-fin ray, consisting of 22–27 pored scales. Olfactory capsule with two nostrils, anterior a short tube, posterior pore-like. Cheeks and opercles naked, body scaled up to the parietal commissure with small, elliptical cycloid scales. Pseudobranch short, with five lobes.

A few (four to six) conical teeth on vomer, none elsewhere on palate. Jaw teeth conical, slightly curved, anterior largest, decreasing irregularly in size posteriorly. Inner patch of small teeth behind symphysis in both jaws, an inner row continuing posteriorly half as far as the outer row.

Colour pattern (alcohol-preserved specimens)—plain yellow-brown with a somewhat elliptical dark blotch (about three-quarters eye diameter) on shoulder above opercle. The blotch was apparently unocellated (ocellated in many congrogadids), but the material is somewhat faded.

Etymology

The specific name *sam* (treated as a noun in apposition) is the acronym for the South African Museum, Cape Town, whose ichthyologists, Dr P. A. Hulley and Miss E. Louw, have always been most co-operative and good company.

Natalichthys leptus sp. nov.

Fig. 3

Holotype

SAM–28938, 57,2 mm SL (63,9 mm TL), Umhlangakulu River, Natal, South Africa (30°04′10″S 30°21′47″E ?). No further data, but see discussion.

Paratype

SAM–28939, 49,7 mm SL (56,9 mm TL), collected with holotype.

Diagnosis

Differs from the other two species in the genus in fin-ray counts (DI/48, A 39 v. DI/42 or 52–53, A 32 or 42–43), in having the first dorsal-fin ray branched (v. unbranched), in a single dorsal procurrent caudal-fin ray (v. two),

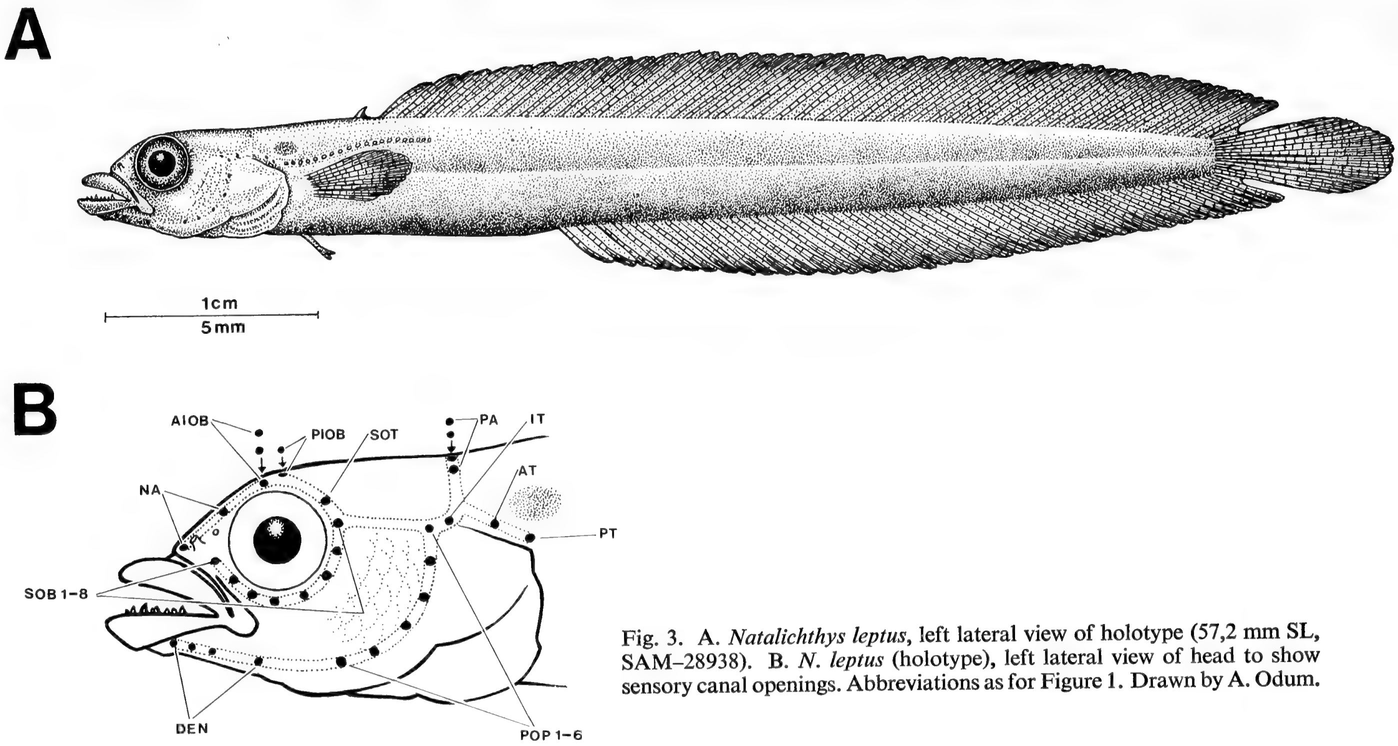

Fig. 3. A. *Natalichthys leptus*, left lateral view of holotype (57,2 mm SL, SAM–28938). B. *N. leptus* (holotype), left lateral view of head to show sensory canal openings. Abbreviations as for Figure 1. Drawn by A. Odum.

and in possessing scales on the cheeks. It differs from *N. sam* in having nine (v. ten) pectoral-fin rays, and in having two or no vomerine teeth (v. four to six). Additional differences from *N. ori* include a single ventral procurrent caudal-fin ray (v. two) and a lower number of gill rakers on the lower limb (five to six v. seven to eight).

Description

A small (57,2 mm SL maximum recorded SL) congrogadid known only from two specimens collected off Natal. The following counts and measurements are given first for the holotype, with values for the paratype in parentheses where different. As per cent standard length: soft dorsal-fin base 69,2 (74,8); anal-fin base 55,6 (59,6); snout tip to dorsal-fin spine origin 23,0 (22,5); snout tip to first dorsal-fin ray origin 25,3 (25,2); snout tip to first anal-fin origin 41,4 (41,6); head length 17,5 (16,9). As per cent head length: head depth at parietal commissure 54,0 (54,8); body depth at anal-fin origin 49,0 (53,8); eye diameter 26,0 (26,2); snout length 25,0; bony interorbital 7,0 (7,1); upper-jaw length 36,0 (38,1); lower-jaw length 55,0 (54,8); pectoral-fin length 53,0 (51,2); pelvic-fin length 21,0 (25,0); length of first dorsal-fin ray 21,0 (23,8); tenth 45,0 (42,6); twentieth 47,0 (46,4); thirtieth 54,0 (53,6); fortieth 55,0 (53,6); penultimate 46,0 (54,8); length of first anal-fin ray 21,0 (25,0); tenth 29,0 (34,5); twentieth 32,0 (38,1); thirtieth 35,0 (41,7); penultimate 40,0 (47,6).

Dorsal fin I/48, all rays branched; A 39, all rays branched; pectoral fin 9; pelvic fin I,2, spine rudimentary; caudal fin with one dorsal procurrent ray, five branched principal dorsal and five branched principal ventral rays, and a single ventral procurrent ray. Both dorsal and ventral procurrent rays with a few striations in holotype, no striations in paratype. Caudal fin connected to dorsal and anal fins by a membrane which reaches about one-third along the length of the last dorsal- and anal-fin rays.

Sensory canal openings (Fig. 3B—all pores bilateral except where otherwise stated): nasal double, with one just posterior to upper lip and the other just behind posterior nostril; an anterior interorbital, and a single, median posterior interorbital (paratype only); a supraotic; eight suborbitals; six in preopercular canal; four in dentary. An intertemporal; anterior and posterior posttemporal; and two parietal pores.

Gill membranes fused to each other in ventral midline, but free from isthmus. Six branchiostegal rays, gill rakers on first arch with two to three epibranchial, one in angle and five to six ceratobranchial ($= 2 - 3 + 1 + 5 - 6$). A single, short, incomplete lateral line ending beneath the third to fourth ray of soft dorsal fin; consisting of 20–24 pored scales. Olfactory capsule with two nostrils, anterior a short tube, posterior pore-like. Cheeks, but not opercles, with small, elliptical, cycloid scales, body scaled to parietal commissure with similar scales. Pseudobranch with six lobes in holotype, five in paratype.

A single minute tooth on either side of the head of the vomer in paratype, none in holotype; rest of palate edentate. Jaw teeth stoutly conical, decreasing in size posteriorly. A short inner row of five teeth in upper jaw, three in lower jaw.

Colour pattern (alcohol-preserved specimens)—plain yellow-brown, with a diffuse, elliptical dark blotch (about three-quarters eye diameter) on shoulder above opercle. Blotch apparently unocellated.

Etymology

From the Greek *leptos*, like a scale or peel, thin, fine, small, delicate; in allusion to the scaled cheeks of the new species. Treated as a noun in apposition.

DISCUSSION

Two of the species, *N. ori.* and *N. leptus*, were in the same lot. The only data accompanying the lot consisted of the catalogue number, and 'Umhlangakulu River, Natal' Congrogadids have not previously been recorded from fresh or estuarine waters. It seems probable that these specimens were collected off the mouth of the river, in the sea. Additional circumstantial evidence for this comes from Barnard's statement (1927: 871) that *Halidesmus scapularis* had been collected from the Natal coast at 50 fathoms. This specific statement of depth and place indicates that he had specimens with that data. There are no specimens of *H. scapularis* from that depth and locality at the South African Museum (where Barnard worked). The South African Museum specimens labelled as *H. scapularis* from Natal represent the material forming this paper. The specimens here described as *N. sam* were collected in 1958 (31 years after publication of Barnard's monograph), and therefore cannot represent his material. Thus it is probable that the lot on which Barnard based his statement of range and depth is the one now labelled as being from Umhlangakulu River. The original catalogue entry for this lot (SAM–17340) is in Barnard's handwriting (E. Louw, pers. comm.).

A further point is of interest here. Although Gilchrist & Thompson's 1917*b*) statement of Port Natal as a locality for *H. scapularis* appears to be taken directly from Günther's (1871) description of the types (see introduction), it is possible that they may have had additional specimens identified as *H. scapularis* from Natal. In this context, P. Heemstra (pers. comm.) informed the author that there is an 'Umhlangankulu' estuary served by a short (6,5 km) river located at 30°56′45″S 30°18′E, which thus lies some 34 km south-west of Port Shepstone. P. A. Hulley (pers. comm.) searched the original catalogues of the R.S. *Pieter Faure* and found the following: '14 March, 1901. Umhlangakulu [sic] River NW by N, 7½ miles. Dredge, 12.50–1.00 p.m.'. The co-ordinates for this station would then be 31°04′10″S 30°21′47″E. The evidence, although circumstantial, appears to indicate strongly that *N. ori* and *N. leptus* were taken at this station.

In summary, then, it appears probable that (i) Gilchrist & Thompson's (1917*b*) record of *H. scapularis* was taken directly from Günther's description and (ii) that the specimens of *N. ori* and *N. leptus* were collected at 30°04′10″S 30°21′47″E off the Natal south coast near Port Edward at a depth of 90 m (50 fm.) on 14 March 1901.

ACKNOWLEDGEMENTS

I thank the South African Museum for allowing me to report on the specimens and Dr P. Hulley and Miss E. Louw for the information on the Faure stations, catalogue data and geography. Dr P. Heemstra of the J.L.B. Smith Institute of Ichthyology, Grahamstown, kindly sent me the co-ordinates for the Umhlangankulu River. Drs E. J. Crossmand and A. R. Emery of the Royal Ontario Museum commented on the manuscript, and Mr Anker Odum (ROM) expertly prepared the figures for me.

REFERENCES

Barnard, K. H. 1927. A monograph of the marine fishes of South Africa. Part II. *Ann. S. Afr. Mus.* **21**: 419–1065.

Gilchrist, J. D. F. & Thompson, W. W. 1917*a*. A catalogue of the sea fishes recorded from Natal. Part I. *Ann. Durban Mus.* **1**(4): 255–290.

Gilchrist, J. D. F. & Thompson, W. W. 1917*b*. A catalogue of the sea fishes recorded from Natal Part II. *Ann. Durban Mus.* **1**(4): 291–431.

Günther, A. 1871. Report on several collections of fishes recently obtained for the British Museum. *Proc. zool. Soc. Lond.* **1871**: 652–675.

Hubbs, C. L. & Lagler, K. F. 1964. *Fishes of the Great Lakes Region.* Ann Arbor: University of Michigan Press.

Smith, J. L. B. 1952. The fishes of the family Haliophidae. *Ann. Mag. nat. Hist.* (12) **5**: 85–101.

Smith, J. L. B. 1961. *The Sea Fishes of Southern Africa.* 4th ed. South Africa: Central News Agency.

Smith, J. L. B. & Smith, M. M. 1966. *Fishes of the Tsitsikama Coastal National Park.* South Africa: National Parks Board of Trustees.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
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(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
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(c) Scientific names, but not their vernacular derivatives
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Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

RICHARD WINTERBOTTOM

A NEW GENUS AND THREE NEW SPECIES OF THE FAMILY CONGROGADIDAE (PISCES, PERCIFORMES) FROM NATAL, SOUTH AFRICA

VOLUME 83 PART 2 NOVEMBER 1980 ISSN 0303-2515

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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DECAPOD AND ISOPOD CRUSTACEANS FROM THE WEST COAST OF SOUTHERN AFRICA, INCLUDING SEAMOUNTS VEMA AND TRIPP

By

BRIAN KENSLEY

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By

BRIAN KENSLEY

Smithsonian Institution, Washington, D.C.

(With 9 figures)

[*MS. accepted 15 July 1980*]

ABSTRACT

Seven species of isopods (including *Stenetrium vemae* sp. nov. and *Jaeropsis monsmarinus* sp. nov.) and nineteen species of decapods (including *Pseudodromia cacuminis* sp. nov. and *Macropodia cirripilus* sp. nov.) are recorded from seamounts Vema and Tripp, and the Lüderitz area. Zoogeographically, the isopods show strong affinities with the South African fauna, while the decapods include mainly South African and west African forms, with single Indo-Pacific and Austral species.

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INTRODUCTION

The benthic fauna of the continental shelf and seamounts off the west coast of South Africa has barely been investigated. What information exists is to be found in scattered reports, and we are still a long way from even a superficial overview.

The material dealt with in this report comes from several sources and emphasizes the fragmentary state of our knowledge. It was thought useful, however, to publish several new records and species, and to summarize the little that is known about Seamount Vema's crustacean fauna.

Seamount Vema, first discovered in 1957, was visited by personnel from the University of Cape Town and the South African Museum in 1964 and 1966. In 1978 the University of Cape Town did further collecting on the summit peak. Lying about 650 km off the west coast of South Africa at 31°38′S 08°02′E (Fig. 1), and rising steeply from the 5 000 m deep sea-floor, the summit plateau averages about 40 m below the surface. Collecting on this plateau has been done both with air-lift dredge and by scuba divers (see Grindley 1967). Most

Ann. S. Afr. Mus. **83**(2), 1980: 13–32, 9 figs.

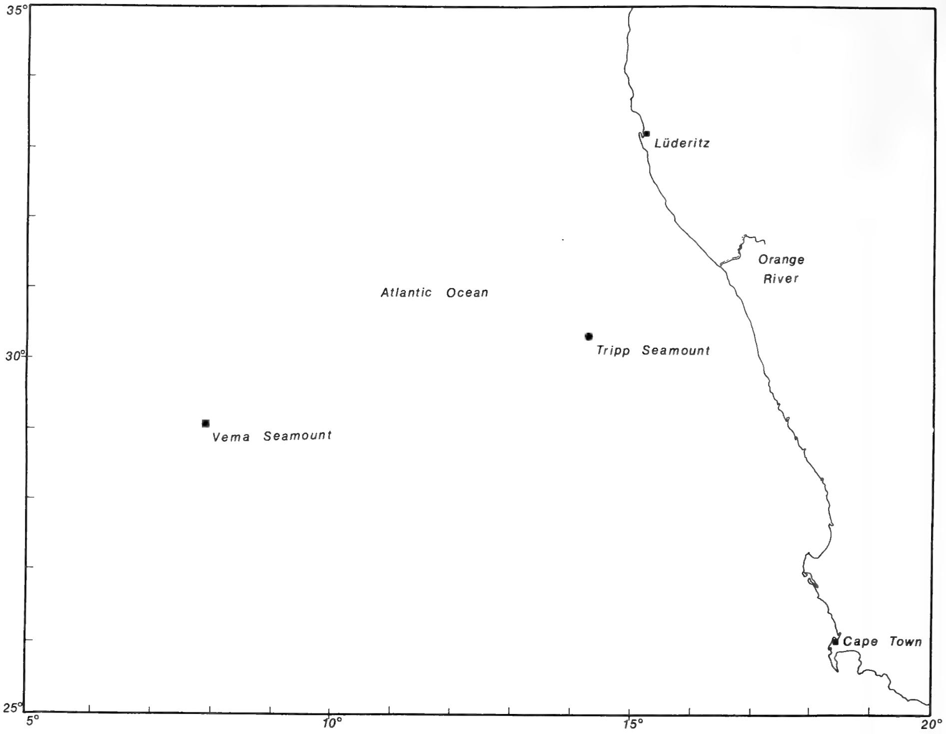

Fig. 1. Map showing localities.

of this material has been deposited in the South African Museum, while a preliminary account of the fauna was given by Berrisford (1969). The Decapoda in this latter report were given preliminary identifications by J. Forest and D. Guinot of the Paris Museum.

Material from Seamount Tripp was collected in the late 1960s by the then Division of Sea Fisheries and the South African Museum, and a few specimens came from commercial fishing boats on the west coast. Seamount Tripp (20°36′S 14°15′E) has received even less attention than Vema, the three specimens mentioned here having been accidentally caught during hydrographic operations. The summit is about 150 m below the sea surface.

Abbreviations used

CL—carapace length
CW—carapace width
IK—Isaacs Kidd trawl
juv.—juvenile(s)
ovig.—ovigerous
SAM—South African Museum
USNM—United States National Museum
VEM—Vema station numbers

SYSTEMATIC DISCUSSION

Order ISOPODA

SPECIES LIST

Family Idoteidae	*Material*	*Station No.*	*Locality*	*Distribution*
Glyptidotea lichtensteini (Krauss)	2 juvs	VEM 2.3	Vema, 39 m	Lüderitz to Transkei
	3 juvs	VEM 4.3	Vema, 40 m	
Paridotea ungulata (Pallas)	1 ♂	VEM 2.2	Vema, 39 m	Walvis Bay to East London; Australia; New Zealand; Chile; Argentina
Family Cirolanidae				
Cirolana saldanhae Barnard	1 ovig. ♀	VEM 2.3	Vema, 39 m	Orange River mouth to Saldanha Bay
	1 damaged			
	1 juv.	VEM 4.3	Vema, 40 m	
	1 ♀	VEM 4.6	Vema, 42 m	
Family Sphaeromatidae				
Cymodoce unguiculata Barnard	1 ♀	VEM 4.6	Vema, 42 m	Lüderitz to False Bay
Cymodocealla sublevis Barnard	1 ♀	VEM 4.2	Vema, 40 m	Lüderitz to East London
Family Stenetriidae				
Stenetrium vemae sp. nov.	2 ovig. ♀	VEM 2.1	Vema, 39 m	—
	2 ovig. ♀	VEM 2.2	Vema, 39 m	
	2 ♀ 3 ♂			
	4 ovig. ♀	VEM 2.3	Vema, 39 m	
	4 ♀ 8 ♂			
	1 ♂	VEM 4.1	Vema, 40 m	
	1 ♀	VEM 4.2	Vema, 40 m	
	1 ♂	VEM 4.6	Vema, 42 m	
Family Jaeropsidae				
Jaeropsis monsmarinus sp. nov.	1 ♀ 1 ♂	VEM 4.3	Vema, 40 m	—

Family **Stenetriidae**

Stenetrium vemae sp. nov.

Figs 2–3

Description

Male

Body about three and one-half times longer than wide, with scattered setae dorsally. Cephalon broader than long, with well-developed dorsal reniform eyes; anterolateral corners produced, acute; antennal spine of frontal margin triangular, acute; rostrum wider than long, pentagonal, two anterior margins with tiny teeth, apex an obtuse angle somewhat dorsally flexed. Pereonites 1–4 with anterolateral corners acute, posterolateral corners rounded; midventral keel hardly developed, with tiny denticle on pereonites 1–3, absent on 4; pereonites 5–7 with anterolateral corners rounded, posterolateral corners of 5 rounded, 6 bluntly produced, 7 acute; midventral keel with strong posterior spine on 6 and 7. First pleonite short, reduced; pleotelson wider than long, with single strong lateral tooth in posterior half of margin, followed by sinuous margin leading to rounded apex; middorsal region gently convex, barely demarked from lateral regions.

Antennular peduncle 3-segmented, basal segment broader and longer than two distal segments, second segment shorter than third, bearing elongate simple setae; flagellum of 29–30 articles. Basal antennal segment produced into spinose process on outer distal angle; second segment shorter than first; third segment outer distal margin deeply excavate for insertion of large setiferous scale; fourth segment less than half length of third. Mandibular palp 3-segmented, basal segment with single, strong fringed seta; second segment

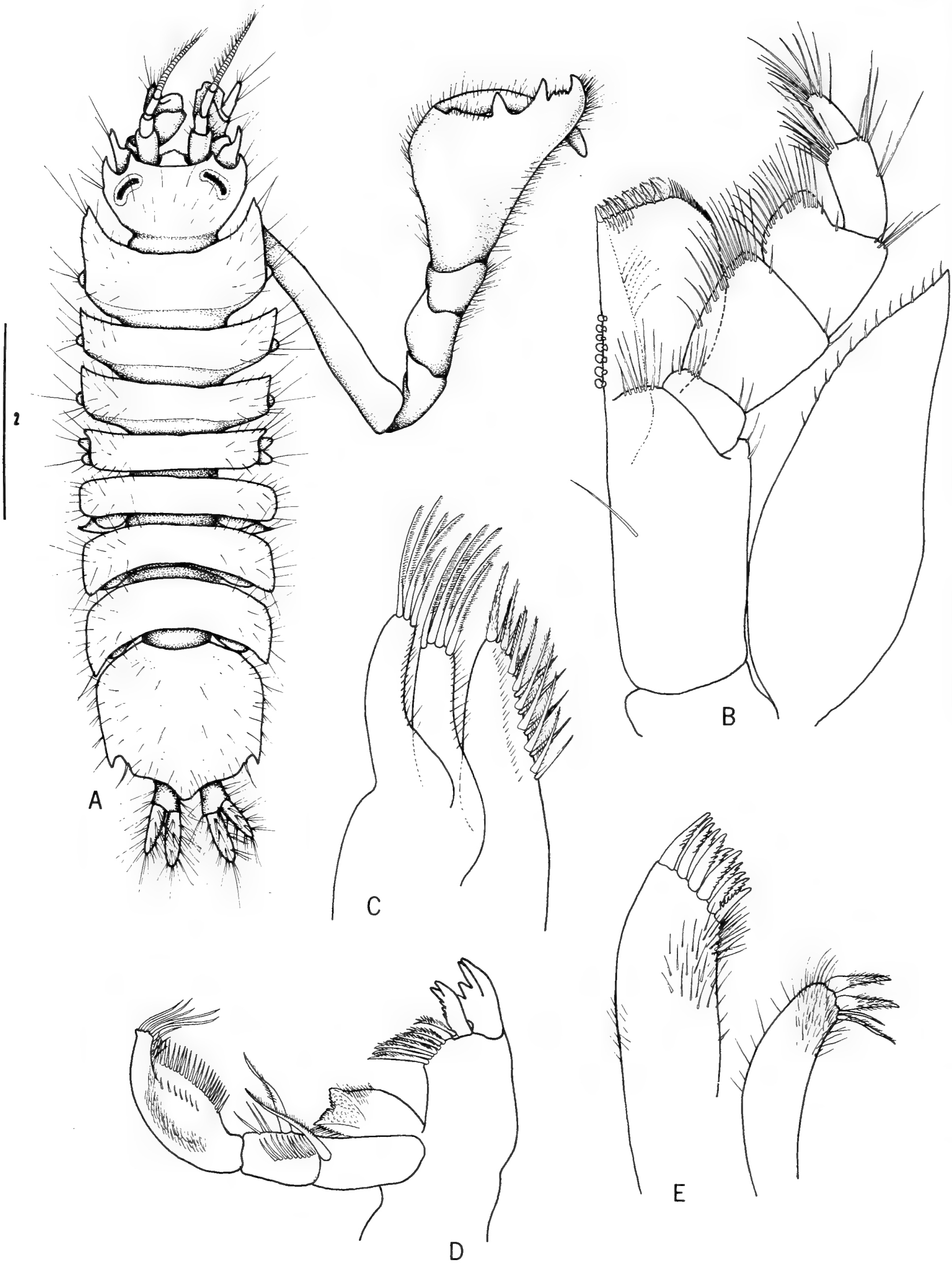

Fig. 2. *Stenetrium vemae*.
A. Holotype in dorsal view. B. Maxilliped. C. Maxilla 2. D. Mandible. E. Maxilla 1.

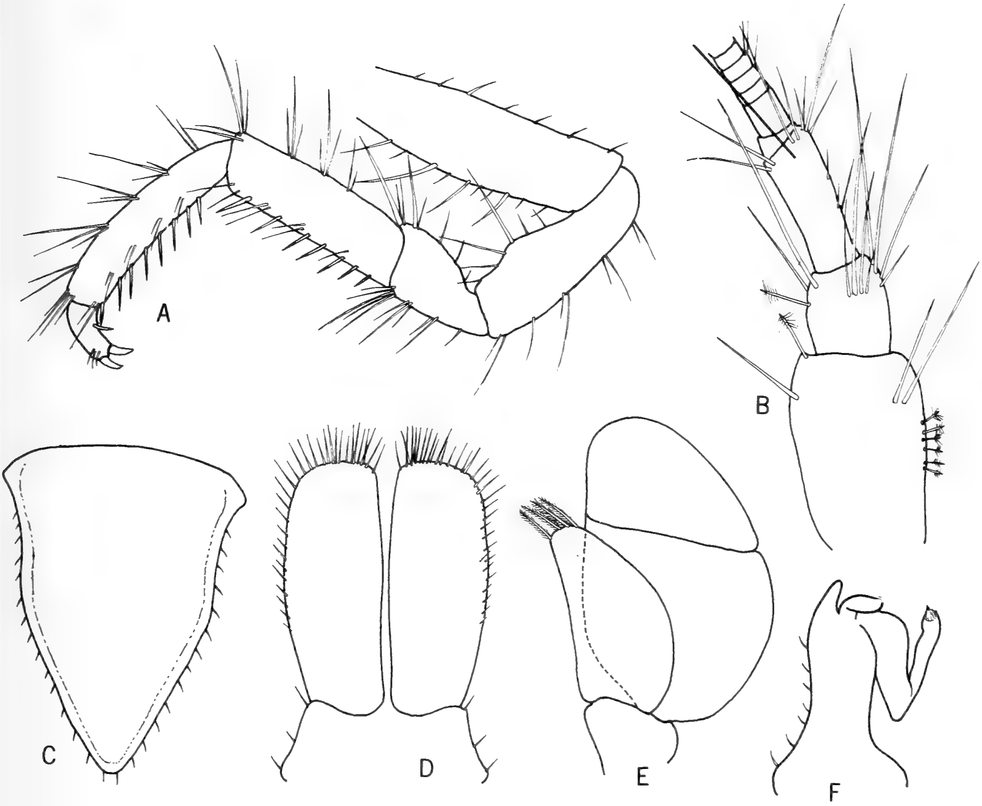

Fig. 3. *Stenetrium vemae*.
A. Pereopod 2. B. Antennular peduncle. C. Operculum ♀. D. Pleopod 1 ♂. E. Pleopod 3 ♂. F. Pleopod 2 ♂.

with row of short spines and single, strong fringed seta; terminal segment strongly curved, with row of spines on inner margin, several elongate setae on distal narrowed part; left mandible with incisor of four large cusps, sclerotized lacinia of two strong cusps and serrate spine; spine row of six serrate spines; molar bearing short marginal spines, roughened distal surface; right mandible lacking lacinia; spine row of sixteen serrate spines. Maxilla 1 outer ramus with eleven strong dentate spines; inner ramus distally with two strong and two slender setae. Maxilla 2 both lobes of outer ramus each with five elongate fringed spines; inner ramus with eight fringed spines and several setae. Maxilliped exopod apically acute; palp of five segments, each with numerous simple setae; endite with seven coupling hooks on median margin, several fringed spines and seven or eight flattened fringed scales. Pereopod 1 almost equal to entire body in length; dactylus strongly curved, longer than propodal palm; propodus widening distally, palm with strong tooth at about midlength, outer half of palm somewhat produced into lobe bearing two strong teeth separated by three tiny teeth; carpus, merus, and ischium together shorter than propodus, merus and ischium with triangular acute process on upper margin; basis elongate-cylindrical. Pereopods 2–7 similar, ambulatory; dactylus biunguiculate; propodus and carpus with slender spines on ventral margin. Pleopod 1 rami distally rounded-truncate, with short setae. Remaining pleopods typical of genus. Uropod with basis shorter than rami; latter terete, setose, inner ramus longer than outer.

Female

Pereopod 1 strongly setose, much shorter than in male; dactylus with row of short serrate spines on cutting edge; propodal palm with row of curved serrate spines. Operculum triangular, lateral margins slightly sinuous, apex narrowly rounded.

Material

Holotype SAM–A16780 ♂ TL 7,5 mm VEM 2.2
Paratypes SAM–A16781 4 ovig. ♀, 4 ♀, 8 ♂ VEM 2.3
Paratypes USNM 173516 2 ovig. ♀, 1 ♀, 2 ♂ VEM 2.2
Additional material SAM–A16782 2 ovig. ♀ VEM 2.1
SAM–A16783 1 ♂ VEM 4.1
SAM–A16784 1 ♀ VEM 4.2
SAM–A16785 1 ♂ VEM 4.6

Remarks

Using Wolff's (1962: 22) key to the genus *Stenetrium* the present material can be run down to *S. diazi* Barnard, 1920, from South Africa. The two species are undoubtedly similar, especially in the elongate form and structure of pereopod 1 of the mature male. Several differences separate the two species: the rostrum of *S. diazi* has a concave anterior margin, the rami of pleopod 1 ♂ are acutely rounded on the inner distal angle, while pereopod 1 ♂, although having a somewhat elongate propodus, does not have the outer distal lobe bearing two large teeth separated by three tiny teeth; instead it possesses two blunt, closely opposed teeth near the articulation.

Etymology

The specific name is derived from the type locality, Seamount Vema.

Family **Jaeropsidae**

Jaeropsis monsmarinus sp. nov.
Figs 4–5

Description

Male

Body about three times longer than wide, with numerous scattered, short setules dorsally. Cephalon with lateral margins entire, apex rounded.

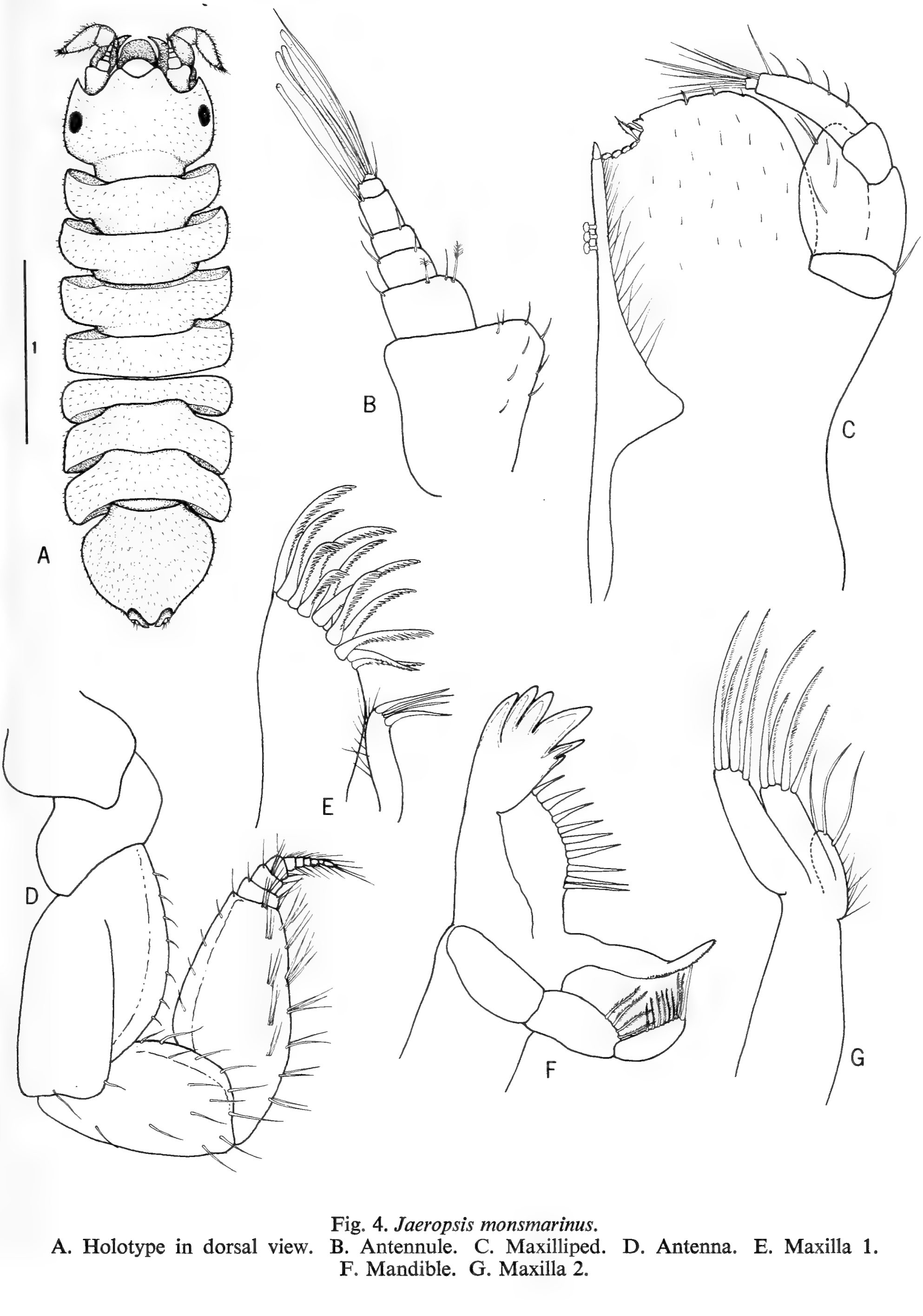

Fig. 4. *Jaeropsis monsmarinus*.
A. Holotype in dorsal view. B. Antennule. C. Maxilliped. D. Antenna. E. Maxilla 1. F. Mandible. G. Maxilla 2.

Antennule with broad basal segment equal in length to following six segments; three distal articles bearing aesthetascs. Antennal peduncle 5-segmented; two basal segments short; flagellum of nine very short articles. Mandibular palp 3-segmented, two distal segments bearing several fringed setae; incisor of six cusps; spine row of nine strong spines; molar elongate-slender with tiny denticles on lower margin. Maxilla 1 outer ramus with twelve strong serrate spines; inner ramus with four distal setae. Maxilla 2, two outer lobes each with four elongate fringed spines; inner lobe with three distal simple setae. Maxillipedal palp 5-segmented, segments 1 and 2 broad, three distal segments narrow; endite broad, inner distal angle excavate, with strong delimiting spine, four flattened denticles, and two short fringed spines; median margin with three coupling hooks. Pereopod 1 dactylus biunguiculate, remaining pereopods triunguiculate. Pleopod 1 two rami fused for two-thirds of length, terminal setose part narrowly triangular. Uropod with apically rounded hook on inner distal angle of basis; reduced rami bearing elongate simple setae.

Material

Holotype SAM–A 16786 ♂ TL 3,1 mm VEM 4.3
Allotype USNM 173517 ♀ TL 3,0 mm VEM 4.3

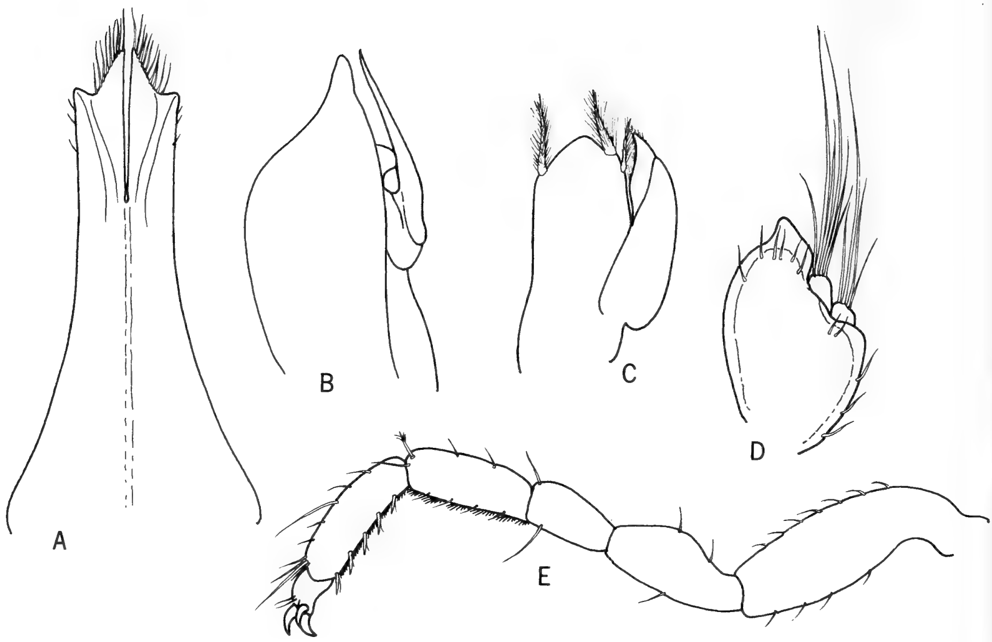

Fig. 5. *Jaeropsis monsmarinus*.
A. Pleopod 1 ♂. B. Pleopod 2 ♂. C. Pleopod 3 ♀. D. Uropod. E. Pereopod 2.

Remarks

The present species belongs to the groups of species possessing well-separated obliquely-inserted uropods (Barnard 1965: 200), which includes *J. stebbingi* Kensley, 1975, *J. paulensis* Vanhöffen, 1914, and *J. waltervadi* Kensley, 1975. Both *J. waltervadi* and *J. stebbingi* each possess a pleon with serrate margins. *J. monsmarinus* most closely resembles *J. paulensis*, especially in rostral shape and mouthparts. Vanhöffen's species, however, does not have a hook on the inner distal angle of the uropod, while the triangular terminal part of the pleopod 1 ♂ is broader than in the present species. Considering the isolated nature of Vema, *J. monsmarinus* possibly represents a population of *J. paulensis* (known from Gough, St Paul and Amsterdam Islands) which has become genetically isolated.

Etymology

The specific name is the Latin for 'seamount'.

Order DECAPODA

SPECIES LIST

* material not seen

	Material	*Station No.*	*Locality*	*Distribution*
Family **Penaeidae**				
Funchalia villosa (Bouvier)	11 ♂ 7 ♀ 40 juv.		Vema, from tuna stomach	eastern and western North Atlantic, Caribbean, South and Central Atlantic to Natal
Family **Oplophoridae**				
Notostomus auriculatus Barnard	1 ♀	IK 52	Vema	off Cape Point
Family **Alpheidae**				
* *Alpheus macrocheles* (Hailstone)			Vema	Mediterranean, Great Britain, Antilles, Guinea, Sao Tome
Synalpheus huluensis africanus Crosnier & Forest	5 ♂ 5 ovig. ♀ 12 juv.	VEM 2.3	Vema, 39 m	Guinea, Sao Tome, Cape Verde Is., Principe, Annobon
	1 ♀	VEM 4.6	Vema, 42 m	
Family **Hippolitidae**				
Eualus ctenifera (Barnard)	1 ♂ 11 ♂ 16 ♀ 1 ovig. ♀	VEM 2.2	Vema, 39 m	Port Elizabeth to Natal, Walter's Shoal
	1 ♀	VEM 3.2	Vema, 48 m	
	1 ♀	VEM 3.3	Vema, 50 m	
Family **Crangonidae**				
**Pontophilus sculptus* (Bell)			Vema	False Bay to Durban, Mediterranean, North Atlantic
Family **Palinuridae**				
Jasus tristani Holthuis			Vema	Tristan da Cunha
Family **Paguridae**				
* *Pagurus chevreuxi* Bouvier			Vema	Mediterranean
Pagurus cuanensis (Bell)	1 ♂	VEM 4.5	Vema, 42 m	False Bay to Port Elizabeth, North Atlantic, west Africa, Mediterranean
Family **Galatheidae**				
Eumunida picta Smith	1 ♀		Off Lüderitz	North-western Atlantic, Cuba, Florida, New Zealand, Australia
	1 ♂ 1 ♀		Seamount Tripp	
Galathea sp.	1 ♂	VEM 2.3	Vema, 39 m	
Family **Lithodidae**				
Lithodes murrayi Henderson	2 ♂		Off Lüderitz	St Paul and Amsterdam Is. Prince Edward Is., Crozet Is., off Natal
	3 ♂		Off South West Africa	
Family **Dromiidae**				
Pseudodromia cacuminis sp. nov.	1 ♂	VEM 3.2	Vema, 48 m	
	1 ♂	VEM 4.2	Vema, 40 m	
	1 ♀	VEM 4.4	Vema, 40 m	
	1 ♀	VEM 4.6	Vema, 42 m	
Family **Homolidae**				
Paromola alcocki (Stebbing)	1 ♀		Off Lüderitz 800 m	Port Elizabeth, Mozambique, Maldives
Paromola cuvieri (Risso)	1 ♂		Off Lüderitz, 800 m	eastern North Atlantic, Mediterranean, west Africa
	1 ovig. ♀		Seamount Tripp	

	Material	*Station No.*	*Locality*	*Distribution*
Family **Majidae**				
Macropodia cirripilus sp. nov.	1 ♀ 1 ♂	VEM 4.4 VEM 15M	Vema, 40 m Vema, 40 m	
Family **Xanthidae**				
Pilumnus sp.	1 ♂ 4 juv. 1 ♂	VEM 2.3 VEM 3.3	Vema, 39 m Vema, 50 m	
* *Pseudactaea corallina* (Alcock)			Vema	Indo-Pacific
Family **Grapsidae**				
Plagusia chabrus (Linnaeus)	1 ♂ 1 ovig. ♀		Vema	South West Africa to Natal, Chile, Juan Fernandez, Australia, New Zealand

Family **Lithodidae**

Lithodes murrayi Henderson

Lithodes murrayi Henderson, 1888: 43, pl. 4. Hale, 1941: 272, pl. 3 (figs 3–4). Yaldwyn & Dawson, 1970: 275, figs 1–3. Arnaud, 1971: 167; Kensley, 1977: 166, fig. 3.

Previous records

Possession Is., Prince Edward Is. 620 m; Macquarie Is. 120 m; Crozet Is., New Zealand, 764 m; Zululand to Durban, South Africa, 600–810 m.

Material

SAM–A 16206 ♂ CL 89 mm CW 90 mm off Lüderitz, 800 m
SAM–A 15358 ♂ CL 101 mm CW 102 mm off Lüderitz, 800 m
SAM–A 16211 3 ♂♂ CL 109–118 mm CW 106–120 mm off South West Africa

Remarks

These first Atlantic records of *L. murrayi* represent a considerable extension in the range of what was regarded as a southern Indian Ocean species.

Family **Dromiidae**

Pseudodromia cacuminis sp. nov.

Figs 6–7

Description

Female

Carapace, abdomen, and pereopods covered with short spiky hairs, becoming dense in supraorbital, rostral, and abdominal margins. Carapace wider than long, dorsally convex; front bluntly trilobed, median lobe set at lower level than lateral lobes, ventrally keeled, dorsally visible; single, rounded lateral lobe present; anterolateral and supraorbital areas bearing numerous short spines; scattering of tiny spines in rostral area. Abdomen 7-segmented, terminal segment broadly rounded; no trace of uropods. Sternal grooves ending together on broad rounded-truncate sternal plate between bases of chelipeds.

Eyestalk with scattered spinules. Antennular peduncle segments with few scattered spinules; flagellum of six articles, barely extending to distal end of antennal peduncle. Antennal peduncle segments with scattered spinules; flagellum of about fifteen articles, extending well beyond orbit. Maxilliped 1 with triangular epipodite. Maxilliped 2 with narrow epipodite and gill. Maxilliped 3 segments 3 to 6 with tiny spinules on outer surface, slender epipodite and gill present. Chelipeds equal; palm of chela longer than finger and thumb; dactylus with cutting edge of seven rounded cusps; terminal teeth fitting between two terminal teeth of propodal finger; outer surface of propodus, carpus, merus, and ischium bearing scattered spinules. Pereopods 2 and 3

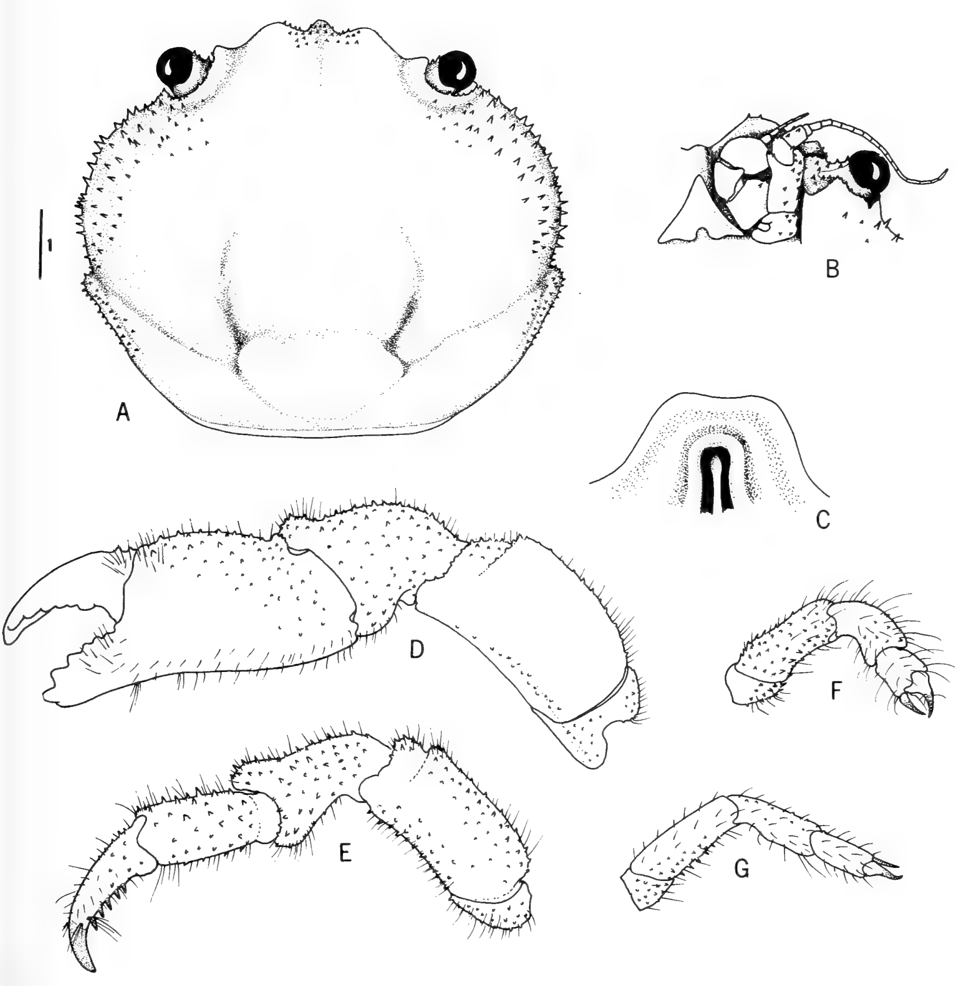

Fig. 6. *Pseudodromia cacuminis.*
A. Holotype carapace in dorsal view. B. Ventral view of orbit and antennae. C. Sternum ♀. D. Cheliped. E. Pereopod 2. F. Pereopod 4. G. Pereopod 5.

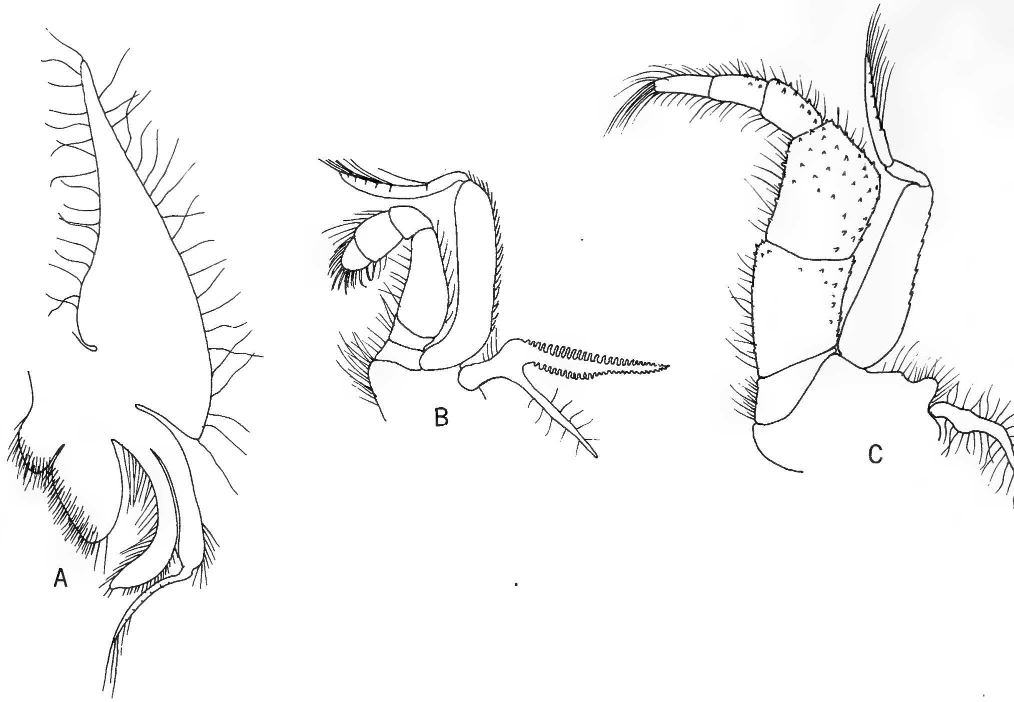

Fig. 7. *Pseudodromia cacuminis.*
A. Maxilliped 1. B. Maxilliped 2. C. Maxilliped 3.

ambulatory, similar; dactyli with strong corneous unguis and five spines on ventral margin; dactylus, propodus, carpus, and merus with scattered spinules. Pereopod 4, dactylus forming pincer with strong curved terminal spine of propodus; spinules on carpus, merus, and ischium. Pereopod 5 slightly longer and more slender than pereopod 4; curved dactylus forming pincer with strong straight spine of propodus; spinules on carpus, merus, and ischium. Branchial formula: 8 gills (on maxillipeds 2 and 3, and pereopods 1–5) + 3 epipods (on maxillipeds 1–3).

Material

Holotype SAM–A 16787 ♀ CL 6,0 mm CW 6,6 mm VEM 4.4
Paratype SAM–A 16788 immature ♂ CL 2,9 mm CW 3,0 mm VEM 4.2
Paratypes USNM 173518 ♀ CL 4,4 mm CW 4,8 mm VEM 4.6
immature ♂ CL 2,9 mm CW 3,1 mm VEM 3.2

Remarks

The lack of epipodites on the pereopods, the tridentate rostral area of the carapace, and a fifth pereopod longer than the fourth, place this material in the genus *Pseudodromia* Stimpson.

Of the five species of *Pseudodromia* described, the Vema material most closely resembles *P. spinosissima* Kensley, 1977, from deep water off the east coast of South Africa. However, the overall carapace shape of the two species differs, as does the carapace ornamentation (uniformly scattered spinules and long hairs in *P. spinosissima*, patchy spinules and short spiky hairs in *P. cacuminis*).

Etymology

The specific name 'cacuminis', meaning pointed as in a peak, refers to the type locality, viz. the summit of Seamount Vema.

Family **Homolidae**

Paromola alcocki (Stebbing)

Thelxiope (*Moloha*) *alcocki:* Barnard, 1950: 341.
(See Gordon 1950 for full synonymy.)

Previous records

Algoa Bay, South Africa, 80 m; Mozambique, 312 m; Maldive Islands, 229 m.

Material

SAM–A16207 ♀ CL (excluding rostrum) 42 mm, rostral length 8,5 mm, supraorbital spine length 12,5 mm, west of Lüderitz, about 800 m.

Remarks

This specimen closely resembles the type from South Africa, especially in the relatively elongate pereopodal spination. The supra-orbital spines, however, are relatively longer and more slender. The specimen differs markedly from the type of *P. alcocki faughni* Serene & Lohavanijaya, 1973, from the South China Sea, especially in its lack of strong setation, and in its stronger carapace and pereopodal spination.

Paromola cuvieri (Risso)

Paromola cuvieri: Monod, 1956: 79, fig. 89.

Previous records

Eastern North Atlantic and southern Scandinavia; Mediterranean to west Africa.

Material

SAM–A16789 ovigerous	♀ CL 105 mm, CW 83 mm, Seamount Tripp, 150 m.
SAM–A16790	♂ CL 120 mm, CW 102 mm, off Lüderitz, 19°55′S 11°43′E.

Remarks

Although not previously recorded from southern Africa. *P. cuvieri* is being commercially fished in the Lüderitz area.

Family **Majidae**

Macropodia cirripilus sp. nov.

Figs 8–9

Description

Male

Carapace piriform, dorsally convex. Scattered curved hairs over entire carapace and abdomen. Rostrum of two relatively short parallel spines, reaching distal end of third antennal peduncle segment. Supra-orbital eaves with four or five short spines; strong nuchal spine present; hepatic region with few scattered spine-tubercles; strong dorsolateral spine on protogastric region; metagastric region convex with medial tubercle; convex bulbous branchial region with several scattered tubercles; cardiac region convex, lacking tubercles. Abdomen 6-segmented; third segment widest, with convex lateral areas; distal margin of terminal segment evenly convex; all segments with weakly-raised middorsal longitudinal ridge.

Eyestalk with curved anterior margin, produced into rounded papilla, posterior margin straight; cornea oval, as wide as eyestalk base. Outer margin of antennular fossa spinose; interantennular spine situated at end of acutely triangular grooved process; basal peduncular segment of antennule inflated, with row of four or five small spines. Basal antennal peduncular segment narrow, with few small proximal spines and two more elongate spines distally; second segment with single small distal spine; third segment longer than second, unarmed. Epistome broader than long, flattened. Maxilliped 3 ischium wider than merus, medial margin with several small tubercle-spines, exterior surface with scattered tubercles; outer distal margin of merus with five spines, few tubercles on external surface. Chelipeds subequal, only slightly longer than middorsal carapace length (including rostrum); finger and thumb shorter than palm; both cutting edges shallowly serrate, single spine at dactylar base; upper surface of palm with few scattered tubercles; lower margin with row of seven small spines; carpus shorter than palm, with few strong dorsal spines and strong proximal tubercle on outer surface; merus one and one-half times length of carpus, with row of spines on upper and lower margins; ischium about one-third length of merus, with row of spines on ventral margin. Ambulatory pereopods decreasing in length posteriorly; pereopod 2 dactylus almost straight, unarmed ventrally, almost as long as propodus. Dactylus of pereopod 3 with subapical secondary spine. Pereopods 4 and 5, dactyli curved, with strong subapical secondary spine plus row of smaller spines. Pleopod 1 ♂ basally broad, tapering distally to curved rounded apex.

Female as in male, except for abdomen.

Material

Holotype SAM–A 16791 ♂ CL 5,0 mm CW 3,1 mm (across branchial areas)
VEM 15M
Allotype USNM 173519 ♀ CL 6,0 mm CW 3.9 mm VEM 4.4

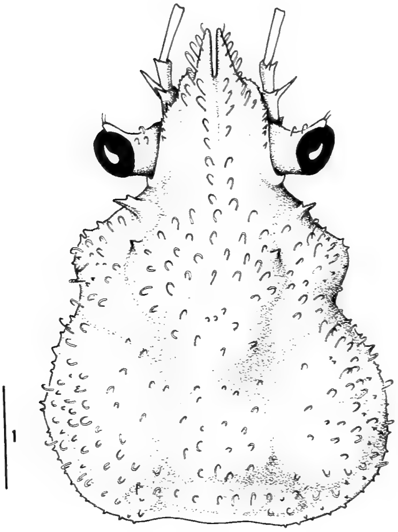

Fig. 8. *Macropodia cirripilus.*
Holotype in dorsal view.

Remarks

Of the seven species of *Macropodia* mentioned by Monod (1956), the present species resembles *M. rostrata* (Linnaeus), and that only to a limited extent. This similarity lies in the shape of the male abdomen and pleopod 1, and to a lesser degree, in the maxilliped 3. The carapace of *M. rostrata*, however, is much more strongly spinose, while the ambulatory pereopods do not become as strongly armed as in *M. cirripilus*. Further, the basal antennal segment is unarmed. None of the five species from the Mediterranean (Forest & Zariquiey Alvarez 1964) bears any close resemblance to *M. cirripilus*. The species referred to by Barnard (1950: 15, fig 2j) as *Macropodia formosa* var., from off the Natal coast, shows a similarity in the antennal and antennular spination and in the rostrum, but the carapace is less spinose and the proportions are quite different. The dactyli of the fourth and fifth pereopods, although possessing ventral spines, lack the strong subterminal spine seen in *M. cirripilus*.

Etymology

The specific name is derived from the two Latin words 'cirrus', a curl, and 'pilus' a hair, and refers to the characteristic curled hairs of the integument of this species.

Family **Xanthidae**

Pilumnus sp.

Pilumnus hirsutus non Stimpson, Barnard, 1950: 263, fig. 49 (d–g).

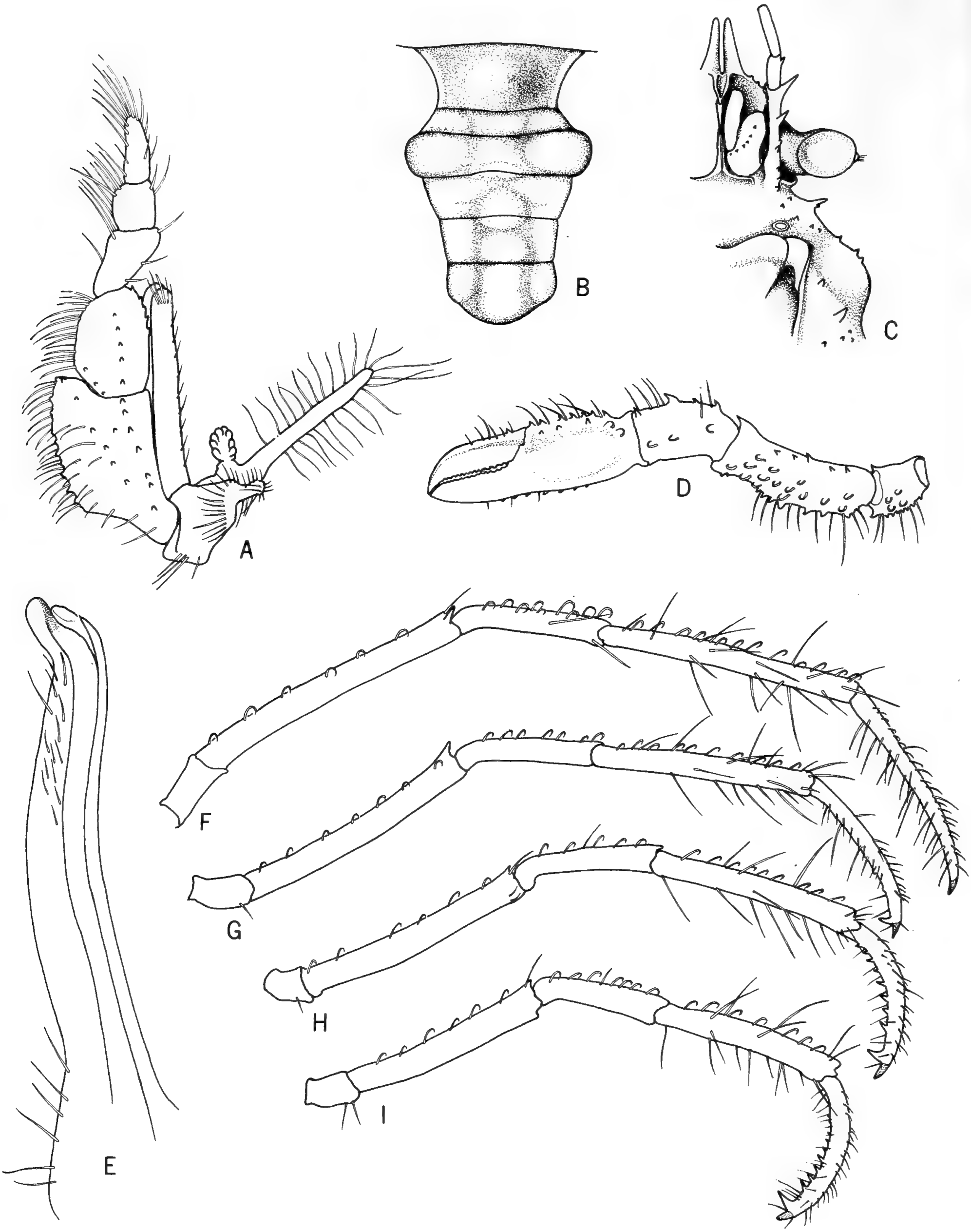

Fig. 9. *Macropodia cirripilus*.
A. Maxilliped 3. B. Abdomen ♂. C. Ventral view of orbit and antennae. D. Cheliped. E. Pleopod 1 ♂. F. Pereopod 2. G. Pereopod 3. H. Pereopod 4. I. Pereopod 5.

Previous records

False Bay, Port Elizabeth, Port Shepstone, Durban.

Material

SAM–A 16792	1 ♂ 4 juv.	39 m	Vem 2.3
SAM–A 16793	1 ♂	50 m	Vem 3.3

Remarks

The six small specimens from Vema agree well with the South African material with which it has been compared. The true identity of this species, however, is an open question. Barnard (1950) was careful to note that his figures and description were based solely on South African material, which he suspected differed from the Indo-Pacific *P. hirsutus* Stimpson. Comparison with material from the Indo-Pacific shows some distinct differences. The Vema/South African species possesses stiff hairs as well as longer flexible hairs. The larger chela is proportionally squatter, with a shorter fixed finger in the Vema/South African species. Unfortunately, the latter material is dry and in poor condition, making further comparison difficult.

Comparison with the most closely related west African form, *Pilumnus inermis* A. Milne Edwards & Bouvier, also reveals several differences, especially in the carapace hairs.

ZOOGEOGRAPHIC DISCUSSION

Although the summit plateau of Seamount Vema is of somewhat limited area (about 8 km in diameter), it supports a relatively rich fauna dominated by encrusting and cryptic forms. Berrisford (1969, table 1) summarized the affinities of the 105 species of invertebrates identified. Of these, 25 per cent were South African species, 27 per cent had a scattered (cosmopolitan) distribution, 28 per cent were endemic, and 10 per cent had Indo-Pacific affinities. Millar (1968) found the ascidian fauna of Vema to have strong affinities with South Africa and no components in common with Tristan da Cunha.

Vema is about 11×10^6 years old (Simpson & Heydorn 1965), and older than Tristan. Apart from the fish and the spiny lobster species, there are few species in common, even though the prevailing oceanic conditions need not reinforce isolation. Vema is bathed in South Atlantic Central Water, with what was initially interpreted as local subsurface upwelling of Antarctic Intermediate water having a strong northerly-flowing component (Simpson & Heydorn 1965: 251). Welsh & Visser (1970), however, suggest that this apparent upwelling, which also occurs further south away from any topographical features such as seamounts, is really cyclonic upwelling caused by a 'dying' eddy moving northward. These eddies are formed in the area where the Agulhas Current meets the West Wind Drift.

The fish, being mainly pelagic forms, can be regarded as part of the Vema fauna only in the widest sense, while Penrith (1967) has recorded only one endemic species. The problem of recruitment of *Jasus tristani* is less simple, but with a planktonic life of several months, phyllosomata originating at Tristan would need to be transported in a north-easterly direction, perhaps by offshoots of the West Wind Drift encountering the north-flowing Benguela System, for successful colonization. This obviously happens, judging from the population discovered in the later 1950s. Since then, Vema's spiny lobster population has been heavily exploited. By 1967 Heydorn reported the summit almost denuded of *Jasus*, while the divers of the 1978 cruise did not see any lobsters, neither were any specimens of the grapsid crab *Plagusia chabrus* noted. This latter species was fairly commonly seen on the earlier visits. How long a time is required for this population to recover will probably be answered only by a theoretical exercise in population dynamics.

The isopods, with their strong South African affinity and lacking planktonic larvae for dispersal, perhaps reached Vema clinging to drifting kelp. The major alga of the summit is *Ecklonia biruncinata*, which also occurs off the southern Cape coast, and would provide ideal shelter for clinging animals.

Seventeen species of decapods are included in this brief discussion of zoogeography (the two mesopelagic species mentioned being excluded). Of these seventeen, six have been recorded from South Africa, including three from the east coast only (*Eualus ctenifera*, *Paromola alcocki*, *Lithodes murrayi*); *Pontophilus sculptus*, known from False Bay to Natal and also from the Mediterranean, north-western Atlantic, and Angola; *Pilumnus* sp. recorded as *P. hirsutus* from the east and south coast; and *Plagusia chabrus*, an essentially cold-temperate austral species known from South West Africa to Natal, Australia, New Zealand, Chile, and Juan Fernandez. *Lithodes murrayi* was previously regarded as an austral form, but has been recorded from deep water off Natal (Kensley 1977).

Pseudactaea corallina is a true Indo-Pacific species and has not been recorded from the east coast of South Africa.

The two new species described here, viz. *Pseudodromia cacuminis* and *Macropodia cirripilus*, are the only 'endemics'.

Five species have been recorded from West Africa; *Alpheus macrocheles*, *Synalpheus huluensis africanus*, and *Pagurus cuanensis* (also known from the Mediterranean) are regarded as true West African forms; *Paromola cuvieri* and *Eumunida picta* have a much wider range. *Pagurus chevreuxi* is known only from the Mediterranean.

With an age of eleven million years, it is not difficult to envisage colonization of Seamount Vema by West African/Mediterranean species. The species from the Indo-Pacific and the east coast of South Africa, however, must have been faced with greater problems of colonization. Perhaps the most feasible explanation is that planktonic larval forms of these species, present in southward-flowing Agulhas water, were caught in the pockets of Agulhas water eddying northward in the South Atlantic as previously mentioned. The temperature regime in this series of events would not be a barrier to colonization. Although there is so-called upwelling of Antarctic Intermediate water in the vicinity of Vema, above the 75 m depth line the temperatures are fairly uniform (Welsh & Visser 1970: 2), being between 18° and 21° C, and comparable with east coast shallow-water temperatures.

ACKNOWLEDGEMENTS

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REFERENCES

Arnaud, P. M. 1971. *Lithodes murrayi* Henderson, 1888 (Crustacea, Decapoda, Anomura) dans les eaux côtières des îles Crozet (SW de l'Océan Indien). *Tethys* **3**: 167–172.

Barnard, K. H. 1920. Contributions to the Crustacean Fauna of South Africa. No. 6. Further additions to the list of marine Isopoda. *Ann. S. Afr. Mus.* **17**: 319–438.

Barnard, K. H. 1950. Descriptive catalogue of South African Decapod Crustacea (Crabs and Shrimps). *Ann. S. Afr. Mus.* **38**: 1–837.

Barnard, K. H. 1965. Isopoda and Amphipoda collected by the Gough Island Scientific Survey. *Ann. S. Afr. Mus.* **48**: 195–210.

Berrisford, C. D. 1969. Biology and zoogeography of Vema Seamount: a report on the first biological collection made on the summit. *Trans. R. Soc. S. Afr.* **38**: 387–398.

Forest, J. & Zariquiey, R. A. 1964. Le genre *Macropodia* Leach en Méditerranée. 1. Description et étude comparative des espèces (Crustacea Brachyura Majidae). *Bull. Mus. natn. Hist. nat., Paris* (2) **36**: 222–244.

Gordon, I. 1950. Crustacea: Dromiacea. Part I. Systematic account of the Dromiacea collected by the 'John Murray' Expedition Part II. The morphology of the spermatheca in certain Dromiacea. *Scient. Rep. John Murray Exped.* **9**: 201–253.

Grindley, J. 1967. Research on the Vema Seamount. *Comm. Fish. News, S. Afr.* **2**: 14–19.

Hale, H. M. 1941. Decapod Crustacea. *Rep. B.A.N.Z. antarct. Res. Exped.* (B) **4**: 259–285.

Henderson, J. R. 1888. Report on the anomura collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. Voy. Challenger* **27**: 1–221.

Heydorn, A. E. F. 1967. Research on the Vema Seamount. *S. Afr. Ship. News Fish. Ind. Rev.* **12**: 79–83.

Kensley, B. 1975. Five species of *Jaeropsis* from the southern Indian Ocean. (Crustacea, Isopoda, Asellota). *Ann. S. Afr. Mus.* **67**: 367–380.

Kensley, B. 1977. The South African Museum's *Meiring Naude* cruises. Part 2. Crustacea, Decapoda, Anomura and Brachyura. *Ann. S. Afr. Mus.* **72**: 161–188.

Millar, R. H. 1968. A collection of Ascidians from the Vema Seamount. *Trans. R. Soc. S. Afr.* **38**: 1–22.

Monod, T. 1956. Hippidea et Brachyura Ouest-africains. *Mem. Inst. fr. Afr. Noire* **45**: 1–674.

Penrith, M. J. 1967. The fishes of Tristan da Cunha, Gough Island, and the Vema Seamount. *Ann. S. Afr. Mus.* **48**: 523–548.

Serene, R. & Lohavanijaya, P. 1973. The Brachyura (Crustacea: Decapoda) collected by the Naga Expedition including a review of the Homolidae. *Naga Rep.* **4** (4): 1–187.

Simpson, E. & Heydorn, A. E. F. 1965. Vema Seamount. *Nature, Lond.* **207**: 249–251.

Vanhöffen, E. 1914. Die Isopoden der Deutschen Südpolar-Expedition 1901–1903. *Dt. Südpol.-Exped.* **15**: 447–598.

Welsh, J. G. & Visser, G. A. 1970. Hydrological observations in the south-east Atlantic Ocean. 2. The Cape Basin. *Investl Rep. Div. Fish. Rep. S. Afr.* **83**: 1–5.

Wolff, T. 1962. The systematics and biology of the bathyal and abyssal Isopoda Asellota. *Galathea Rep.* **6**: 1–320.

Yaldwyn, J. C. & Dawson, E. W. 1970. The stone crab *Lithodes murrayi* Henderson: the first New Zealand record. *Rec. Dominion Mus.* **6**: 275–284.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
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Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

BRIAN KENSLEY

DECAPOD AND ISOPOD CRUSTACEANS FROM THE WEST COAST OF SOUTHERN AFRICA, INCLUDING SEAMOUNTS VEMA AND TRIPP

VOLUME 83 PART 3 MARCH 1981 ISSN 0303-2515

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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1. MATERIAL should be original and not published elsewhere, in whole or in part.

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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FIRST RECORD OF THE MELON-HEADED WHALE *PEPONOCEPHALA ELECTRA* FROM SOUTH AFRICA

By

PETER B. BEST
&
PETER D. SHAUGHNESSY

Cape Town Kaapstad

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By

PETER B. BEST

&

PETER D. SHAUGHNESSY

Sea Fisheries Institute, Cape Town

(With 7 figures and 4 tables)

[*MS. accepted* 17 *July* 1980]

ABSTRACT

An adult male *Peponocephala electra* that stranded at Hout Bay (34°03′S 18°21′E) in July 1976 was the first record of the species from South Africa and the South Atlantic. Details of the animal's external appearance, body measurements, organ weights, parasites, stomach contents, skull measurements and skeletal characters are given. Differences in coloration and head and flipper shape between this species and *Feresa attenuata* are demonstrated.

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INTRODUCTION

At about 07h40 on 16 July 1976 a single small whale stranded alive on the beach at Hout Bay (34°03′S 18°21′E). It was placed in the water four times by the harbour master, but each time the animal returned to the beach. Finally it was taken to the harbour where it was placed in the water from a jetty, but the animal then stranded on a near-by slipway, where it died half an hour later (at about 10h00).

Later the same day the whale was examined by staff of the marine mammal laboratory of the Sea Fisheries Institute, and was found to be a melon-headed whale[1] (*Peponocephala electra*), the first such record for South Africa. A cast of the head was prepared and the whole skeleton was presented to the South African Museum (ZM 38245).

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[1] As there appears to be no Afrikaans (or Dutch—Van Bree 1975) name for this species, the authors suggest 'bolkopdolfyn'.

Ann. S. Afr. Mus. **83** (3), 1981: 33–47, 7 figs, 4 tables.

EXTERNAL APPEARANCE

The animal was a male, 248 cm long, and was generally undamaged apart from a few superficial cuts and abrasions caused by stranding. It was photographed about an hour after death, while the colour pattern was still rather prominent (Figs. 1–6).

The general body coloration was bluish-black overall (Fig. 1). Both upper and lower jaws, however, were irregularly edged with white as far back as the angle of the gape (Fig. 2). On the belly of the animal there was also a greyish-white 'blaze' in the midline extending from the throat to the anal slit (Fig. 3). The shape of this blaze was similar to the 'throat chevron-genital patch pattern' (Mitchell 1970) seen in pilot whales (especially *Globicephala melaena*), false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), and Risso's dolphins (*Grampus griseus*), particularly juveniles. On the throat this blaze was roughly bracket-shaped, rapidly narrowing posteriorly to a thin mid-ventral streak between the flippers. The blaze gradually widened on the abdomen to form a lozenge-shaped mark extending approximately from the umbilicus to the anus. Only at its posterior extremity (where the blaze formed a V terminating at the anterior end of the anal slit) were its outer margins well defined.

The animal had a healed scar roughly elliptical in outline under the left flipper (probably attributable to the small shark *Isistius* (Jones 1971)). The only other feature of the body coloration was a well-defined pale band on the dorsal midline of the head from the blowhole to the tip of the snout, which broadened anteriorly to cover most of the front of the head (Fig. 4). This band appears equivalent to the 'apex of melon to blowhole stripes' described by Mitchell (1970) for *Tursiops* and other species of delphinid cetaceans. It is just apparent in figures of *P. electra* provided by Nishiwaki & Norris (1966), being masked by highlights in most pictures, but has not been described previously for this species, nor for *F. attenuata*.

In other respects the animal was very similar in coloration to the pygmy killer whale. However it lacked the pale grey lateral coloration described for *F. attenuata* by Nishiwaki *et al.* (1965). As this feature fades rapidly after death, its absence on this *P. electra* carcass cannot be taken unequivocally as applying to the animal in life. Bryden *et al.* (1977*b*), however, assert that this coloration is not present in *Peponocephala*, and it could not be detected on a captive animal (seen by P.B.B.) at Sea Life Park, Hawaii, on 23 March 1980.

The dorsal fin of the Hout Bay specimen had presumably been damaged, as the trailing edge was ragged (Fig. 5).

The external measurements of the whale were taken as recommended by the Committee on Marine Mammals, American Society of Mammalogists (Norris 1961). As only ten specimens of this species appear to have been measured previously the data from all eleven animals (expressed as proportions of the total body length) are presented in Table 1. The specimen measured by

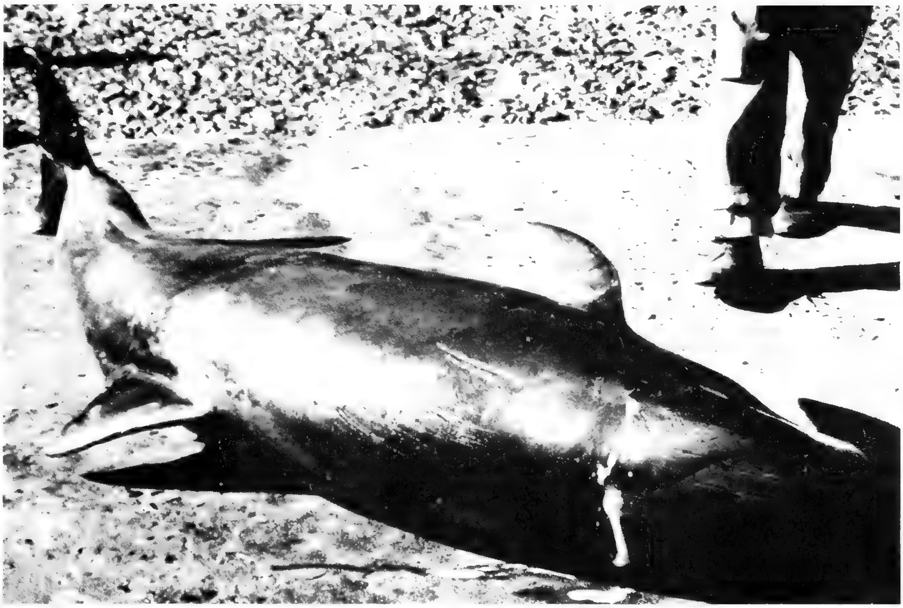

Fig. 1. General body coloration of the *Peponocephala electra* that stranded at Hout Bay.

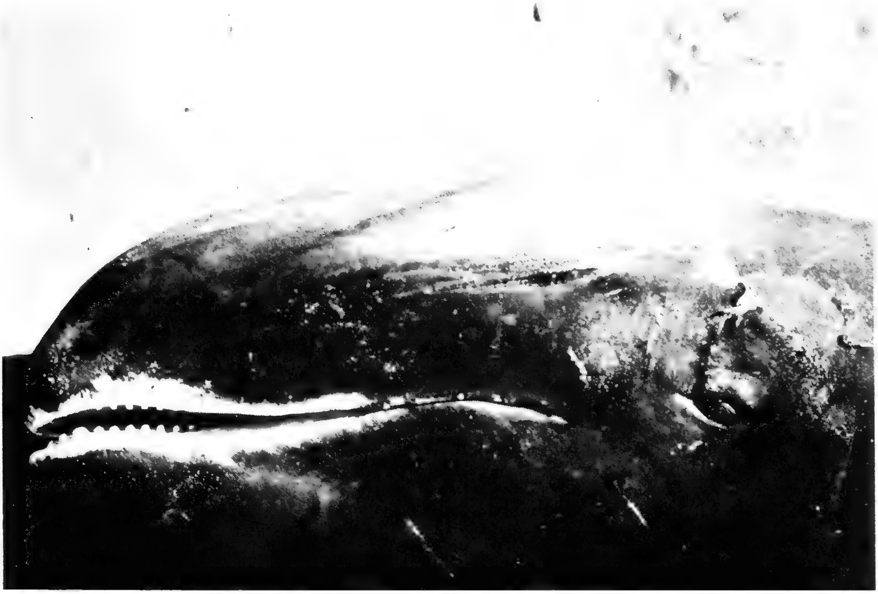

Fig. 2. Head of the *Peponocephala electra* that stranded at Hout Bay showing white edging to the upper and lower jaws.

Fig. 3. Belly of the *Peponocephala electra* that stranded at Hout Bay showing a greyish-white 'blaze' along the midline.

Fig. 4. Head of the *Peponocephala electra* that stranded at Hout Bay showing a pale band from the blowhole to the snout.

Fig. 5. Dorsal fin of the *Peponocephala electra* that stranded at Hout Bay.

Pilleri & Gihr (1973–4) was a mounted skin and hence the measurements may not be strictly comparable.

At least some of the measurements given for specimen C15 appear to be erroneous, particularly those concerning the position of the genital aperture and anus, which (although the animal was a male) are placed further posteriorly than in any of the females measured. The data for this animal have therefore been excluded from subsequent analyses. Although the remaining sample is small (six males, three females and one of unknown sex), a comparison between sexes of the proportional measurements indicates some apparent differences (apart from those concerned with the position of the anus and genital aperture). In males the anal girth appears larger (29,1–38,6% cf 26,1–28,8%), the flippers longer (17,5–20,4% cf 16,2–17,0%, or 13,0–15,8% cf 11,7–12,5%), the dorsal fin greater in height (8,4–10,9% cf 7,3–8,0%) and the tail flukes broader from the notch to their anterior margin (6,1–7,2% cf 5,1–5,5%) than in females. These apparent differences cannot all be accepted as evidence of sexual dimorphism until ontogenetic changes in body proportions of *P. electra* have been investigated: the present sample is too small for such an analysis, but it may be significant that only one of the three females was sexually mature, while four of the six males could be classified as mature (Bryden *et al.* 1977*b*). Differences in the anal girth may reflect the more anterior position of the opening in males. Alternatively, they may be indicative of real

TABLE 1
Body measurements of *Peponocephala electra.*

Measurement	ZM 38245 (♂)		Males						Females			Unknown sex
			Japan[1]	AMNH 43000[2]	C2[3]	MM9[3]	C14[4]	C15[4]	C12[4]	C13[4]	C16[4]	Songkla[5]
	cm	%	%	%	%	%	%	%	%	%	%	%
Tip of upper jaw to deepest part of notch in flukes	248	100	(260) 100	(273) 100	(267,7) 100	(223) 100	(264) 100	(204,5) 100	(228,8) 100	(211,2) 100	(257) 100	(237) 100
Tip of upper jaw to centre of anus	168	67,7	—	68,5	65,1	66,4	66,3	82,2	69,5	70,8	70,0	—
Tip of upper jaw to centre of genital aperture	144	58,1	—	55,9	54,7	57,0	56,8	76,3	66,0	67,5	66,5	—
Tip of upper jaw to tip of dorsal fin	138	55,6	—	—	62,8	60,1	60,2	72,9	58,0	57,3	56,4	—
Tip of upper jaw to ant. insertion of dorsal fin	106	42,7	—	43,2	—	—	—	—	—	—	—	40,5[6]
Tip of upper jaw to centre of umbilicus	118	47,6	—	—	43,5	—	39,8	50,9	47,3	53,0	46,7	—
Tip of upper jaw to ant. insertion of flipper	53	21,4	—	21,1	19,0	20,2	20,3	26,7	23,1	23,4	17,5	20,3
Tip of upper jaw to angle of gape	28	11,3	—	11,0	10,1	9,9	9,5	13,4	11,0	10,4	10,5	9,7[7]
Tip of upper jaw to centre of eye	36	14,5	12,9	13,6	13,6	13,5	13,4	17,7	14,9	14,4	13,7	12,7
Tip of upper jaw to blowhole	32	12,9	13,3	14,9	14,3	13,0	14,8	17,8	12,9	14,7	14,6	13,5
Tip of upper jaw to external auditory meatus	—	—	—	—	16,2	—	16,3	—	18,1	17,5	16,5	—
Girth, at axilla	139	56,0	—	—	50,4	54,3	58,7	66,0	47,8	49,5	57,6	—
Girth, maximum	147	59,3	—	—	51,8	57,8	65,2	66,0	49,8	50,8	58,8	—
Distance of maximum girth from tip of upper jaw	99	39,9	—	—	40,8	39,5	32,2	—	35,7	38,4	—	—
Girth, at anus	93,5	37,7	—	38,3	36,2	29,1	38,6	34,7	26,1	26,8	28,8	—
Girth, midway anus to notch in flukes	45,5	18,3	—	—	—	—	—	—	—	—	—	—
Height of body at same locality	40	16,1	—	—	—	—	—	—	—	—	—	—
Projection of upper jaw beyond lower	2,3	0,9	0,4	—	0,3	0,2	1,5	1,1	0,3	0,6	0,2	—
Centre of eye to angle of gape (direct)	7,5	3,0	—	—	3,1	3,8	3,6	4,7	3,7	4,1	3,7	—
Centre of eye to centre of blowhole (direct)	26	10,5	—	8,2	8,7	—	8,3	8,3	10,1	10,0	9,5	(L)7,2 (R)8,0
Blowhole, width	4,5	1,8	—	1,6	1,8	—	1,9	2,0	1,5	2,2	1,5	1,5
Blowhole, length	2,5	1,0	—	—	0,9	—	0,9	0,6	0,7	0,5	0,5	—
Eye, height	0,5	0,2	—	—	0,5	0,9	0,6	0,7	0,3	0,4	0,5	—
Eye, length	4	1,6	—	1,1	1,0	1,3	1,1	1,6	1,2	1,4	1,2	0,8
Genital slit, length	36	14,5	—	—	7,9	6,7	5,7	11,9	7,0	9,9	2,9	—
Anal slit, length	5,5	2,2	—	—	3,3	2,2	2,1	0,8	0,6	0,8	0,7	—
Flipper, length, ant. insertion to tip R	43,7	17,6	20,4[9]	18,1[8]	19,3[8]	17,9[8]	19,1[8]	22,2[8]	16,6[8]	16,2[8]	17,0[8]	—
L	43,5	17,5										
Flipper, length, axilla to tip R	33	13,3	15,8[10]	—	14,6[8]	13,0[8]	13,0[8]	16,6[8]	12,5[8]	11,7[8]	12,4[8]	14,4[11]
L	34,5	13,9										
Flipper, width, maximum R	13	5,2	6,2[8]	—	6,2[8]	4,9[8]	5,6[8]	6,2[8]	4,5[8]	4,4[8]	5,1[8]	5,1[8]
L	13,5	5,4										
Dorsal fin, height	22	8,9	9,6	8,4	10,9	9,0	9,7	8,3	7,3	7,7	8,0	8,4
Dorsal fin, length of base	52	21,0	15,4	16,1	17,1	14,8	16,3	16,4	14,4	10,4	10,5	11,4
Width of flukes, tip to tip	52	21,0	25,6	22,9	27,8	20,4	24,4	22,7	18,6	18,9	22,8	19,4[12]
Distance from nearest point on ant. border of flukes to notch R	16	6,5	—	—	6,6[8]	7,2[8]	6,1[8]	6,1[8]	5,2	5,1	5,5	—
L	16	6,5										
Depth of notch in flukes	3,5	1,4	—	1,4	1,8	5,8	1,3	2,1	1,4	1,6	1,1	—

[1] Nakajima & Nishiwaki (1965).
[2] Goodwin (1945).
[3] Bryden *et al.* (1977*a*).
[4] Bryden *et al.* (1977*b*).
[5] Pilleri & Gihr (1973–4).
[6] Presumably to anterior insertion, though this is not specified.
[7] 'Length of lips'.
[8] Side not specified.
[9] Radial length (side not specified).
[10] Ulnar length (side not specified).
[11] 'Length of flipper', side not specified.
[12] 'Tail fluke, width'.

sexual dimorphism. The largest male *P. electra* yet measured (273 cm long (Goodwin 1945)) had a pronounced protuberant keel posterior to the anus, similar to that seen in adult males of some stocks of delphinid species (e.g. eastern Pacific *Stenella longirostris* (Perrin 1972)). There is also a suggestion of a similar but smaller keel in the male 267,7 cm long illustrated by Bryden *et al.* (1977*a*). The apparently greater anal girth in male *P. electra* could reflect the development of this protuberant keel, if it should be found to be a consistent feature of the males of this species.

By comparison with the only species with which it is likely to be confused, *F. attenuata*, the melon-headed whale has a relatively longer head section. Measurements from the tip of the snout to the angle of gape, eye and blowhole as a proportion of the total body length are all greater in *P. electra* than in *F. attenuata* (Table 2). This distinction does not extend as far as the anterior insertion of the flipper, suggesting that the real difference between the two species lies in the length of the rostrum. No other distinctions in body proportions could be found between the two species.

TABLE 2

Comparison of body measurements (expressed as a proportion of body length) between *Peponocephala electra* and *Feresa attenuata*.

	P. electra[1]			*F. attenuata*[2]		
Measurement	n	mean	range	n	mean	range
Tip of snout to centre of eye	10	13,7	12,7–14,9	19	10,1	8,1–12,0
Tip of snout to angle of gape	9	10,4	9,7–11,3	17	6,9	5,4– 8,9[3]
Tip of snout to blowhole	10	13,9	12,9–14,9	19	9,8	6,7–11,9
Tip of snout to anterior insertion of flipper	9	20,7	17,5–23,4	18	19,8	16,8–22,6

[1] From Table 1 (C15 excluded).

[2] From Best (1970), Bryden (1976), Nishiwaki *et al.* (1965), Perrin & Hubbs (1969), and Pryor *et al.* (1965).

[3] Excluding a value of 11 per cent (Bryden 1976) which appears atypical as it places the angle of gape posterior to the blowhole, a situation not recorded in any of the other specimens measured to date.

From a photographic comparison, however, the flippers of *P. electra* (Fig. 6) appear to be more pointed at the tip and with a straighter trailing edge than those of *F. attenuata* (Best 1970; Bryden *et al.* 1977*a*; Nakajima & Nishiwaki 1965; Nishiwaki *et al.* 1965; Perrin 1976; Pilleri & Gihr 1973–4; Pryor *et al.* 1965; Rancurel 1974; Yamada 1954). This distinction has been noted by Bryden *et al.* (1977*b*), and may arise from differences in the arrangement of bones in the flipper (see below). To illustrate the distinction, outline drawings of flippers of *P. electra* and *F. attenuata* are shown in Figure 7.

LIFE HISTORY DATA

The animal weighed 206 kg entire on a platform scale, but its weight in parts totalled 209,8 kg (Table 3). As dissection of a large cetacean normally creates significant weight-loss (Lockyer 1976), one of the two weighings must

Fig. 6. Flipper of the *Peponocephala electra* that stranded at Hout Bay.

TABLE 3

Weight of *Peponocephala electra* in parts and weights of various organs.[1]

Part	Weight lb	kg	%
Blubber	97	(44,0)	21,0
Axial muscle, dorsal	91	(41,3)	19,7
ventral	52	(23,6)	11,2
Head[2]	65	(29,5)	14,1
Vertebral column (including tail)	46	(20,9)	9,9
Ribcage	46	(20,9)	9,9
Flippers & scapulae	18	(8,1)	3,9
Viscera	47,5	(21,5)	10,3
Total	462,5	(209,8)	100
Organ			
Heart (minus clots)		1,025	
Lungs & trachea		5,245	
Liver		3,310	
Kidneys, left		0,575	
right		0,560	
Spleen		0,075	
Intestines		3,750	
Adrenals, left		0,0068	
right		0,0092	
Diaphragm		1,455	
Oesophagus		0,360	
Bladder		0,130	
Stomach (plus contents)		2,455	

[1] Parts were weighed on a spring balance graduated in pounds.

[2] Including associated blubber and muscle.

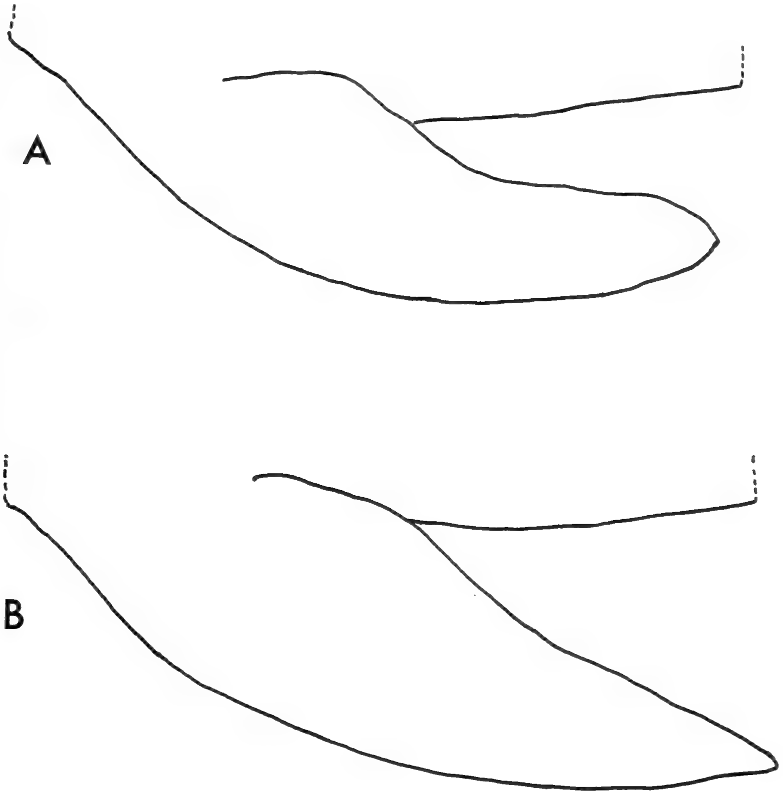

Fig. 7. Outlines of left flipper.
A. *Feresa attenuata* (from Nishiwaki *et al.* 1965).
B. *Peponocephala electra* (SAM–ZM38245).

be incorrect. The platform scale belonged to a commercial fishing company in Hout Bay and was regularly assayed, and hence its accuracy should perhaps be considered more reliable. Repeat weighings on this scale, however, produced differences of up to 2,5 kg depending on the position of the animal on the platform. The highest weight obtained (206 kg) has been adopted as the most accurate, given the apparent weight of the animal in parts.

This is the largest *P. electra* weighed to date. Bryden *et al.* (1977*b*) provided data for a foetus (3,9 kg) and three immature animals (78, 100 and 100 kg), while a calf from the eastern tropical Pacific Ocean weighed 15 kg (Perrin 1976).

No external parasites were found, despite an examination of the body surface, eye, blowhole, mouth, anal and genital slits, and appendages. 'Whale lice' (Miyazaki & Wada 1978) and traces of barnacle attachments on the tail flukes (Bryden *et al.* 1977*a*) have been recorded previously.

Numerous internal parasites were found. Longitudinal strips of blubber were cut transversely at 10 to 13 cm intervals, and the number of cestode cysts (probably *Phyllobothrium* sp.) counted. These totalled 58, ofwhich about 90 per cent were in the posterior half of the body. Cestode cysts (*Phyllobothrium chamissonii*) were also found in the abdomen grouped around the rectum (32), in the mesentery of the small intestine (2), in the diaphragm (2), and in the muscle (1). Nematodes (*Anisakis simplex*) were found in the oesophagus (36) and in the stomach (chiefly the second), where they weighed 20 g. The large and small intestines were opened for about 25 cm at 2 m intervals: one incomplete acanthocephalan (probably *Bolbosoma* sp.) was found in the rectum and 2 nematode fragments (probably *Anisakis simplex*) at about the midlength of the small intestine. Parasites were not found in the heart, liver, lungs, kidneys, or bladder.

Parasitic cysts in the blubber (unidentified) and *Phyllobothrium chamissonii* (= *Monorygma* sp.) cysts in the stomach wall or between the peritoneum and abdominal muscles in the inguinal region of *P. electra* have been recorded previously (Bryden *et al.* 1977*a*; Cannon 1977; Dailey & Brownell 1972). Nakajima & Nishiwaki (1965) reported the presence of unidentified stomach nematodes, while Cannon (1977) described *Anisakis simplex* and *A. typica* from the stomach of *P. electra*. Bryden *et al.* (1977*a*), Dawbin *et al.* (1970), and Nakajima & Nishiwaki (1965) all record the presence of small thread-like worms or nematodes in the air sinuses of the head, identified by Bryden *et al.* (1977*a*) as *Stenurus* sp. and by Cannon (1977) as *S. globiocephalae*. The air sinuses of the Hout Bay specimen were unfortunately not examined. Dailey & Brownell (1972) also list the trematode *Nasitrema* sp. and the nematode *Halocercus* sp. as 'new host records' for this species, without specifying the host tissue.

The stomach contained 2 upper beaks and 1 lower beak of *Loligo reynaudi* and 1 lower beak of a juvenile ommastrephid squid, a squid pen, 2 fish otoliths (*Merluccius* sp.) and some sand. There are no previously identified stomach contents for this species. As indicated by Leatherwood & Walker (1979), however, stomach contents of stranded cetaceans should be interpreted with a great deal of caution: in *Lissodelphis borealis* these authors found many near-shore fish species not representative of the normal known distribution of the dolphin and which were probably ingested just prior to stranding.

The faeces were bright green with much mucus, indicating that the animal was either sick or had not fed for some time (Ridgway 1972).

The testes (without epididymides) weighed 760 g (left) and 1 035 g (right), and measured 34 × 7,4 × 3,9 cm (left) and 38 × 8,8 × 4,6 cm (right). Bryden *et al.* (1977*b*) have summarized the known reproductive data for male *P. electra*, comprising a total of five animals. A male with a combined testis weight of 1 359 g was shown histologically to be sexually mature, so it is reasonable to assume that the Hout Bay animal was also mature.

SKELETON

The skull dimensions of the Hout Bay specimen were measured using a pair of 55 cm vernier calipers. To avoid ontogenetic differences, comparison with previously measured skulls (Table 4) has been confined to animals with a condylobasal length (CBL) exceeding 440 mm: this limit was chosen on the basis of the determination of skulls with a CBL of 415 mm as adolescent and a CBL of 456 mm as adult (Dawbin *et al.* 1970), and the description of a skull with a CBL of 440,2 mm as 'approaching adulthood' (Bryden *et al.* 1977*a*). The Hout Bay specimen could clearly be classified as adult from the robust rostrum, strongly developed supraoccipital crest, the degree of fusion of sutures, the advanced ossification of the mesethmoid, the degree of filling-in of the cranial hiatus and the posterior extension of the vomer in the basicranial trough (Dawbin *et al.* 1970).

TABLE 4

Skull measurements of *Peponocephala electra*

	ZM 38245			Previous records[1]
	mm	% CBL	n	Range of % CBL
Condylobasal length	477	100	—	—
Rostrum length	258	54,1	12	52,3–55,6
Rostrum basal width	136	28,5	12	27,6–31,0
Rostrum width 60 mm ant. to antorbital notches	116	24,3	11	22,2–26,5
Rostrum width at middle	97	20,3	11	17,3–25,2
Premaxillae, width at same point	46	9,6	7	8,7–14,25
Tip of snout to blowhole	320	67,1	7	68,7–70,4
Tip of snout to pterygoid	300	62,9	5	62,5–66,5
Preorbital width	245	51,4	11	50,5–54,4
Postorbital width	263	55,1	12	53,6–57,6
Orbital width	249	52,2	7	51,3–54,6
Blowhole, width at	61	12,8	7	11,9–16,6
Zygomatic breadth	263	55,1	11	54,0–57,6
Greatest width of premaxillaries	101	21,2	12	19,9–23,6
Width of braincase across parietals	197	41,3	10	37,7–44,0
Length of upper toothrow L	186	39,0	11	36,6–40,7
R	184	38,6	11	35,3–40,9
Hinder edge of upper toothrow L	184	38,6	5	38,6–41,0
to tip of premaxillae R	185	38,8	5	37,5–41,2
Length of lower toothrow L	164	34,4	8	34,6–38,6
R	163	34,2	8	33,8–39,2
Hinder edge of lower tooth L	170	35,6	5	35,6–38,2
row to tip of mandible R	170	35,6	5	34,4–38,5
Mandible length	384	80,5	9	79,4–81,8
Coronoid height	95	19,9	9	17,7–20,5
Length of symphysis	38	8,0	7	6,7– 9,2
Post-temporal length	97[2]	20,3	10	17,1–21,0
Post-temporal height	62[2]	13,0	10	11,0–15,3
Width at ¾ rostrum length	72	15,1	5	14,7–16,9
Cranial height	154	32,3	6	28,5–40,4
Cranial length, internal	154	32,3	5	27,8–33,9[3]
Tooth count[4] RU	22		14	21–26
LU	21		14	20–25
RL	22		13	22–25
LL	22		13	22–25

[1] From Bryden *et al.* (1977*a*), Dawbin *et al.* (1970), and Van Bree & Cadenat (1968).

[2] Left side only.

[3] Plus one outlying value of 18,7 per cent (Bryden *et al.* 1977*a*).

[4] Count of alveoli.

Nearly all the skull dimensions (expressed as percentages of CBL) of the Hout Bay animal fall within the range previously recorded for 'adult' *P. electra.* One exception is the measurement tip of snout to blowhole, which appears shorter than any previously recorded. Comparison of the outline of the nares with figures provided by Dawbin *et al.* (1970) and by Van Bree & Cadenat (1968), however, suggest that either the Hout Bay specimen was atypical, or that the anterior margin of the nares was damaged. The dimensions of the tooth rows in general are close to or below the lower limits of the previously reported ranges, but the number of teeth (= alveoli) present is also at or just above the lower limit recorded for other adults.

Many of the teeth showed extensive wear at the tip, particularly in the lower jaw, so that the occlusal surfaces were flattened. The maximum diameter of the five largest teeth in the upper and lower jaws (measured with dial calipers) averaged 6,3 and 6,6 mm respectively, while three of the relatively unworn teeth (all from the upper jaw) had overall dimensions (length × maximum diameter) of 8,8 × 5,8, 7,7 × 5,9 and 7,6 × 5,8 mm. The teeth of *P. electra* are, therefore, somewhat smaller than those of *F. attenuata,* where the five largest teeth in upper and lower jaws of two specimens averaged 21,2 × 6,8 mm (upper), 23,2 × 7,4 mm (lower), and 19,2 × 6,4 mm (upper), 22,0 × 8,0 mm (lower) (Nishiwaki *et al.* 1965).

The vertebral column of the Hout Bay specimen was composed of eighty-one vertebrae: previous vertebral counts for *P. electra* have been eighty-one (Bryden *et al.* 1977*a*, Goodwin 1945) and eighty-two (Nakajima & Nishiwaki 1965). Comparison of counts of vertebrae in different regions of the column with published data is impossible when the criteria used for distinguishing the regions are not specified (as indicated by De Smet 1977). Adopting De Smet's nomenclature, the vertebral formula of the Hout Bay specimen was as follows: Cv = (4) + 3, Th.v. = 12, I.Th.ℓ = 2, X = 18, Y = 31, Z = 11. Total = 81.

All epiphyses were fused to their centra, confirming the status of the animal as adult.

Vertebrae numbers 46 and 47 (the 7th and 8th of the caudal series) were partly fused together by their left transverse processes, clearly a pathological condition.

There were 14 thoracic ribs on the right side and 13 on the left, 6 of which on each side possessed a definite capitulum and tubercle. Each side of the 7th thoracic vertebra, however, possessed a spur 14 to 17 mm long on the ventral surface of the transverse process, while at similar positions on each side of the 8th thoracic vertebra there was a small protuberance. Similar structures were figured or described by Dawbin *et al.* (1970), also on the 7th and 8th thoracic vertebrae, and described as rib neck vestiges: in an animal from Australia these structures were present on the 8th, 9th and 10th thoracic vertebrae (Bryden *et al.* 1977*a*.) A 'spur' on the 7th thoracic was also described by Nakajima & Nishiwaki (1965). Vestigial catapophyses were present on the 6th to 11th thoracic vertebrae: Bryden *et al.* (1977*a*) found them on the 7th to 10th vertebrae.

The 5th rib on the left side of the thorax bore evidence of a healed fracture at a point about 40 per cent of its length from the capitulum.

Unlike *F. attenuata*, where the flippers normally contain four carpal bones (Best 1970), the Hiratsuka specimen of *P. electra* had five carpals in both flippers (Nakajima & Nishiwaki 1965). As determined by radiography, the Hout Bay specimen had five carpals in the right flipper and six in the left, the sixth being a small, almost circular element in contact with the cuneiform, hamate and fourth metacarpal bones.

The phalangeal formula was

Left I : 3, II : 8, III : 6, IV : 3, V : 2
Right I : 3, II : 8, III : 6, IV : 4, V : 2

The minute terminal phalanges on the 2nd to 5th digits shown in Nakajima & Nishiwaki's (1965) X-rays were (apart from R IV) absent. There was no indication of the bilateral asymmetry reported by Bryden *et al.* (1977*a*).

Despite Nakajima & Nishiwaki's (1965) contention that the phalangeal formula of *P. electra* resembled that of *F. attenuata*, there is some indication that the relative numbers of phalanges in digits II and III differ. In 21 flippers of *F. attenuata* examined by Nishiwaki *et al.* (1965), 76 per cent had a difference of only one phalange between digits II and III, and 24 per cent a difference of two phalanges. In both the Hiratsuka and Hout Bay specimens of *P. electra*, there was a difference of two phalanges between these digits, while Bryden *et al.* (1977*a*) gave the range for *P. electra* as 8–9 phalanges for digit II and 6–7 for digit III. This apparent difference between *P. electra* and *F. attenuata* may account for the difference in flipper shape mentioned above.

The sternum consisted of four elements, of which the most posterior was very small, as in the specimen examined by Nakajima & Nishiwaki (1965), but unlike their example all four elements were unfused. There were ten pairs of sternal ribs, as opposed to the nine found by Nakajima & Nishiwaki (1965).

DISCUSSION

Since Perrin (1976) summarized the known records of *P. electra*, and illustrated their distribution, there have been several additional published records. Caldwell *et al.* (1976) documented four specific records from the island of St Vincent in the southern Caribbean. Bryden *et al.* (1977*a*) described two specimens from Queensland and one from the Queensland–New South Wales border of Australia. A mass stranding of fifty-three individuals on Moreton Island, Queensland, was later described by Bryden *et al.* (1977*b*), and these authors also listed two previously unpublished records for the Australian region —an immature male stranded at Tweed Heads, New South Wales, in February 1967, and a sighting of a group of 100 off Stadbroke Island, Queensland, in May 1975. Miyazaki & Wada (1978) mentioned an animal of this species collected at sea in the western tropical Pacific. Perrin (1976) also omitted from his figure the record from Derby, Western Australia listed by Dawbin *et al.* (1970).

The nearest published records of the species to South Africa are an animal harpooned in mid-Atlantic at 03°03′N 24°40′W (Goodwin 1945) and a skeleton from the central Indian Ocean from Gan Island, Addu Atoll, Maldive Islands, at about 00°30′S 73°20′E (Dawbin *et al.* 1970). In addition, however, there are six skulls (one with an incomplete skeleton) of this species in the British Museum (Natural History) that were collected from stranded animals on the south side of Aldabra Atoll (09°20′S 46°25′E) near a place called Dune Jean Louis in September 1974. The catalogue numbers are 1980.147 to 1980.152 (M. C. Sheldrick *in litt.* 14 January 1980). The Hout Bay animal, therefore, represents not only the first record for South Africa but also the first record for the South Atlantic, and a major apparent range extension.

P. electra is usually considered to occur in tropical (Rice 1977) or tropical and subtropical waters (Van Bree & Cadenat 1968). Under this assumption the South African record, at 34°03′S and at the southern end of the cold Benguela Current system, may represent an animal at the probable extreme end of its range.

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REFERENCES

Best, P. B. 1970. Records of the pygmy killer whale, *Feresa attenuata*, from southern Africa, with notes on behaviour in captivity. *Ann. S. Afr. Mus.* 57: 1–14.

Bryden, M. M. 1976. Observations on a pygmy killer whale, *Feresa attenuata*, stranded on the east coast of Australia. *Aust. Wildl. Res.* **3**: 21–28.

Bryden, M. M., Dawbin, W. H., Heinsohn, G. E. & Brown, D. H. 1977*a*. Melon-headed whale, *Peponocephala electra*, on the east coast of Australia. *J. Mammal.* **58**: 180–187.

Bryden, M. M., Harrison, R. J. & Lear, R. J. 1977*b*. Some aspects of the biology of *Peponocephala electra* (Cetacea: Delphinidae). I. General and reproductive biology. *Aust. J. mar. Freshwat. Res.* **28**: 703–715.

Caldwell, D. K., Caldwell, M. C. & Walker, R. V. 1976. First records for Fraser's dolphin (*Lagenodelphis hosei*) in the Atlantic and the melon-headed whale (*Peponocephala electra*) in the Western Atlantic. *Cetology* **25**: 1–4.

Cannon, L. R. G. 1977. Some aspects of the biology of *Peponocephala electra* (Cetacea: Delphinidae). II. Parasites. *Aust. J. mar. Freshwat. Res.* **28**: 717–722.

DAILEY, M. D. & BROWNELL, R. L. Jr. 1972. A checklist of marine mammal parasites. *In:* RIDGWAY, S. H., *ed. Mammals of the Sea, Biology and Medicine*: 528–589. Springfield, Illinois: Thomas.

DAWBIN, W. H., NOBLE, B. A. & FRASER, F. C. 1970. Observations on the electra dolphin, *Peponocephala electra. Bull. Br. Mus. nat. Hist. Zool.* **20**: 173–201.

DE SMET, W. M. A. 1977. The regions of the cetacean vertebral column. *In*: HARRISON, R. J., *ed. Functional Anatomy of Marine Mammals* **3**: 59–80. London: Academic Press.

GOODWIN, G. G. 1945. Record of a porpoise new to the Atlantic. *J. Mammal.* **26**: 195.

JONES, E. C. 1971. *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. *Fishery Bull., Wash.* **69**: 791–798.

LEATHERWOOD, S. & WALKER, W. A. 1979. The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern North Pacific. *In:* WINN, H. E. & OLLA, B. L., *eds. Behavior of marine animals. Current perspectives in research.* **3**: 85–141. New York: Plenum.

LOCKYER, C. 1976. Body weights of some species of large whales. *J. Cons. perm. int. Explor. Mer* **36**: 259–273.

MITCHELL, E. 1970. Pigmentation pattern evolution in delphinid cetaceans: an essay in adaptive coloration. *Can. J. Zool.* **48**: 717–740.

MIYAZAKI, N. & WADA, S. 1978. Observation of cetacea during whale marking cruise in the western tropical Pacific, 1976. *Scient. Rep. Whales Res. Inst., Tokyo* **30**: 179–195.

NAKAJIMA, M. & NISHIWAKI, M. 1965. The first occurrence of a porpoise (*Electra electra*) in Japan. *Scient. Rep. Whales Res. Inst., Tokyo* **19**: 91–104.

NISHIWAKI, M., KASUYA, T., KAMIYA, T., TOBAYAMA, T. & NAKAJIMA, M. 1965. *Feresa attenuata* captured at the Pacific coast of Japan in 1963. *Scient. Rep. Whales Res. Inst., Tokyo* **19**: 65–90.

NISHIWAKI, M. & NORRIS, K. S. 1966. A new genus, *Peponocephala*, for the odontocete cetacean species *Electra electra. Scient. Rep. Whales Res. Inst., Tokyo* **20**: 95–100.

NORRIS, K. S. 1961. Standardized methods for measuring and recording data on the smaller cetaceans. *J. Mammal.* **42**: 471–476.

PERRIN, W. F. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. *Fishery Bull., Wash.* **70**: 983–1003.

PERRIN, W. F. 1976. First record of the melon-headed whale, *Peponocephala electra*, in the eastern Pacific, with a summary of world distribution. *Fishery Bull., Wash.* **74**: 457–458.

PERRIN, W. F. & HUBBS, C. L. 1969. Observations on a young pygmy killer whale (*Feresa attenuata* Gray) from the eastern tropical Pacific Ocean. *Trans. S. Diego Soc. nat. Hist.* **15**: 297–308.

PILLERI, G. & GIHR, M. 1973–4. Contribution to the knowledge of the cetaceans of Southwest and Monsoon Asia (Persian Gulf, Indus Delta, Malabar, Andaman Sea and Gulf of Siam). *Invest. Cetacea* **5**: 95–149.

PRYOR, T., PRYOR, K. & NORRIS, K. S. 1965. Observations on a pygmy killer whale (*Feresa attenuata* Gray) from Hawaii. *J. Mammal.* **46**: 450–461.

RANCUREL, P. 1974. Echouage en masse du cétacé *Peponocephala electra* aux Nouvelles-Hébrides. *Biol. Conserv.* **6**: 233–235.

RICE, D. W. 1977. A list of the marine mammals of the world. *NOAA Tech. Rep. NMFS SSRF* **711**: 1–15.

RIDGWAY, S. H. 1972. Homeostasis in the aquatic environment. *In*: RIDGWAY, S. H., *ed. Mammals of the Sea, Biology and Medicine:* 590–747. Springfield, Illinois: Thomas.

VAN BREE, P. J. H. 1975. Preliminary list of the cetaceans of the southern Caribbean. *Stud. Fauna Curaçao* **48**: 79–87.

VAN BREE, P. J. H. & CADENAT, J. 1968. On a skull of *Peponocephala electra* (Gray, 1846) (Cetacea, Globicephalinae) from Sénégal. *Beaufortia* **14**: 193–202.

YAMADA, M. 1954. An account of a rare porpoise, *Feresa* Gray from Japan. *Scient. Rep. Whales Res. Inst., Tokyo* **9**: 59–88.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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PETER B. BEST
&
PETER D. SHAUGHNESSY

FIRST RECORD OF THE MELON-HEADED WHALE *PEPONOCEPHALA ELECTRA* FROM SOUTH AFRICA

VOLUME 83 PART 4 FEBRUARY 1981 ISSN 0303–2515

ANNALS

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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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THE SOUTH AFRICAN MUSEUM'S *MEIRING NAUDE* CRUISES

PART 12

CRUSTACEA DECAPODA OF THE 1977, 1978, 1979 CRUISES

By

BRIAN KENSLEY

Cape Town Kaapstad

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PART 12

CRUSTACEA DECAPODA OF THE 1977, 1978, 1979 CRUISES

By

Brian Kensley

Smithsonian Institution, Washington, D.C.

(With 11 figures)

[*MS. accepted 1 October 1980*]

ABSTRACT

Ninety-five species of Macrura, Anomura, and Brachyura Decapoda from deep water off the east coast of South Africa are recorded. Of the fifteen new records for the area, *Odontozona spinosissima*, *Uroptychus edwardi*, and *Paralomis roeleveldae* are described as new, while the second record of *Sergia inequalis* Burkenroad is noted.

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INTRODUCTION

As a continuation of the reports on the South African Museum's *Meiring Naude* cruises on the east coast of South Africa, the present paper deals with the Decapoda taken during the three cruises of 1977, 1978 and 1979. The decapods of the two earlier cruises have already been reported (Kensley 1977*a*, 1977*b*).

The area of the continental shelf investigated during all these cruises stretches from Durban in the north to the Transkei coast (Fig. 1), in depths ranging from 100 to 2 800 m. Although abbreviated station data are provided for the stations mentioned in this paper, fuller information on these cruises may be obtained from Louw (1980).

Abbreviations used throughout: SAM—South African Museum catalogue number; SM—*Meiring Naude* station number; CL—carapace length; CW—carapace width; RL—rostral length; ovig.—ovigerous; juv.—juvenile.

Ann. S. Afr. Mus. **83** (4), 1981: 49–78, 11 figs.

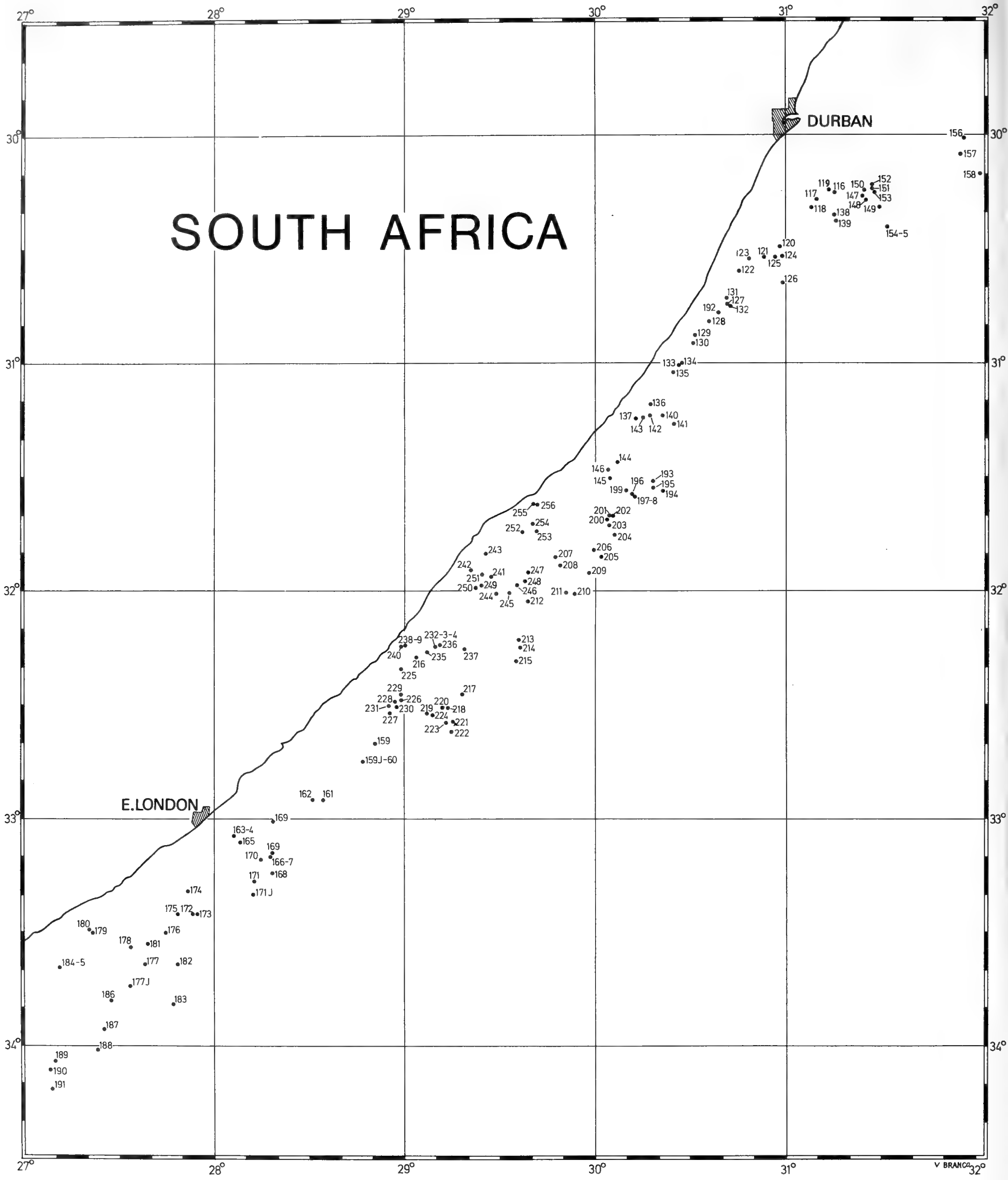

Fig. 1. Map showing localities of collecting stations.

SPECIES LIST

SUBORDER PENAEIDEA

Family **Aristeidae**

Subfamily Aristeinae

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
Aristaeomorpha foliacea (Risso)	119	4	—	4	9
	121	—	—	1	—
Plesiopenaeus edwardsianus (Johnson)	121	1	—	—	—
	227	1	—	—	—
Plesiopenaeus nitidus Barnard	119	1	—	2	59
	121	9	—	6	—
	134	1	—	3	—

Subfamily Benthesicyminae

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
Bentheogennema intermedia (Bate)	145	1	—	—	—
	194	—	—	1	—
**Bentheogennema pasithea* (De Man)	224	1	—	—	—
Benthesicymus investigatoris Alcock & Anderson	134	—	—	4	—
Gennadas bouvieri Kemp.	139	2	—	3	—
	140	1	—	3	—
	148	—	—	2	—
	160	1	—	—	—
	208	1	—	—	—
	218	—	—	2	—
	220	—	—	1	—
Gennadas capensis Calman	139	2	—	—	—
	140	—	—	1	—
	148	1	—	4	—
	153	1	—	2	—
	154	—	—	2	—
	211	1	—	—	—
	218	1	—	—	—
	224	1	—	—	—
Gennadas gilchristi Calman	119	2	—	1	—
	126	5	—	2	—
	132	1	—	—	—
	139	22	—	17	—
	140	8	—	8	—
	145	5	—	6	—
	148	48	—	30	—
	153	19	—	33	—
	154	23	—	24	—
	160	—	—	1	—
	167	2	—	1	—
	168	2	—	1	—
	173	2	—	3	—
	174	1	—	—	—
	182	4	—	2	—
	186	2	—	—	—
	187	—	—	2	—
	195	1	—	—	—
	205	—	—	1	—
	208	2	—	4	—
	209	11	—	4	—
	211	—	—	7	—

* New record

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	218	43	—	26	—
	220	4	—	3	—
	221	3	—	8	—
	223	16	—	14	—
	224	16	—	11	—
Gennadas incertus (Balss)	126	—	—	1	—
	139	1	—	1	—
	140	1	—	—	—
	145	1	—	1	—
	148	1	—	3	—
	173	1	—	1	—
	218	—	—	1	—
	220	1	—	—	—
	221	—	—	1	—
Gennadas kempi Stebbing	139	1	—	—	—
	194	—	—	1	—
	195	1	—	1	—
	201	2	—	—	—
	203	5	—	5	—
	208	3	—	4	—
	209	1	—	1	—
	214	—	—	1	—
	218	3	—	—	—
	220	—	—	5	—
	221	6	—	2	—
Gennadas parvus Bate	119	—	—	1	—
	139	3	—	5	—
	140	1	—	—	—
	145	1	—	—	—
	148	2	—	1	—
	153	—	—	1	—
	167	—	—	1	—
	194	1	—	1	—
	199	1	—	—	—
	209	1	—	3	—
	211	—	—	2	—
	218	2	—	1	—
	223	—	—	1	—
	224	1	—	—	—
Gennadas propinquus Rathbun	119	1	—	—	—
	126	—	—	1	—
	139	—	—	2	—
	140	1	—	—	—
	148	1	—	4	—
	157	—	—	1	—
	159	—	—	1	—
	167	—	—	1	—
	199	—	—	2	—
Gennadas scutatus Bouvier	119	—	—	2	—
	126	—	—	2	—
	132	3	—	2	—
	139	2	—	6	—
	140	1	—	1	—
	148	—	—	2	—
	153	1	—	4	—

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	154	1	—	2	—
	157	—	—	1	—
	160	2	—	—	—
	167	1	—	—	—
	168	1	—	—	—
	182	2	—	2	—
	218	1	—	1	—
	221	1	—	—	—
Gennadas tinayrei Bouvier	119	1	—	—	—
	126	—	—	1	—
	132	—	—	1	—
	148	1	—	—	—
	153	1	—	1	—
	154	1	—	—	—
	157	1	—	—	—
	160	—	—	1	1
	168	1	—	—	—
	171	1	—	—	—
	189	2	—	—	—
	218	2	1	—	—
	220	1	—	—	—
	221	1	—	—	—
Family **Solenoceridae**					
Haliporoides triarthrus Stebbing	119	1	—	—	—
**Hymenopenaeus halli* Bruce	119	—	—	—	4
	121	—	—	1	—
Family **Sergestidae**					
Petalidium foliaceum Bate	209	2	—	—	—
**Petalidium obesum* (Krϕyer)	139	—	—	3	—
	140	1	—	5	—
	157	1	—	1	—
	167	—	—	1	—
	195	1	—	1	—
	201	1	—	—	—
	203	—	—	3	—
	209	—	—	1	—
	214	1	—	2	—
	220	2	—	2	—
Sergestes arcticus Krϕyer	132	—	—	—	1
	139	—	—	—	1
	148	—	—	1	—
	171	—	—	—	2
	187	1	—	—	—
Sergestes armatus Krϕyer	126	—	—	1	—
	132	—	—	1	—
	138	—	—	1	—
	139	—	—	—	1
	140	—	—	2	1
	145	1	—	1	1
	148	3	—	4	—
	154	1	—	—	—
	157	1	—	2	—
	168	—	—	1	—
	183	—	—	—	1

* New record

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	190	—	—	1	—
	191	—	—	—	3
	195	1	—	—	—
	197	2	—	1	—
	199	—	—	2	—
	211	—	—	1	—
	218	—	—	1	—
	220	1	—	1	—
	221	1	—	1	—
	223	—	—	2	—
	224	2	—	—	—
Sergestes atlanticus H. Milne Edwards	119	1	—	—	—
	126	—	—	1	1
	132	1	—	1	1
	138	1	—	1	—
	140	1	—	—	—
	153	1	—	1	—
	154	2	—	1	—
	167	—	—	1	—
	168	1	—	—	—
	190	—	—	1	—
Sergestes curvatus Crosnier & Forest	133	—	—	1	—
	138	—	—	—	2
	144	—	—	1	—
	145	—	—	2	—
	148	1	—	—	—
	154	2	—	—	1
	157	—	—	—	1
	175	1	—	—	1
	218	—	—	1	—
	250	1	—	—	—
Sergestes disjunctus Burkenroad	126	—	—	—	3
	132	—	—	2	3
	139	1	—	2	—
	145	1	—	—	—
	148	1	—	—	—
	153	—	—	1	—
	154	—	—	—	1
	191	—	—	—	3
Sergestes orientalis Hansen	119	1	—	3	—
	126	1	—	2	—
	132	3	—	12	—
	139	—	—	4	—
	140	—	—	3	—
	145	—	—	3	—
	148	2	—	4	1
	153	2	—	9	—
	154	4	—	3	—
	159	—	—	2	—
	160	1	—	—	—
	168	1	—	3	3
	173	—	—	1	—
	183	1	—	1	—
	186	1	—	—	—
	190	1	—	—	—

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	191	5	—	4	—
	221	—	—	1	—
	223	—	—	1	—
Sergestes sargassi Ortmann	119	—	—	1	—
	126	—	—	2	—
	132	—	—	2	1
	145	—	—	1	—
	154	1	—	1	—
	157	—	—	—	1
	168	1	—	1	—
Sergestes pectinatus Sund	126	—	—	1	—
	145	—	—	1	—
	148	—	—	1	—
	153	—	—	1	—
	168	—	—	1	—
	221	—	—	1	—
Sergia creber (Burkenroad)	148	—	—	1	1
**Sergia gardineri* (Kemp)	63	1	—	1	—
	88	—	—	2	6
	126	—	—	1	—
	140	1	—	1	—
	153	—	—	1	—
	154	1	—	1	—
	157	1	—	3	—
Sergia grandis (Sund)	148	1	—	—	—
	173	—	—	1	—
	185	—	—	1	—
	190	1	—	—	—
**Sergia inequalis* (Burkenroad)	194	1	—	—	—
Sergia laminatus (Burkenroad)	126	—	—	—	1
	132	—	—	—	2
	138	—	—	1	—
	139	—	—	—	3
	145	—	—	1	—
	148	2	—	1	—
	153	1	—	6	—
	154	1	—	—	—
	157	2	—	1	—
	160	—	—	1	—
	171	2	—	1	—
	173	1	—	1	—
	182	1	—	—	—
	187	1	—	2	—
	195	—	—	1	—
	208	—	—	1	—
	209	—	—	1	—
	218	5	—	24	—
	220	2	—	1	—
	223	4	—	3	—
Sergia potens (Burkenroad)	121	—	—	1	—
Sergia prehensilis (Bate)	119	1	—	3	—
	126	—	—	1	1
	132	4	—	5	—

* New record

	SM Station *no.*	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	138	—	—	1	1
	139	1	—	—	—
	140	2	—	1	—
	145	1	—	1	—
	148	7	—	1	—
	153	1	—	3	—
	154	4	—	1	—
	157	5	—	—	—
	168	2	—	—	—
	171	—	—	1	—
	173	2	—	—	—
	174	—	—	2	—
	182	1	—	—	—
	190	3	—	1	—
	191	1	—	—	—
	194	1	—	3	—
	195	1	—	—	—
	197	3	—	6	—
	199	1	—	12	—
	204	1	—	—	—
	211	1	—	—	—
	214	1	—	—	—
	218	3	—	3	—
	220	2	—	1	—
	221	2	—	—	—
	223	4	—	1	—
	224	1	—	—	—
Sergia regalis (Gordon)	139	2	—	—	—
	140	—	—	1	—
	148	—	—	—	2
	153	—	—	1	—
	154	1	—	—	—
Sergia scintillans (Burkenroad)	119	—	—	—	1
	132	1	—	1	—
	138	—	—	1	—
	139	—	—	—	1
	140	—	—	—	1
	153	—	—	—	1
	154	1	—	—	—
	157	1	—	—	—
	159	—	—	—	1
	160	—	—	—	4
	167	—	—	—	19
	168	—	—	—	4
	170	—	—	—	1
	171	—	—	—	2
	191	—	—	1	1
	209	1	—	—	—
Sergia talismani (Barnard)	123	—	—	—	1
	140	—	—	—	1
	145	—	—	—	1
	153	—	—	1	2
	154	2	—	1	—
	157	1	—	—	—
	190	—	—	1	—

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
SUBORDER STENOPODIDEA					
Family **Stenopodidae**					
**Odontozona spinosissima* sp. nov.	250	—	—	1	—
SUBORDER CARIDEA					
Family **Oplophoridae**					
Acanthephyra armata A. Milne Edwards	119	—	—	11	—
	131	—	—	1	—
	134	—	—	1	—
**Acanthephyra curtirostris* Wood-Mason & Alcock	139	—	—	2	—
	157	—	—	4	2
	187	—	—	—	1
	208	—	—	1	—
	209	—	—	1	—
Acanthephyra eximia Smith	119	—	—	—	2
	132	—	—	2	—
	145	—	—	3	—
	148	—	1	4	—
	153	2	—	—	—
	154	1	—	—	3
	157	—	2	1	—
	168	—	—	—	1
	173	—	—	2	—
Acanthephyra pelagica (Risso)	194	2	—	—	—
	195	—	—	1	—
	208	1	—	2	6
	220	1	—	—	—
	221	—	—	1	1
**Acanthephyra prionota* Foxton	157	—	—	1	—
	201	—	—	1	—
	203	1	—	1	—
Acanthephyra quadrispinosa Kemp	132	2	—	—	—
	138	2	—	1	9
	139	3	—	7	—
	140	4	—	1	4
	145	—	—	2	3
	148	8	23	11	37
	153	3	2	2	8
	154	1	2	2	9
	157	2	—	—	—
	160	1	1	2	4
	167	—	—	—	1
	170	3	—	—	1
	171	—	—	2	1
	173	—	—	1	1
	182	2	—	—	1
	197	1	2	1	3
	199	3	6	—	2
	201	1	—	—	—
	205	2	—	—	1
	208	—	1	—	—
	209	3	0	0	4
	211	1	1	—	14

* New record

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	218	7	11	3	17
	220	1	—	1	9
	221	1	1	1	6
	223	8	6	1	7
	224	1	1	—	6
Acanthephyra stylorostrata (Bate)	203	1	—	—	—
	208	1	—	1	—
Hymenodora gracilis Smith	220	1	—	—	2
**Meningodora miccyla* (Chace)	96	1	—	—	—
	139	1	—	—	—
	157	1	—	—	—
	224	1	—	—	—
Meningodora mollis Smith	194	—	1	—	—
	203	—	—	4	—
	214	—	—	2	—
	218	1	—	—	—
	221	—	—	1	—
	223	—	—	2	—
**Meningodora vesca* (Smith)	145	1	—	—	—
Notostomus auriculatus Barnard	208	—	—	—	1
	209	1	—	—	—
	220	—	—	1	—
Notostomus elegans A. Milne Edwards	148	—	—	1	—
	157	—	—	—	1
	221	—	—	1	—
Notostomus gibbosus A. Milne Edwards	209	—	—	1	—
Oplophorus gracilirostris A. Milne Edwards	119	—	—	1	—
Oplophorus spinicauda A. Milne Edwards	119	—	—	—	1
	126	—	—	—	3
	132	—	—	1	1
	145	—	—	1	—
	183	—	—	1	2
	191	—	—	1	—
	211	—	—	1	—
Oplophorus typus H. Milne Edwards	237	—	1	—	—
**Systellaspis cristata* (Faxon)	139	—	—	—	2
	157	—	—	—	1
	218	—	—	1	—
Systellaspis debilis (A. Milne Edwards)	132	1	—	—	5
	139	2	2	3	—
	140	1	—	—	—
	145	1	1	2	1
	148	2	2	1	3
	153	—	—	2	1
	154	—	1	—	1
	157	3	1	5	—
	159	—	1	—	—
	160	2	3	6	—
	167	3	—	3	—
	168	—	—	1	3
	171	—	—	—	1
	182	—	—	3	—
	187	3	2	14	—

* New record

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
	190	1	3	12	—
	197	—	1	1	—
	199	3	2	1	—
	209	1	1	1	—
	218	—	1	—	—
	221	2	—	1	—
	223	1	—	—	—
	224	1	—	—	—
Family **Stylodactylidae**					
Stylodactylus stebbingi Hayashi & Miyake	132	—	—	—	1
Family **Pasiphaeidae**					
Eupasiphae gilesii Wood-Mason & Alcock	224	—	—	1	—
Leptochela robusta Stimpson	184	—	—	—	1
Parapasiphae sulcatifrons Smith	195	—	—	1	—
	208	—	—	1	—
	218	—	—	—	4
Pasiphaea meiringnaudei Kensley	119	—	—	2	—
	121	—	—	2	1
	209	—	—	—	1
	227	1	—	1	—
Pasiphaea sivado (Risso)	119	7	—	2	3
	139	—	—	—	1
	148	—	—	—	1
	153	—	—	—	1
	157	—	—	—	1
	209	—	—	—	1
Family **Pandalidae**					
Heterocarpus dorsalis Bate	121	2	—	—	—
	129	—	—	1	—
Heterocarpus laevigatus Bate	129	—	—	—	1
	131	1	—	1	—
Heterocarpus tricarinatus Alcock & Anderson	237	—	—	1	—
Parapandalus richardi (Coutière)	119	—	—	—	1
	126	1	—	—	—
	145	—	1	—	—
	148	1	—	—	—
	154	—	1	—	—
	168	—	—	—	1
	187	—	1	—	—
Plesionika longirostris (Borradaile)	132	—	—	1	—
	160	—	—	—	1
Plesionika martia (A. Milne Edwards)	119	9	—	5	48
	121	2	1	1	—
	123	1	—	—	—
	134	—	—	1	—
	226	—	—	—	4
	227	1	—	—	—
	232	2	—	—	—
	233	6	1	7	1
	237	1	2	2	—
Family **Crangonidae**					
Metacrangon jacqueti bellmarleyi (Stebbing)	174	—	—	1	—
Pontophilus sculptus (Bell)	179	—	—	1	—
	185	1	1	—	—

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
SUBORDER PALINURA					
Family **Polychelidae**					
Stereomastis sculpta (Smith)	134	—	1	—	—
Family **Palinuridae**					
Projasus parkeri (Stebbing)	131	1	—	—	—
	233	1	—	1	1
	237	5	—	2	4
SUBORDER ANOMURA					
Family **Axiidae**					
Calocaris alcocki McArdle	150	—	—	1	—
Family **Lithodidae**					
**Paralomis roeleveldae* sp. nov.	121	—	—	1	—
Family **Galatheidae**					
Munida sanctipauli Henderson	237	1	—	1	—
Munida sp.	129	—	1	—	—
Family **Chirostylidae**					
**Uroptychus edwardi* sp. nov.	134	—	1	—	—
Uroptychus nitidus (A. Milne Edwards)	117	1	—	1	—
	121	1	4	16	—
Uroptychus simiae Kensley	233	1	—	—	1
SUBORDER BRACHYURA					
Family **Dromiidae**					
Pseudodromia spinosissima Kensley	163	1	—	1	—
	233	1	—	—	—
Family **Cymonomidae**					
Corycodus disjunctipes (Stebbing)	232	1	—	1	—
Cymonomus trifurcus Stebbing	129	—	—	1	—
	162	1	—	—	—
	232	—	—	3	—
	250	1	—	—	—
	226	1	—	—	—
Family **Homolidae**					
* *Homolochunia valdiviae* Doflein	237	1	—	—	—
Family **Dorippidae**					
Ethusa sp.	121	1	—	—	—
Family **Calappidae**					
Mursia armata De Haan	239	1	—	—	—
Family **Majidae**					
Inachus guentheri (Miers)	185	1	1	—	—
Macropodia formosa Rathbun	239	1	—	—	—
Pleistacantha moseleyi (Miers)	234	2	—	—	—
Family **Hymenosomatidae**					
Hymenosoma orbiculare Desmarest	180	—	—	—	1

* New record

	SM Station no.	♂♂	*ovig.* ♀♀	♀♀	*juv.*
Family **Atelecyclidae**					
**Trachycarcinus glaucus* Alcock & Anderson	121	1	—	—	—
Family **Geryonidae**					
Geryon sp.	121	—	—	1	—
	233	2	—	2	—
Family **Goneplacidae**					
Goneplax rhomboides (Linnaeus)	237	1	—	—	—
Litocheira kingsleyi (Miers)	233	—	2	1	1
	237	2	2	—	1
Pilumnoplax heterochir (Studer)	226	2	—	—	—
	232	1	1	—	—
	237	1	—	—	—

STATION DATA

B — Bongo net
BT — Beam trawl
HD — Heavy dredge
RMT — Rectangular midwater trawl

SM Station no.	Position	Depth (m)	Gear
63	27°10′S 33°14′E	140	RMT
88	27°51′S 32°55′E	297	RMT
96	28°14′S 32°49′E	465	RMT
99	28°23′S 32°41′E	920	BT
119	30°14′S 31°13′E	750	RMT
121	30°32′S 30°52′E	900–625	BT
123	30°33′S 30°48′E	690	HD
126	30°39′S 30°59′E	464	RMT
129	30°53′S 30°31′E	850	HD
131	30°43′S 30°40′E	780	BT
132	30°45′S 30°42′E	830	RMT
133	31°01′S 30°26′E	212	B
134	31°00′S 30°27′E	900	BT
138	30°21′S 31°15′E	830	RMT
139	30°22′S 31°16′E	250	RMT
140	31°14′S 30°20′E	1120	RMT
144	31°26′S 30°06′E	212	B
145	31°30′S 30°04′E	1129	RMT
148	30°17′S 31°25′E	750	RMT
150	30°14′S 31°25′E	1000	HD
153	30°15′S 31°28′E	664	RMT
154	30°24′S 31°32′E	500	RMT
157	30°05′S 31°57′E	750	RMT
159	32°40′S 28°50′E	690	RMT
160	32°45′S 28°47′E	583	RMT
162	32°55′S 28°31′E	630	HD
163	33°04′S 28°06′E	90	HD
167	33°10′S 28°17′E	1091	RMT
168	33°14′S 28°18′E	816	RMT
170	33°10′S 28°14′E	708	RMT

* New record

SM Station no.	Position	Depth (m)	Gear
171	33°16′S 28°13′E	792	RMT
173	33°25′S 27°54′E	683	RMT
174	33°19′S 27°52′E	760	HD
175	33°25′S 27°49′E	212	B
179	33°30′S 27°22′E	80	HD
180	33°29′S 27°21′E	80	HD
182	33°38′S 27°49′E	1517	RMT
183	33°48′S 27°47′E	474	RMT
184	33°39′S 27°11′E	86	HD
185	33°39′S 27°11′E	90	HD
186	33°48′S 27°27′E	583	RMT
187	33°55′S 27°25′E	982	RMT
189	34°04′S 27°10′E	212	B
190	34°06′S 27°08′E	658	RMT
191	34°11′S 27°08′E	542	RMT
194	31°34′S 30°20′E	2166	RMT
195	31°33′S 30°18′E	1050	RMT
197	31°35′S 30°11′E	150	RMT
199	31°33′S 30°08′E	250	RMT
201	31°40′S 30°03′E	1333	RMT
203	31°42′S 30°03′E	1750	RMT
204	31°45′S 30°04′E	212	B
205	31°51′S 30°01′E	585	RMT
208	31°53′S 29°48′E	1320	RMT
209	31°55′S 29°57′E	1260	RMT
211	32°00′S 29°50′E	415	RMT
214	32°15′S 29°36′E	1390	RMT
218	32°30′S 29°13′E	916	RMT
220	32°31′S 29°11′E	1416	RMT
221	32°34′S 29°15′E	1170	RMT
223	32°34′S 29°13′E	670	RMT
224	32°33′S 29°09′E	663	RMT
226	32°28′S 28°58′E	710	HD
227	32°32′S 28°55′E	790	BT
232	32°14′S 29°10′E	620	HD
233	32°15′S 29°09′E	580	BT
234	32°15′S 29°09′E	520	BT
237	32°15′S 29°09′E	650	BT
239	32°14′S 29°00′E	90	BT
250	31°59′S 29°22′E	200	HD
254	31°42′S 29°40′E	860	BT

SYSTEMATIC DISCUSSION

Family **Aristeidae**

Bentheogennema pasithea (De Man)

Bentheogennema pasithea: Crosnier, 1978: 31, figs 13c–d, 14d. [Full synonymy.]

Previous records

Formosa; Caroline and Gilbert Islands; Indonesia; India; Somalia; Seychelle Islands; Nosi Be, Madagascar.

Material

1 ♂ CL (incl. rostrum) 12,5 mm SM 224 32°33′S 29°09′E 600–663 m.

Family **Sergestidae**

Petalidium obesum (Krφyer)

Fig. 2

Sergestes obesus Krφyer, 1859: 257, 279, pl. 4 (fig. 10a–f).
Sergestes sanguineus Chun, 1889: 538 (mastigopus larva).
Petalidium obesum: Hansen, 1896: 968; 1903: 56; 1922: 190, pl. 11 (figs 3–4). Burkenroad, 1937: 324. Wasmer, 1974: 165.
Petalidium foliaceum non Bate, Illig, 1927: 282, figs 1–5.

Previous records

Off Cape Verde, Canary Islands, Azores Islands (Hansen); off Lüderitz; Cape Point (Illig).

Remarks

Burkenroad (1937) noted that his new species *P. suspiriosum* differed from other species of the genus in the gill structure, in having two arthrobranchs above pereopod 4, instead of one as in *P. obesum*, or none as in *P. foliaceum* (see Wasmer 1974: 165). Hansen (1922: 193), in discussing the gill formula of *P. obesum*, mentioned that there was frequently a rudimentary gill above pereopod

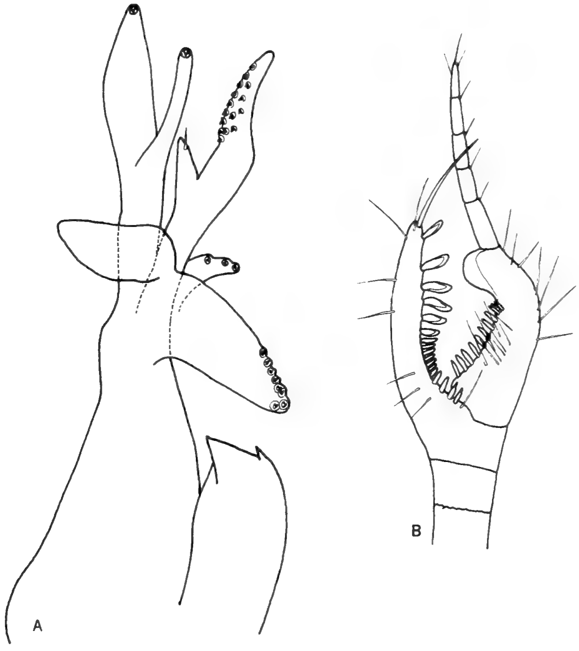

Fig. 2. *Petalidium obesum*. A. Petasma. B. Outer antennular flagellum ♂.

4, and that its absence was probably due to mutilation along with bad preservation. The thirty-one specimens in the present collection agree with *P. foliaceum* in lacking a gill above pereopod 4.

The petasma agrees well with Hansen's figures, although slight differences are noted: the longer lobe of the lobus terminalis has only a single terminal hook (three in Hansen's description), while the shorter lobe of the lobus armatus carries three (not two) hooks in the present material. Hansen's figure of the telsonic apex does not show the two distolateral spines seen in the Indian Ocean material.

The rostrum is variable, in fact, it shows the same range of variation as Illig (1927, fig. 1) illustrates for *P. foliaceum*. As Illig's figure of the petasma more closely resembles that of *P. obesum* (lacking the two distinctive stumpy lobus armatus lobes of *P. foliaceum* Bate), there is strong reason to believe that Illig's specimens from the South Atlantic were *P. obesum*.

As the integument of *Petalidium* is very delicate, carapace lengths are difficult to measure; however, the average carapace length of four males of *P. obesum* is 7,1 mm, while the two males of *P. foliaceum* have carapace lengths of 12,0 mm each.

Sergia inequalis (Burkenroad)

Fig. 3

Sergestes inequalis Burkenroad, 1940: 51.
Sergestes (*Sergia*) *inequalis:* Yaldwyn, 1957: 9.

Description

Male

Rostrum with relatively slender apical spine, lacking dorsal denticle, anterior margin oblique. Carapace with cervical sulcus becoming obsolete dorsally; postcervical sulcus distinct across dorsum; suprabranchial ridge strong. Cornea reaching beyond midpoint of basal antennular peduncle segment. Latter subequal in length to second segment; third segment somewhat shorter. Scaphocerite reaching to midpoint of third antennular peduncle segment, with twelve small opaque-spot photophores. Maxilliped 3 slender, slightly longer than pereopod 1. Outer uropodal ramus with spine on outer margin at about distal third, with twelve opaque-spot photophores near inner margin. Telson apically acute.

Petasma: processus uncifer with small apical spine; lobus armatus short, tapering, extended laterally, with eleven hooks; lobus accessorius subequal in length to lobus armatus, but broader, with about twenty hooks; processus ventralis broad, outer margin sinuous, apically acute, reaching to lobus accessorius and lower lobus connectens lobe; lobus connectens lower lobe slender, extending laterally, curved downwards, with ten to twelve terminal hooks, upper lobe short, extended upwards; lobus terminalis directed laterally, short, squat, with three

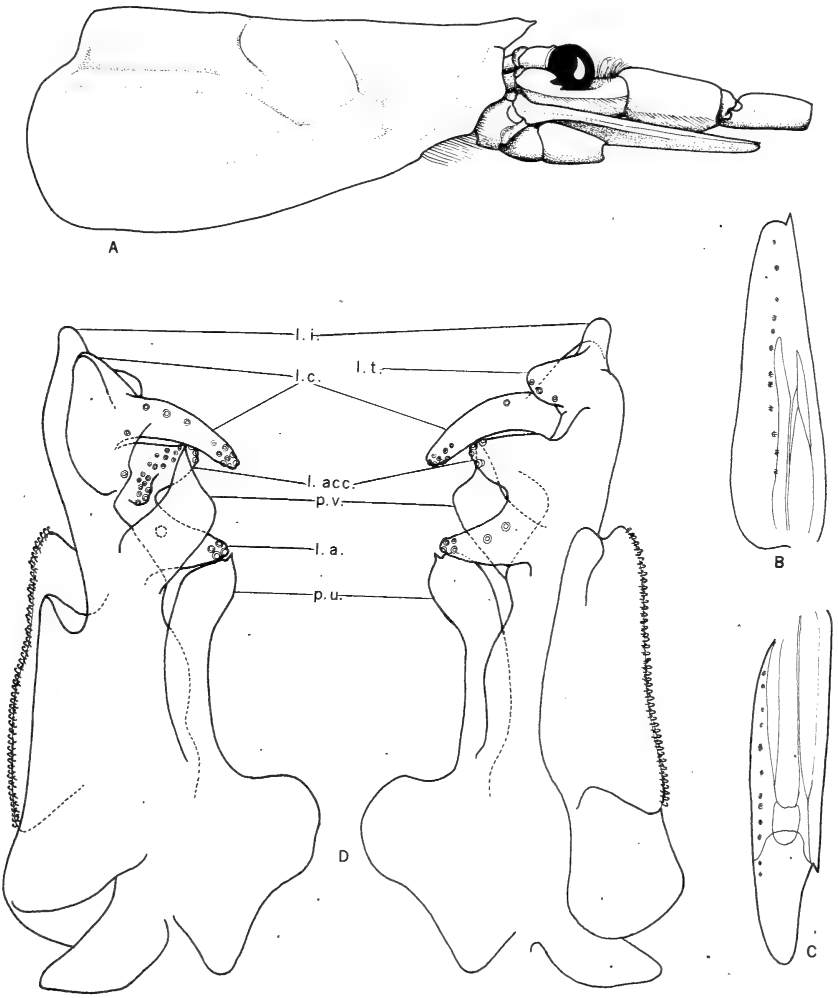

Fig. 3. *Sergia inequalis*. A. Carapace in lateral view. B. Scaphocerite. C. Outer uropodal ramus. D. Anterior and posterior view of petasma. l.a.—lobus armatus, l.acc.—lobus accessorius, l.c.—lobus connectens, l.i.—lobus inermis, l.t.—lobus terminalus, p.u.—processus uncifer, p.v.—processus ventralis.

terminal hooks; lobus inermis extending beyond lobus terminalis, short, distally rounded.

Previous records

Dana Expedition station 3768 7°33′S 115°22′E 810 m, off Sunda Islands, Java Sea.

Material

SAM–A16810 1 ♂ CL (incl. rostrum) 11,5 mm SM 194 31°34′S 30°20′E 1150–2166 m.

Remarks

Burkenroad (1940) described *S. inequalis* from a single male, but provided no figures. The species has not been recorded since. From Burkenroad's description of the petasma, there can be little doubt that the present male is the same species.

Family **Stenopodidae**

Odontozona spinosissima sp. nov.

Figs 4–5

Description

Female

Translucent integument bearing numerous flattened spines. Carapace with strong cervical, postcervical, and hepatic grooves; rostrum compressed, with twelve dorsal teeth, two ventrodistal teeth, and strong ventrolateral ridge running into orbital margin posteriorly. Orbital spine set back from margin, larger than surrounding spines; strong antennal spine set slightly back from margin; pterygostomian spine marginal; forwardly-directed carapace spines posterior to cervical groove arranged in more or less vertical cinctures. Pleonal segments dorsolaterally bearing numerous closely packed ridges and grooves; pleonite 3 largest, dorsally smoothly convex; pleura of pleonites 1 and 2 ventrally rounded, pleuron 1 about one-third width of pleuron 2, bearing transverse ridges and grooves; pleuron 4 ventrally truncate, bearing spines and ridges, small marginal tooth posteroventrally, two posterolateral teeth; pleuron 5 with stronger posteroventral tooth plus three smaller posterolateral marginal teeth, bearing spines laterally; pleuron 6 ventrally truncate, with small posteroventral denticle, bearing spines laterally. Telson (apex damaged) with at least one pair of lateral spines; two strong, rounded dorsal ridges present.

Eye reaching to about midlength of rostrum; mediodorsal surface of eyestalk armed with spines, those overlapping cornea relatively elongate. Basal segment of antennular peduncle with flattened apically acute lobe on outer margin. Scaphocerite with spines on outer margin, elongate setae on inner; basal peduncular segment with one ventral and two large dorsolateral marginal spines plus numerous smaller scattered spines; second and third segments with scattered ventral spines. Mandibular palp 3-segmented, first segment short, second and third segments subequal, latter with numerous setae. Maxilla 1 with slender palp; distal lobe with nine spines and several setae on straight inner margin, proximal lobe broadly rounded, setose. Maxilla 2 with broad scaphognathite, slender palp, four narrow endites. Maxilliped 1 with broad bilobed epipod, slender exopod, 3-segmented endopod. Maxilliped 2 exopod with peduncle equal in length to flagellum; endopod merus largest segment, equal in

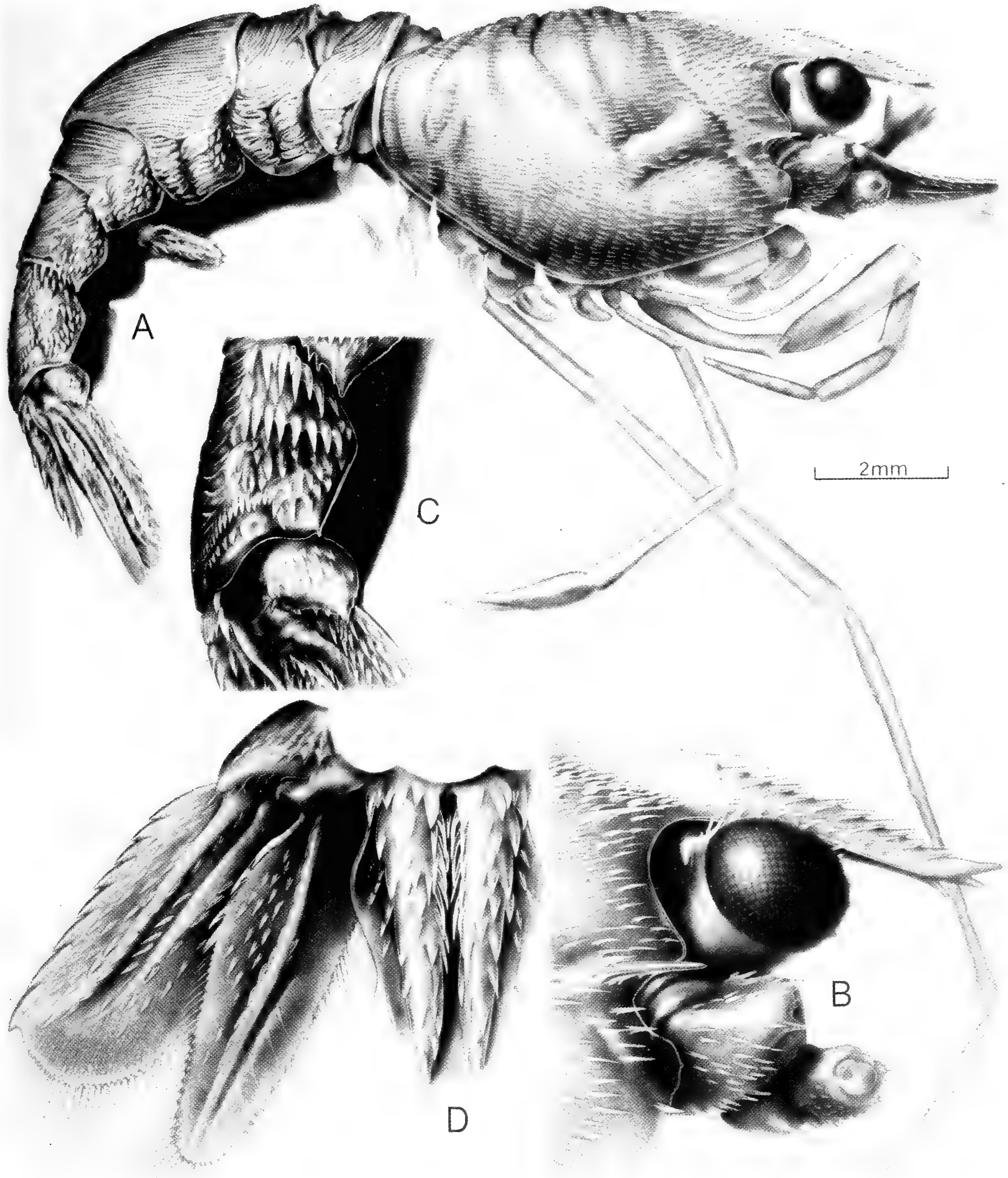

Fig. 4. *Odontozona spinosissima*. A. Holotype in lateral view. B. Anterior carapace. C. Pleonite 6 and uropodal base. D. Telson (damaged) and left uropod.

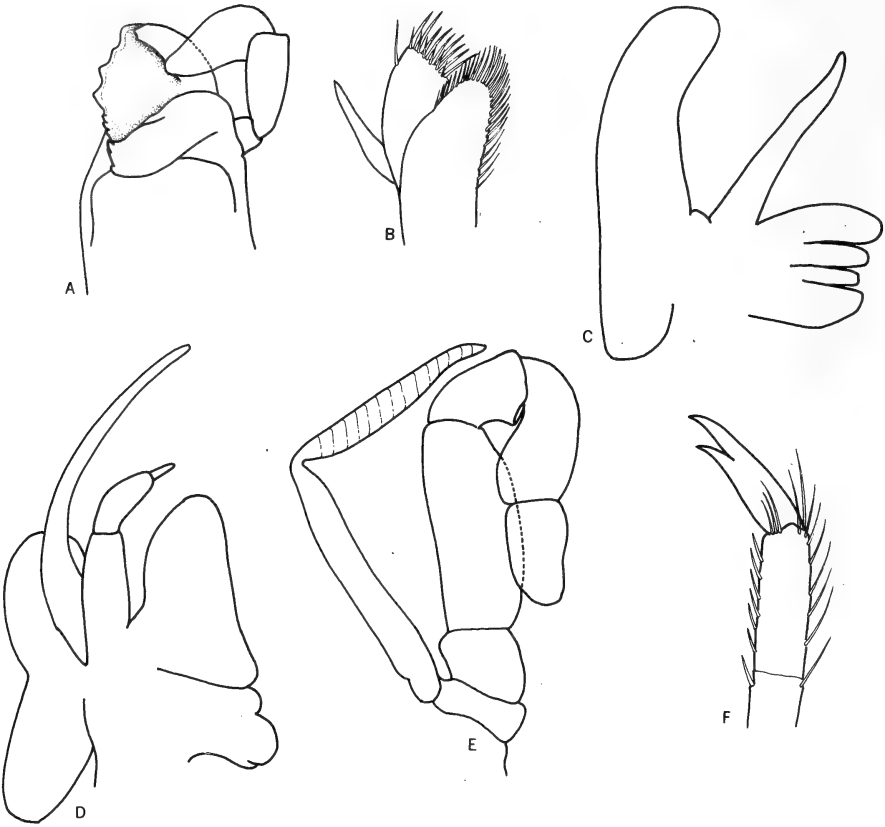

Fig. 5. *Odontozona spinosissima.* A. Mandible. B. Maxilla 1. C. Maxilla 2. D. Maxilliped 1. E. Maxilliped 2. F. Pereopod 5 dactylus.

length to dactylus and carpus together. Maxilliped 3 with elongate exopod; elongate setae on inner margins of five distal endopodal segments. Epipodites present on pereopods 1–4. Pereopod 1 chela three-quarters length of carpus, equal in length to merus. Pereopod 4 elongate, slender, propodus half length of carpus consisting of six subsegments, with fine spinules on posterior margin; carpus of eight subsegments; merus about two-thirds length of carpus. Pereopod 5 dactylus biunguiculate; propodus of six subsegments; carpus of nine subsegments; merus about two-thirds length of carpus. Pleopod 1 uniramous, peduncle very short, ramus elongate-lanceolate, with setose margins. Uropodal basis with strong distal tooth and several smaller marginal teeth plus several surface spines; outer ramus broader than inner, with eight teeth on outer margin, distally broadly rounded; dorsal surface with two strong rounded ridges, bearing scattered spines; inner ramus distally narrower than outer ramus, with four spines on outer proximal margin, single rounded ridge dorsally, with scattered dorsal spines.

Material

Holotype SAM–A16811 1 ♀ CL (incl. rostrum) 7,0 mm RL 2,4 mm SM 250 31°59′S 29°22′E 150–200 m.

Remarks

Although only a single damaged specimen is available, this species is so markedly distinctive as to deserve description.

The genus *Odontozona* Holthuis is characterized by the possession of a compressed body, cinctures of anteriorly-directed spines on the carapace, maxilliped 3 possessing a large exopod, but lacking external spinules on the ischium, biunguiculate dactyli on pereopods 4 and 5, and a uropodal endopod having two dorsal ridges (Holthuis 1946: 5).

O. spinosissima bears a strong resemblance to *O. sculpticaudata* Holthuis, described from a single ovigerous female from Sape Straits, east of Soembawa, Indonesia, especially in the abdominal sculpturing. From examination of Holthuis's type and from the description, these two species differ in several easily-observed features, summarized in the following table.

	O. sculpticaudata	*O. spinosissima*
Rostral dentition . .	5/2	12/2
Pleon sculpture . .	Few grooves and ridges	Many grooves and ridges
Pleuron 1	Blunt anterior tooth present	Rounded
Pleonite 3	Transverse carina present	No transverse carina
Pleura 4 & 5 . . .	Anterior and posterior tooth present	Anterior tooth absent posterior tooth present
Uropodal rami . . .	Lacking dorsal spines	Numerous dorsal spines present
Outer uropodal ramus .	6 marginal teeth	8 marginal teeth

Etymology

The specific name derives from the extremely spinose condition of the carapace and pleon.

Family **Chirostylidae**

Uroptychus edwardi sp. nov.

Figs 6–7

Description

Female

Carapace middorsal length (excluding rostrum) almost three-quarters greatest carapace width; dorsally smooth, gently convex, widest across branchial

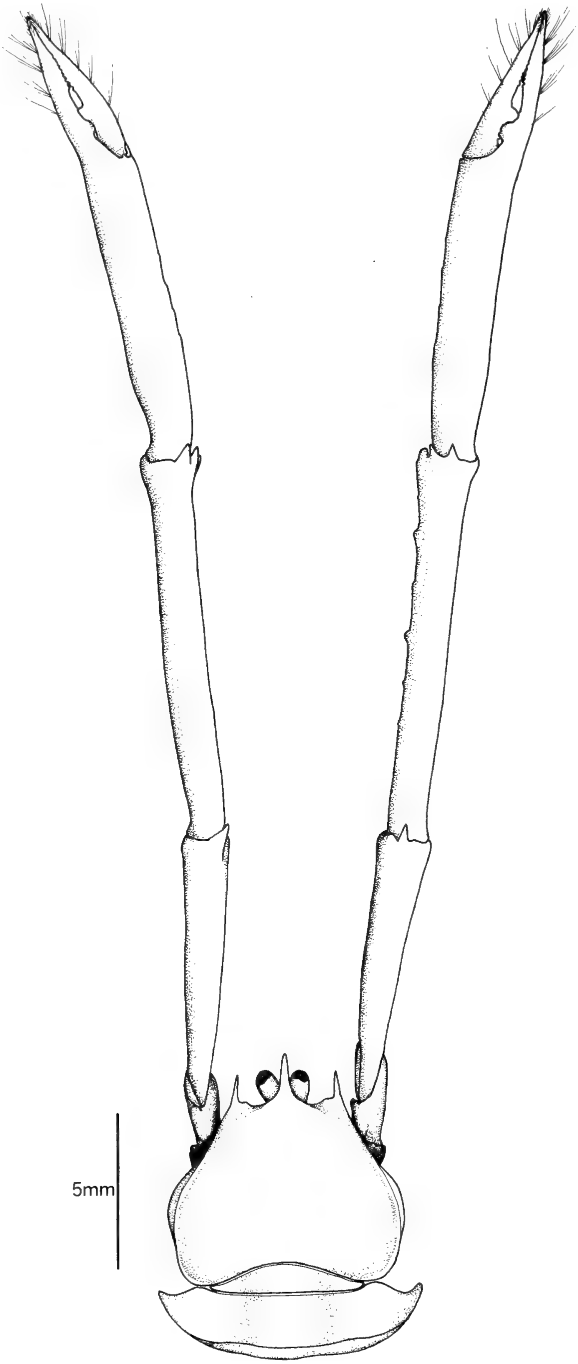

Fig. 6. *Uroptychus edwardi.* Holotype in dorsal view.

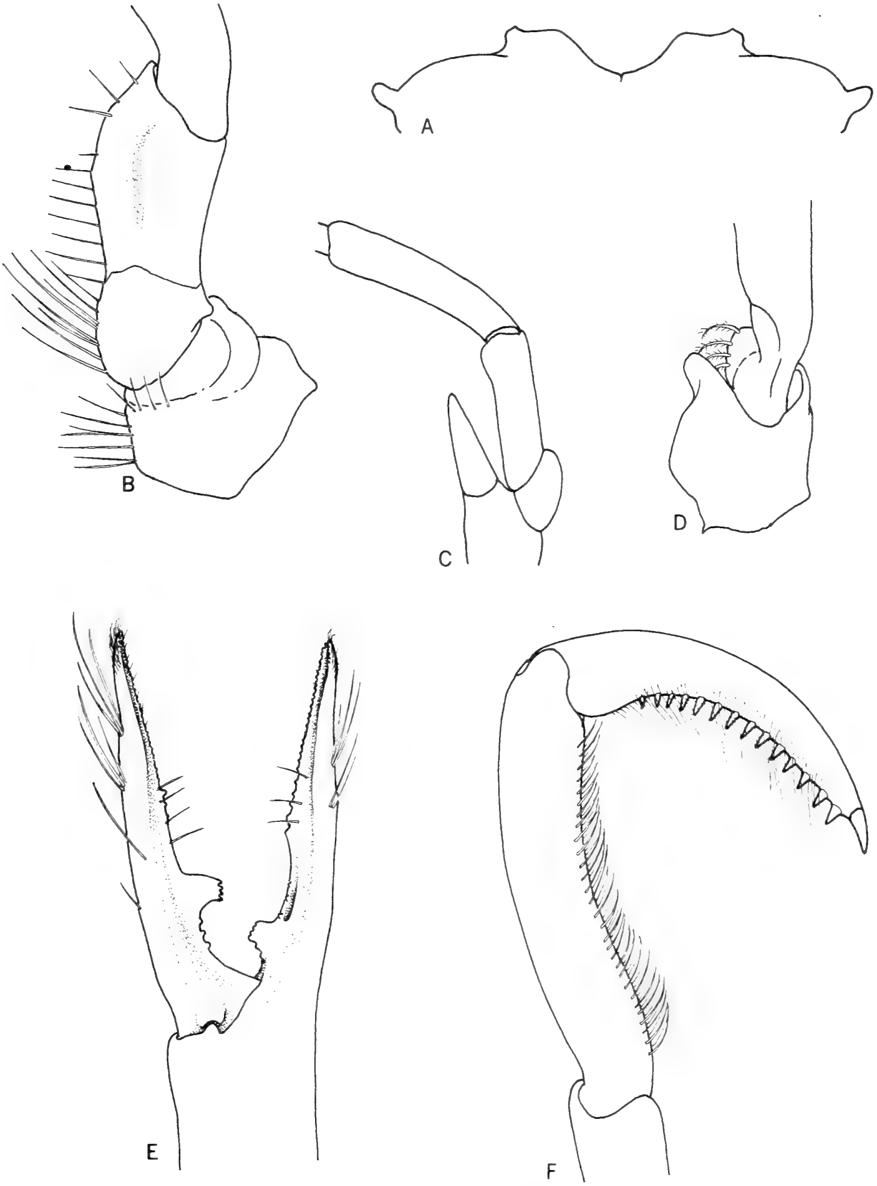

Fig. 7. *Uroptychus edwardi.* A. Anterior sternum. B. Three basal segments of maxilliped 3 endopod. C. Antennal peduncle. D. Basal antennular segment. E. Chela. F. Dactylus and propodus of ambulatory pereopod.

regions; anterior margins somewhat sinuous between spiciform rostrum and anterolateral spines; posterodorsal margin concave. Ventrolateral carapace plate ending anteriorly in short spine. Sternum with smoothly even median concavity, with tiny median slit. Sternites of maxilliped 3 and pereopod 1 laterally rounded.

Basal antennular segment with unarmed rounded distal lobe. Antennal peduncle segments unarmed, acicle not reaching end of second segment. Chelipeds slender, five and a half times length of carapace (including rostrum); dactylus about half length of propodal palm; distal half of finger and thumb distinctly narrowed, grooved on inner faces, with outer cutting edges finely denticulate; proximal half of dactylus bearing strong, finely denticulate process on cutting margin, fitting closely against and distal to similar process on fixed finger; carpus four-fifths length of propodus (including fixed finger), two distal spines present, four or five low tubercles medioventrally; merus about two-thirds length of carpus, with strong distodorsal spine. Propodi of ambulatory pereopods slightly curved, with dense band of setae on ventral margin; dactyli curved, with row of conical spines and numerous fine setae on ventral margin.

Material

Holotype SAM–A16033 1 ovigerous ♀ CL (incl. rostrum) 7,0 mm CW 8,0 mm SM 134 31°00′S 30°27′E 900 m.

Remarks

Although only a single female of this species is available, it is sufficiently distinct to warrant description.

U. edwardi belongs to that group of species of *Uroptychus* possessing a carapace wider than long, and lacking dorsal spination. The spiciform rostrum and anterolateral spines distinguish *U. edwardi* from all other species of this group, including *U. siraji* Tirmizi, *U. onychodactylus* Tirmizi, *U. foulisi* Kensley, *U. suluensis* Van Dam, *U. setosidigitalis* Baba, *U. scambus* Benedict, and *U. glyphodactylus* MacGilchrist. The two latter species most closely resemble the present species, especially in the short but spiciform anterolateral carapace spines, but both species possess broadly triangular rostra.

Etymology

Station SM 134, at which *U. edwardi* was captured, lies on the continental shelf off Port Edward, hence the specific name.

Family **Lithodidae**

Paralomis roeleveldae sp. nov.

Figs 8–9

Description

Female

Carapace (including rostrum) slightly longer than wide, covered with short, rounded tubercles of varying sizes; regions well defined. Gastric region strongly convex, with large acute tubercle at middorsal point and two smaller tubercles in posterior part; margin with two or three strong spines; cardiac region defined by grooves; branchial region with large acute tubercle at about midpoint,

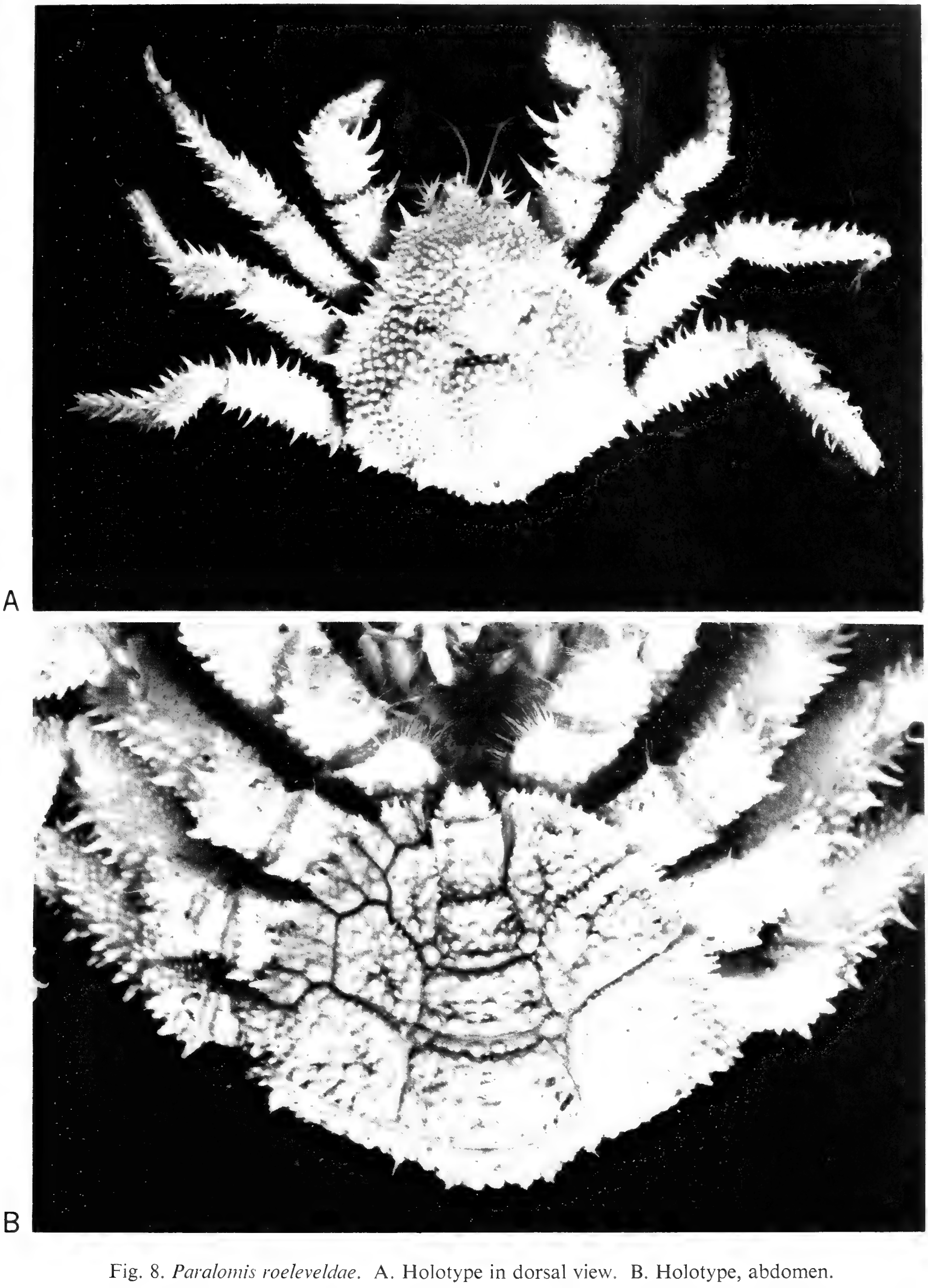

Fig. 8. *Paralomis roeleveldae*. A. Holotype in dorsal view. B. Holotype, abdomen.

anterior margin with two strong spines; two large contiguous spinose tubercles at posterolateral angle, single large tubercle between posterolateral angle and midpoint of posterior margin. Rostrum of strong inferior median spine with three small median spines dorsal to median spine, and two strong dorsolateral spines with a pair of small anterior spines at base. Abdomen with second somite a single plate covered with conical tubercles. Median and lateral plates of somites 3–5 bearing rounded-flattened and smaller conical tubercles. Lateral plates of left side bearing short spinose tubercles. On right side, lateral plate of somite 3 bearing small marginal plate at distal angle. Somite 4 with two marginal plates, each divided marginally and carrying fine spines. Somite 5 similar to somite 4. Somite 6 rectangular, terminal somite short, with two terminal spines. Median plates 4 and 5 each with deep transverse groove proximally.

Eyestalks with single relatively strong terminal spine extending beyond cornea and several tiny spines dorsally. Antennules unarmed. Basal antennal peduncle segment with single distal spine; second segment with laterodistal spine and three or four smaller spines at base; acicle with five strong spines (including terminal spine) on outer margin, several smaller spines dorsally and on inner margin. Maxilliped 3 with small spine on inner distal margin of second endopod segment (ischium); outer surface of merus granular.

Left cheliped slightly shorter and less robust than right, spination and granulation similar; spines of upper distal region of merus becoming stronger than

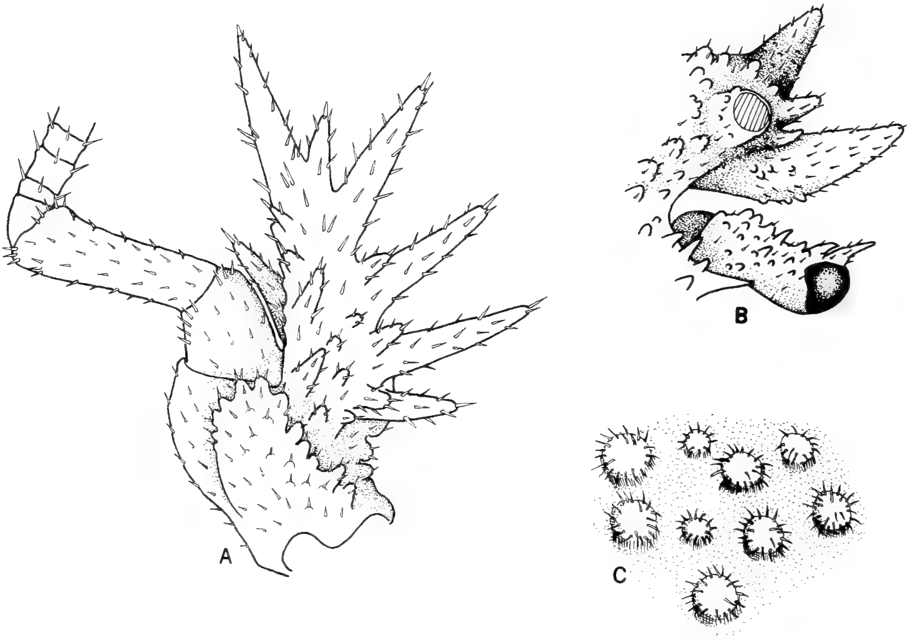

Fig. 9. *Paralomis roeleveldae*. A. Basal antennal segments. B. Rostrum (lateral spine broken) and eyestalk. C. Carapace tubercles enlarged.

spinose-granulations of outer face, with several elongate spines on inner and dorsal surfaces; fingers of chela subequal to palm in length; propodi with several elongate spines on inner margin. Right chela with two or three rounded proximal cusps on cutting edges of finger and thumb, tips subacute, corneous; left chela lacking cusps, tips subacute, corneous. Ambulatory pereopods 2–4 with strong spines on dorsal margins of carpi and meri, surfaces granulate-spinose, lower margins with strong spines, dactyli unarmed except for single proximal tubercle.

Material

Holotype SAM–A16045 1 ♀ CL (incl. rostrum) 50,0 mm CW 45,0 mm SM 121 30°32′S 30°52′E 625–900 m.

Remarks

The present species appears to be most closely related to *Paralomis investigatoris* Alcock & Anderson, 1899, from deep water off the coast of Travancore, India. This resemblance lies especially in the overall carapace shape, similarity of the carapace and abdominal tuberculation, and pereopodal armature. Several differences separate the two species, however, including the lack of stronger spinose tubercles on the carapace and marginal abdominal spines in the Indian species, and the lack of basal rostral spines and the relatively more slender chelipeds in *P. roeleveldae*. Alcock & Anderson (1899) mention the similarity of their species to *P. aspera* Faxon from the Pacific coast of Panama. Although Faxon's species resembles *P. roeleveldae* in the general shape and carapace armature, it lacks longer carapace tubercles, elongate marginal spines, the inferior rostrum is multidentate, and the pereopods lack elongate spines.

Paralomis seagranti Eldredge (1976) from Guam, although superficially similar to the present species, possesses a relatively more elongate carapace, elongate setae on the appendages, relatively short marginal carapace spines, fewer antennal acicle spines, shorter spines on the setose ambulatory pereopods, while lacking a large gastric spine and spines on the posterior carapace margin.

This is the first record of the genus from the South-western Indian Ocean.

Etymology

The species is named for Martina Roeleveld of the South African Museum, in thanks for her help during the *Meiring Naude* cruises.

Family **Atelecyclidae**

Trachycarcinus glaucus Alcock & Anderson

Figs 10–11

Trachycarcinus glaucus Alcock & Anderson, 1899: 8. Alcock, 1899: 59, pl. 2 (fig. 2). Alcock & MacGilchrist, 1905: pl. 76 (figs 1–2). Guinot & Sakai, 1970: 203.

Previous records

Off Travancore coast, southern India, 860 m.

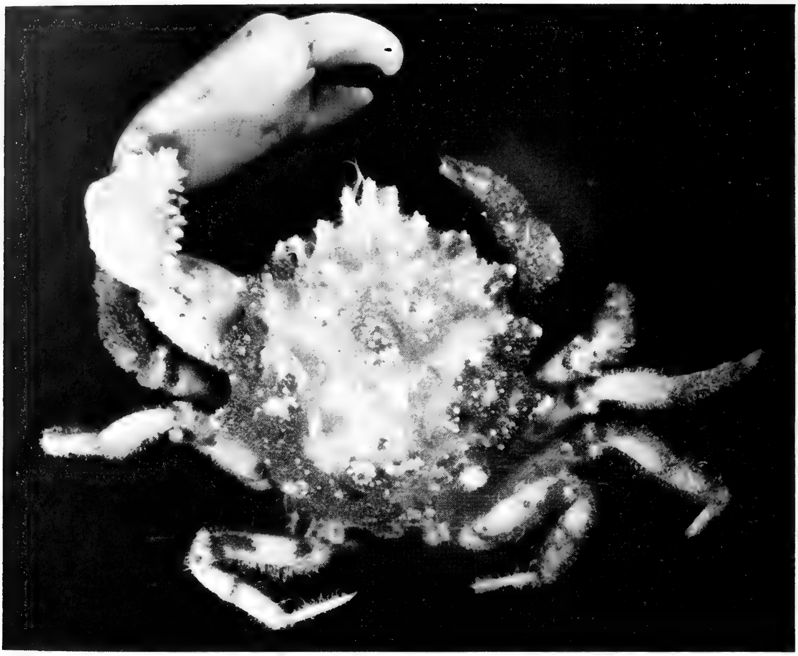

Fig. 10. *Trachycarcinus glaucus.* Male in dorsal view.

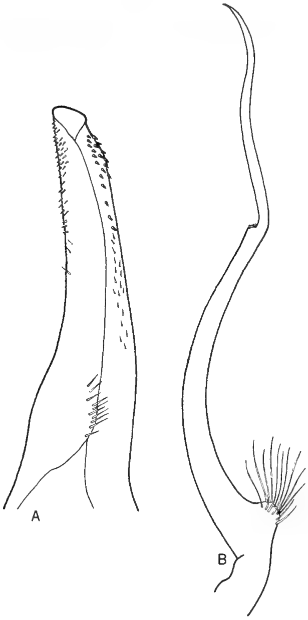

Fig. 11. *Trachycarcinus glaucus.* A. Pleopod 1 ♂. B. Pleopod 2 ♂.

Material

SAM–A16018 1 ♂ CL (incl. rostrum) 23,7 mm CW 22,0 mm SM 121 625–900 m.

Remarks

The largest male from Travancore measured CL 18,5 mm, CW 14,5 mm. The present male is thus probably the largest known.

ACKNOWLEDGEMENTS

My sincere thanks are due to Captain G. Foulis and the crew of the R.V. *Meiring Naude* and to my scientific colleagues on the cruises; to the Trustees and Director of the South African Museum, Cape Town, for making the decapod material available to me; Dr D. Platvoet of the Zoologisch Museum, Amsterdam, for the loan of type material of *Odontozona*; Carolyn Bartlett Gast (Smithsonian Institution) for the beautiful figures of *Odontozona spinosissima*; Messrs Michael Carpenter (Smithsonian Institution) and Sidney Kannemeyer (South African Museum) for assistance with the photographs; and to Drs F. A. Chace, Jr., and R. B. Manning of the Department of Invertebrate Zoology, Smithsonian Institution, for critically reading and commenting on the manuscript.

REFERENCES

Alcock, A. 1899. *An account of the deep-sea Brachyura collected by the Indian Marine Survey Ship 'Investigator'*. Calcutta: Trustees of the Indian Museum.

Alcock, A. & Anderson, A. R. S. 1899. Natural history notes from H.M. Royal Indian Marine Survey Ship 'Investigator', Commander T. H. Heming, R.N., commanding. Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897–98. *Ann. Mag. nat. Hist.* (7) **3**: 1–27.

Alcock, A. & MacGilchrist, A. C. 1905. Illustrations of the Zoology of the Royal Indian Marine Survey Ship 'Investigator', under the Command of Captain T. H. Heming, R.N. *Ill. Zool. 'Investigator'* 11, plates 68–76.

Burkenroad, M. D. 1937. The Templeton Crocker Expedition. 12. Sergestidae (Crustacea Decapoda) from the Lower Californian Region, with descriptions of two new species and some remarks on the Organs of Pesta in *Sergestes*. *Zoologica, N.Y.* **22**: 315–329.

Burkenroad, M. D. 1940. Preliminary descriptions of twenty-one new species of pelagic Penaeidea (Crustacea Decapoda) from the Danish Oceanographical Expeditions. *Ann. Mag. nat. Hist.* (11) **6**: 35–54.

Chun, C. 1889. Bericht über eine nach den Canarischen Inseln im Winter 1887–88 ausgeführte Reise. *Sber. preuss. Akad. Wiss.* **1889**: 519–553.

Crosnier, A. 1978. Crustacés Décapodes Peneides Aristeidae (Benthesicyminae, Aristeinae, Solenocerinae). *Faune Madagascar* **46**: 1–197.

Eldredge, L. G. 1976. Two new species of lithodid (Anomura, Paguridea, Lithodidae) crabs from Guam. *Micronesica* **12**: 309–315.

Guinot, D. & Sakai, T. 1970. Un nouveau *Trachycarcinus*, *T. elegans* sp. nov. (Crustacea Decapoda Brachyura). *Bull. Mus. natn. Hist. nat., Paris* (2) **42**: 201–205.

Hansen, H. J. 1896. On the development and the species of the Crustaceans of the genus *Sergestes*. *Proc. zool. Soc. Lond.* **1896**: 936–970

Hansen, H. J. 1903. The Crustaceans of the genera *Petalidium* and *Sergestes* from the 'Challenger', with an account of luminous organs. *Proc. zool. Soc. Lond.* **1903**: 52–79.

HANSEN, H. J. 1922. Crustacés Décapodes (Sergestidés) provenant des campagnes des Yachts Hirondelle et Princesse-Alice (1885–1915). *Res. Camp. sci. Monaco* **64**: 1–232.

HOLTHUIS, L. B. 1946. The Decapoda Macrura of the Snellius Expedition. I. *Temminckia* **7**: 1–178.

ILLIG, G. 1927. Die Sergestiden der Deutschen Tiefsee-Expedition, 3. Natantia. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **23**: 279–354.

KENSLEY, B. 1977*a*. The South African Museum's *Meiring Naude* Cruises. Part 2. Crustacea, Decapoda, Anomura and Brachyura. *Ann. S. Afr. Mus.* **72**: 161–188.

KENSLEY, B. 1977*b*. The South African Museum's *Meiring Naude* Cruises. Part 5. Crustacea, Decapoda, Reptantia and Natantia. *Ann. S. Afr. Mus.* **74**: 13–44.

KRØYER, H. 1859. Forsog til en monographisk fremstelling af kraebsdyrslaegten Sergestes. *K. danske Vidensk. Selsk. Skr.* **4**: 217–304.

LOUW, E. 1980. The South African Museum's *Meiring Naude* Cruises. Part 10. Station data 1977, 1978, 1979. *Ann. S. Afr. Mus.* **81**: 187–205.

WASMER, R. A. 1974. A description of *Petalidium suspiriosum* Burkenroad, 1937 (Decapoda, Natantia). *Crustaceana* **27**: 159–169.

YALDWYN, J. C. 1957. Deep-water Crustacea of the genus *Sergestes* (Decapoda Natantia) from Cook Strait, New Zealand. *Zoology Publs Vict. Univ. Coll.* **22**: 1–27.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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figures of plates are enclosed in parentheses to distinguish them from text-figures
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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
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BRIAN KENSLEY

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PART 12
CRUSTACEA DECAPODA OF THE 1977, 1978, 1979 CRUISES

VOLUME 83 PART 5 FEBRUARY 1981 ISSN 0303-2515

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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THE FRESHWATER AMPHIPODA (CRUSTACEA) OF SOUTH AND SOUTH WEST AFRICA

By

CHARLES L. GRIFFITHS

Cape Town Kaapstad

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THE FRESHWATER AMPHIPODA (CRUSTACEA) OF SOUTH AND SOUTH WEST AFRICA

By

Charles L. Griffiths

Zoology Department, University of Cape Town

(With 8 figures)

[*MS. accepted 9 September 1980*]

ABSTRACT

Sixteen species and one variety of freshwater Amphipoda are recognized, of which two, *Paramelita flexa* sp. nov. and *Sternophysinx alca* sp. nov., are described as new. The fauna is composed of three taxonomically and geographically distinct elements—a single species of Ingolfiellidae recorded from South West Africa, a group of three *Sternophysinx* species which occur in the Transvaal, and twelve species and one variety of *Paramelita* which are restricted to the south-western Cape Province.

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INTRODUCTION

The freshwater amphipod fauna of South Africa was last reviewed by Barnard (1927), who recorded a total of eleven species and one variety, all but one of which were assigned to the genus *Gammarus* (=*Paramelita*). The taxonomic positions of all these species have subsequently been revised, and four further valid species and one invalid species have been described from the southern African region. Considerable collections of unidentified material have also accumulated. The time thus appears opportune for an updated review of the fauna and of the distribution records of the various species. In the course of such an analysis the collections of the South African Museum, Cape Town and the Albany Museum, Grahamstown, as well as material sent by A. J. Cannone of the University of the Witwatersrand have been examined. The material includes a number of new locality records as well as two new species, which are described below. The opportunity is also taken to provide keys to the known species of *Paramelita* and *Sternophysinx*, and to illustrate the taxonomically important features of each species.

Ann. S. Afr. Mus. **83** (5), 1981: 79–97, 8 figs.

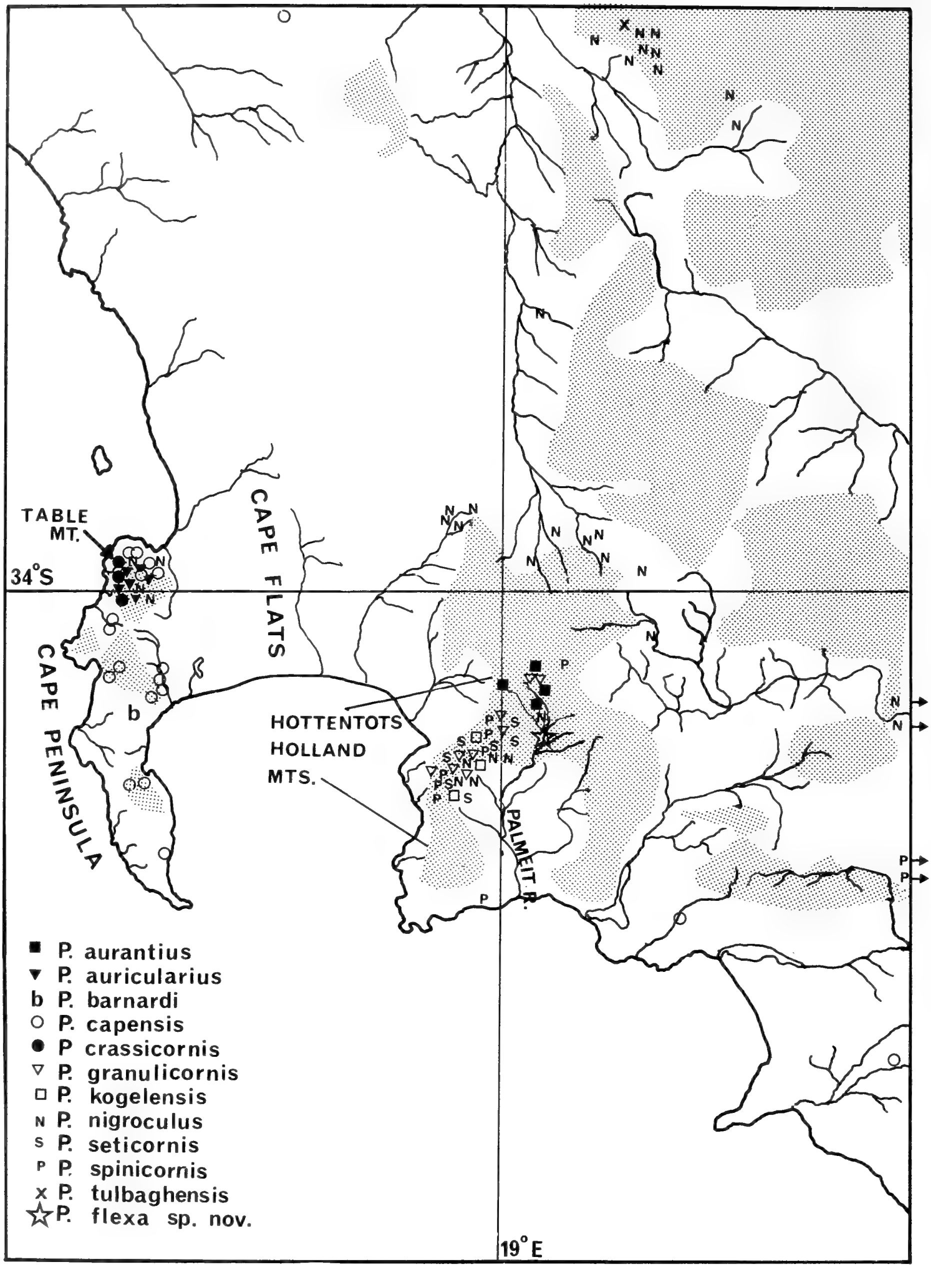

Fig. 1. Map of the south-western Cape Province showing distribution records of *Paramelita* species.

Only truly freshwater and subterranean species are included in this analysis, estuarine forms having been treated by Griffiths (1976). The freshwater fauna is clearly divided into three elements. Of these the ingolfiellid *Leleupiella* is known only from northern South West Africa, *Sternophysinx* (three species) is recorded only from the Transvaal, and *Paramelita* (twelve species and one variety) is restricted to the south-western Cape.

In accordance with modern practice, the pereiopods are numbered 3–7, so that they correspond to the pereon segments on which they occur. It should be noted that, while this system is used by Holsinger & Straskraba (1973) and Thurston (1973), authors such as Methuen (1911*a*, 1911*b*) and Barnard (1916, 1927, 1966) number the pereiopods 1–5.

SYSTEMATICS

KEY TO THE GENERA OF SOUTHERN AFRICAN FRESHWATER AMPHIPODA

1. Body vermiform, coxae minute, widely separated, pleopods reduced to small lobes . . . . *Leleupiella* (p. 96)
   Body laterally compressed, coxae well developed, contiguous or overlapping, pleopods large, biramous 2
2. Coxae not overlapping, pereon segments 2–7 with bladder-like medioventral processes . . . . *Sternophysinx* (p. 91)
   Coxae overlapping, pereon segments bearing accessory gills but lacking medioventral processes . . . . *Paramelita* (p. 81)

Superfamily CRANGONYCTOIDEA Bousfield, 1973

Family **Paramelitidae** Bousfield, 1977

Paramelita Schellenberg, 1926

The species described by Barnard (1916, 1927) were transferred from *Gammarus* to *Paramelita* by Schellenberg (1937). In a revision of the family Gammaridae, Bousfield (1977) subsequently placed this genus in his new family Paramelitidae.

Paramelita spp are restricted to fully freshwater habitats, both in surface streams and in caves. All known records are from the south-western Cape Province, South Africa. The recorded distribution patterns within the genus are given in Figure 1.

KEY TO SPECIES OF *PARAMELITA*

1 Eyes conspicuous, black (Fig. 6A–B) 2
  Eyes small, white, invisible in preserved material (Fig. 4A) 3

2 Posterior margins of antenna 2 and pereiopods 2–7 densely setose posteriorly, especially in ♂ (Fig. 6A) . . . . *nigroculus* var. *persetosus*
  Posterior margins of antenna 2 and pereiopods 3–7 moderately setose, lacking setal brushes (Fig. 6B) . . . . *nigroculus*

3 Peduncle of antenna 2 ♂ greatly enlarged and/or with articles 3 or 4 posterodistally lobed or toothed (Fig. 3A, D–E) 4
  Peduncle of antenna 2 ♂ not enlarged, articles 3 and 4 not lobed or toothed (Figs 4A, 2D) . . 8

4 Article 3 of antenna 2 ♂ posterodistally lobed (Figs 3A, 5A)........................5
Article 3 of antenna 2 ♂ not lobed..6

5 Antenna 2 ♂ linear, coxa 4 quadrangular, pereiopod 3 chelate in adult ♂ (Fig. 3A–C).... *auricularius*
Antenna 2 ♂, article 5 attached at right angles to 4, coxa 4 posteriorly excavate, pereiopod 3 ♂ normal (Fig. 5A, G)..*flexa* sp. nov.

6 Antenna 2 ♂, article 4 with a strong posterodistal tooth, article 5 attached normally to 4 (Fig. 3D) ....*spinicornis*
Antenna 2 ♂, article 4 not toothed, article 5 bent at right angles to 4 (Fig. 3E)..........7

7 Coxa 4 not posteriorly excavate, dactyls of pereiopods 3–7 each with a single spinule (Fig. 3F–G)..*crassicornis*
Coxa 4 distinctly excavate posteriorly, dactyls of pereiopods 3 and 4 with two spinules, of 5 with three spinules and of 6 and 7 with four spinules (Fig. 3H–I)............*tulbaghensis*

8 Palm of gnathopod 2 distinctly oblique (Fig. 2A)................................9
Palm of gnathopod 2 transverse or slightly oblique (shorter than hind margin) (Fig. 2I–J) 10

9 Coxa 4 strongly excavate posteriorly, uropod 3 strongly setose (Fig. 4A–B)......*capensis*
Coxa 4 shallowly excavate posteriorly, uropod 3 spinose, not setose (Fig. 2B–C)..*barnardi*

10 Coxa 4 distinctly excavate posteriorly (Fig. 2E)................................11
Coxa 4 quadrate, lacking posterior excavation (Fig. 2H)..........................12

11 Peduncle of antenna 2 densely setose posteriorly, article 2 of outer ramus of uropod 3 obsolete (Fig. 2D, F)..*seticornis*
Peduncle of antenna 2 not strongly setose, outer ramus of uropod 3 with distinct second joint (Fig. 2G) ....*kogelensis*

12 Article 2 of gnathopod 2 with a group of spines on posterior margin, palm strongly convex, with distinct defining tooth (Fig. 2I)................................*granulicornis*
Article 2 of gnathopod 2 not spinose, palm moderately convex, lacking defining tooth (Fig. 2J) ....*aurantius*

Paramelita aurantius (K. H. Barnard, 1927)

Fig. 2J

Gammarus aurantius Barnard, 1927: 173–174; pl. 10, figs 6, 16.

Remarks

One of a closely related group of species comprising *P. aurantius*, *P. granulicornis*, *P. kogelensis*, and *P. seticornis*. Distinguished by the quadrate coxa 4, sparsely setose antenna 2, and absence of a defining tooth and of spines on gnathopod 2.

Distribution

Hottentots Holland Mountains, south-western Cape.

Paramelita auricularius (K. H. Barnard, 1916)

Fig. 3A–C

Gammarus auricularius Barnard, 1916: 209–210, pl. 27, figs 26–68; 1927, 169–170.

Remarks

The ear-like lobe on article 3 of antenna 2 ♂ distinguishes this species from all others except *P. flexa* sp. nov., from which it differs in the shape of coxa 4,

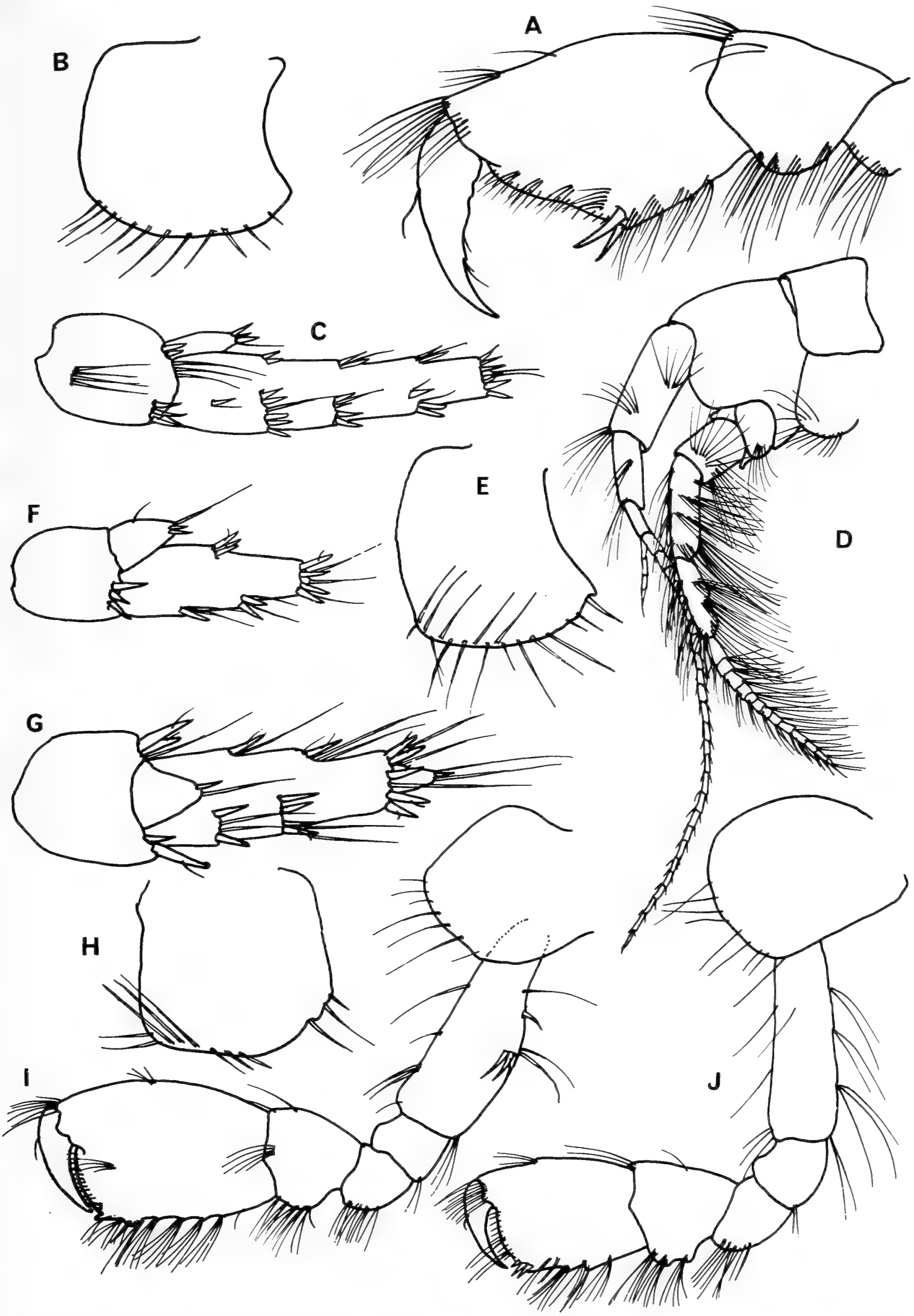

Fig. 2. A–C. *Paramelita barnardi*, female, 9 mm. A. Gnathopod 2. B. Coxa 4. C. Uropod 3. D–F. *Paramelita seticornis*, male, 5 mm. D. Head and antennae. E. Coxa 4. F. Uropod 3. G. *Paramelita kogelensis*, male, 6 mm. Uropod 3. H–I. *Paramelita granulicornis*, male, 6 mm. H. Coxa 4. I. Gnathopod 2. J. *Paramelita aurantius*, male, 7 mm. Gnathopod 2.

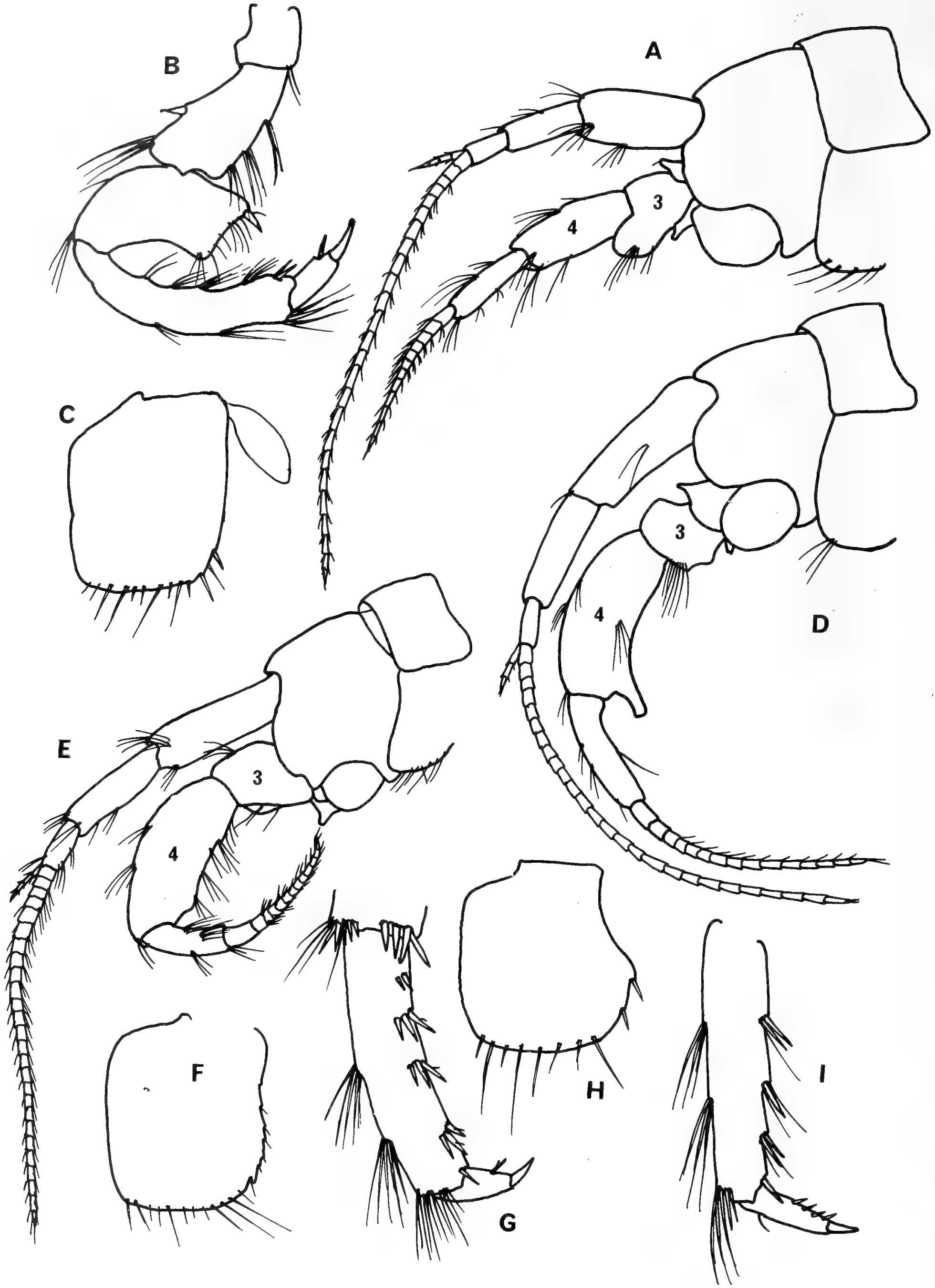

Fig. 3. A. *Paramelita auricularius*, male, 5,5 mm. Head and antennae. B–C. Male, 6 mm. B. Pereiopod 3. C. Coxa 4. D. *Paramelita spinicornis*, male, 8 mm. Head and antennae. E–G. *Paramelita crassicornis*, male, 8 mm. E. Head and antennae. F. Coxa 4. G. Articles 6 and 7 of pereiopod 7. H–I. *Paramelita tulbaghensis*, male, 7 mm. H. Coxa 4. I Articles 6 and 7 of pereiopod 7.

non-flexed antenna 2, and in the extraordinary subchelate condition of pereiopod 3 in the adult ♂.

Distribution

Top of Table Mountain only.

Paramelita barnardi Thurston, 1973

Fig. 2A–C

Paramelita barnardi Thurston, 1973: 159–168, figs 1–3.

Remarks

Similar to *P. capensis* but distinguished by the weakly excavate coxa 4 and spinose (not setose) uropod 3.

Distribution

Known only from the type locality, a cave above Kalk Bay on the Cape Peninsula.

Paramelita capensis (K. H. Barnard, 1916)

Fig. 4

Gammarus capensis Barnard, 1916: 203–205, pl. 27, figs 20–22; 1927: 169.
Paramelita ctenodactyla Schellenberg, 1926: 367, fig. 57.

Remarks

The degree of setation of the pleon segments and of pereiopods 5–7 is very variable, ranging from the condition shown in Figure 4A to one in which the dorsal surface of the pleon and the anterior margins of articles 2–6 of pereiopods 5–7 are densely clothed in setae. Antenna 2 may be as long as and sturdier than antenna 1. A wide variety of forms may be collected from the same stream, suggesting that the various forms are not of any taxonomic significance.

C. capensis may be recognized by its large size (15–25 mm) at maturity, unmodified antennae, oblique palm of gnathopod 2, deeply excavate coxa 4, and setose uropod 3.

Distribution

Widely distributed from Clanwilliam in the north to Bredasdorp in the east.

Paramelita crassicornis (K. H. Barnard, 1916)

Fig. 3E–G

Gammarus crassicornis Barnard, 1916: 207–209, pl. 27, figs 24–25.

Remarks

The unusual form of antenna 2 ♂, in which the peduncle is enlarged and bent between articles 4 and 5, is found only in this species, *P. flexa* sp. nov. and *P. tulbaghensis*. *P. crassicornis* is recognized by the quadrate coxa 4, the single

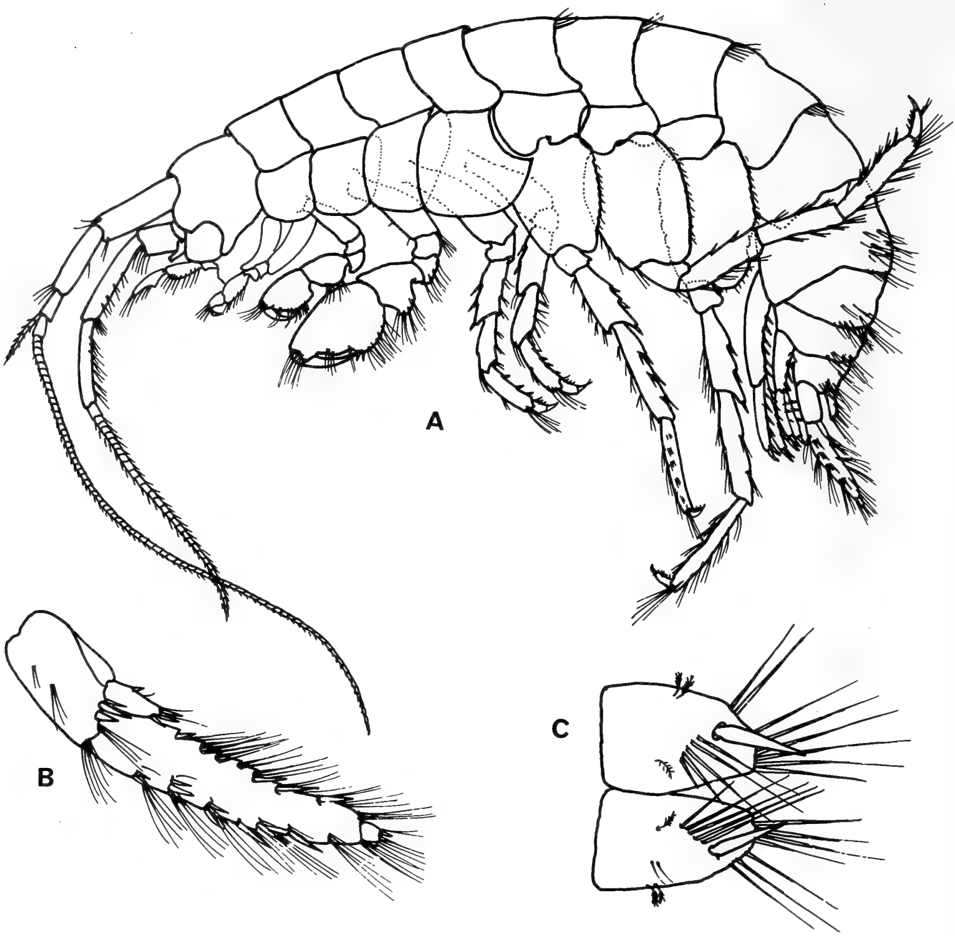

Fig. 4. *Paramelita capensis*, male, 18 mm. A. Lateral aspect. B. Uropod 3. C. Telson.

spinule on article 7 of pereiopods 3–7 and the absence of a posterodistal lobe on article 3 of antenna 2 ♂.

Distribution

Northern and western slopes of Table Mountain.

Paramelita flexa sp. nov.

Fig. 5

Description (of male, 7 mm)

Head slightly shorter than pereon segments 1 and 2 together, anterolateral lobes deep, rounded-truncate, eyes invisible in alcohol. Antenna 1 as long as body, flagellum 1,5 times length of peduncle, 26-articulate, accessory flagellum 5-articulate. Antenna 2 somewhat shorter but stouter than 1, article 3 strongly

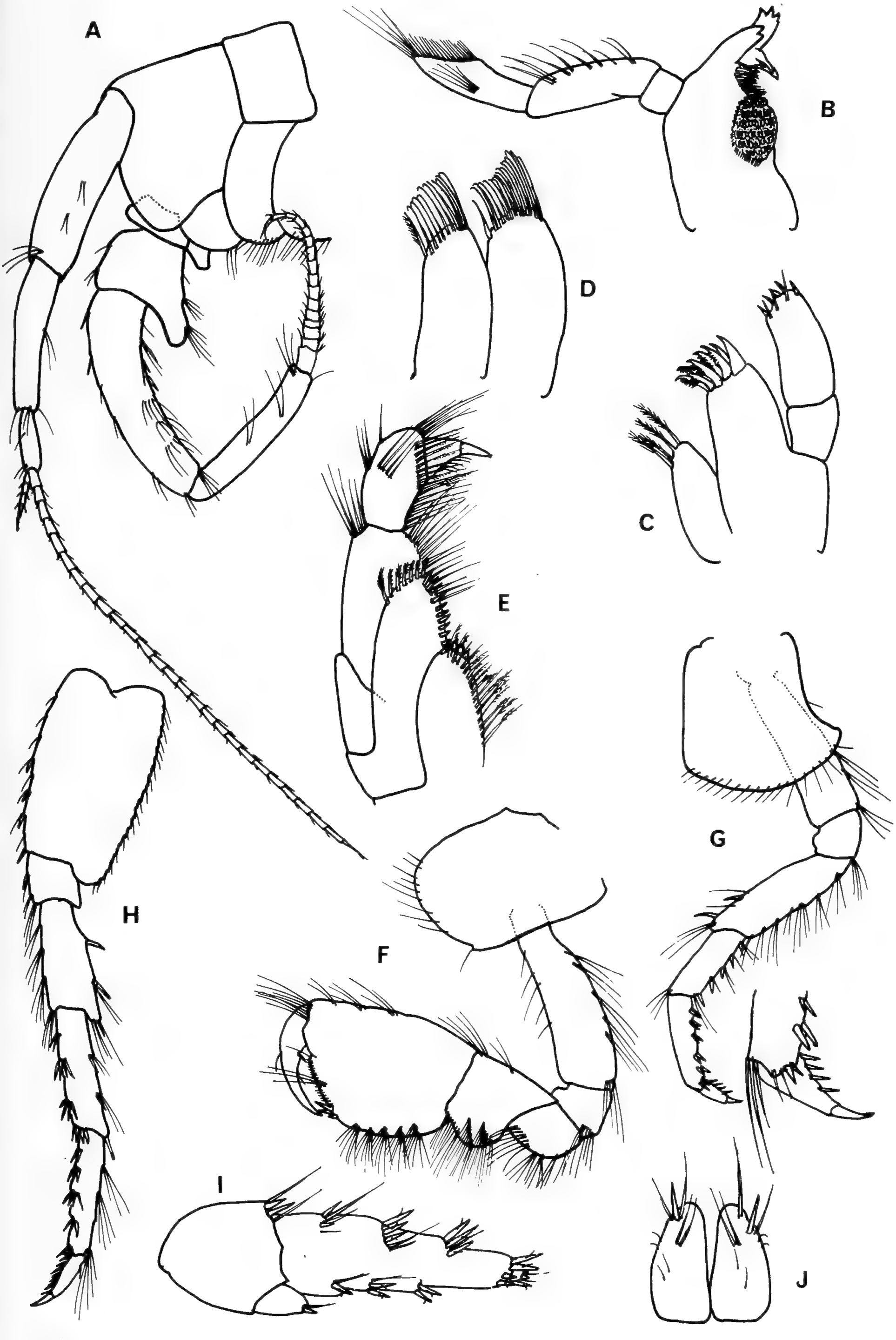

Fig. 5. *Paramelita flexa* sp. nov., male, 7 mm. A. Head and antennae. B. Mandible. C. Maxilla 1. D. Maxilla 2. E. Maxilliped. F. Gnathopod 2. G. Coxa 4 and pereiopod 4. H. Pereiopod 7. I. Uropod 3. J. Telson.

lobed posterodistally, article 4 three times length of 3, curved ventrally, article 5 bent almost at right angles to 4, flagellum 16-articulate. Cutting-edge of mandible 5-toothed, lacinia mobilis (left side) with four teeth, spine row of nine strongly pectinate spines, molar strongly triturative, palp articles 2 and 3 subequal, distal half of 3 lined with dense row of short setae. Inner plate of maxilla 1 with four plumose setae, outer plate bearing ten stout toothed spines, palp exceeding outer plate, with five terminal spines and three subterminal setae. Inner plate of maxilla 2 a little shorter and narrower than outer plate, both strongly setose terminally. Inner plate of maxilliped with three short blunt spines and fifteen plumose setae, outer plate bearing twelve medial spine-teeth and seven terminal pectinate setae, palp densely setose medially.

Pereon segments dorsally smooth, coxae 1–3 slightly deeper than corresponding segments, rounded-quadrate, coxa 4 distinctly excavate posteriorly, 5 and 6 bilobed, 7 rounded-quadrate. Gnathopods 1 and 2 of similar structure but 2 slightly the larger, article 6 slightly longer than wide, palm convex, slightly oblique, defined by three short stout spines, dactyl as long as palm. Pereiopods 3 and 4 of similar structure, article 4 slightly produced anterodistally, 5 with five posterior spines, 6 with six pairs of spines posteriorly, 7 with four spinules posteriorly. Pereiopods 5–6, articles 4, 5 and 6 subequal, dactyl with seven spinules anteriorly. Pereiopod 7 similar to 5 and 6 but dactyl with nine spinules.

Pleon segments 1–3 each with a few setae along posterodorsal margin, first pleonal epimeron rounded, 2 and 3 quadrate, each with long plumose setae just above distal margin, posterior margin with short setae in minute notches. Pleon segments 4–6 each with a few dorsal setae, uropod 1 extending slightly beyond 2, rami equal, inner ramus of uropod 2 slightly the shorter, uropod 3 exceeding 2 by half length of outer ramus, peduncle as broad as long, inner ramus short, half length of peduncle, terminating in a short spine and one seta, outer ramus twice length of peduncle, three groups of spines on each margin, apex strongly spinose, concealing minute second article. Telson slightly longer than broad, cleft almost to base, each lobe with one large subapical spine between two long setae, dorsal margin with two long and two short setae, plus one pair of minute setae on lateral margin.

Holotype

Albany Museum MISC 52B, male, 7 mm.

Type locality

Palmiet River (34° 09′S 19°01′E), beneath bridge on main Elgin–Grabouw road, south-western Cape, 20 October 1952.

Material

Two juveniles from the same sample as the type specimen and an ovigerous female and four further juveniles collected by the author on 7 December 1979 from the same locality (SAM–A16776).

Etymology

From the Latin *flexus* (bending), an allusion to the flexion of antenna 2 between articles 4 and 5.

Relationships

The posterodistal lobe on article 3 of antenna 2 of this species is similar to that found in *P. auricularius*. Antenna 2 in *P. auricularius* is, however, linear, whereas in *P. flexa* sp. nov. article 5 is attached at right angles to article 4, in a manner similar to that occurring in *P. crassicornis* and *P. tulbaghensis*. *P. auricularius* may also be distinguished from *P. flexa* sp. nov. in the form of coxa 4 and pereiopod 3 as well as by its distribution, which is limited to Table Mountain.

Paramelita granulicornis (K. H. Barnard, 1927)

Fig. 2H–I

Gammarus granulicornis Barnard, 1927: 175–177, pl. 10, figs 10–11, 20.

Remarks

The second gnathopod of this species, with its spinose article 2 and convex, transverse palm, defined by an acute tooth, is diagnostic. The square coxa 4 and spinose posterior margin of article 2 of pereiopod 4 also aid in identification.

Distribution

Hottentots Holland Mountains.

Paramelita kogelensis (K. H. Barnard, 1927)

Fig. 2G

Gammarus kogelensis Barnard, 1927: 172–173, pl. 10, figs 9, 21.

Remarks

Closely related to *P. seticornis* but differs in the degree of setation of the peduncle of antenna 2 (both species have the flagellum setose) and in details of the spination of the pereiopods and of uropod 3.

Distribution

Hottentots Holland Mountains.

Paramelita nigroculus (K. H. Barnard, 1916)

Fig. 6

Gammarus nigroculus Barnard, 1916: 206–207, pl. 27, fig. 23; 1927: 168–169.

Remarks

The dark eyes distinguish the species, which is otherwise similar to *P. capensis*. Although a variety based on degree of setation (var. *persetosus*) is recognized, the degree of setation is very variable, even within individual samples.

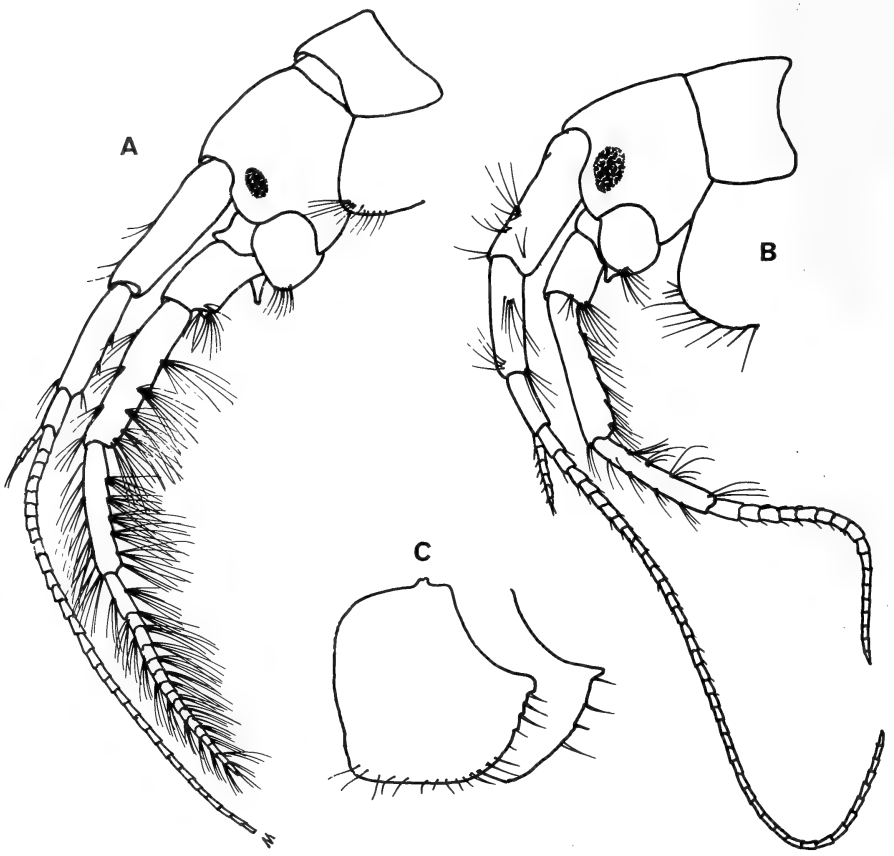

Fig. 6. A. *Paramelita nigroculus* var. *persetosus*, male, 13 mm. Head and antennae. B–C. *Paramelita nigroculus*, male, 12 mm. B. Head and antennae. C. Coxa 4 (both sides).

Distribution

The most common and widely distributed *Paramelita* species, occurring from Tulbagh and the Cedarberg in the north to Swellendam in the east.

Paramelita seticornis (K. H. Barnard, 1927)

Fig. 2D–F

Gammarus seticornis Barnard, 1927: 171–172, pl. 10, figs 7, 17.

Remarks

A small form, mature at 5 mm, distinguished from the allied *P. kogelensis* by the form of antenna 2 ♂.

Distribution

Hottentots Holland Mountains.

Paramelita spinicornis (K. H. Barnard, 1927)

Fig. 3D

Gammarus spinicornis Barnard, 1927: 174–175, pl. 10, figs 8, 18–19.

Remarks

The form of antenna 2 ♂ in this species is characteristic.

Distribution

Hottentots Holland Mountains eastwards to Swellendam.

Paramelita tulbaghensis (K. H. Barnard, 1927)

Fig. 3H–I

Gammarus tulbaghensis Barnard, 1927: 170–171, pl. 10, figs 5, 15.

Remarks

The enlarged and bent peduncle of antenna 2 ♂ is similar to that of *P. crassicornis,* but coxa 4 is excavate posteriorly and there are more spinules on the dactyls of the pereiopods (two in pereiopods 3 and 4, three in pereiopod 5, and four in pereiopods 6 and 7). Lacks the lobe on article 3 of antenna 2 ♂ found in *P. flexa* sp. nov.

Distribution

Known only from the type locality in the Sneeuwgat Valley, Tulbagh, south-western Cape.

Pseudocrangonyx–Sternophysinx family group (Bousfield, 1977)

Sternophysinx Holsinger & Straskraba, 1973

Originally erected to accommodate *Crangonyx robertsi* and two new species from the Transvaal, *Sternophysinx* was transferred from the Gammaridae to a new Superfamily Bogidielloidea by Bousfield (1977) and again to the Superfamily Crangonyctoidea by Bousfield (1978). The genus has not been recorded outside the Transvaal and is hence geographically isolated from *Paramelita.* Morphologically *Sternophysinx* may readily be distinguished from *Paramelita* by the smaller, non-overlapping coxae and distinctive bladder-like sternal processes on pereon segments 2–7.

KEY TO SPECIES OF *STERNOPHYSINX*

1 Article 2 of pereiopods 5–7 widened, with distinct posterodistal lobe (Fig. 7A–B)........2
Article 2 of pereiopods 5–7 narrowly tapering, without posterodistal lobe (Fig. 7C–D)....3

2 Articles 6, or 5 and 6 of pereiopods 5–7 bearing long threadlike setae posteriorly, dactyls with 2–5 anterior spines (Fig. 7A).......................................*filaris*
Articles 5 and 6 of pereiopods 5–7 lacking thread-like setae, dactyls with single anterior spine (Fig. 7B)...*robertsi*

3 Palm of gnathopods 1 and 2 evenly convex, body length about 5 mm at maturity........ *transvaalensis*
Palm of gnathopods 1 and 2 excavate (Fig. 8H, I), body length at maturity about 10–12 mm *alca* sp. nov.

Sternophysinx alca sp. nov.

Figs 7D, 8

Description (of female, 15 mm)

Antenna 1 about half length of body, flagellum 22-articulate, accessory flagellum uni-articulate, about as long as first segment of primary flagellum. Antenna 2 somewhat shorter than 1, gland cone prominent, flagellum 9-articulate. Mandible with large triturative molar, spine row of eight spines, palp well developed, articles 2 and 3 subequal. Palp of maxilla 1 bi-articulate, bearing seven terminal spines, outer plate with six serrate spines apically, inner plate with two terminal plumose setae. Both inner and outer plates of maxilla 2 strongly setose apically, inner plate with two long subterminal plumose setae. Inner plate of maxilliped armed with three short thick spines, outer plate with thirteen medial and terminal spines, palp 4-segmented.

Pereon dorsally smooth. Coxa 1 slightly produced anteroventrally, coxae 2–4 quadrate, 4 not strongly excavate posteriorly, 5 and 6 bilobed, 7 semicircular. Gnathopod 1 short but stout, palm defined by large pair of spines,

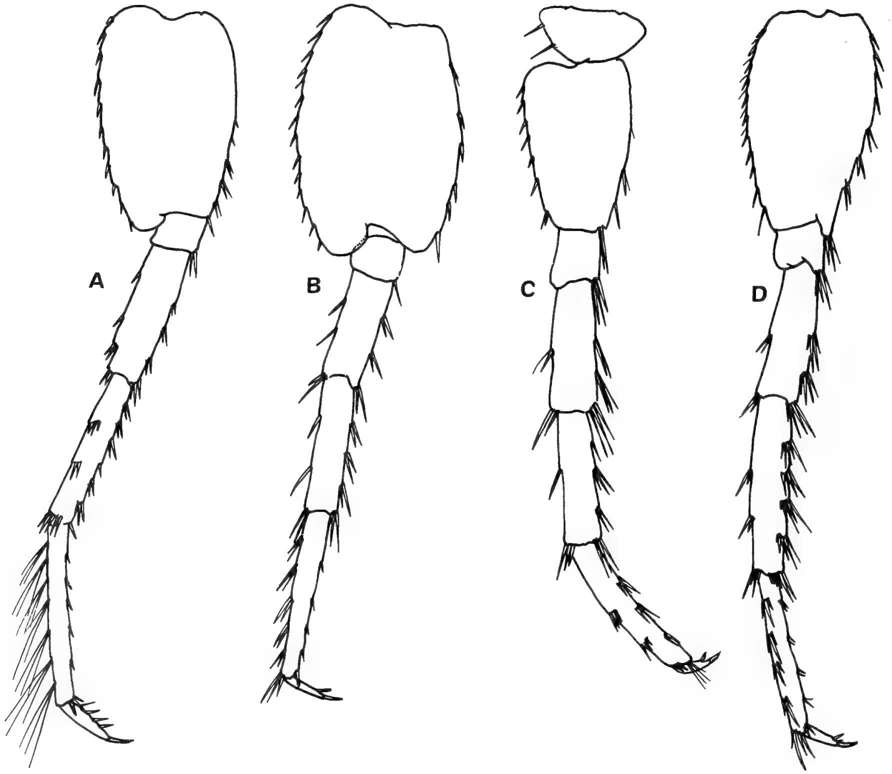

Fig. 7. Pereiopod 7 in *Sternophysinx* species. A. *S. filaris*, male, 8 mm. B. *S. robertsi*, male, 8 mm. C. *S. transvaalensis*, male, 5 mm. D. *S. alca*, female, 13 mm.

posterior margin bearing three further pairs of large spines, palmar margin lined by short setae, with semicircular excision and small tooth at its midpoint, dactyl exceeding palm, nail long, bearing small secondary process at its base. Gnathopod 2 as 1 but article 2 slender, more elongate and without anterior setae. Pereiopods 3 and 4 with article 2 slightly expanded and with long slender setae equally spaced along posterior margin. Pereiopod 5 considerably shorter than 6 or 7, article 2 not expanded, lacking posterodistal lobe, dactyl with two spines. Pereiopods 6 and 7 similar to 5 but much longer, extending to end of uropods, dactyl with single spine. Pereon segments 2–7 each with bladder-like median sternal process.

Pleon segments 1–4 each with few small setae along posterodorsal margin. Pleonal epimera rounded-quadrate, two small setules at posterodistal corner of each, posterior margins almost straight. Uropod 1 extending slightly beyond 2, outer ramus slightly the shorter, both rami dorsally and terminally spinose. Uropod 3 considerably exceeding 1 and 2, outer ramus with five groups of setae along ventral and four along dorsal margin, inner ramus minute, rounded, bearing single terminal seta. Telson slightly longer than broad, apically emarginate, each lobe with four large terminal spines.

Holotype

SAM–A16775, female, 13 mm.

Type locality

Peppercorn's Cave, Makapansgat, Transvaal (24°09′S 29°12′E) collected from a small clear pool, June 1979, by A. J. Cannone of the Zoology Department, University of the Witwatersrand.

Material

Twenty-five individuals from Peppercorn's Cave and from Ficus Cave, Makapansgat.

Etymology

Named for Dr Al Cannone, who discovered this species and allowed the author to describe it.

Relationships

The excavation and tooth on the palm of gnathopods 1 and 2 readily identify this species. *S. alca* sp. nov. is also distinguished from *S. robertsi* and *S. filaris* by the narrowly tapering article 2 of pereiopods 5–7, and from *S. transvaalensis* by its larger body size and by details of spination of the pereiopods. The species is found in the same pools as *S. robertsi.*

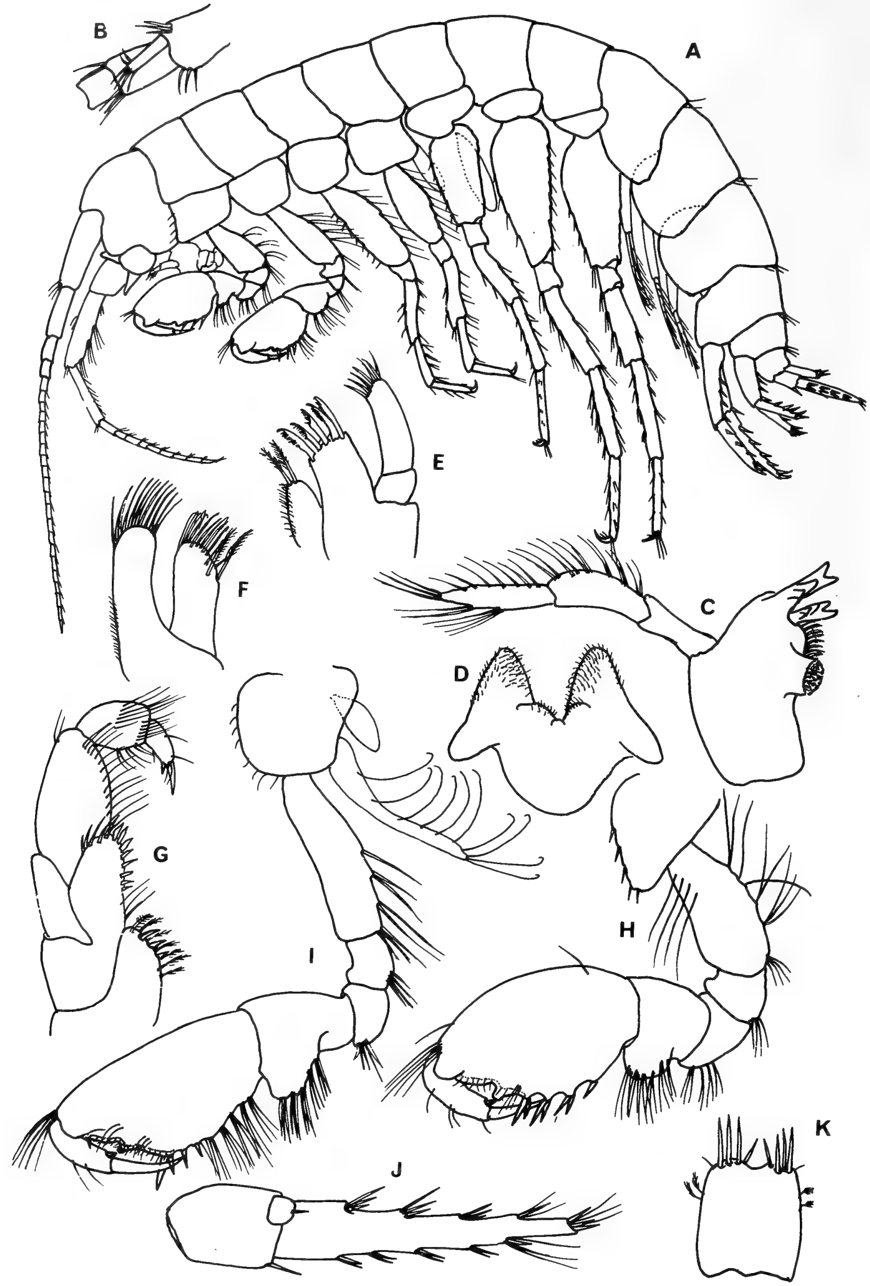

Fig. 8. *Sternophysinx alca* sp. nov., female, 15 mm. A. Lateral aspect. B. Accessory flagellum. C. Mandible. D. Lower lip. E. Maxilla 1. F. Maxilla 2. G. Maxilliped. H–I. Gnathopods 1, 2. J. Uropod 3. K. Telson.

Sternophysinx filaris Holsinger & Straskraba, 1973

Fig. 7A

? *Eucrangonyx robertsi (partim.)* Methuen, 1911*a*: 948–957, pls 49–51.
Sternophysinx filaris Holsinger & Straskraba, 1973: 75–76, figs 2–3.

Remarks

Distinguished by the thread-like setae along the posterior margins of articles 5 and 6 of pereiopods 5 and 6 and of article 6 of pereiopod 7. The material reported from Irene by Methuen (1911*a*) should probably be allocated to *S. filaris*, rather than *S. robertsi*, the latter being positively known only from the Makapan Caves area some 200 km to the north.

Distribution

Sterkfontein Caves, and (?) Irene, Transvaal.

Sternophysinx robertsi (Methuen, 1911)

Fig. 7B

Eucrangonyx robertsi Methuen, 1911*a*: 948–957, pls 49–51; 1911*b*: 96–101.
Barnard, 1927: 141, 209.
[*Non*]*Crangonyx robertsi*: Barnard, 1949: 523–525 (=*Sternophysinx transvaalensis*).

Remarks

The expanded article 2 of pereiopods 5–7 distinguishes this species from *S. transvaalensis* and *S. alca* sp. nov., while the posterior pereiopods are shorter than those of *S. filaris*, lack thread-like seta on articles 5 and 6 and have only a single spine on article 7. The material identified as *S. robertsi* by Barnard (1949) —SAM–A8372—has been re-examined and transferred to *S. transvaalensis*.

Distribution

Makapan Caves and springs in the vicinity.

Sternophysinx transvaalensis Holsinger & Straskraba, 1973

Fig. 7C

Crangonyx robertsi (*non* Methuen, 1911*a*): Barnard, 1949: 523–525.
Sternophysinx transvaalensis Holsinger & Straskraba, 1973: 76–79, figs. 4–5.

Remarks

The small size, smoothly convex palm of gnathopods 1 and 2, unexpanded article 2 of pereiopods 5–7, and absence of long setae on these appendages serve to identify this species. The material identified as *Crangonyx robertsi* by Barnard (1949) has been re-examined and the structure of pereiopod 7 (Fig. 7C) clearly identifies it as belonging to *S. transvaalensis*.

Distribution

Surface streams in the northern Drakensberg region.

Suborder INGOLFIELLIDEA Hansen, 1903

Family **Ingolfiellidae** Hansen, 1903

Leleupiella Karaman, 1959

Leleupiella eggerti Ruffo, 1964

Leleupiella eggerti Ruffo, 1964: 1019–1031, figs 1–2.
Ingolfiella opisthodorus Barnard, 1966: 189–197, figs 1–2.

Remarks

First described by Ruffo (1964) from Tsumeb, this species was subsequently redescribed as new in a posthumous paper by Barnard (1966). No further material has been recorded. *L. eggerti* is the only ingolfiellid recorded from South or South West Africa and is notable for its large size (up to 25 mm). The elongate body form, minute coxae and carpochelate gnathopods readily distinguish the Ingolfiellidae from members of the Crangonyctoidea.

Distribution

Recorded from boreholes near Tsumeb, South West Africa.

ACKNOWLEDGEMENTS

My thanks to Dr A. J. Cannone, who initiated this project by bringing to my attention the material described herein as *Stenophysinx alca* sp. nov. Additional material was kindly lent by the South African Museum and the Albany Museum, Grahamstown. Mrs Leonora Freeland typed the manuscript.

REFERENCES

BARNARD, K. H. 1916. Contributions to the crustacean fauna of South Africa. 5. The Amphipoda. *Ann. S. Afr. Mus.* **15**: 105–302.

BARNARD, K. H. 1927. A study of the freshwater isopodan and amphipodan Crustacea of South Africa. *Trans. R. Soc. S. Afr.* **14**: 139–215.

BARNARD, K. H. 1949. A fresh-water amphipod from Mont-aux-Sources. *Ann. Natal Mus.* **11**: 523–525.

BARNARD, K. H. 1966. The occurrence of the genus *Ingolfiella* (Crustacea, Amphipoda) in South Africa, with description of a new species. *Ann. Mag. nat. Hist.* **13**: 189–197.

BOUSFIELD, E. L. 1973. *Shallow-water gammaridean Amphipoda of New England.* New York: Cornell University Press.

BOUSFIELD, E. L. 1977. A new look at the systematics of gammaroidean amphipods of the world. *Crustaceana, Suppl.* **4**: 282–316.

BOUSFIELD, E. L. 1978. A revised classification and phylogeny of amphipod crustaceans. *Trans. R. Soc. Can.* (IV) **16**: 343–390.

GRIFFITHS, C. L. 1976. *Guide to the benthic marine amphipods of southern Africa.* Cape Town: South African Museum.

HOLSINGER, J. R. & STRASKRABA, M. 1973. A new genus and two new species of subterranean amphipod crustaceans (Gammaridae) from South Africa. *Ann. Spéléol.* **28**: 69–79.

METHUEN, P. A. 1911*a*. On an amphipod from the Transvaal. *Proc. zool. Soc. Lond.* **2**: 948–957.

METHUEN, P. A. 1911*b*. Transvaal Crustacea. Part 2. Notice of a freshwater amphipod from South Africa. *Ann. Transv. Mus.* **3**: 96–101.

Ruffo, S. 1964. Studi sui Crostacei Anfipodi. 58. Un nuovo Ingolfiellide delle acque sotterranee dell' Africa di Sud Ovest. *Boll. Zool.* **31**: 1019–1034.

Schellenberg, A. 1926. Die Gammariden der Deutschen Südpolar-Expedition 1901–1903. *Dt. Südpol.-Exped.* **18**: 235–414.

Schellenberg, A. 1937. Kritische Bemerkungen zur Systematik der Süsswassergammariden. *Zool. Jb.* **69**: 469–516.

Thurston, M. H. 1973. A new species of *Paramelita* (Crustacea: Amphipoda) from South Africa. *Ann. S. Afr. Mus.* **62**: 159–168.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

CHARLES L. GRIFFITHS

THE FRESHWATER AMPHIPODA (CRUSTACEA) OF SOUTH AND SOUTH WEST AFRICA

VOLUME 83 PART 6 FEBRUARY 1981 ISSN 0303-2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

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    - Address(es) of author(s) (institution where work was carried out)
    - Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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(a) Author's name and year of publication given in text, e.g.:

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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THE GENERA *DICYNODON* AND *DIICTODON* AND THEIR BEARING ON THE CLASSIFICATION OF THE DICYNODONTIA (REPTILIA, THERAPSIDA)

By

MICHAEL A. CLUVER
&
NICHOLAS HOTTON III

Cape Town Kaapstad

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By

MICHAEL A. CLUVER
South African Museum, Cape Town
&
NICHOLAS HOTTON III
Smithsonian Institution, Washington, D.C.

(With 30 figures and 1 table)

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ABSTRACT

The Late Permian dicynodont genera *Dicynodon, Oudenodon, Diictodon* and *Kingoria* are diagnosed on the basis of skull details seen in the primary type material. Many of the species previously included under *Dicynodon* have been referred to other genera, but no attempt at assessing the validity of these types at the species level has been made. *Diictodon* has the greatest stratigraphical range among the four genera, occurring throughout the three zones of the Lower Beaufort of the South African Karoo, while the characteristic features of *Dicynodon* can be identified in modified form in a number of Triassic genera. *Dicynodon* and *Oudenodon* appear to be more closely related to each other than to *Diictodon*. *Kingoria*, with several unusual features in the palate and lower jaw, holds the least in common with other Late Permian genera. Recognition of the characters distinguishing the four genera from each other should aid future studies on the systematics and evolution of this important therapsid group.

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INTRODUCTION

The infra-order Dicynodontia represents a Late Permian and Triassic radiation of herbivorous therapsids. Its first appearance in the lowermost *Tapinocephalus* Zone of the South African Karoo's Beaufort Group coincides

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with that of the earliest known South African land vertebrates. Although dicynodonts, mainly of Triassic age, are now known from east Africa, India, China, Antarctica, Europe, and North and South America, the most complete record of the group is the South African one against which the other more restricted occurrences must be compared.

The evolution of the Dicynodontia, as far as can be traced in features of the skull morphology, chiefly involved numerous modifications of a basic innovation of the feeding process, and in terms of general skull structure the earliest and latest known representatives of the infra-order are essentially similar. Chief among the departures from the primitive condition are the tendency for replacement of the upper and lower dentitions by horny beaks, the establishment of a sliding quadrate-articular jaw joint, and the lateral migration of a portion of the external jaw adductor musculature to a new site of origin on the lateral surface of the temporal arch.

The dicynodont skull is consequently a highly distinctive one, and from the time of its original description by Owen (1845*a*) has frequently been described and figured in its many variations. However, the great abundance of specimens collected from numerous Beaufort localities, and the preference for detailed skull roof characters shown in the taxonomic work of earlier palaeontologists, combined to create a large number of poorly diagnosed dicynodont 'species' divided among a number of 'genera' of doubtful validity. In the bibliographic work of Haughton & Brink (1954), which takes into at least partial account revisions by Van Hoepen (1934) and Toerien (1953), no fewer than 111 South African species are assigned to the catch-all genus *Dicynodon*. Since the bulk of these dicynodonts is known from the Permian part of the Beaufort succession, it is among these forms that the taxonomic confusion is at its worst.

It has long been recognized that this state of affairs has served to obscure the potential importance of the Dicynodontia in a variety of fields of study. Attempts at rectifying the situation have resulted in a number of detailed studies on selected dicynodont groups; the cranial morphology of *Placerias* (Camp & Welles 1956), *Kingoria* (Cox 1959), *Daptocephalus* (Ewer 1961), *Lystrosaurus* (Cluver 1971), and *Oudenodon* (Keyser 1975) is now well known and these genera serve as standards of comparison with other forms.

Following the work of Toerien (1953), more attention has been paid to details of the palate and lower jaw (e.g. Cluver 1970, 1974*a*, 1974*b*, 1975; Keyser 1975). Cluver (1970) recognized previously undescribed cranial features in specimens of Permian age identified as *Dicynodon testudirostris*. Subsequent comparisons have shown that these features are not present in the type specimen (BMNH 36233) of *Dicynodon lacerticeps*, upon which Owen's (1845*a*) original description of *Dicynodon* was based. Rather, they are found in the type specimen (AMNH 5308) of *Diictodon galeops* Broom, 1913. It is now clear that the genus *Diictodon* is valid and distinct from *Dicynodon*, has greater stratigraphical and geographical ranges than previously suspected, and is abundant in certain Upper Permian Karoo localities (Cluver & Hotton 1979). Furthermore, comparisons based on type material confirm the validity of the genera *Oudenodon* and *Kingoria*, as revised and defined by Keyser (1975) and Cox (1959) respectively. In the following sections, expanded diagnoses of these two genera are included to allow full comparison with *Dicynodon* and *Diictodon*. Diagnoses of these four important dicynodont genera help to remove much of the uncertainty surrounding the status of the type specimens currently assigned to *Dicynodon*. Locality and stratigraphic information with respect to type specimens has been taken from Haughton & Brink (1954) and Kitching (1970, 1977). The latter author's division of the Permian part of the Beaufort group into *Tapinocephalus*, *Cistecephalus*, and *Daptocephalus* zones is followed.

GENERAL SKULL MORPHOLOGY

The highly distinctive skull structure of dicynodonts (Figs 1–9) is modelled around a jaw mechanism unique among tetrapods. The preorbital portion of the skull is short, and the temporal region expanded to accommodate a greatly enlarged temporal musculature. The temporal muscles arose medially from a broad, flat process of the postorbital that covers much of the parietal in most forms.

The highest areas of origin are marked by bony parietal ridges which in some dicynodonts meet in the midline to form a longitudinal crest behind the parietal foramen. Lateral portions of the temporal muscles arose from a flattened zygoma formed chiefly by the squamosal, and posterior portions from a laterally expanded process of the squamosal that slants downward and forward with respect to the zygoma.

The quadrate is inserted into the distal end of the ventral process of the squamosal and is covered laterally by the quadratojugal (Figs 3–4). In lateral aspect the squamosal process appears to be suspended from the back of the skull, and its function as a support for the quadrate and an origin for jaw muscles is most accurately reflected by the term suspensorium.

The lateral expansions of the squamosals give a plate-like configuration to the otherwise rather massive occiput (Fig. 8). The bones shared between the occiput and the short, stout basis cranii tended to fuse very early in life.

The jaws (Figs 3, 7–9) are short, stout, beak-like and generally toothless. In the upper jaw the premaxillae are fused in the midline and firmly sutured to the maxillae and more posterior parts of the palate. In the lower jaw the dentaries are fused at the symphysis, which is remarkably robust and deep. Coronoid bones are lacking and prominent coronoid processes are seldom developed on the dentaries. In life, the temporal musculature slanted sharply forward from its origins in the temporal fossa to insert on the coronoid region and on the lateral face of the dentary, about half-way between the articulation of the lower jaw and the tip of the symphyseal beak. In some forms the lateral part of the insertion, which is bounded dorsally by the coronoid margin of the dentary and ventrally by the mandibular fenestra, is expanded laterally into a shelf-like structure (lateral shelf, Crompton & Hotton 1967) (Figs 3, 8). Deeper portions

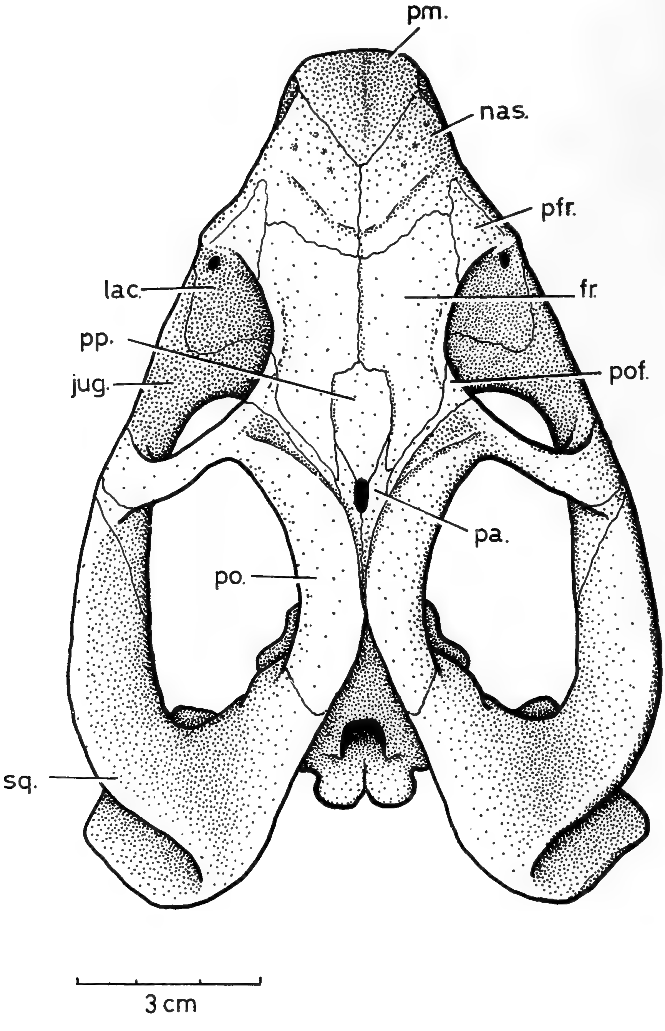

Fig. 1. *Dicynodon* sp. SAM–B88. Skull in dorsal view.

of the temporal musculature inserted inside the jaw ramus, in and around the adductor (Meckelian) fossa (Cluver 1974*a*, 1975).

The articulation of the lower jaw is unique in that both bearing surfaces are essentially convex (Figs 3, 7, 9), that of the articular being about twice as long as that of the quadrate. This can be construed as clear evidence of longitudinal sliding of the lower jaw during the bite, and the angle at which muscular force was applied shows that the motion during which the bite was most effective was one of retraction.

The toothless margins of the premaxillae and maxillae are usually sharp-edged. Except in *Endothiodon* and its closest allies, the middle of the maxilla is

Fig. 2. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in dorsal view. Scale: 5 cm.

thickened and produced downward as a caniniform process. Because of its thickness the caniniform process is triangular in cross-section presenting lateral, medial and posterior surfaces. In those forms in which it is present, the tusk erupts from the ventromedial surface of this process. In some forms, small non-caniniform teeth erupt from the flat medial surface of the maxilla (and in some cases from the premaxilla as well). A secondary palate, analogous to that which is found in cynodont mammal-like reptiles and mammals, is present and consists chiefly of a broad, plate-like posterior expansion of the fused premaxillae.

A finely-punctate sculpture is developed on the anterior and dorsal surfaces of the dentary symphysis, on the external surfaces of the premaxillae and palatines (in most forms), and on most external surfaces of the maxillae. It may be assumed that during life these surfaces were covered by horn because of their resemblance to bone surfaces that are covered by horn in living turtles and birds.

The three-sided caniniform process exhibits sculpture on its medial and lateral surfaces, but its posterior surface is smooth. The large masticatory muscles passed just behind the posterior surface, the smoothness of which suggests a place of attachment for a large and muscular *Mundplatte*, which in life lay in front of the temporal musculature in the corner of the mouth (Cluver 1975). The posterior surfaces of the caniniform processes thus provide useful

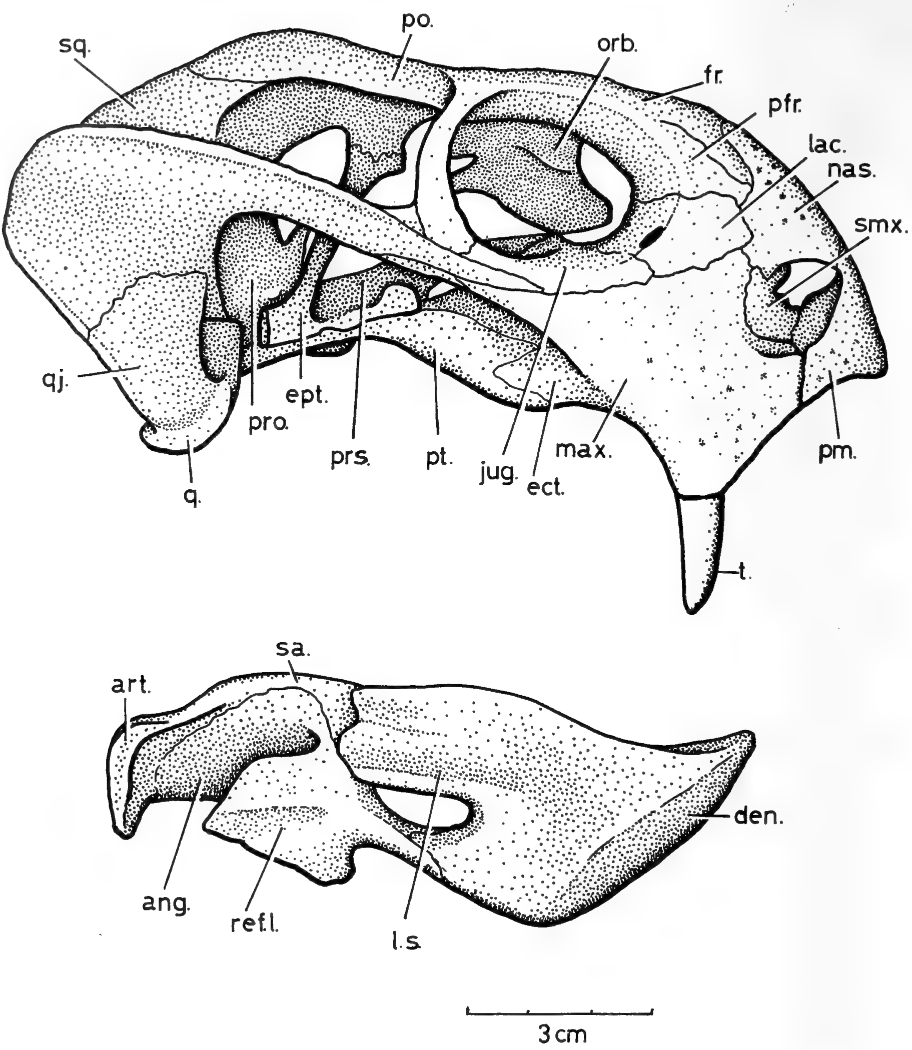

Fig. 3. *Dicynodon* sp. SAM–B88. Skull and lower jaw in lateral view.

landmarks for the corners of the mouth, and the mouth opening can be delimited posteriorly by a line drawn between the medial sides of the backs of the caniniform processes at the general level of the ventral margins of the premaxillae. The posterior margin of the mouth, defined here in functional terms, corresponds closely to that defined by Cruickshank (1968) on more exclusively anatomical grounds, i.e. the front of the choanae.

As confirmed by Agnew (1959), the skull is akinetic, and premaxillae, maxillae, palatines, pterygoids and ectopterygoids are firmly knit in the palate. In addition, the pterygoids are so closely and complexly sutured to the basis cranii a little behind their midlength (Olson 1944) (Figs 5–6) that, except in serial section, they appear fused to it.

The blade-like palatine rami of the pterygoids are elongate and oriented anteroposteriorly; there are no transverse pterygoid flanges. Between them the palatine rami enclose a deep, rather broad vault, into the front of which the choanae open. Anteriorly this vault, which may be termed the interpterygoid fossa, is partially roofed by the vomers and dorsal wings of the palatines (Fig. 5). The vomers enter the interpterygoid fossa as a single midline structure arising from the back of the premaxilla between the choanae, and bifurcate posteriorly at a variable distance behind the secondary palate. This bifurcation forms the anterior margin of the variably narrow fusiform or ovoid interpterygoid vacuity, which pierces the roof of the interpterygoid fossa. Through the interpterygoid vacuity the ventral edge of the slender parasphenoid rostrum may be seen in well-preserved and carefully prepared skulls. Only the interpterygoid vacuity, so restricted, is homologous with the phylogenetically ancient interpterygoid vacuity of less specialized reptiles and anthrocosaurian amphibians, and presumably was inherited with little change from such ancestors. The interpterygoid fossa, which has come to surround the interpterygoid vacuity, is a new entity formed in dicynodonts by rearrangement of the palatine rami of the pterygoids

Fig. 4. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in lateral view. Scale: 5 cm.

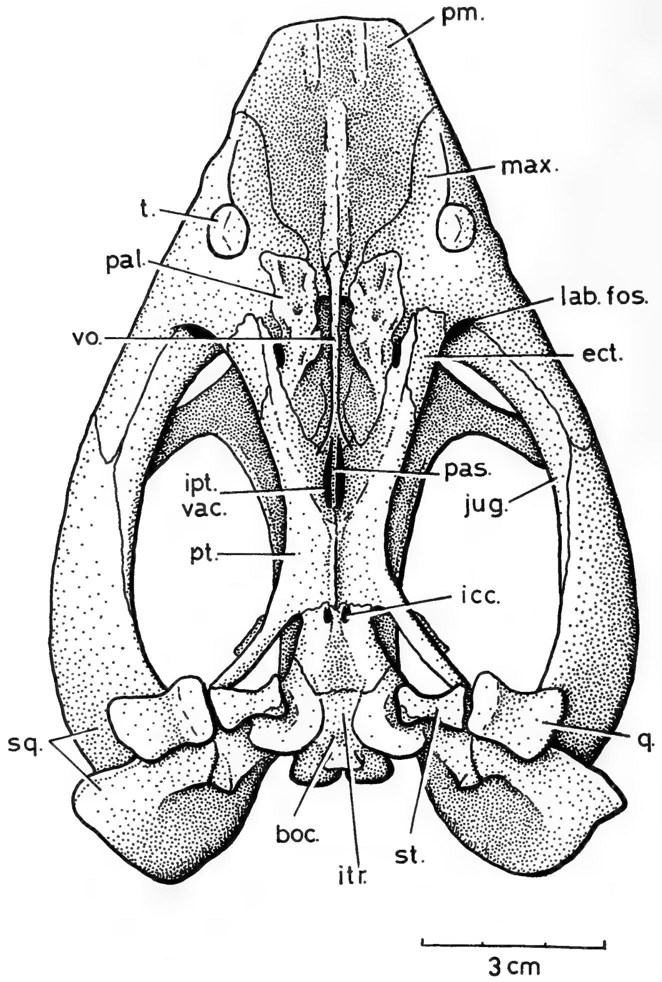

Fig. 5. *Dicynodon* sp. SAM–B88. Skull in ventral view.

and the formation of a secondary palate. The fossa is as distinctive of dicynodonts as the structure and function of their peculiar jaw articulation, to which its development is probably closely related.

THE GENUS *DICYNODON* (Figs 1–11)

Dicynodon Owen

Diagnosis

Medium-sized to large dicynodonts (average skull length 100 mm to over 400 mm), single pair of maxillary tusks in upper jaw, lower jaw edentulous. Postorbitals tend to cover parietals behind parietal foramen. Septomaxilla merges smoothly with outer surface of snout, does not meet lacrimal. Low boss formed over external nares by nasals. Caniniform process of maxilla arises as ventral extension of palatal rim. Palatal rim sharp-edged, uninterrupted by notch. Palatal portion of palatine large, makes short contact with premaxilla. Vomers form long, narrow septum in interpterygoid fossa, interpterygoid vacuity short. Ectopterygoid small, displaced laterally. Labial fossa present between maxilla, palatine and jugal. Pterygoid makes short contact with maxilla. Basioccipital tubera separated by intertuberal ridge. Fused dentaries carry narrow dentary tables .dorsal edge of dentary carries deep sulcus behind dentary tables. Rear of dentary extended dorsally to form weak coronoid process. Mandibular fenestra large, bounded dorsally by lateral dentary shelf.

Dicynodon lacerticeps Owen

Dicynodon lacerticeps Owen, 1845*a*: 59, pls 3–4.

Type specimen

Skull and lower jaw, BMNH 36233.

Locality

Tarka prolongation of the Winterberg, Cape Province.

Fig. 6. *Dicynodon* sp. SAM–B88. Stereophotograph of skull in ventral view. Scale: 5 cm.

Fig. 7. *Dicynodon* sp. SAM–B88. Stereophotograph of lower jaw in lateral view. Scale: 5 cm.

Horizon

Daptocephalus Zone.

Diagnosis

As for genus.

Remarks

Owen published two accounts of *Dicynodon lacerticeps* in 1845, both based on a lecture delivered by him before the Geological Society of London on 8 January of that year. The paper which appeared in the *Transactions of the Geological Society* (Owen 1845*a*) with illustrations of the fossil specimens is regarded as having priority here; in a subsequent paper in the same journal Owen (1856: 233) refers to this description as 'my former account' of the new forms. The paper which appeared in the *Proceedings of the Geological Society* (Owen 1845*b*) is a shortened version of the *Transactions* article.

One reason for the uncertainty surrounding the status of the many described species of *Dicynodon* is the poor preservation of the type specimen of *Dicynodon lacerticeps* itself (Figs 10–11). The specimen is a fairly complete skull and lower jaw, but much of the surface bone is damaged and sutures are subsequently difficult or impossible to trace. However, recent preparation has exposed several

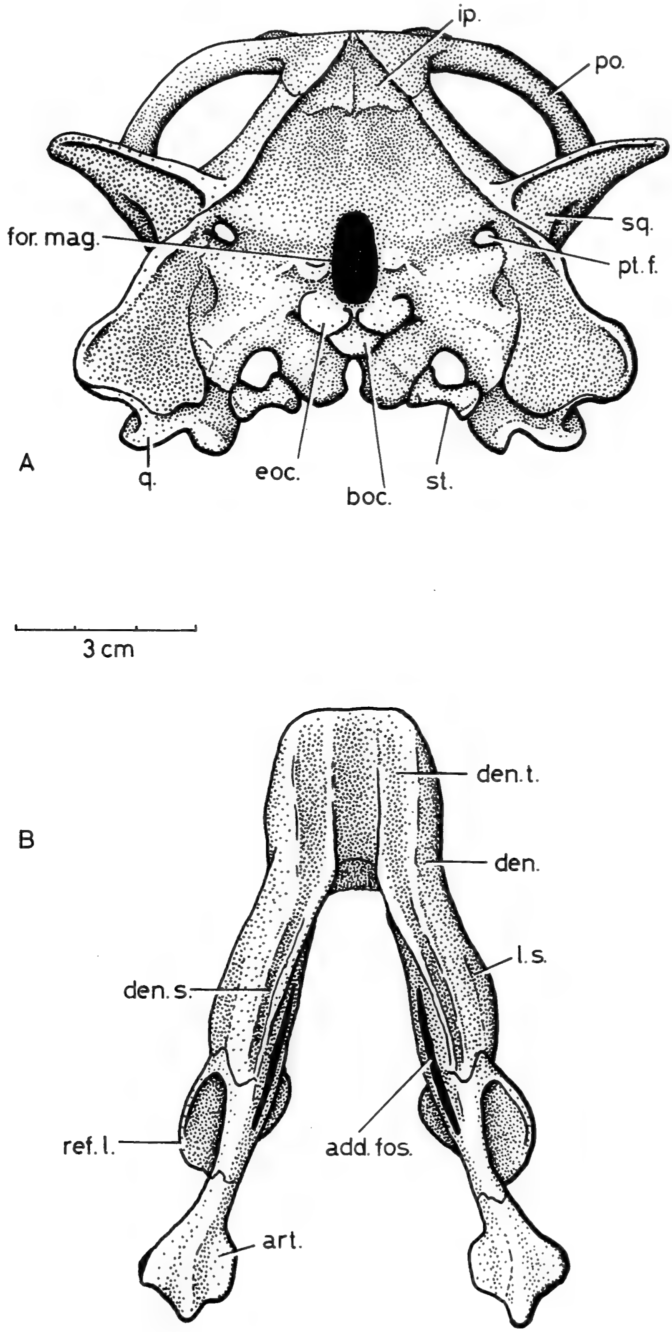

Fig. 8. *Dicynodon* sp. SAM–B88. A. Occipital view of skull. B. Lower jaw in dorsal view.

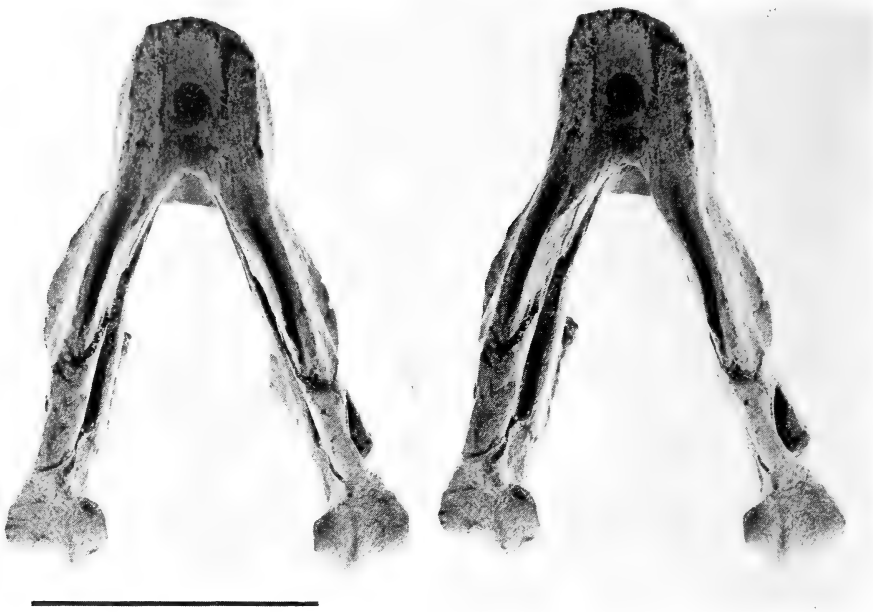

Fig. 9. *Dicynodon* sp. SAM–B88. Stereophotograph of lower jaw in dorsal view. Scale: 5 cm.

key areas of the skull and enough can now be seen to distinguish it from other dicynodont genera founded on better type material.

The dorsal skull surface is gently curved from the parietal region to the tip of the snout, and in lateral view the skull appears relatively deep. The postorbitals approach each other very closely behind the parietal foramen, but may be separated by a thin parietal crest. A large, leaf-like preparietal and a clear postfrontal are present, as well as a relatively small prefrontal. The prefrontal may be separated from the lacrimal on the side of the snout by a narrow posterior process of the nasal, but poor preservation does not allow confirmation of this point.

The sharp-edged palatal rim is continued on to the anterior part of the caniniform process without interruption, and in lateral view forms a continuous arc. A pair of powerful maxillary tusks are present, as are two anterior premaxillary ridges on the palatal surface of the premaxilla. Matrix obscures the area where the more posterior, median ridge is normally found in dicynodonts.

The basioccipital tubera are joined by a raised area of the basicranium, the intertuberal ridge, as seen in *Lystrosaurus* (Cluver 1971). The deepest part of the ridge is on the basioccipital, behind the basioccipital-basisphenoid suture. Only the rear of what appears to have been a wide interpterygoid vacuity is preserved. The palatines are large, but their anterior palatal portions are partly obscured and their relationships with the maxillae and premaxillae cannot be determined.

In the poorly preserved lower jaw, dentary tables are present and the dorsal edge of the dentary appears to be excavated in the form of a longitudinal sulcus.

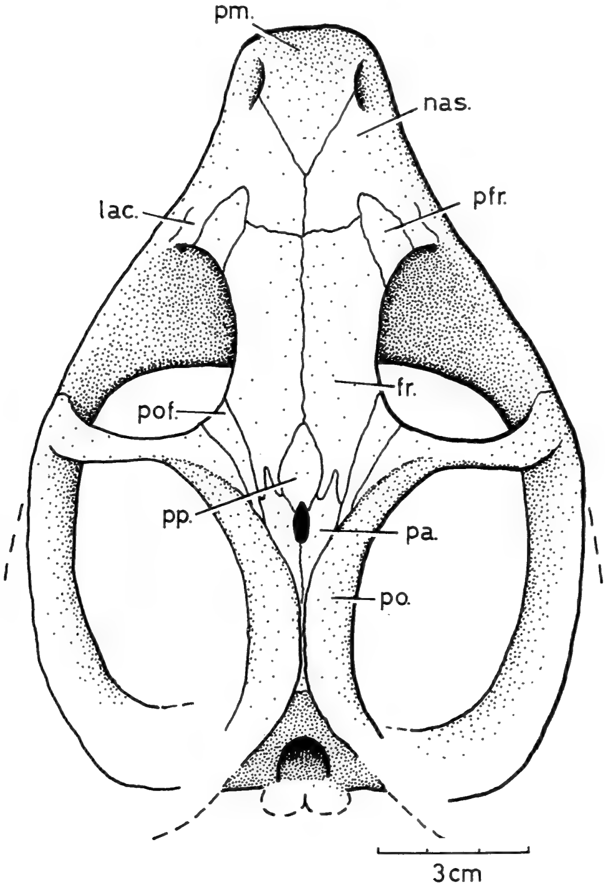

Fig. 10. *Dicynodon lacerticeps* BMNH 36233. Type specimen. Skull in dorsal view, partially reconstructed and with distortion corrected.

In spite of the poor condition of the type specimen, the combination of characters which can be determined in it is sufficient to permit referral of additional, fully preserved specimens (Figs 1–9) to *Dicynodon lacerticeps* and to allow the formulation of a full generic diagnosis. The species listed below may be retained in the genus *Dicynodon* on the basis of type material; an analysis of the validity of these species is beyond the scope of this generic-level revision, but future work will undoubtedly result in the establishment of a smaller number of valid species.

Dicynodon testudiceps Owen

Dicynodon testudiceps Owen, 1845*a*: 71, pls 5–6.

Type specimen

Anterior part of skull, BMNH 47051.

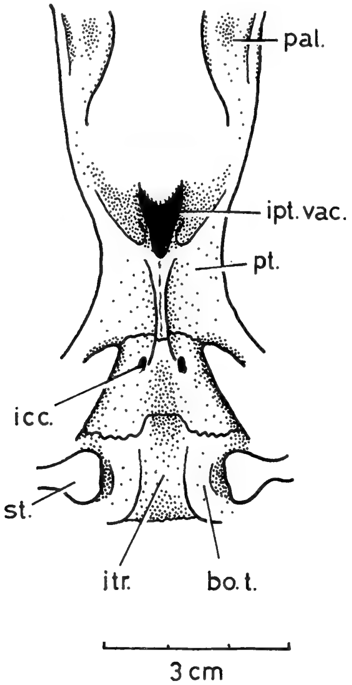

Fig. 11. *Dicynodon lacerticeps* BMNH 36233. Type specimen. Partial ventral view of skull, distortion corrected.

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon leoniceps Owen

Dicynodon leoniceps Owen, 1876: 32, pls 24–26.

Type specimen

Skull, BMNH 47047.

Locality

Gats River, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Van Hoepen (1934) proposed this species as the type of a new genus, *Daptocephalus*. Comparison of the type specimen with the type of *Dicynodon lacerticeps* shows that large size is the only feature that can be used to distinguish

Daptocephalus from *Dicynodon*. The species *leoniceps*, which may prove to be a valid one, is accordingly reassigned to *Dicynodon*.

Dicynodon lissops Broom

Dicynodon lissops Broom, 1913: 450, fig. 11.

Type specimen

Skull, AMNH 5508.

Locality

Wilgerbosch, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon leontops Broom

Dicynodon leontops Broom, 1913: 451, fig. 12.

Type specimen

Skull AMNH 5582.

Locality

Bethulie, Orange Free State.

Horizon

Daptocephalus Zone.

Dicynodon alticeps Broom & Haughton

Dicynodon alticeps Broom & Haughton, 1913: 37, pl. 7.

Type specimen

Skull, SAM–2347.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon watsoni Broom

Dicynodon watsoni Broom, 1921: 653, fig. 32.

Type specimen

Skull, SAM–7849.

Locality

East of New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon gilli Broom

Dicynodon gilli Broom, 1932: 176, fig. 60.

Type specimen

Skull, SAM–4008.

Locality

Watervlei, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon venteri Broom

Dicynodon venteri Broom, 1935*b*: 69, fig. 10.

Type specimen

Skull, TM 199.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon validus Broom

Dicynodon validus Broom, 1935*b*: 70, fig. 11.

Type specimen

Skull, TM 252.

Locality

Leeukloof, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon microdon Broom

Dicynodon microdon Broom, 1936: 376, figs 22–23.

Type specimen

Skull, TM 267.

Locality

Bethesda Road, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon luckhoffi Broom

Dicynodon luckhoffi Broom, 1937: 306, fig. 6.

Type specimen

Skull, SAM–K1219

Locality

Zuurplaats, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon macrodon Broom

Dicynodon macrodon Broom, 1940*a*: 81, fig. 10A–B.

Type specimen

Skull, RC 22.

Locality

Grootfontein, Murraysburg district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon cadlei Broom

Dicynodon cadlei Broom, 1940*a*: 82, fig. 11.

Type specimen

Skull, RC 23.

Locality

Hoeksplaas, Murraysburg district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon calverleyi Broom

Dicynodon calverleyi Broom, 1940*b*: 179, fig. 21.

Type specimen

Skull, RC 39.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon grahami Broom

Dicynodon grahami Broom, 1940*b*: 180, fig. 22.

Type specimen

Skull, RC 39.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon trigonocephalus Broom

Dicynodon trigonocephalus Broom 1940*b*: 182, fig. 24.

Type specimen

Skull, RC 38.

Locality

Klipfontein, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon aetorhamphus Broom

Dicynodon aetorhamphus Broom, 1948: 605, figs 23A, 24A.

Type specimen

Skull, RC 85.

Locality

Hoeksplaas, Murraysburg district, Cape Province.

Horizon

Cistecephalus Zone.

Dicynodon leontocephalus Broom

Dicynodon leontocephalus Broom, 1950: 246, fig. 1.

Type specimen

Skull, RC 96.

Locality

Springfontein (Springfield), Middelburg district, Cape Province.

Horizon

Daptocephalus Zone.

Dicynodon clarencei Broom

Dicynodon clarencei Broom, 1950: 247, fig. 2.

Type specimen

Skull, RC 77.

Locality

Hanover, Cape Province.

Horizon

Cistecephalus Zone.

THE GENUS *OUDENODON* (Figs 12–17)

Oudenodon Owen

Diagnosis

Medium-sized to large dicynodonts (skull length ranging from 100 mm to over 300 mm), teeth lacking in both upper and lower jaws. Postorbitals well separated on skull roof by parietals. Septomaxilla recessed within external naris, lacrimal may extend forward above maxilla to posterior margin of naris. Nasal forms boss over naris. Maxilla carries weak caniniform process, with sharp-edged posterior crest. Palatal portion of palatine large, meeting posterior border of premaxilla. Vomers form short septum in anterior part of interpterygoid fossa, interpterygoid vacuity long and narrow. Basipterygoid region constricted. Ectopterygoid large, pterygoid does not contact maxilla. Dentaries carry narrow dentary tables, dorsal edge of dentary carries deep sulcus. Coronoid process weak or absent. Weak lateral dentary shelf above large mandibular fenestra.

Oudenodon baini Owen

Oudenodon baini Owen, 1860: 46, pl. 1 (fig. 1).

Type specimen

Skull lacking lower jaw, BMNH 36232.

Locality

Near Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Diagnosis

As for genus.

Discussion

The almost complete type skull (Figs 12–15) has been fully prepared and detailed comparisons with other dicynodont taxa are possible. The most dis-

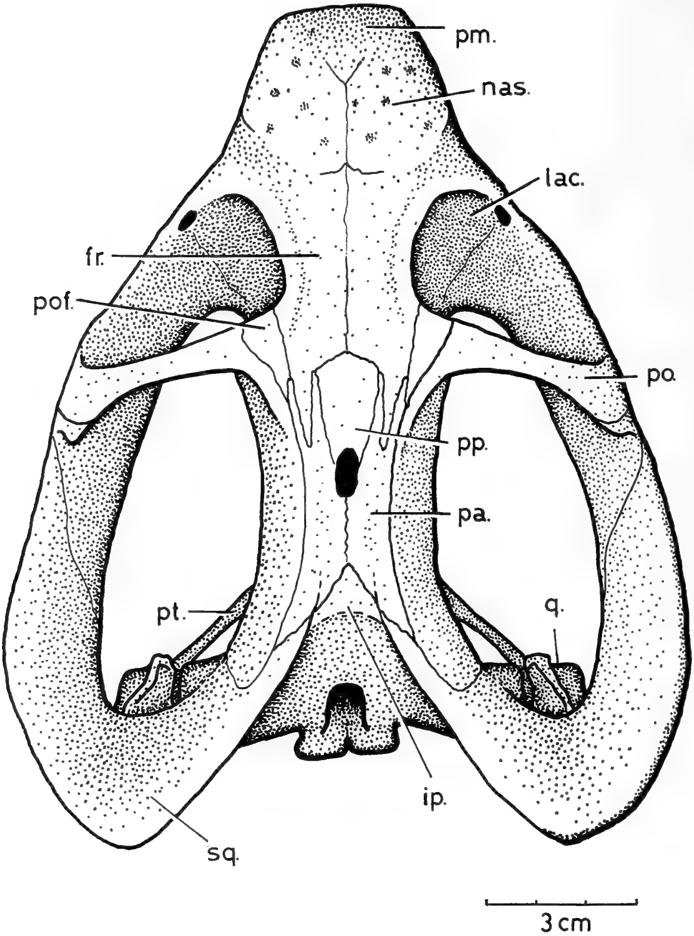

Fig. 12. *Oudenodon baini* BMNH 36232. Type specimen. Skull in dorsal view.

tinctive features in the palate are the long, narrow interpterygoid vacuity, the deep and relatively narrow secondary palate, the sharp maxillary crest behind the caniniform process, and the absence of maxillary tusks. These characteristics, taken together with the wide parietal exposure in the skull roof, are sufficient to permit referral of more fully preserved specimens to *Oudenodon* for inclusion of lower jaw features in the generic diagnosis.

In lateral view (Figs 15–16) the skull of *Oudenodon* is not as deep as that of *Dicynodon*, and the anterior surface of the short snout lies almost at right angles to the flat surface of the dorsal skull roof. The palatal rim in front of the caniniform process is blunt, but the usual pair of anterior premaxillary ridges is

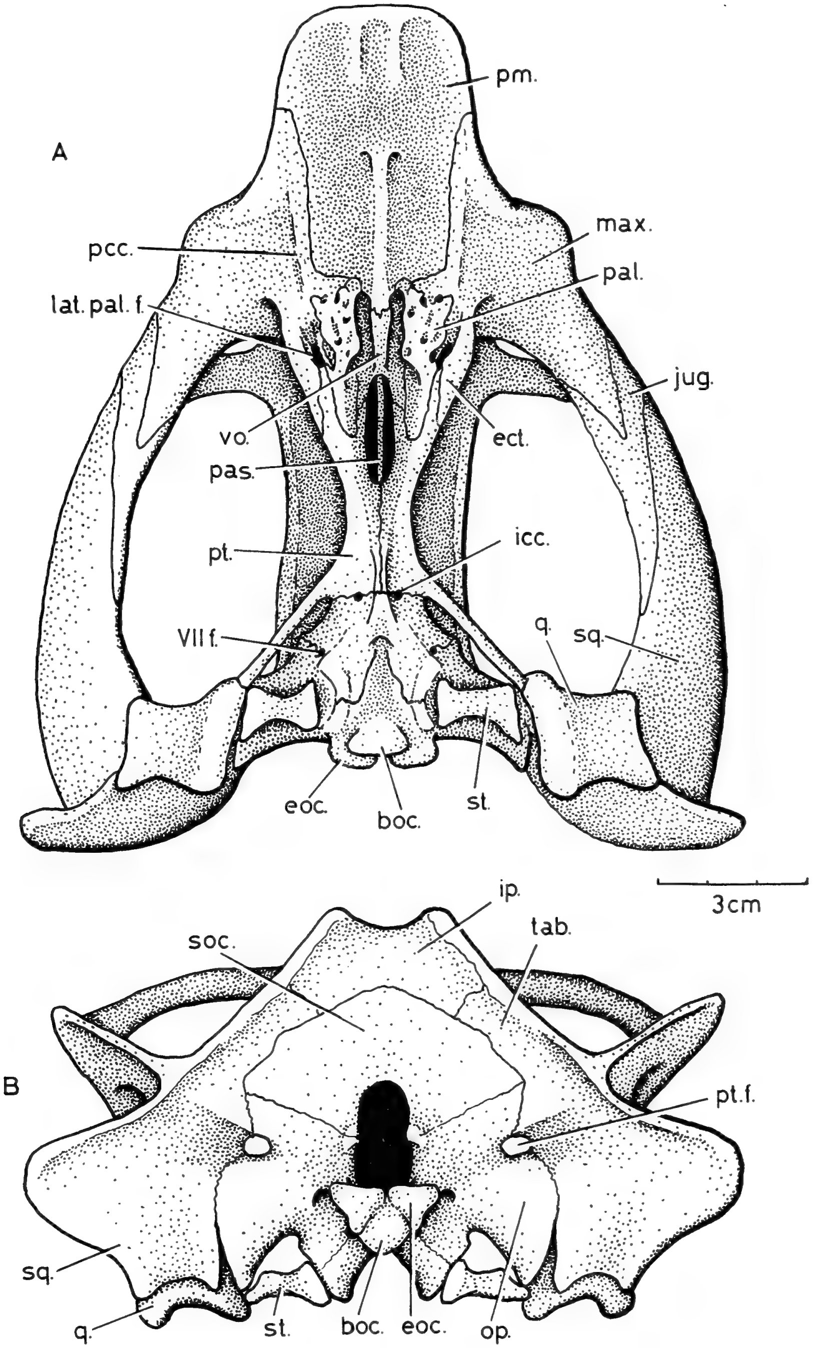

Fig. 13. *Oudenodon baini* BMNH 36232. Type specimen. A. Skull in ventral view. B. Occipital view.

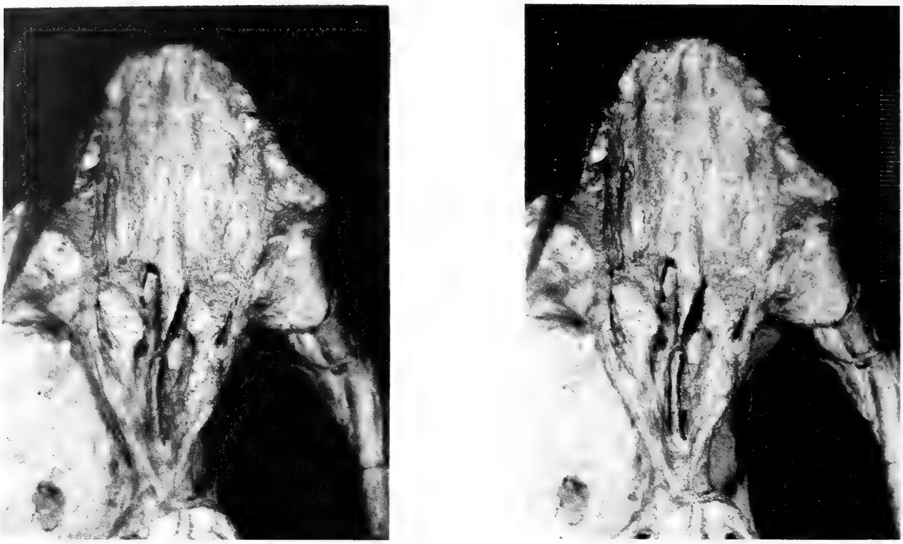

Fig. 14. *Oudenodon baini* BMNH 36232. Type specimen. Stereophotograph of palate. Scale: 8 cm.

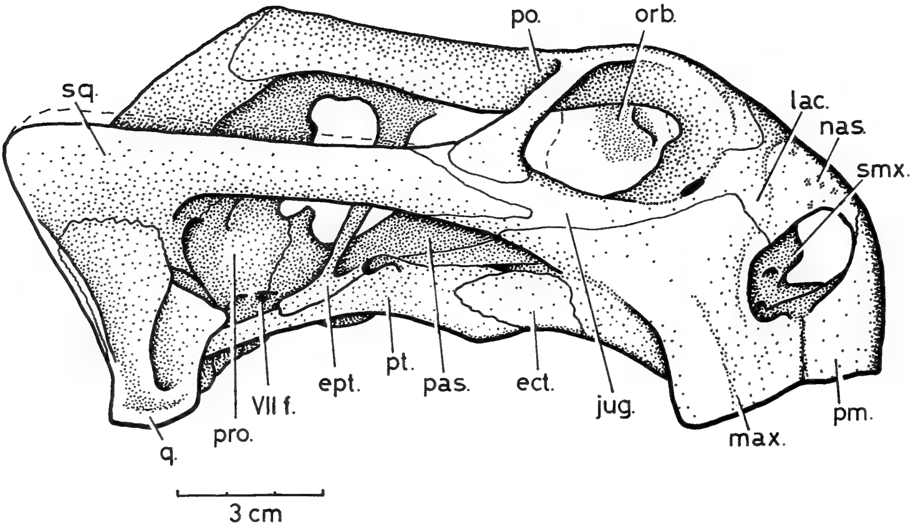

Fig. 15. *Oudenodon baini* BMNH 36232. Type Specimen. Skull in lateral view.

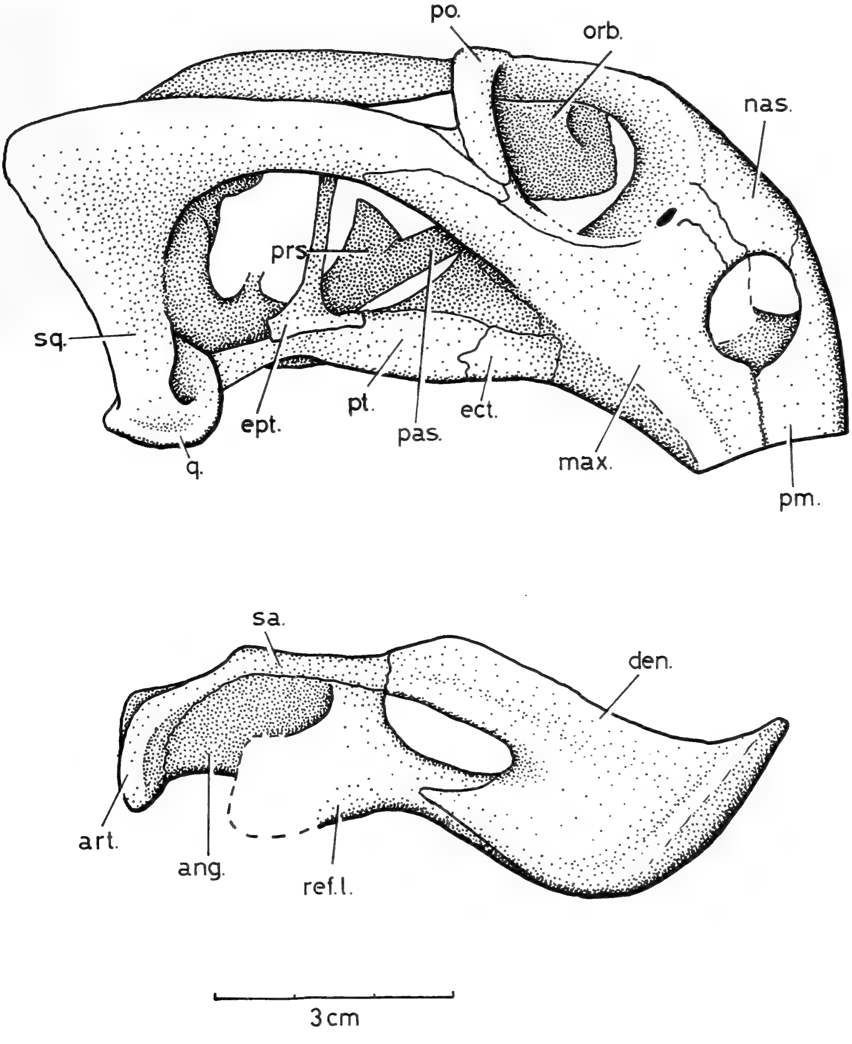

Fig. 16. *Oudenodon* sp. SAM–6045. Skull and jaw in lateral view.

present. In general shape and in the possession of dentary tables and a dorsal dentary sulcus, the lower jaw is essentially similar to that of *Dicynodon*.

Keyser (1975) has reviewed the species of *Oudenodon* and lists all type material fully; it is unnecessary to repeat the information here. Keyser recognizes only three species, these being *Oudenodon baini* Owen, *Oudenodon grandis* (Haughton), and *Oudenodon luangwaensis* (Boonstra) and suggests that the large number of other dicynodont types that can be assigned to the genus are synonyms of *Oudenodon baini*.

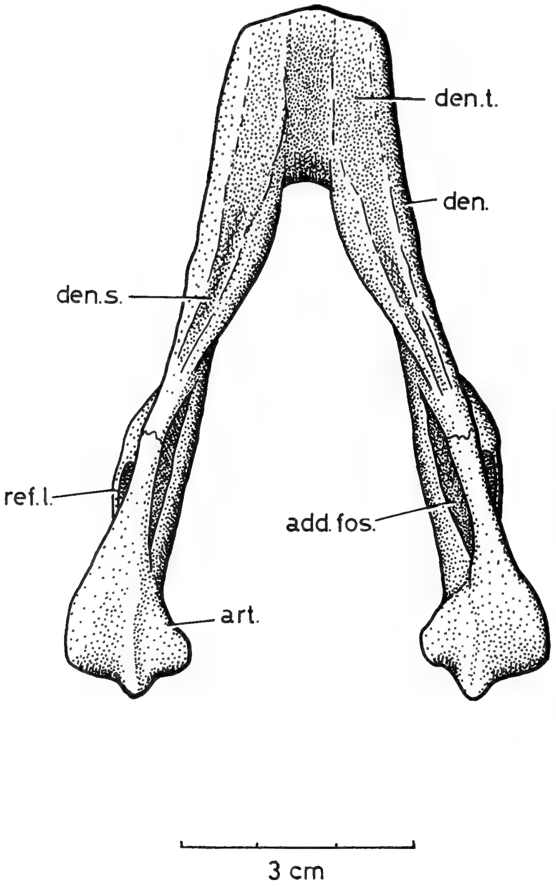

Fig. 17. *Oudenodon* sp. SAM–6045. Lower jaw in dorsal view.

THE GENUS *DIICTODON*

Diictodon Broom

Diagnosis

Medium-sized dicynodonts (average skull length 110 mm), jaws either lacking teeth altogether, or bearing a single pair of maxillary tusks. Postorbitals tend to cover parietals behind pineal foramen. Septomaxilla recessed within external naris, maxilla rises high in side of snout to meet the nasal. Nasal forms boss over external naris. Maxilla carries prominent caniniform process, clearly demarcated from anterior maxillary palatal rim. Sharp anterior edge of caniniform process set medially to anterior palatal rim. Palatal portion of palatine small, does not meet premaxilla. Vomers form short septum in interpterygoid

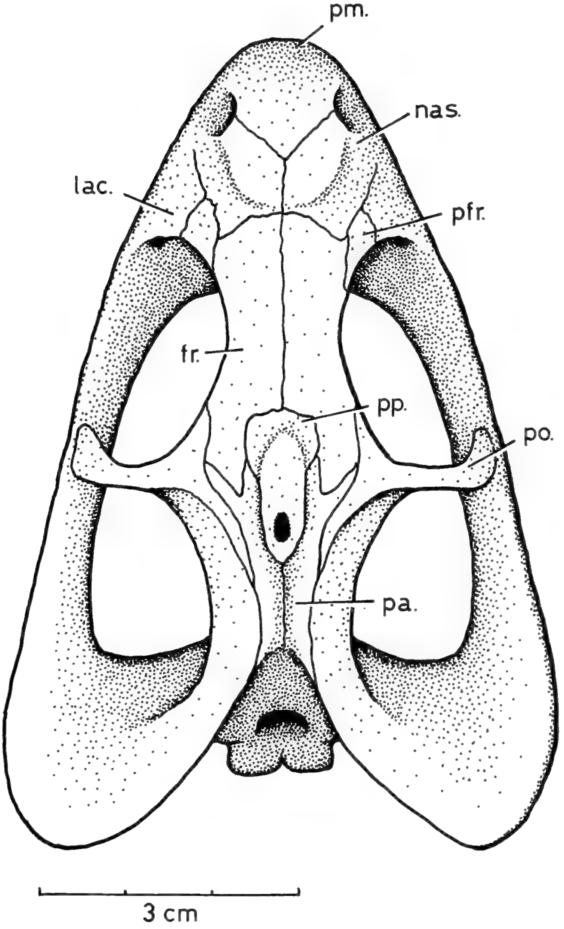

Fig. 18. *Diictodon galeops* AMNH 5308. Type specimen. Skull in dorsal view.

fossa. Interpterygoid vacuity long. Ectopterygoid large, separating pterygoid from maxilla. Fused dentaries carry wide dorsal dentary tables, with high medial borders. Rear of dentary table extended medial to level of inner surface of jaw ramus. Dorsal edge of dentary rounded behind dentary table, no coronoid process present. Mandibular fenestra large, no expanded lateral dentary shelf for insertion of adductor musculature.

Diictodon galeops Broom

Diictodon galeops Broom, 1913: 453, fig. 15.

Type specimen

Skull lacking lower jaw, AMNH 5308.

Locality

'Slachter's Nek', Somerset East district, Cape Province.

Horizon

Upper Permian, *Cistecephalus* Zone.

Diagnosis

Preparietal bone large, surrounding parietal foramen. Postfrontals absent, caniniform processes and maxillary tusks small. Parietals partially exposed between postorbitals behind parietal foramen.

Remarks

The type skull (Figs 18–21) is well preserved but lacks the lower jaw, quadrates and stapes. Small tusks are present. Distinctive features of the specimen are the inflated preparietal bone, which surrounds the parietal opening, and the absence of postfrontals on the skull roof. No septomaxillae can be seen, and it is likely that these bones became disassociated from the skull, as the stapes and quadrates evidently did, prior to fossilization.

The postorbitals approach each other behind the pineal opening but do not cover the parietals fully. The maxilla rises high in the side of the snout and meets the nasal so that the lacrimal is confined to the orbital border. In ventral view it can be seen that the base of the caniniform process is offset medially to the palatal rim in the form of an anteriorly facing blade, separated from the palatal rim by a clear notch (Figs 20–21). Besides the usual single median and double

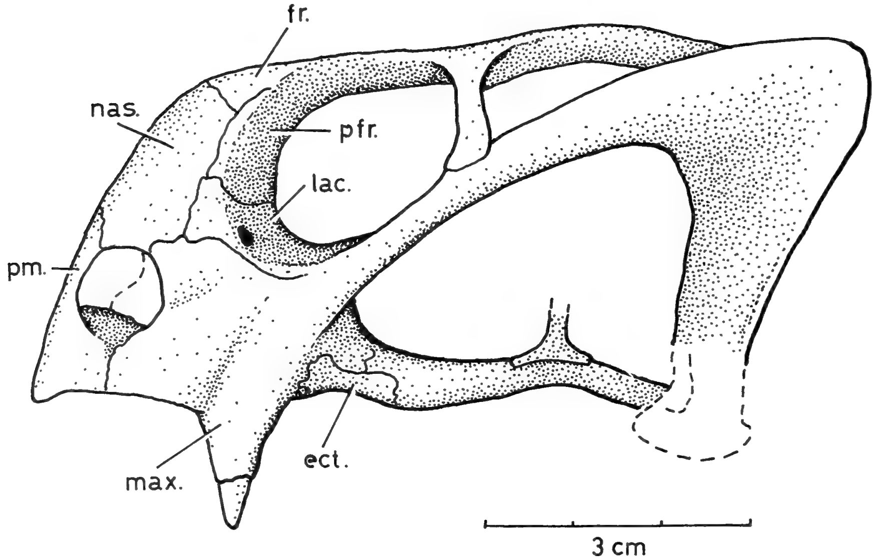

Fig. 19. *Diictodon galeops* AMNH 5308. Type specimen. Skull in lateral view.

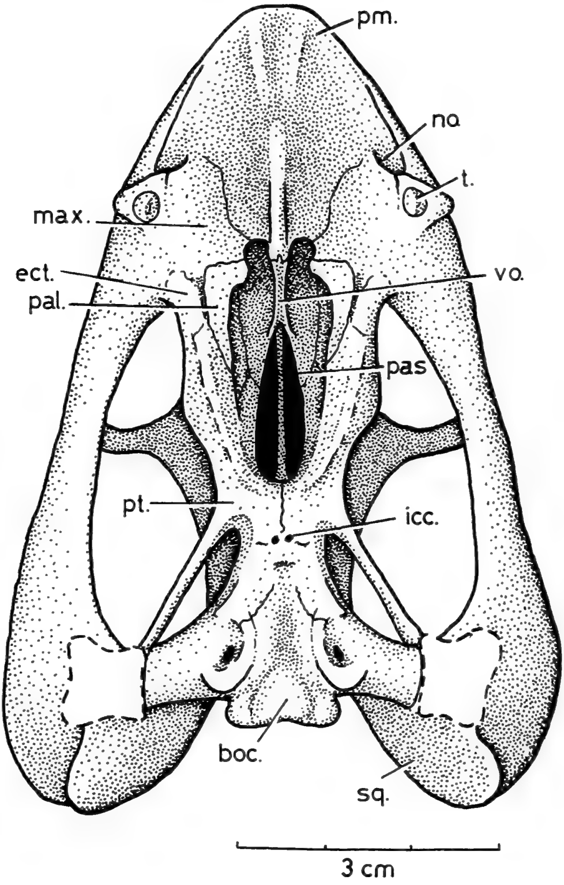

Fig. 20. *Diictodon galeops* AMNH 5308. Type specimen. Skull in ventral view.

anterior palatal ridges, there is a more lateral ridge on each side of the secondary palate, medial to the caniniform process. The palatal portion of the palatine is small, and does not meet the premaxilla. The long, wide interpterygoidal vacuity extends far forward to where the vomers unite and descend to meet the posterior spine of the premaxilla. The lateral pterygoidal borders of the interpterygoid fossa are strongly constructed, but there is no pterygoid-maxilla contact.

Diictodon feliceps (Owen)

Dicynodon feliceps Owen, 1876: 45, pl. 43.

Type specimen

Skull, BMNH 47052.

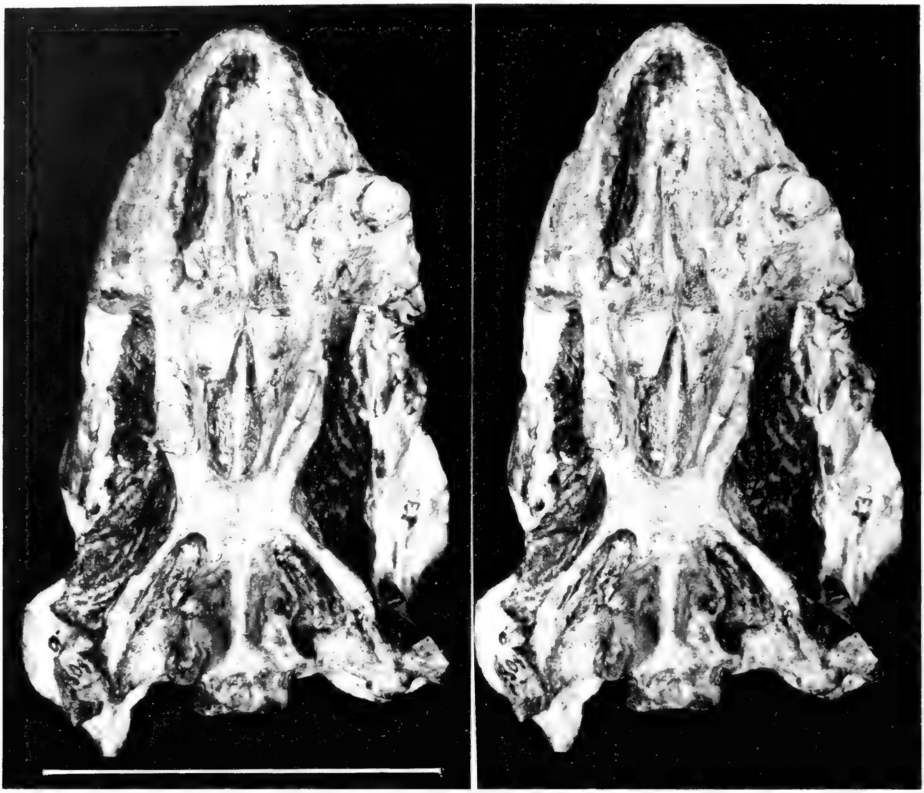

Fig. 21. *Diictodon galeops* AMNH 5308. Type specimen. Stereophotograph of palate. Scale: 5 cm.

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Diagnosis

Postorbitals cover parietals behind parietal foramen, parietal foramen not surrounded by preparietal. Narrow postfrontal exposed on dorsal skull roof. Caniniform process large, maxillary tusks present or absent.

Remarks

The species *feliceps* is the earliest described form which shows the characteristics of *Diictodon* as diagnosed above, but examination of dicynodont type material shows that a number of other described species of *Dicynodon*, including

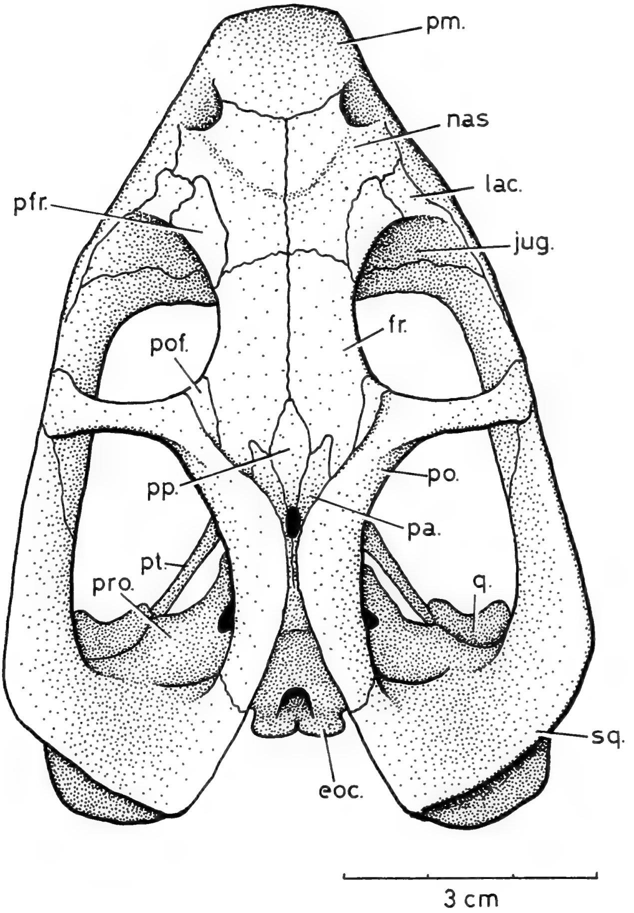

Fig. 22. *Diictodon testudirostris* SAM–10086. Skull in dorsal view.

D. testudirostris (see Cluver 1970), closely resemble the species *feliceps* and can be referred to the genus *Diictodon* (Figs 22–26).

An analysis of the validity of these species is outside the scope of the present generic level revision and, as in the case of *Dicynodon* and *Oudenodon*, the list below is compiled only on the basis of type material which can be included under *Diictodon*. Future investigations may well result in a smaller number of recognizable species.

Diictodon jouberti (Broom)

Dicynodon jouberti, Broom, 1905: 331.

Type specimen

Skull, SAM–695.

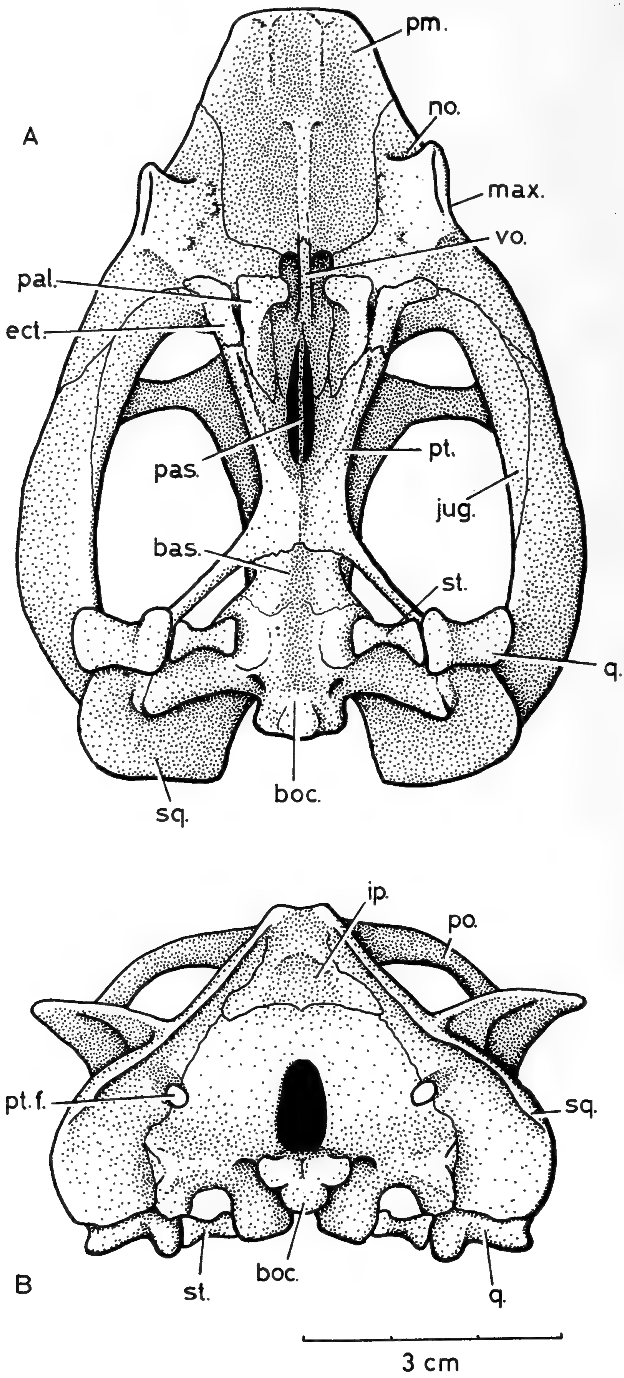

Fig. 23. *Diictodon testudirostris* SAM–10086. A. Skull in ventral view. B. Occipital view.

Locality

Gouph Tract, or Koup, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon psittacops (Broom)

Dicynodon psittacops Broom, 1912: 869, pl. 92.

Type specimen

Skull and skeleton, AMNH 5534.

Locality

Beaufort West district, Cape Province.

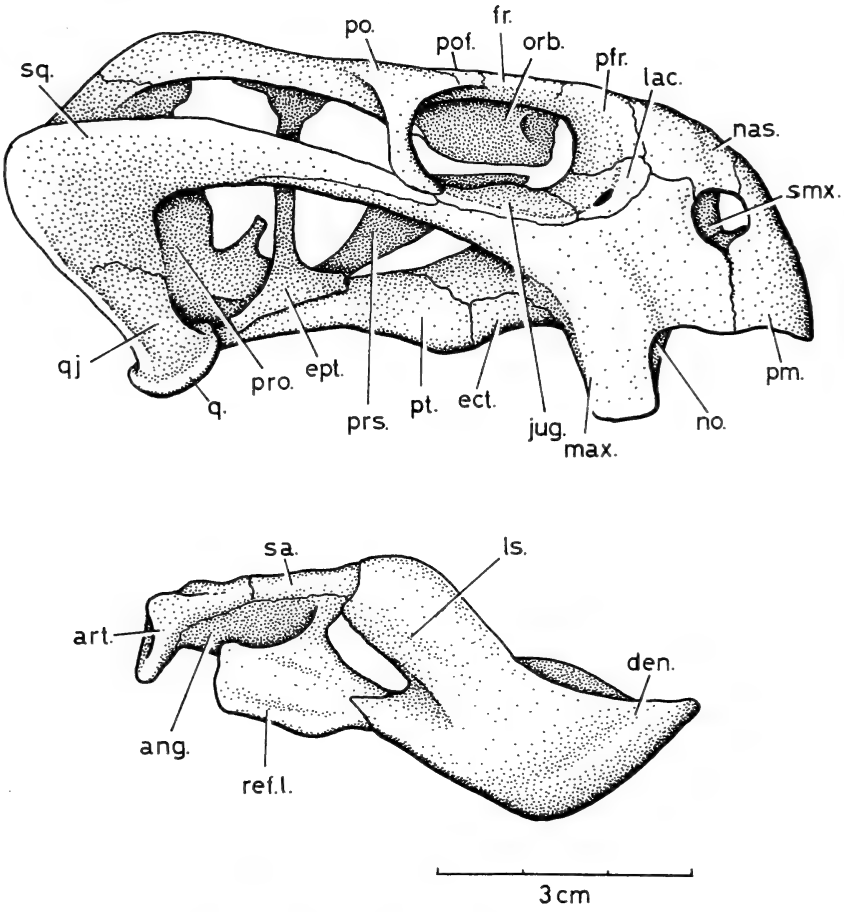

Fig. 24. *Diictodon testudirostris* SAM–10086. Skull and lower jaw in lateral view.

Horizon

Cistecephalus Zone.

Diictodon ictidops (Broom)

Dicynodon ictidops Broom, 1913: 466, figs 5–6.

Type specimen

Skull, AMNH 5510.

Locality

Beaufort West commonage, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon palustris (Broom)

Emydorhynchus palustris Broom, 1913: 456, fig. 19.

Type specimen

Skull, AMNH 5512.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Remarks

The type specimen, although poorly preserved, displays a sufficient number of characters to warrant its referral to *Diictodon*, which has page priority. Additional preparation of the type (TM 241) of *Emydorhynchus formosus* Broom, 1935*a* (mislaid at present, E.S. Vrba 1979 pers. comm.), will be needed to determine if this species should also be included in *Diictodon*.

Diictodon testudirostris (Broom & Haughton)

Dicynodon testudirostris Broom & Haughton, 1913: 36, pl. 7.

Type specimen

Skull, SAM–2354.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

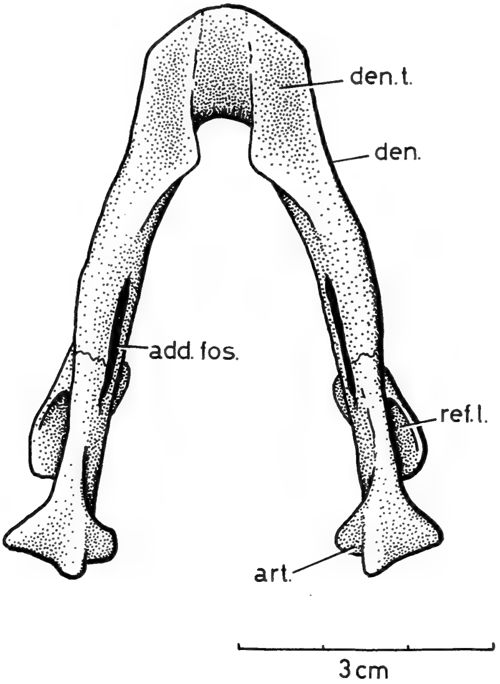

Fig. 25. *Diictodon testudirostris* SAM–10086. Lower jaw in dorsal view.

Fig. 26. *Diictodon testudirostris* SAM–10078. Stereophotograph of occlusal surfaces of upper and lower jaws. Scale: 5 cm.

Diictodon pygmaeus (Broom & Haughton)

Dicynodon pygmaeus Broom & Haughton, 1917: 123, fig. 23.

Type specimen

Skull, SAM–2664.

Locality

Dunedin, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon sollasi (Broom)

Dicynodon sollasi Broom, 1921: 648, figs 28–29.

Type specimen

Skull, SAM–7420.

Locality

Biesjiespoort, Victoria West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon macrorhynchus (Broom)

Dicynodon macrorhynchus Broom, 1921: 657, fig. 36.

Type specimen

Skull, BMNH R.4954.

Locality

New Bethesda, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Diictodon haughtonianus (Huene)

Dicynodon haughtonianus Huene, 1931: 186, fig. 25.

Type specimen

Skull, Institüt für Geologie und Paläontologie, University of Tübingen.

Locality

Blaauwkrans, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon rubidgei (Broom)

Dicynodon rubidgei Broom, 1932: 189, fig. 62F.

Type specimen

Skull, BMNH 47081.

Locality

Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon nanus (Broom)

Diictodon nanus, Broom, 1936: 379, fig. 25A.

Type specimen

Skull, TM 268.

Locality

Houd Constant, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

Diictodon grimbeeki (Broom)

Dicynodon grimbeeki Broom, 1935*a*: 7, figs 6–7.

Type specimen

Skull, TM 253.

Locality

Leeukloof, Beaufort West district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon huenei (Broili & Schröder)

Dicynodon huenei Broili & Schröder, 1937: 118, figs 1–4.
Oudenodon huenei (Broili & Schröder) Toerien, 1953: 97.

Type specimen

Skull, University of Munich, 1934 vii 46.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon broomi (Broili & Schröder)

Dicynodon broomi Broili & Schröder, 1937: 132, figs 5–13.

Type specimen

Skull, University of Munich, 1934 viii 47a.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon grossarthi (Broili & Schröder)

Dicynodon grossarthi Broili & Schröder, 1937: 150, figs 14–18.

Type specimen

Skull, University of Munich, 1934 viii 48.

Locality

La-de-da, Beaufort West district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon whitsonae (Broom)

Dicynodon annae Broom, 1940*b*: 181, fig. 23.
Dicynodon whitsonae (Broom) Toerien, 1954: 937.

Type specimen

Skull, RC 42.

Locality

Wellwood, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Diictodon pseudojouberti (Boonstra)

Dicynodon pseudojouberti Boonstra, 1948: 60.

Type specimen

Skull, SAM–774.

Locality

Prince Albert Road, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon vanderhorsti (Toerien)

Dicynodon vanderhorsti Toerien, 1953: 91, fig. 60.

Type specimen

Skull, BPI 175.

Locality

Antjiesfontein, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon antjiesfonteinensis (Toerien)

Dicynodon antjiesfonteinensis Toerien, 1953: 93, figs 61–62.

Type specimen

Skull, BPI 219.

Locality

Antjiesfontein, Prince Albert district, Cape Province.

Horizon

Tapinocephalus Zone.

Diictodon tienshanensis (Sun)

Dicynodon tienshanensis Sun, 1973: 56.

Type specimen

Skull, in Institute of Vertebrate Palaeontology and Palaeoanthropology, Peking.

Locality

'Turfan Basin', Sinkiang Province, People's Republic of China.

Horizon

Lower Ko-Ko-Ya Group, Upper Permian.

Remarks

Cluver & Hotton (1979) pointed out that the specimen mentioned by Yuan & Young (1934) and described as *Dicynodon tienshanensis* by Sun (1973) can be referred to the genus *Diictodon*. The specimen in question is to date the only *Diictodon* recorded outside South Africa.

THE GENUS *KINGORIA* (Figs 27–30)

Kingoria Cox

Diagnosis

Medium-sized dicynodonts (average skull length 160 mm), jaws lacking teeth altogether or bearing a single pair of maxillary tusks. Parietals exposed between postorbitals behind parietal foramen. Septomaxilla recessed within opening of naris, maxilla rises high in side of snout to meet nasal. Low boss formed by nasal. Maxilla carries prominent caniniform process, palatal rim continued without interruption on to anterior blade of caniniform process. Rear of caniniform process extended as keel to level of ectopterygoid. Palatal portion of palatine very small, but making contact with greatly expanded premaxilla. Vomers form short septum in interpterygoid fossa, interpterygoid vacuity long and narrow. Ectopterygoid large, separating pterygoid from maxilla. Basipterygoid region constricted. Fused dentaries taper to form rounded anterior tip of lower jaw, no dentary tables present. Dorsal edge of dentary narrow, lateral dentary shelf widely expanded. Coronoid process weak or absent. Mandibular fenestra reduced or absent. Angular forms sharp ventral keel behind reflected lamina.

Kingoria nowacki (Huene)

Dicynodon nowacki von Huene, 1942: 156, fig. 2.
Kingoria nowacki (von Huene) Cox, 1959: 321.

Type specimen

Skull, Institüt für Geologie und Paläontologie, University of Tübingen, K–12.

Locality

Kingori, Tanzania.

Horizon

Kawinga Formation (Charig 1963).

Diagnosis

As for genus.

Discussion

A diagnosis of *Kingoria*, which has been fully described and characterized by Cox (1959), is provided only in the interest of completeness. Cox suggested that *Dicynodon galecephalus* Broom was related to or congeneric with *Kingoria*, but detailed examination of dicynodont type material shows that this is only one of a number of species previously included under *Dicynodon* which may be assigned to *Kingoria*. A potential problem of priority and nomenclature exists in that, on the basis of the poorly preserved type, *Dicynodontoides parringtoni* Broom, 1940*b*, appears to be related to or congeneric with *Kingoria*. In the

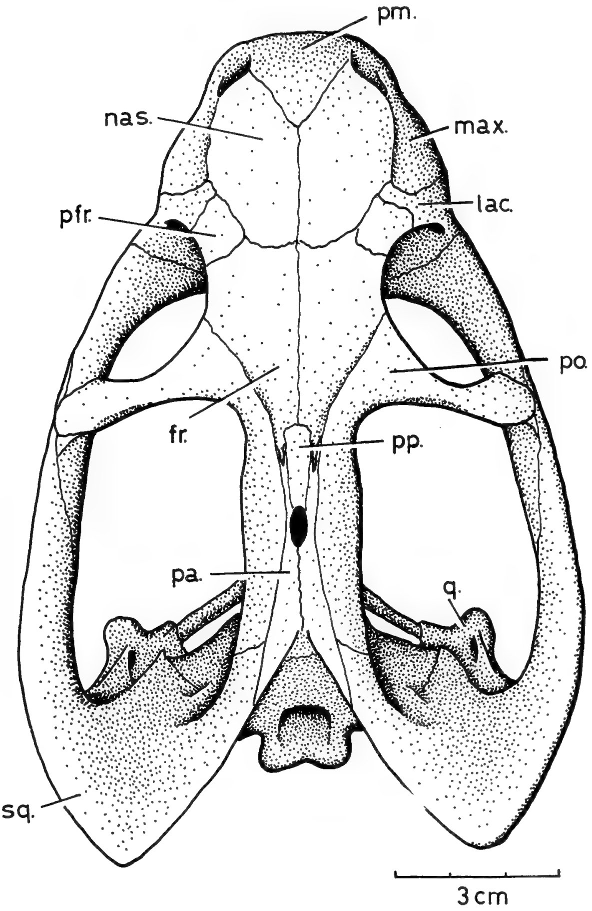

Fig. 27. *Kingoria nowacki*. Skull in dorsal view (after Cox 1959).

interests of stability, it is proposed that at this stage *Dicynodontoides* be retained as a separate genus, distinct from but related to *Kingoria*, until preparation of the type specimen (RC 45) allows a full comparison with the type of *Kingoria nowacki* to be made.

Kombuisia frerensis Hotton, 1974, from the lower Triassic *Cynognathus* zone, is the only Triassic form so far described that can be related to the upper Permian *Kingoria*.

Kingoria recurvidens (Owen)

Dicynodon recurvidens Owen, 1876: 46, pl. 69.

Type specimen

Skull, BMNH 40709.

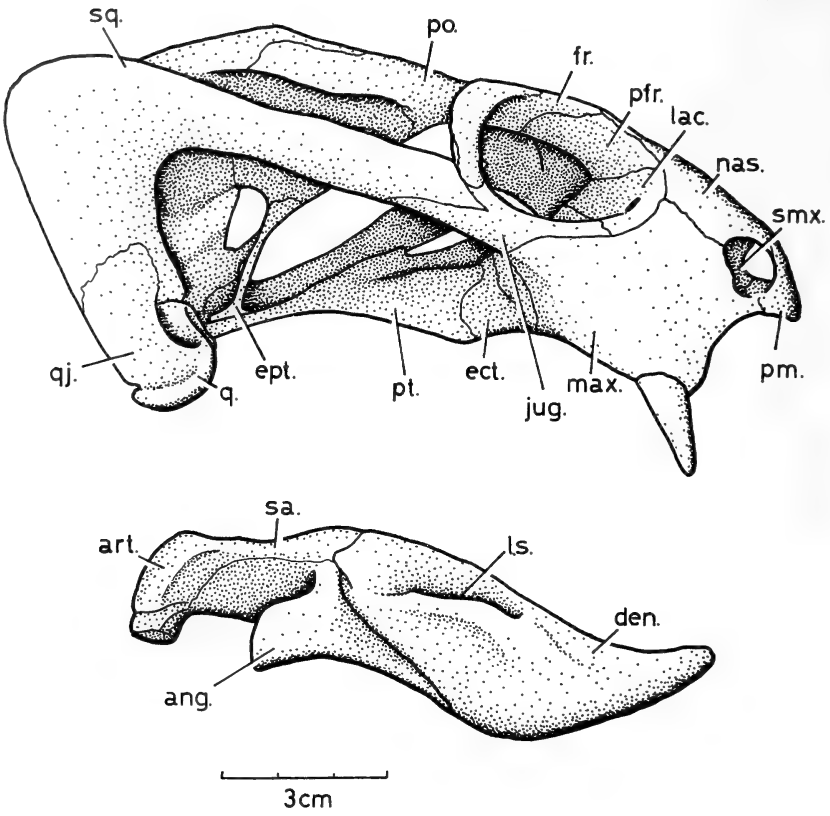

Fig. 28. *Kingoria nowacki.* Skull and lower jaw in lateral view (after Cox 1959).

Locality

Fort Beaufort, Cape Province.

Horizon

Cistecephalus Zone.

Kingoria gracilis (Broom)

Oudenodon gracilis Broom, 1901: 162.

Type specimen

Skull, SAM–590.

Locality

Pearston, Cape Province.

Horizon

Cistecephalus Zone.

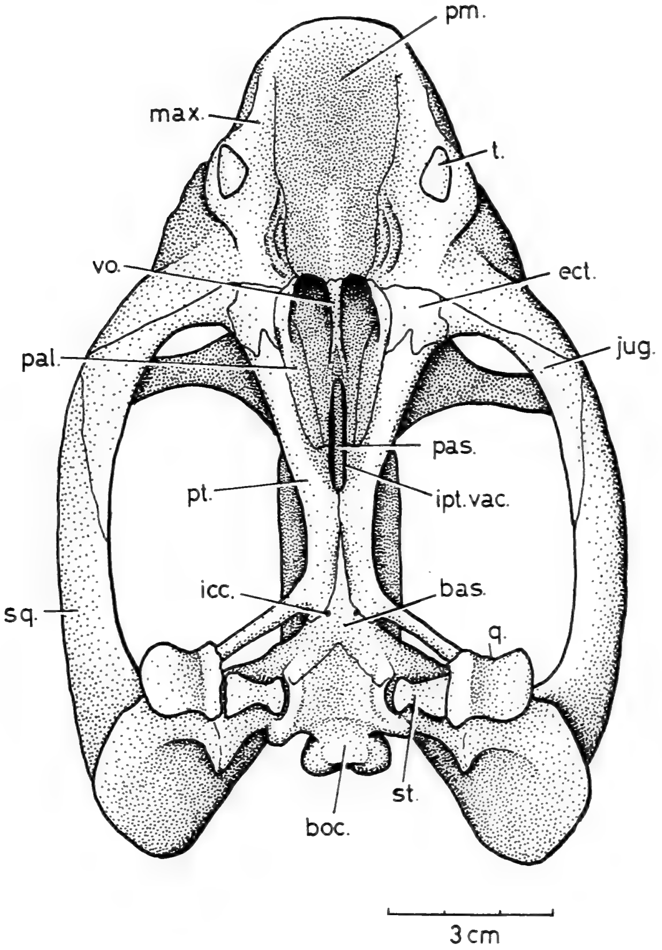

Fig. 29. *Kingoria nowacki*. Skull in ventral view (after Cox 1959).

Kingoria grahami (Broom)

Dicynodon grahami Broom, 1940*b*: 180, fig. 22.

Type specimen

Skull, RC 40.

Locality

St Olives, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone

Kingoria howardi (Broom)

Dicynodon howardi Broom, 1948: 604, fig. 22A.

Type specimen

Skull, RC 83.

Locality

Riversdale, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

Kingoria duvenhagei (Broom)

Dicynodon duvenhagei Broom, 1948: 607, fig. 25.

Type specimen

Skull, RC 64.

Locality

Doornkloof, Graaff-Reinet district, Cape Province.

Horizon

Daptocephalus Zone.

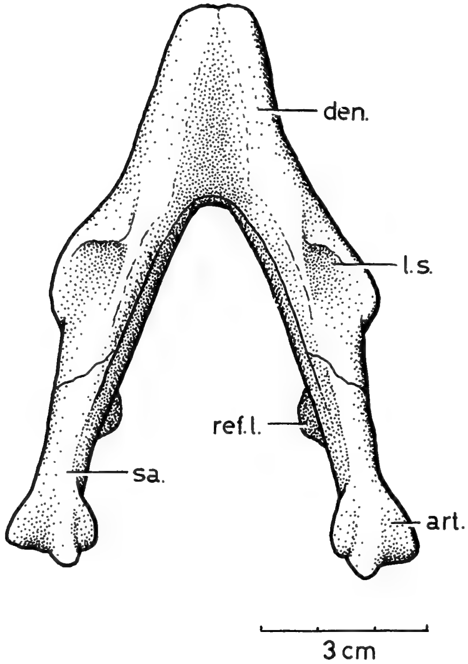

Fig. 30. *Kingoria nowacki*. Lower jaw in dorsal view (after Cox 1959).

Kingoria galecephala (Broom & Robinson)

Dicynodon galecephalus Broom & Robinson, 1948: 404.
Kingoria galecephala (Broom & Robinson) Cox, 1959: 324.

Type specimen

Skull, RC 97.

Locality

Ferndale, Graaff-Reinet district, Cape Province.

Horizon

Cistecephalus Zone.

INTERRELATIONSHIPS OF *DICYNODON*, *OUDENODON*, *DIICTODON*, AND *KINGORIA*

Recognition of four central Permian dicynodont genera on the basis of the diagnoses given above has brought a clear picture of dicynodont interrelationships a step closer. While a full review of dicynodonts based on diagnoses of all genera cannot be attempted here, comparisons between *Dicynodon*, *Oudenodon*, *Diictodon*, and *Kingoria* nevertheless suggest closer relationships among some genera than among others (see Table 1).

In terms of lower jaw and palatal morphology, *Dicynodon* and *Oudenodon* resemble each other closely. It is unlikely that these similarities, involving dentary tables, a dorsal dentary sulcus, a deeply vaulted secondary palate with high palatal rim, and a large palatal development of the palatine, would have arisen as a consequence of convergence, and the differences which are seen in the palatal structure of the two genera are very likely the result of permanent loss of the maxillary tusk in *Oudenodon* and accompanying modification of masticatory function.

Diictodon resembles *Dicynodon* and *Oudenodon* in the presence of dentary tables, but the structure of the dorsal edge of the dentary as well as the palatal rim, caniniform process, and palatine sets the genus well apart from the others.

On the basis of palatal and lower jaw structure, *Kingoria* holds only a remote relationship with the other genera. The lower jaw, with flared lateral dentary shelves, blunt anterior tip, and highly reduced mandibular fenestra, is unique and, taken in conjunction with palatal structure, suggests an origin of the genus well separated from that of *Dicynodon*, *Oudenodon* or *Diictodon*.

Of the four genera discussed above, *Diictodon* has the greatest stratigraphic range. Specimens that can be referred to the genus are common in collections from the *Tapinocephalus* Zone, and are extremely abundant in certain *Cistecephalus* Zone localities. In addition, a specimen of *Diictodon* has been identified from the Upper Permian of Tienshan, China (Cluver & Hotton, 1979). The genus appears to persist to the very top of the *Daptocephalus* Zone, but has not been recorded from the Triassic Karoo formations. *Dicynodon*, *Oudenodon*, and

TABLE 1
Distribution of character states

	Dicynodon	*Oudenodon*	*Diictodon*	*Kingoria*
postcaniniform crest		×		
palatal rim continuous	×	×		×
palatal rim notched			×	
broad inter-temporal region		×		×
narrow inter-temporal region	×		×	
tusks present	×			
tusks absent		×		
tusks absent or present			×	×
dorsal sulcus in dentary	×	×		
dentary tables	×	×	×	
dentary tables absent				×
weak dentary shelf	×	×	×	
wide dentary shelf				×
septomaxilla recessed		×	×	×
septomaxilla exposed	×			
large palatine	×	×		
small palatine			×	×

Kingoria have not been identified from *Tapinocephalus* Zone localities, but all three are relatively common in the *Daptocephalus* Zone. *Oudenodon* appears to be better represented in *Cistecephalus* Zone localities than are *Dicynodon* or *Kingoria*, but whereas *Oudenodon* did not survive the Permian–Triassic transition, both *Kingoria* and *Dicynodon* can claim relationships with Triassic genera. *Kombuisia frerensis* (Hotton, 1974) is clearly a specialized relative of *Kingoria*, while the features that set *Dicynodon* apart from the other Permian genera are seen in modified form in *Lystrosaurus* and *Kannemeyeria* (Cluver 1971), as well as in many of the later, non-South African genera for which good descriptions exist (see Keyser & Cruickshank 1979). Future revision of the group of which *Dicynodon* is an early and primitive member will very likely show it to be geographically and stratigraphically the most wide-ranging dicynodont taxon.

Further speculation on the relationships of *Dicynodon*, *Oudenodon*, *Diictodon* and *Kingoria* would be fruitless before the status of other Permian dicynodonts has been clarified, in particular the pristerodontid genera and the primitive forms from the lowermost *Tapinocephalus* zone of the Beaufort series. However, recognition of the distinctive morphological features characterizing the four genera as set out above should aid materially in revealing what will undoubtedly prove to be a highly complex phylogeny of dicynodonts.

ACKNOWLEDGEMENTS

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REFERENCES

Agnew, J. D. 1959. Cranio-osteological studies in *Dicynodon grimbeeki* with special reference to the sphenethmoid region and cranial kinesis. *Palaeont. afr.* **6**: 77–107.

Boonstra, L. D. 1948. On the anomodont reptiles from the *Tapinocephalus* zone of the Karroo System. *In:* Royal Society of South Africa. *Robert Broom Commemorative volume:* 57–64. Cape Town: Royal Society of South Africa.

Broili, F. & Schröder, J. 1937. Beobachtungen an Wirbeltieren der Karrooformation. XXVIII. Über einige neue Anomodontier aus der *Tapinocephalus* Zone. *S. B. bayer. Akad. Wiss.* **1937**: 118–168.

Broom, R. 1901. On the structure and affinities of *Udenodon. Proc. zool. Soc. Lond.* **1901**: 162–190.

Broom, R. 1905. Notice of some new fossil reptiles from the Karroo Beds of South Africa. *Rec. Albany Mus.* **1**: 331–337.

Broom, R. 1912. On some new fossil reptiles from the Permian and Triassic beds of South Africa. *Proc. zool. Soc. Lond.* **1912**: 859–876.

Broom, R. 1913. On some new genera and species of dicynodont reptiles, with notes on a few others. *Bull. Am. Mus. nat. Hist.* **32**: 441–457.

Broom, R. 1921. On some new genera and species of anomodont reptiles from the Karroo beds of South Africa. *Proc. zool. Soc. Lond.* **1921**: 647–674.

Broom, R. 1932. *The mammal-like reptiles of South Africa.* London: Witherby.

Broom, R. 1935*a*. A new genus and some new species of mammal-like reptiles. *Ann. Transv. Mus.* **18**: 1–12.

Broom, R. 1935*b*. On some new genera and species of Karroo fossil reptiles *Ann. Transv. Mus.* **18**: 55–72.

Broom, R. 1936. On some new genera and species of Karroo fossil reptiles with notes on some others. *Ann. Transv. Mus.* **18**: 349–386.

Broom, R. 1937. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proc. zool. Soc. Lond.* **1937**: 299–318.

Broom, R. 1940*a*. Some new Karroo reptiles from the Graaff-Reinet District. *Ann. Transv. Mus.* **20**: 71–87.

Broom, R. 1940*b*. On some new genera and species of fossil reptiles from the Karroo Beds of Graaff-Reinet. *Ann. Transv. Mus.* **20**: 157–192.

Broom, R. 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Trans. R. Soc. Edinb.* **61**: 577–929.

Broom, R. 1950. Three new species of anomodonts from the Rubidge collection. *Ann. Transv. Mus.* **21**: 246–250.

Broom, R. & Haughton, S. H. 1913. On the two new species of *Dicynodon. Ann. S. Afr. Mus.* **12**: 36–39.

Broom, R. & Haughton, S. H. 1917. Some new species of Anomodontia (Reptilia). *Ann. S. Afr. Mus.* **12**: 119–125.

Broom, R. & Robinson, J. T. 1948. Some new fossil reptiles from the Karroo Beds of South Africa. *Proc. zool. Soc. Lond.* **118**: 392–407.

Camp, C. L. & Welles, S. P. 1956. Triassic dicynodont reptiles. Part I. The North American genus *Placerias. Mem. Univ. Calif.* **13**: 255–304.

Charig, A. J. 1963. Stratigraphical nomenclature in the Songea Series of Tanganyika. *Rec. geol. Surv. Tanganyika* **10**: 47–53.

Cluver, M. A. 1970. The palate and mandible in some specimens of *Dicynodon testudirostris* Broom & Haughton (Reptilia, Therapsida). *Ann. S. Afr. Mus.* **56**: 133–153.

Cluver, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus. Ann. S. Afr. Mus.* **56**: 155–274.

Cluver, M. A. 1974*a*. The skull and mandible of a new cistecephalid dicynodont. *Ann. S. Afr. Mus.* **64**: 137–155.

Cluver, M. A. 1974*b*. The cranial morphology of the Lower Triassic dicynodont *Myosaurus gracilis. Ann. S. Afr. Mus.* **66**: 35–54.

Cluver, M. A. 1975. A new dicynodont from the *Tapinocephalus* Zone (Karoo System, Beaufort Series) of South Africa, with evidence of the jaw adductor musculature. *Ann. S. Afr. Mus.* **67**: 7–23.

Cluver, M. A. & Hotton, N. 1979. The dicynodont genus *Diictodon* (Reptilia, Therapsida) and its significance. *Proc. IV International Gondwana Symposium, 1977, Calcutta*: 176–183.

Cox, C. B. 1959. On the anatomy of a new dicynodont genus, with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 321–367.

Crompton, A. W. & Hotton, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla* **109**: 1–51.

Cruickshank, A. R. I. 1968. A comparison of the palates of Permian and Triassic dicynodonts. *Palaeont. afr.* **11**: 23–31.

Haughton, S. H. & Brink, A. S. 1954. A bibliographic list of Reptilia from the Karroo beds of Africa. *Palaeont. afr.* **2**: 1–187.

Hotton, N. 1974. A new dicynodont (Reptilia, Therapsida) from *Cynognathus* zone deposits of South Africa. *Ann. S. Afr. Mus.* **64**: 157–165.

Huene, F. Von. 1931. Beitrag zur Kenntnis der Fauna der südafrikanischen Karrooformation. *Geol. palaeont. Abh.* (N.F.) **18**: 158–228.

Huene, F. Von. 1942. Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. *Palaeontographica* **94**: 154–184.

Keyser, A. W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. *Mem. geol. Surv. Rep. S. Afr.* **67**: 1–110.

Keyser, A. W. & Cruickshank, A. R. I. 1979. The origins and classification of Triassic dicynodonts. *Trans. geol. Soc. S. Afr.* **82**: 81–108.

EWER, R. F. 1961. The anatomy of the anomodont *Daptocephalus leoniceps* (Owen). *Proc. zool. Soc. Lond.* **136**: 375–402.

KITCHING, J. W. 1970. A short review of the Beaufort zoning in South Africa. *In: IUGS 2nd Symposium Gondwana Stratigraphy and Palaeontology:* 309–312. Cape Town, Johannesburg: CSIR.

KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Mem. Bernard Price Inst. palaeont. Res.* **1**: 1–131.

OLSON, E. C. 1944. The origin of mammals based on the cranial morphology of the therapsid suborders. *Spec. Pap. geol. Soc. Am.* **55**: 1–136.

OWEN, R. 1845*a*. Report on the reptilian fossils of South Africa. Part 1. Description of certain fossil crania, discovered by A. G. Bain in sandstone rocks at the south eastern extremity of Africa, referable to an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or sub-order of Sauria. *Trans. geol. Soc. Lond.* **7**: 59–84.

OWEN, R. 1845*b*. Description of certain fossil crania, discovered by A. G. Bain, Esq., in sandstone rocks at the south-eastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. *Proc. geol. Soc.* **4**: 500–504.

OWEN, R. 1856. Report on the reptilian fossils of South Africa. Part II. Description of the skull of a large species of *Dicynodon* (*D. tigriceps*, Ow.), transmitted from South Africa by A. G. Bain, Esq. *Trans. geol. Soc. Lond.* **7**: 233–240.

OWEN, R. 1860. On some reptilian fossils from South Africa. *Q. Jl. geol. Soc. Lond.* **16**: 49–63.

OWEN, R. 1876. *Descriptive and illustrated catalogue of the fossil Reptilia of South Africa in the collection of the British Museum.* London: British Museum (Natural History).

SUN, A. L. 1973. A new species of *Dicynodon* from Sinkiang: *Vert. Palasiatica* **11**: 52–58.

TOERIEN, M. J. 1953. The evolution of the palate in South African Anomodontia and its classificatory significance. *Palaeont. afr.* **1**: 49–117.

TOERIEN, M. J. 1954. *Lystrosaurus primitivus*, sp. nov. and the origin of the genus *Lystrosaurus*. *Ann. Mag. nat. Hist.* (12) **7**: 934–938.

VAN HOEPEN, E. C. N. 1934. Oor die indeling van die Dicynodontidae na aanleiding van nuwe vorme. *Palaeont. Navors. nas. Mus. Bloemfontein* **2**: 67–101.

YUAN, P. L. & YOUNG, C. C. 1934. On the discovery of a new *Dicynodon* in Sinkiang. *Bull. geol. Soc. China* **13**: 563–573.

ABBREVIATIONS

add. fos.	adductor fossa
ang.	angular
art.	articular
bas.	basisphenoid
boc.	basioccipital
bo.t.	basioccipital tuber
den.	dentary
den. s.	dentary shelf
den. t.	dentary table
ect.	ectopterygoid
eoc.	exoccipital
ept.	epipterygoid
for. mag.	foramen magnum
fr.	frontal
icc.	canal for internal carotid artery
ip.	interparietal
ipt. vac.	interpterygoid vacuity
itr.	intertuberal ridge
jug.	jugal
lab. fos.	labial fossa
lac.	lacrimal
lat. pal. f.	lateral palatal fenestra

l.s.	lateral shelf
max.	maxilla
no.	notch
op.	opisthotic
orb.	orbitosphenoid
pa.	parietal
pal.	palatine
pas.	parasphenoid
pcc.	postcaniniform crest
pfr.	prefrontal
pm.	premaxilla
po.	postorbital
pof.	postfrontal
pp.	preparietal
pro.	prootic
prs.	presphenoid
pt.	pterygoid
pt. f.	posttemporal fenestra
q.	quadrate
q.j.	quadratojugal
ref. l.	reflected lamina
sa.	surangular
smx.	septomaxilla
soc.	supraoccipital
sq.	squamosal
st.	stapes
t.	tusk
tab.	tabular
vo.	vomer
VIIf.	foramen for facial nerve
AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
BPI	Bernard Price Institute for Palaeontological Research, Johannesburg
RC	Rubidge Collection, Wellwood, Graaff-Reinet
SAM	South African Museum, Cape Town
TM	Transvaal Museum, Pretoria

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text
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(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
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(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

MICHAEL A. CLUVER
&
NICHOLAS HOTTON III

THE GENERA *DICYNODON* AND *DIICTODON* AND THEIR BEARING ON THE CLASSIFICATION OF THE DICYNODONTIA (REPTILIA, THERAPSIDA)

VOLUME 83 PART 7 AUGUST 1981 ISSN 0303–2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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REVISION OF THE LATE VALANGINIAN CEPHALOPODA FROM THE SUNDAYS RIVER FORMATION OF SOUTH AFRICA, WITH SPECIAL REFERENCE TO THE GENUS *OLCOSTEPHANUS*

By

M. R. COOPER

Cape Town Kaapstad

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By

MICHAEL R. COOPER

*Queen Victoria Museum, Salisbury**

(With 205 figures)

[*MS. accepted 8 August 1980*]

ABSTRACT

The cephalopod fauna from the Sundays River Formation is revised and shown to comprise 14 species and varieties of *Olcostephanus*, 2 species each of *Distoloceras*, *Bochianites* and *Belemnopsis*, and 1 species each of *Neohoploceras*, *Eodesmoceras*, *Partschiceras*, and *Eutrephoceras*. Sexual dimorphism is recognized within *Olcostephanus* and the implications and importance of this phenomenon are discussed at length. The fauna is considered of latest Valanginian (*O. baini* Zone) age. The new genus *Jeanthieuloyites* is proposed for *Rogersites quinquestriatus* Besairie, and one new species of *Olcostephanus*, *O. riccardii* sp. nov., is described.

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INTRODUCTION

In the southern and south-eastern Cape, late Mesozoic sediments occur as a widely scattered series of basins, representing basin infills in uneven terrain. The bulk of these deposits are of non-marine origin, and it is only in the Uitenhage basin (Fig. 1), where these sediments attain their fullest development,

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* Present address: National Museum, Bulawayo

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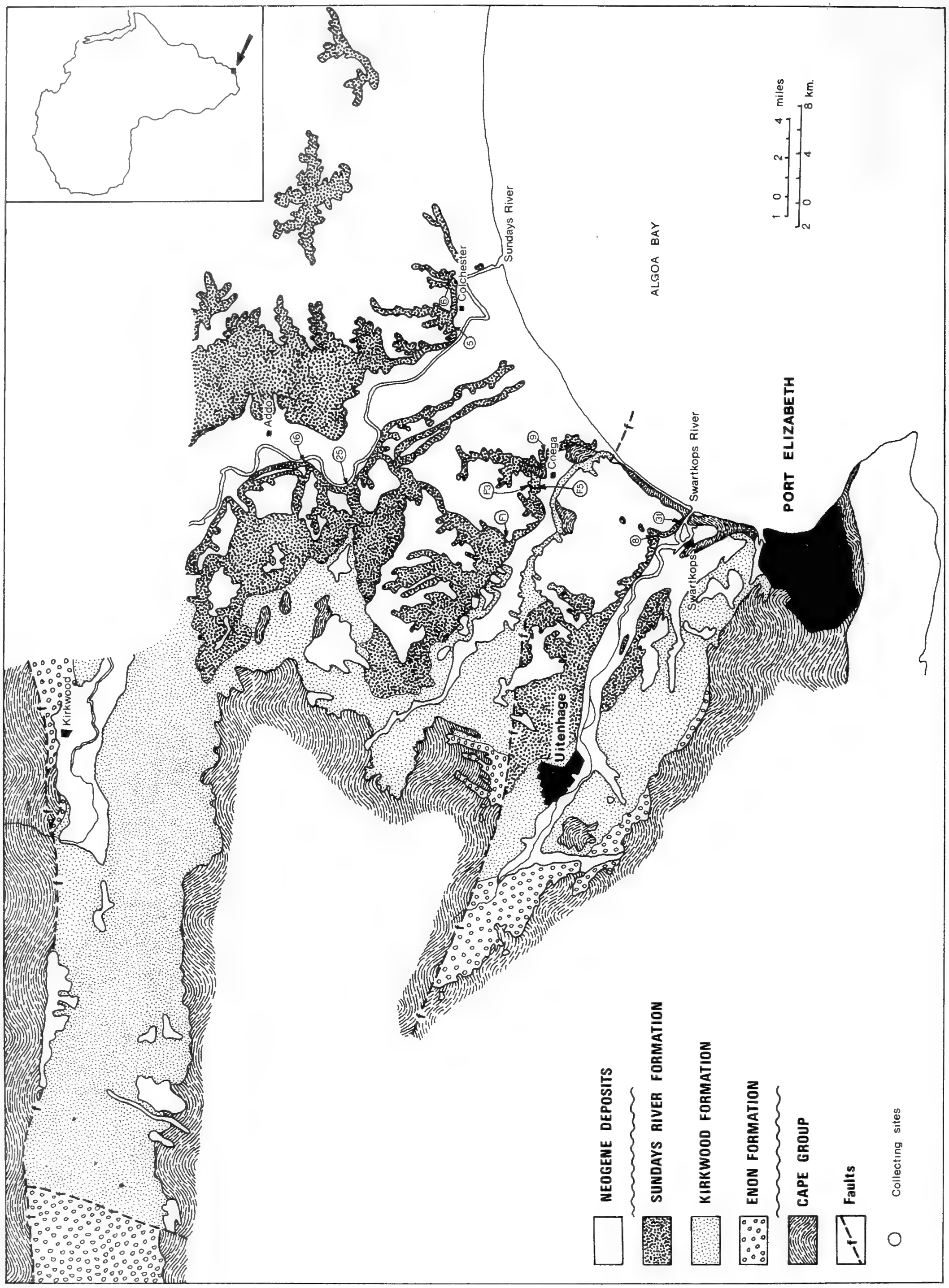

Fig. 1. The geology of the Uitenhage Basin (after Geological Survey Map of 1962).

that the succession is complete. It was to the sediments of this area that Tate (1867) first applied the name 'Uitenhage Beds'.

Within the sediments of the Uitenhage Group (Winter 1973), a tripartite subdivision has long been recognized which, using current lithostratigraphic nomenclature, is:

3. Sundays River Formation
2. Kirkwood Formation
1. Enon Formation

With the break-up Gondwanaland, the depositional history of the area was initially one of rapid deposition of fluviatile sandstones and torrential conglomerates of the Enon Formation, followed by the more quiescent, lagoonal to marginally marine environments of the Kirkwood Formation, finally terminating in the transgressive marine deposits of the Sundays River Formation. It is the rich invertebrate faunas of the latter unit that have provided the main basis for the dating of the Uitenhage Group.

Fossils were first recorded from the Uitenhage Group by Hausmann (1837) who described some molluscs from the Sundays River valley, including the ammonites *Ammonites spinosissimum* and a '*Hamites*' sp., the latter being erroneously compared with the late Albian species *H. intermedius* J. Sowerby and *H. funatus* Brongniart. He considered the fauna to be of Lower Cretaceous age, a determination supported by Goldfuss (1837, 1840) who figured two of Hausmann's shells, whilst Krauss (1843, 1850) assigned a Neocomian age to a small collection of bivalves from the Swartkops River.

In 1851 Portlock (1852) exhibited a collection of fossil plants and molluscs, collected by Rubidge from the Sundays River valley, to which he assigned a probable Jurassic age.

Bain (1856) doubtfully referred the Uitenhage fossils to the Lias, based on the abundance of the supposedly Liassic form, '*Gryphaea incurva*', actually a misidentification of *Aetostreon imbricatum* (Krauss). In an appendix to Bain's paper, Sharpe described a new collection of fossils from the Sundays and Swartkops Rivers, including the ammonites *Ammonites atherstoni* and *A. baini*. An erroneous comparison of these two species with 'Lower Oolite' (Bajocian) forms led Sharpe to conclude that the fauna was most closely related to those from the 'Lower and Middle Oolite' (Bajocian–Bathonian) of Europe.

In 1857 Atherstone suggested a partly Jurassic and partly Cretaceous age for the Uitenhage Group, although Wyley (1859) placed the Enon Formation as low as the New Red Sandstone (Triassic) and correlated the Sundays River Formation with the 'Oolites' (Middle Jurassic).

In his description of several new molluscs from the Uitenhage Group, Tate (1867) considered the deposit to represent a condensed sequence spanning the entire Jurassic period, with the possible exception of the 'Upper Oolite'. Amongst the new forms described were *Ammonites subanceps*, compared with *A. anceps* Reinecke from the 'Middle Oolite' (a Callovian *Reineckia*), *Hamites* *africanus*, and the belemnite *Belemnites africanus* which was compared with the Jurassic *B. aucklandicus.*

Stoliczka (1871), in his monograph of the Cretaceous Bivalvia of southern India, suggested that some of the Uitenhage forms showed Cretaceous rather than Jurassic affinities.

The bivalve *Crassatella complicata* Tate was assigned by Dames (1873) to the genus *Ptychomya* and considered to indicate a Neocomian age, a suggestion supported by a fragment of ammonite which Dames believed to be identical with *Ammonites astieri* d'Orbigny.

Lycett (1879), in the concluding chapter of his monograph of the British fossil trigoniids, expressed the opinion that some of the more characteristic of the Uitenhage forms pointed decisively to a Cretaceous age.

In a critical review of Tate's work, Neumayr (*in* Holub & Neumayr, 1882), besides describing several new bivalves and figuring the holotype of *Crioceras spinosissimum* (Hausmann) for the first time, dealt with the age of the Sundays River faunas at some length. He considered *Olcostephanus atherstoni* (Sharpe), *O. baini* (Sharpe), '*Crioceras*' *spinosissimum* (Hausmann), '*Trigonia*' *ventricosa* Krauss, '*T*'. *conocardiiformis* Krauss, *Crassatella complicata* Tate, and '*Exogyra*' *imbricata* Krauss to be essentially Cretaceous in character. He also considered Tate's *Ammonites subanceps* to possibly represent merely the juvenile whorls of *Crioceras spinosissimum.*

Griesbach (1880), Jones (1884), Moulle (1885), Futterer (1897), and Molengraaf (1900) all assigned a Jurassic age to the Uitenhage Group, while Gürich (1887), Schenk (1888), Molengraaf (1890), and Lemoine (1906), on the other hand, suggested a Lower Cretaceous age.

Pavlow (*in* Pavlow & Lamplugh 1892) assigned both *Ammonites atherstoni* and *A. baini* to the Neocomian subgenus *Holcostephanus* (*Astieria*), thereby suggesting a Lower Cretaceous age for the Sundays River Formation. Moreover, he considered *H. atherstoni* (Sharpe) to be identical to *H. psilostomus* (Neumayr & Uhlig) from northern Germany.

Newton (1896) published a complete list of the known Mollusca from the Uitenhage Group and assigned them a Neocomian age, while Passarge (1904) suggested an Upper Jurassic–Lower Cretaceous age.

Kitchin (1908), in his exhaustive study, gave a concise treatment of the earlier literature and dealt with the age of the fauna at great length. He considered the Cephalopoda to carry the greatest weight in the assignment of an age to the deposit, noting that '. . . the known species of *Holcostephanus* (*sensu stricto*) are almost wholly, if not entirely, confined to strata of Upper Valanginian and Lower Hauterivian age' (p. 30). Having shown that Tate's comparison of many of the Bivalvia with Jurassic forms was erroneous, Kitchin (1908: 39) was led to conclude '. . . that no portion of the Uitenhage Series represents a period of time earlier or later than the Neocomian. It must be said, indeed, that the almost entire restriction of *Holcostephanus sensu stricto* (= *Astieria* Auctorum), to the upper part of the Valanginian and the lower beds of the Hauterivian in Europe suggests much narrower limits, when we consider how important a place is taken by members of this genus in characterizing the cephalopod-fauna of the Uitenhage beds.' Amongst the ammonites, Kitchin (1908) described six new species—*Bochianites glaber, Phylloceras rogersi, Holcostephanus wilmanae, H. modderensis, H. rogersi,* and *H. uitenhagensis,* as well as referring to a *Belemnites* sp. from Coega.

Wegner (1909), in a review of the subgenus *Holcostephanus* (*Astieria*) into which he included all the Uitenhage forms, accepted the majority of these as valid, with the exception of *H. wilmanae* which he considered to represent a variety of *H.* (*Astieria*) *psilostomus* Neumayr & Uhlig.

In 1924 Spath erected the new genus *Rogersites*, type species *R. modderensis* (Kitchin), to include all the Olcostephaninae from the Uitenhage Group without, however, providing a formal diagnosis.

In a revision of the Uitenhage Cephalopoda in 1930, Spath had still not formulated a generic diagnosis for *Rogersites*, but included into it all previously described olcostephanids from the Uitenhage Group, as well as describing the new species *Rogersites kitchini, R. crassicostatus, R. sphaeroidalis, R. otoitoides, Eodesmoceras haughtoni* and the nautiloid *Eutrephoceras uitenhagense.*

AGE OF THE SUNDAYS RIVER FORMATION

Kitchin's (1908) detailed study of the faunas from the Sundays River Formation dispelled any doubt as to the presence of Jurassic forms, while concluding that '. . . the Marine Beds represent not more than the strata at the top of the Valanginian and the base of the Hauterivian'.

Besairie (1936) and Collignon (1962) have recorded rich olcostephanid faunas from Madagascar which include *Olcostephanus atherstoni* (Sharpe), *O. baini* (Sharpe), *O. uhligi* (Collignon) (= *O. fascigerus* Spath), and *Distoloceras spinosissimum* (Hausmann) from the Valanginian of that island. *Partschiceras rogersi* (Kitchin), the type of which was collected midway up the cliffs behind Colchester, and thus high in the marine succession, is reported by Collignon (1962) only from the Lower Valanginian, although Haughton (1963) mentions its occurrence in strata of early Hauterivian age from the same island. Like most phylloceratids, therefore, it is presumably a long-ranging species of little use for detailed biostratigraphic correlation.

Böse (1923) and Imlay (1937, 1938, 1940, 1960) have recorded rich olcostephanid faunas from the Upper Valanginian and Lower Hauterivian of Mexico. Imlay (1937, 1938) considered the upper part of the Taraises Formation to be of early Hauterivian age. His faunal list from these beds included *Olcostephanus, Maderia, Mexicanoceras, Acanthodiscus, Leopoldia, Neocomites, Distoloceras, Valanginites, Thurmannites* (= *Thurmanniceras*), *Bochianites, Kilianella,* and *Dichotomites.* The pyritic olcostephanid nuclei *Maderia* and *Mexicanoceras* are endemic and of no value in biostratigraphic correlation. According to Wright (*in* Arkell *et al.* 1957), *Neocomites, Thurmanniceras,* *Valanginites,* and possibly *Kilianella* are all restricted to Valanginian and older strata. A somewhat older age is also suggested for the lower portion of the Upper Member of the Taraises Formation by the faunal association *Olcostephanus–Bochianites–Distoloceras,* which characterizes the Upper Valanginian of Speeton (England), Verdon (France) and Madagascar, as well as being typical of the Uitenhage Formation. This is supported by the presence of *Kilianella mayranensis* Imlay which closely resembles *K. roubaudiana* (d'Orbigny), the differences hardly warranting specific separation. It seems likely, therefore, that Imlay's fauna should be considered as having come from more than one palaeontological zone, including Upper Valanginian strata.

A re-examination of the Valanginian stratotype led Barbier & Thieuloy (1963) to subdivide the Valanginian into a lower *Kilianella roubaudiana* Zone and an upper *Saynoceras verrucosum* Zone. The so-called 'Astieriaschicht', rich in *Olcostephanus atherstoni* (Sharpe) (Barbier & Thieuloy 1963: 82), is placed at the top of the Valanginian, pending detailed reinvestigation. In 1967, however, Moullade & Thieuloy wrote '. . . il subsiste cependant toujours un large hiatus non caractérisé par les Ammonites entre le Valanginien 'moyen' à *Saynoceras verrucosum* et les termes ultimes du Valanginien supérieur'. The terminal Valanginian was subdivided into a lower zone of *Himantoceras trinodosum* (Thieuloy) and an upper zone of *Sarasinella ambigua* (Uhlig), while the base of the Hauterivian was marked by the appearance of *Acanthodiscus radiatus* (Brugière).

Busnardo & Cotillon (1964) recorded a rich olcostephanid fauna from Bas–Verdon in France, from calcareous marls at the very top of the Valanginian, overlain by so-called Valanginian–Hauterivian passage beds, in turn succeeded by Lower Hauterivian beds with *Acanthodiscus radiatus, Olcostephanus filosus* (Baumberger) and *O.* aff. *psilostomus* (Neumayr & Uhlig). The Upper Valanginian fauna included *O. atherstoni* (Sharpe).

In Argentina, strata with *O. atherstoni* (Sharpe) are apparently overlain (Riccardi *et al.* 1971) by a Lower Hauterivian faunal assemblage with *Acanthodiscus* cf. *radiatus* (Brugière). Riccardi *et al.* (1971) believed their fauna to show close agreement with the 'Astieriaschicht' of the Swiss Jura, but preferred tentatively to date the Argentinian *Olcostephanus atherstoni* assemblage at '. . . late Valanginian to earliest Hauterivian, pending detailed biostratigraphic revision on a world-wide scale'.

At Speeton (Spath 1924) there is an apparent hiatus, possibly only local, during the Upper Valanginian–basal Hauterivian, and derived fossils of this age occur in the black nodules of Division D_2. Spath (1924: 86) considered '. . . the main development of *Olcostephanus,* of which *A. astieri* is the genotype, is at the base of the Hauterivian and uppermost Valanginian'.

The top bed of the Middle Member of the Chichali Formation in the Trans Indus Range of northern Pakistan has yielded a rich *Olcostephanus* fauna (Spath 1939; Fatmi 1977) which leaves little doubt as to its contemporaneity with the Sundays River faunas. Species in common include *O. fascigerus*

Spath, *O. baini baini* (Tate), *O. baini* var. *sphaeroidalis* (Spath), *O. rogersi* (Spath), and perhaps *O. densicostatus* (Wegner) and *O. perinflatus* (Matheron).

Imlay & Jones (1970) recorded *Olcostephanus* cf. *O. atherstoni* Baumberger (*non* Sharpe) (= ? *O. baini* (Sharpe)) from the zone of *Buchia keyserlingi* (Lahusen) in Oregon, considered to be of Middle to Upper Valanginian age, and associated with the genera *Bochianites*, *Neocomites*, *Thurmanniceras*, *Neocraspedites*, and *Polyptychites*.

From Fernão Velosa, in northern Mozambique, Spath (1930) has recorded *Olcostephanus schenki* (Oppel) (= *O. baini* (Sharpe)), and *Haploceras* (*Neolissoceras*) cf. *grasianum* (d'Orbigny). Strata of a similar age also crops out at Mahiba Hill, to the west of Port Amelia, where Newton (1924) recorded fragments of *Lytoceras* together with the belemnite *Duvalia*. From this same locality Spath (1930: 134) also records a '. . . portion of the periphery of a Neocomitid (*Lyticoceras* of the type of *L. regalis* (Bean) or *Neocomites neocomiensis* (d'Orbigny) as figured by Sayn), and the impression of a fragment of the Uitenhage *Bochianites africanus* are decisive and unmistakable'.

The coarse ribbing of the olcostephanids from the Uitenhage Group has long been a distinctive feature. It is of interest to note, therefore, that where the basal Hauterivian is best known (Debelmas & Thieuloy 1963), the associated species of *Olcostephanus* are frequently finely and densely ribbed, with such taxa as *O. filosus* (Baumberger) and *O. sayni* (Kilian) common. *Olcostephanus atherstoni* (Sharpe) also occurs but, as will be shown, represents a stock-name for a number of homoeomorphic macroconchs. The absence of such finely ribbed forms, together with *Acanthodiscus*, from the Sundays River Formation supports the suggestion that this unit should be considered of latest Valanginian age only.

In order to help resolve the Valanginian–Hauterivian boundary problem, it seems necessary to introduce a zone of *Olcostephanus baini* at the top of the Valanginian (Collignon 1962). The following Valanginian–Lower Hauterivian zonal scheme would appear to be of global significance:

Lower Hauterivian	*Crioceratites duvali*
	Acanthodiscus radiatus
Valanginian	*Olcostephanus baini*
	Saynoceras verrucosum
	Kilianella roubaudiana
	Thurmanniceras thurmanni

The Uitenhage fauna may be assigned, therefore, to the assemblage zone of *O. baini*. Besides the Uitenhage species described herein, other important elements of the zone include *Neocomites* spp, *Himantoceras* spp, *Neohoploceras* spp, *Distoloceras* spp, *Sarasinella* spp, *Leopoldia* spp, *Bochianites* spp, *Olcostephanus* spp, together with the less diagnostic *Hemilytoceras liebigi* (Oppel), *Haploceras* (*Neolissoceras*) *grasianum* (d'Orbigny), *Phylloceras thetys* (d'Orbigny), *P. serum* (Oppel) and so on.

SYSTEMATICS

A revision of the Uitenhage ammonite fauna, characterized by the abundance of forms assigned to the genus *Olcostephanus*, some of which have attained unusually large size, has long been overdue, especially in view of the recognition of sexual dimorphism within many groups of the Perisphinctaceae, and more recently in the genus *Olcostephanus* itself (Riccardi *et al.* 1971). Moreover, the erection of numerous species (and genera) within the Olcostephaninae, based upon subtle and generally insignificant differences with no regard for intraspecific variation, has led not only to taxonomic chaos but also to difficulties in interregional correlation.

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

AM	Albany Museum, Grahamstown
BM	British Museum (Natural History), London
LJE, AAS	Geological Survey, Pretoria
MNHP	Natural History Museum, Paris
OUM	Oxford University Museum, Oxford
PEM	Port Elizabeth Museum, Port Elizabeth

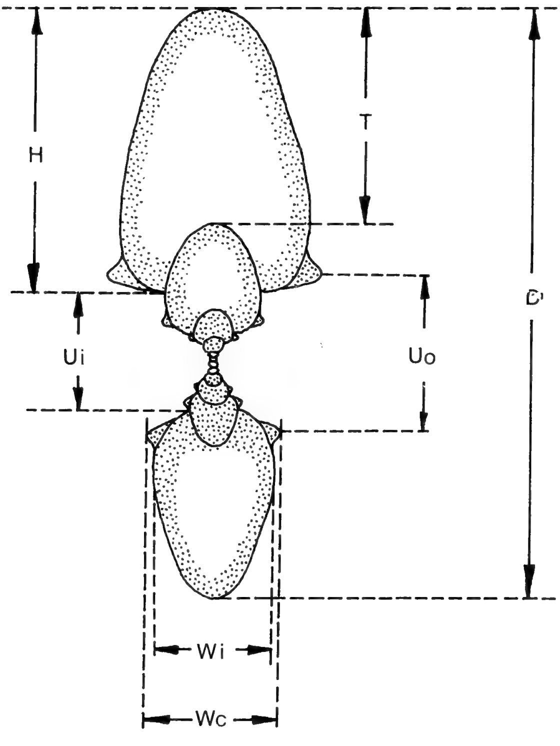

Fig. 2. Schematic diagram showing the measurements discussed in the text.

The abbreviations for measurements given in the text are explained in Figure 2 where D = diameter, H = height, Uo = outer umbilical diameter (between umbilical bullae), Ui = inner umbilical diameter (between umbilical seams), Wi = intercostal width. All measurements are given in millimetres, and dimensions, as a percentage of the diameter, are included 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 *Partschiceras* Fucini, 1920

Type species *Ammonites partschi* Stur, 1851 (*non* Klipstein 1843);
by original designation of Fucini, 1920

Discussion

This is a long-ranging genus, having been recorded from Lower Jurassic (Sinemurian) to Upper Cretaceous (Maastrichtian). It differs from *Phylloceras* in being more inflated with maximum width at mid-flank, and in commonly developing ribs as well as lirae in maturity. Moreover, *Phylloceras* has triphyllic saddles not diphyllic as in *Partschiceras*. Wiedmann (1962 has recently included *Phyllopachyceras* Spath as a junior synonym in this genus.

Partschiceras rogersi (Kitchin, 1908)

Fig. 3

Phylloceras rogersi Kitchin, 1908: 179, pl. 8 (fig. 19, 19a–c). Spath, 1930: 140. Du Toit, 1954: 384. Haughton, 1963: 274.

Non Phylloceras rogersi Kitchin var. nov., Krenkel, 1910: 223, pl. 22 (fig. 9) (= *P. krenkeli* Zwierzycki).

Phyllopachyceras rogersi (Kitchin) Collignon, 1962: 20, pl. 181 (figs 815–816).

Material

The holotype is the only example so far collected from the Sundays River Formation and its present whereabouts is unknown.

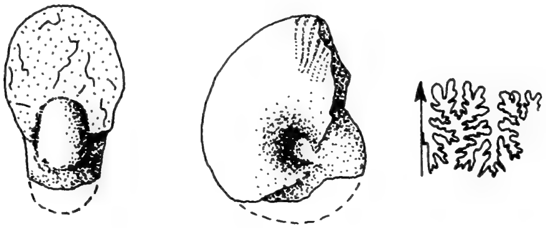

Fig. 3. *Partschiceras rogersi* (Kitchin). The holotype, by monotypy, with part of the suture (after Kitchin 1908). × 1.

Holotype

By monotypy, the original of the specimen figured by Kitchin (1908: 179, pl. 8 (fig. 19, 19a–c)), from the Sundays River Formation, mid-way up the cliffs behind Colchester.

Diagnosis

An immature *Partschiceras* of late Valanginian age characterized by extremely fine, dense lirae, with no sign of ribbing.

Description

A rather inflated, very involute form, with slightly convex flanks and maximum width at mid-flank. Ornament comprises fine, prorsiradiate, flexuous ribs. At a whorl height of 9 mm there are 12 ribs within a 2 mm distance along the venter.

Discussion

Kitchin's holotype, the whereabouts of which is not known, still remains the only record of this species (and genus) from the Sundays River Formation. Since this specimen appears to be immature and the coarse ribbing of this genus appears typically in maturity, the validity of this species is in doubt.

Partschiceras infundibulum (d'Orbigny) appears to be more compressed, whilst also possessing the coarse ribbing not seen in the Uitenhage example.

Phylloceras krenkeli Zwierzycki was established for the specimen figured by Krenkel (1910: 223, pl. 22 (fig. 9)) as *P. rogersi* var. nov., and said to differ from the Uitenhage species in being more compressed, with the greatest width at the umbilical margin and not at mid-flank, having a different suture, and in being more coarsely ribbed, with only eight ribs within a 2 mm distance.

Occurrence

The holotype was collected from mid-way up the cliffs behind Colchester, and thus near the top of the marine succession.

Collignon (1962) has recorded this species from the Lower Valanginian of Madagascar, while Haughton (1963) mentions its occurrence in beds of Lower Hauterivian age from the same island. It would seem, therefore, that *P. rogersi*, like many phylloceratids, is a relatively long-ranging species.

Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily ANCYLOCERATACEAE Meek, 1876
Family **Bochianitidae** Spath, 1922
Subfamily Bochianitinae Spath, 1922
Genus *Bochianites* Lory, 1898

Type species *Baculites neocomiensis* d'Orbigny, 1842;
by original designation of Lory, 1898.

Discussion

This is a relatively long-ranging genus, having been recorded from Tithonian to Hauterivian strata. *Janenschites* was said to have a more denticulate suture than *Bochianites* with long elements, but similar ornament. It has, however, recently (Wiedmann 1962) been included in the synonymy of *Bochianites*.

Bochianites glaber Kitchin, 1908

Fig. 4

Bochianites glaber Kitchin, 1908: 181, pl. 8 (figs 20–21). Hatch & Corstorphine, 1909: 303 fig. 75f. Spath, 1930: 155. Du Toit, 1954: 384. Klinger & Kennedy 1979: 17.

Material

The lectotype, SAM–4695, with some fragments crowded together in the same block of matrix (SAM–12736) from *c.* 2 km upstream from the Swartkops bridge.

Holotype

By lectotype designation herein, the original of *Bochianites glaber* figured by Kitchin (1908: 181, pl. 8 (fig. 20)) from the road below the railway cutting, *c.* 2 km from Rawson bridge on the main line in the Swartkops River Valley.

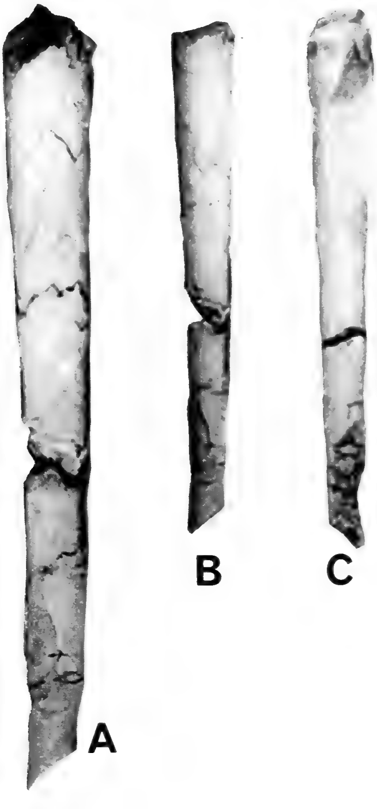

Fig. 4. *Bochianites glaber* Kitchin. A. Ventral view of the lectotype, SAM–4695, × 4. B–C. Ventral and lateral views of the lectotype, × 3.

Diagnosis

A small, very finely ribbed, juvenile *Bochianites*, with an elliptical whorl section at the largest known growth stages.

Description

A small, slowly expanding *Bochianites*, with an initially circular whorl section, becoming elliptical with age. Ornament comprises fine, prorsiradiate lirae, arching across the siphonal line and straight or slightly convex adapically across the dorsum.

Discussion

A number of fragmentary straight shafts within a single block of matrix would seem to belong to this species, the fine ribbing only becoming visible under a hand-lens. No constrictions were observed.

Baculites maldonadi Karsten (1856: 105, pl. 2 (fig. 2)) (Fig. 5) approaches the present species but as they represent different growth stages comparison is difficult. The adapical portion of Karsten's species shows the same thread-like ribbing as *B. glaber*, but adorally it coarsens considerably to resemble *B. africanus*.

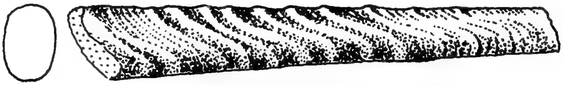

Fig. 5. *Baculites maldonadi* Karsten (after Karsten 1856). × 1.

Whilst there are a number of other *Bochianites* species with which *B. glaber* might be compared, the immature nature and poor preservation of the South African material make such comparisons unwarranted. Indeed, *B. glaber* might even represent the earliest growth stages of *Umgazaniceras thieuloyi* Klinger & Kennedy (1979: 12, figs 1–2, 3A–D, 4–5). As such it is perhaps best regarded as a *nomen dubium*.

Occurrence

At present *B. glaber* is known only from the Sundays River Formation and is thus of latest Valanginian age.

Bochianites africanus (Tate, 1867)

Figs 6–7

Hamites africanus Tate, 1867: 150, pl. 7 (fig. 5). Holub & Neumayr, 1882: 271.
Bochianites africanus (Tate) Kitchin, 1908: 225. Spath, 1930: 153, pl. 14 (figs 2–3), pl. 15 (fig. 3). Du Toit, 1954: 384. Klinger & Kennedy, 1979: 17, fig. 3F–H.

Material

Numerous specimens, including BM–C25227–9, AM–844, 846, SAM–PCU1586–88, 5706, and 12784–88.

Holotype

By the lectotype designation of Spath (1930), the original of Tate's (1867) plate 7, figure 5a, BM–C25228, from Prince Alfred's Rest at the Sundays River mouth.

Diagnosis

A coarsely ribbed species of *Bochianites* with 4–7 prorsiradiate ribs in a distance equal to twice the whorl width and an elliptical to subtrigonal whorl section.

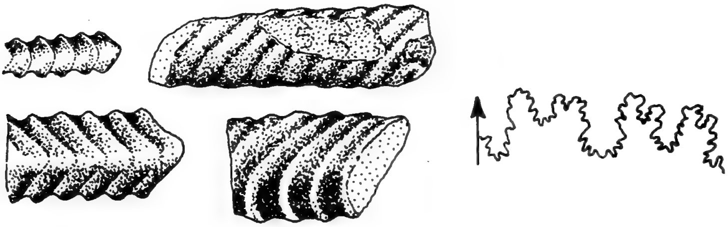

Fig. 6. *Bochianites africanus* (Tate) The syntypes, of which the top right-hand specimen was selected as lectotype (after Tate 1867; composite suture after Spath 1930). × 1.

Description

A slowly expanding, coarsely ribbed *Bochianites* with an elliptical whorl section in immaturity, becoming subtrigonal at large sizes when the maximum width is near the dorsal shoulders. The dorsum is flattened in all but the youngest individuals. Ornament comprises coarse annular ribs, strongly projected on the flanks and sharply arched across the venter. Because of the oblique angle at which the ribbing crosses the distinctly tabulate venter of mature individuals, the ribs are broadest across the venter as well as being asymmetrical with a gentle adapical slope and a steep adoral slope. Rib density varies between 4 and 7 in a distance equal to twice the costal whorl width.

Discussion

Bochianites africanus (Tate) is closest to *B. neocomiensis* (d'Orbigny) (1842*a*, pl. 138 (figs 1–5)) which has, however, an almost perfectly circular whorl section. Spath (1930: 154) considered the present species to be very close to *Baculites granatensis* Karsten (1856: 105, pl. 2 (fig. 1)), to which illustration it certainly bears a considerable resemblance but, according to J.-P. Thieuloy (*in litt.* 1980), the Columbian species (Fig. 8) is a late Cretaceous *Baculites*.

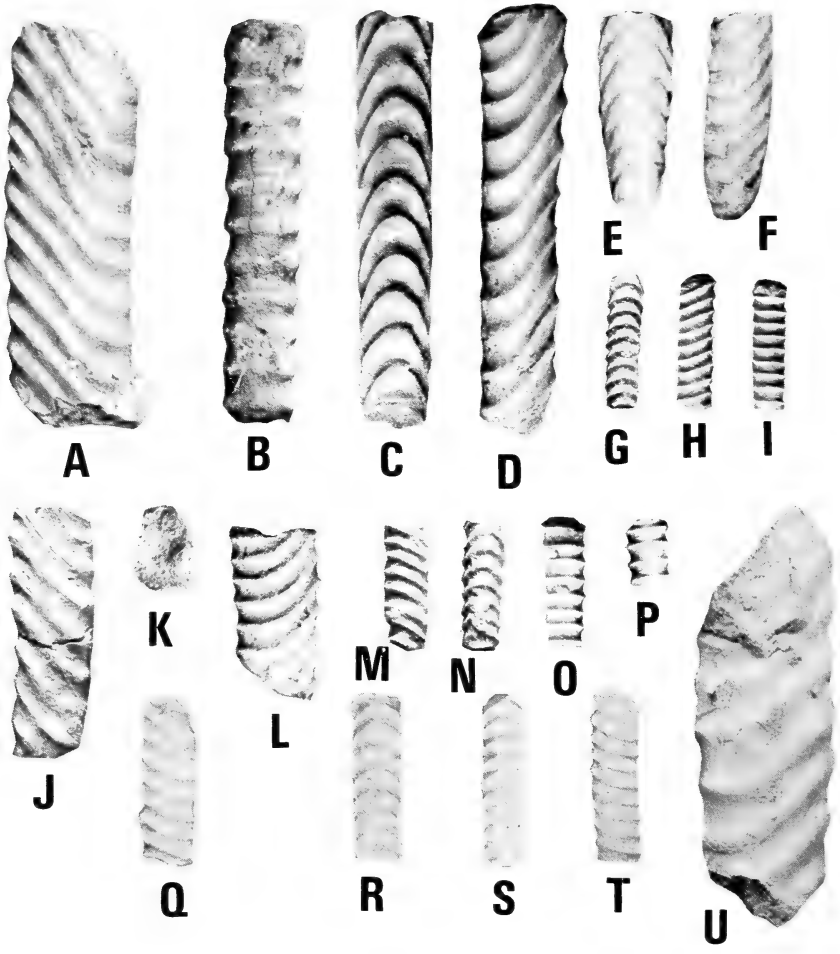

Fig. 7. *Bochianites africanus* (Tate). A. Lateral view of AM–844, × 0,75. B–D. Dorsal, ventral and lateral views of AM–846, × 0,75. E–F. Lateral and ventral views of AM–868, × 0,75. G–I. Ventral, lateral and dorsal views of a specimen in the South African Museum, × 1. J–K. Lateral and cross-sectional views of an unnumbered specimen in the South African Museum, × 0,75. L. Lateral view of SAM–PCU1586, × 1. M–O. Lateral, ventral and dorsal views of a specimen in the South African Museum, × 1. P. Dorsal view of SAM–PCU1587, × 1. Q–R. Lateral and ventral views of a specimen in the South African Museum, × 1. S–T. Ventral and lateral views of a specimen in the South African Museum, × 1. U. Lateral view of an unnumbered specimen in the South African Museum, × 1.

Fig. 8. *Baculites granatensis* Karsten (after Karsten 1856). × 1.

Imlay (1938: 585, pl. 6 (figs 1,11–13)) figured specimens of a *Bochianites* sp. from the Upper Member of the Taraises Formation which he compared with *B. neocomiensis* (d'Orbigny). The ornament is closely comparable with that of *B. africanus*, but since the whorl section was not figured or mentioned its specific assignment is unknown.

Occurrence

Bochianites africanus (Tate) is as yet known only from northern Mozambique and South Africa. It seems surprising that it has not yet been recorded from Madagascar in view of the relative abundance of this species in the Sundays River Formation.

Superfamily PERISPHINCTACEAE Steinmann, 1890

Family **Olcostephanidae** Haug, 1910

Subfamily Olcostephaninae Haug, 1910

Genus *Olcostephanus* Neumayr, 1875

Type species *Ammonites astieri* d'Orbigny, 1840;
by original designation of Neumayr, 1875.

1875 *Olcostephanus* Neumayr
1889 *Holcostephanus* Sayn
1892 *Astieria* Pavlow
1923*a Subastieria* Spath
1923*b Parastieria* Spath
1924 *Rogersites* Spath
1938 *Mexicanoceras* Imlay
1938 *Maderia* Imlay
1964 *Jeannoticeras* Thieuloy
1966 *Taraisites* Cantu Chapa
1966 *Satoites* Cantu Chapa
1977*a Lemurostephanus* Thieuloy

Emended diagnosis

Compressed to strongly inflated cadicones, with strongly arched to well-rounded venters. Primary ribs are usually present on the umbilical wall, commonly terminating in tubercles at the umbilical shoulder (except on the outer whorls of *Parastieria* and *Jeannoticeras*), from which arise straight or slightly curved secondary ribs, usually in fasciculate bundles (in pairs in *Jeannoticeras*). There are commonly 3–4 secondaries per bundle, although there may be as many as 6–9 or as few as 1–2. Secondary ribs may bifurcate on the flanks, while intercalated ribs between bundles are the rule. Ribbing generally passes uninterrupted across the venter, although it may weaken considerably where a ventral furrow is present (i.e. *Mexicanoceras*). Parabolae may or may not be present, but never on the outer whorls of females. This genus is dimorphic; males small and with lappets, females larger and with simple peristomes. Age: Upper Valanginian–Middle Hauterivian.

Discussion

In addition to the objective synonyms *Holcostephanus* and *Astieria,* Wiedmann & Dieni (1968) also placed *Rogersites* within *Olcostephanus* s.s., as well as including *Parastieria* and *Subastieria* within the genus as subgenera. *Capeloites* was considered by these authors to be of dubious status, but, as since shown by Thieuloy (1969), is distinct.

In 1924 Spath erected the new genus *Rogersites,* types species *R. modderensis* (Kitchin), without giving a formal diagnosis. In his revision of the Uitenhage Cephalopoda in 1930, Spath had still not formulated a generic diagnosis for *Rogersites,* but included into it all previously described olcostephanids from the Uitenhage Group. In his monograph of the Cephalopoda of the Neocomian Belemnite Beds of the Salt Range, he (Spath 1939: 11) diagnosed *Rogersites,* stating that '. . . although there are no typical *Rogersites* (e.g. *R. modderensis* Kitchin sp., *R. baini* Sharpe sp. and *R. kitchini* Spath), with few and very coarse primary and secondary ribs and prominent umbilical edge', while further on (p. 31) he refers to '. . . the typical *Rogersites* characters, namely a coronate cadicone and vertical umbilical wall, at large diameters, while retaining coarse ribbing'. At this time Spath was using *Rogersites* both as a genus and a subgenus. Thus (Spath 1939: 11), '. . . there is one common and widely quoted transitional species between *Rogersites* and *Olcostephanus.* This is *O.* (*Rogersites*) *schenki* (Oppel)'. On page 16 he refers to *Rogersites sphaeroidalis* and *R. atherstoni,* but on page 19 states '. . . I previously referred *O. uitenhagensis* to *Rogersites,* but like *R. atherstoni, R. sphaeroidalis* and the many passage forms between these species, *O. uitenhagensis* is one of the transitions from *Rogersites* to *Olcostephanus*'. On page 31 Spath states '. . . *O.* (*R.*) *schenki* is the most strongly and distantly ribbed form of *Olcostephanus* from the Salt Range and the only species that may be compared with such typical *Rogersites* as *R. modderensis* (Kitchin). . . . Since however, no large examples of *O. schenki* have yet been found or recognized, it is uncertain whether it develops the typical *Rogersites* characters.'

Imlay (1938) erected three new genera, all comprising entirely septate pyritic nuclei, within the Olcostephanidae, viz. *Maderia, Mexicanoceras,* and *Ceratotuberculus. Mexicanoceras* was considered '. . . similar in form, sculpture and suture-line to *Olcostephanus.* It differs from *Olcostephanus* in having a ventral furrow on the outer whorls, a more inflated form, broader whorl section, and its much smaller size.' These features are herein considered of only subgeneric value and *Mexicanoceras* is accordingly placed within *Olcostephanus* s. l. *Maderia* was defined by Imlay (1938) as '. . . similar to *Subastieria* (defined by Spath, 1923, p. 32) but exhibits a slight thinning of the ribs along the midventral line of the outer whorls. Compared with *Mexicanoceras* its whorl section is more depressed, its umbilicus wider, and the ventral thinning of the ribs less pronounced.' The importance attached to the very slight weakening of the ribs across the siphonal line in *Maderia* by Imlay (1938) appears unjustified and, in the author's opinion, *Maderia* comprises an heterogeneous assemblage of *Olcostephanus* s.s. and possibly *O.* (*Subastieria*), and is, therefore, superfluous. The genus *Ceratotuberculus* is characterized by the appearance, after the third whorl, of high, thick, ventrolateral bullae, as well as by possessing a ventral furrow, whilst retaining the other olcostephanid characters. If, as suggested by Imlay (1938), this genus is of early Hauterivian age, then it is probably descended from *Saynoceras.* If, however, it is of late Valanginian age, then the differences probably warrant at most subgeneric separation from *Saynoceras.*

Spath (1924) erected the genus *Subastieria* for *Olcostephanus sulcosus* Pavlow, differentiated from *Olcostephanus* by its younger age and highly coronate whorl section. According to Wright (*in* Arkell *et al.* 1957), *Subastieria* closely resembles the inner whorls of some *Rogersites* which, as just shown, is a synonym of *Olcostephanus* s.s. Moreover, Wiedmann & Dieni (1968) have recently shown *Subastieria* to range into the Upper Valanginian, whilst *Olcostephanus* is common in the Lower Hauterivian of the Swiss Jura (Debelmas & Thieuloy 1963). Consequently, not only do *Subastieria* and *Olcostephanus* have the same stratigraphic range, but they are also morphologically very similar. However, in *Subastieria* the whorl section is coronate at all growth stages, whereas microconch forms of *Olcostephanus* become coronate only with the egression of the umbilical seam on the body chamber. This appears to be a subtle but distinct difference, and consequently Wiedmann & Dieni (1968) are provisionally followed in treating it as a valid subgenus.

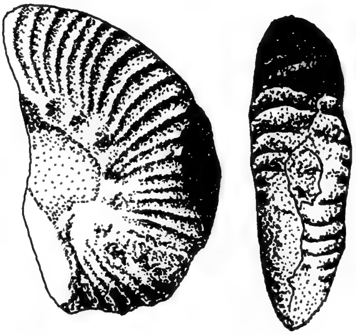

Fig. 9. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe). The holotype of *Taraisites bosei* Cantu Chapa, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

Cantu Chapa (1966) erected the genus *Taraisites* for the specimen of *Astieria* aff. *baini* Sharpe figured by Böse (1923: 76, pl. 2 (figs 3–5)) (Fig. 9 herein), renaming it *T. bosei* Cantu Chapa. This genus was characterized by distant secondary ribbing arising in bundles of 2–3 from the umbilical bullae. As remarked by Riccardi *et al.* (1971), Cantu Chapa's disregard for ontogenetic variation resulted in his separation of, amongst others, the small, coarsely ribbed paratypes of '*Rogersites*' *prorsiradiatus* Imlay, under the new species name of *T. neoleonense*, from the larger and more densely ribbed holotype. Indeed, he included the type of *Olcostephanus baini* (Sharpe) within his new genus, thus separating a microconch from its far more densely ribbed macroconch dimorph. There can be no hesitation in following Riccardi *et al.* (1971) in considering *Taraisites* a synonym of *Olcostephanus* s.s.

Cantu Chapa (1966) also erected the new genus *Satoites* for the supposedly Berriasian *Olcostephanus* sp. nov. figured by Sato (1958: 590, pl. 28 (figs 1–3), fig. 2) (Fig. 10 herein), and considered ancestral to *Mexicanoceras* from which it was said to differ by the absence of a ventral furrow, whilst possessing prominent parabolae. Since the main criterion by which Imlay (1938: 562) distinguished *Mexicanoceras* from *Olcostephanus* was in the presence of a ventral furrow, *Satoites* must be considered a junior synonym of *Olcostephanus* s.s.

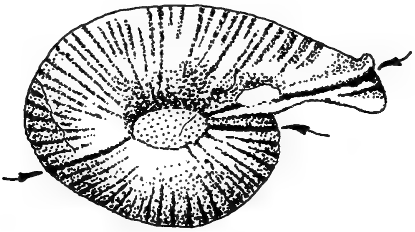

Fig. 10. *Olcostephanus oshimensis* (Cantu Chapa). The type species of the genus *Satoites*, allegedly from the Berriasian of Japan (after Sato 1958). × 1.

Thieuloy (1964: 212) erected the subgenus *Olcostephanus* (*Jeannoticeras*) for *Ammonites jeannoti* d'Orbigny (1840, pl. 56 (figs 3–5)) (Fig. 11 herein), characterized by the absence of umbilical tuberculation in the adult, and by the secondary ribbing which commonly arises in pairs (rarely three) from the primary ribs at the umbilical shoulder. Through C. W. Wright, the writer has seen a collection of *Olcostephanus* (*Parastieria*) from the Lower Hauterivian at Speeton. This subgenus is based upon a microconch species with lappets which upto the body chamber shows numerous primaries giving rise to fine secondaries in twos and threes. At this stage, *Parastieria* is indistinguishable from *Jeannoticeras* and it is only on the body chamber that the broad, flat ribs characteristic of *Parastieria* appear. Further work may show that *Jeannoticeras* is a junior subjective synonym of *Parastieria*, though for the time being they are treated as distinct.

The genus *Dobrodgeiceras* Nikolov (1962: 69) was established for the type species *D. ventrotuberculatum* Nikolov from the Upper Valanginian of Bulgaria, and said to differ from *Valanginites* mainly in the presence of ventral tubercles and more prominent primaries (Nikolov 1962: 69). Thieuloy & Gazay (1967) assigned their entire French fauna to *Dobrodgeiceras wilfridi* (Karakasch)

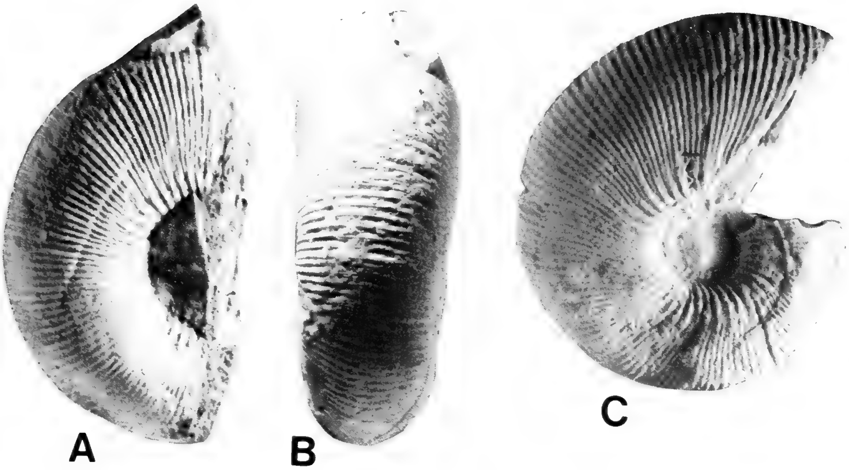

Fig. 11. *Olcostephanus* (*Jeannoticeras*) *jeannoti* (D'Orbigny), × 1. A–B. A specimen in the collections of the University of Paris from the Lower Hauterivian of Montclus, Hautes-Alpes. C. The crushed lectotype in the Natural History Museum, Paris, R3114 (D'Orbigny Collection No. 4865*a*) from the Lower Hauterivian of ?Serrais, Hautes-Alpes. Note the parabola.

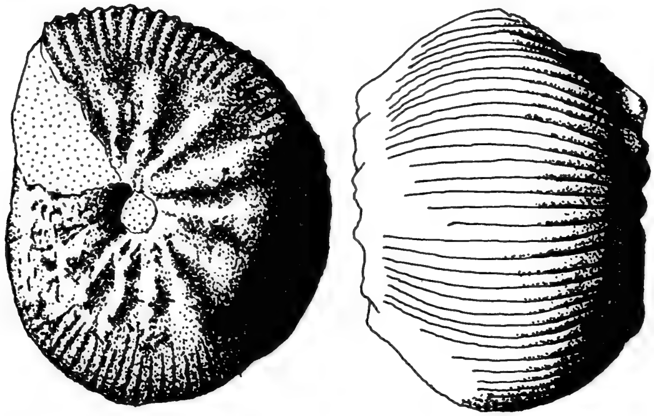

Fig. 12. *Dobrodgeiceras wilfridi* (Karakasch). The holotype of *Holcostephanus wilfridi* Karakasch from the Upper Valanginian of Crimea (after Karakasch 1902). × 1.

(Fig. 12) of which they considered *ventrotuberculatum* merely a subspecies. Riccardi & Westermann (1970) considered that the French sample was derived from a single population, and since '. . . the use of the subspecies category in palaeontology is usually confined to stratigraphically or geographically distinct taxa. . . . The interpretation of this variation as genetic polymorphism is probably correct.' According to Riccardi & Westermann (1970), the position of the flank tubercles in *Dobrodgeiceras* is ventrolateral, and not lateral or periumbilical as described by Thieuloy & Gazay (1967: 77). The similarity with *Valanginites* led Riccardi & Westermann to place *Dobrodgeiceras* within the Polyptychitinae. However, since this subfamily is generally distinguished by the branching of the secondaries, a feature unknown in both *Valanginites* and *Dobrodgeiceras*, there appears no reason why they should not preferably be included within the Olcostephaninae.

Valanginites is a much misunderstood genus although the situation has recently been clarified somewhat by Thieuloy (1977*a*). Thus, a survey of the literature shows that at some time or other most strongly inflated, coarsely ribbed olcostephanids have been referred to this genus. Spath (1930) included *O. perinflatus* (Matheron) and *O. stephanophorus* (Matheron) in this genus, rectifying his mistake in 1939, but now including *O. crassus* (Zwierzycki) and, tentatively, *Holcostephanus bachelardi* Sayn into *Valanginites*. Imlay (1938) erected the species *Valanginites angusticoronatus* for a coarsely ribbed, inflated form which is herein considered to be an *Olcostephanus*, very close to *O. rogersi* (Kitchin) (♀). The only undoubted species of *Valanginites* appear to be the type species *V. nucleus* (Römer), of which *V. utriculus* (Matheron) was considered a synonym by Roch (1930), *V. dolioliformis* (Roch) (Fig. 13), *V. tijerensis* Imlay, *V. psaephoides* (Mayer–Eymar) (including *V. bachelardi* (Sayn)), and *V. simplus* (d'Orbigny). Of these, umbilical tubercles are present in *V. dolioliformis* and *V. tijerensis*.

Leanza (1957) described four species of the Hauterivian genus *Simbirskites* from the Upper Valanginian of Argentina. Rawson (1971: 42), however, considers this material generically misidentified since '. . . all four of Leanza's

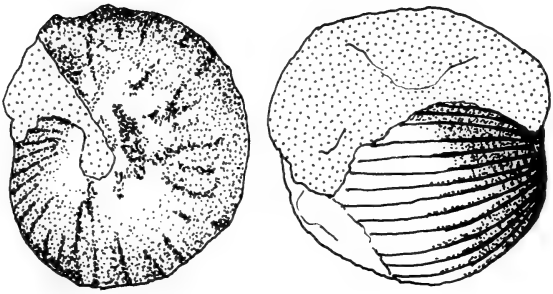

Fig. 13. *Valanginites dolioliformis* (Roch). The holotype from Morocco (after Roch 1930). × 1.

species differ from *Simbirskites* in that the ribs extend straight across the venter instead of curving forwards. Leanza's species appear closer to *Rogersites*; the recorded stratigraphical horizon (late Valanginian) would agree with this.'

The Argentinian material can immediately be precluded from the subgenera *Mexicanoceras*, *Jeannoticeras*, and *Parastieria*. They differ from *Olcostephanus* s.s. (= *Rogersites*) in having prorsiradiate primary ribs throughout ontogeny, in having a gently sloping umbilical wall and rounded umbilical shoulder throughout ontogeny, and in being more evolute. While any one, or even all, of these characters may be found at some growth stage in *Olcostephanus* s.s., they are not known to persist together throughout ontogeny. The sloping umbilical wall, coronate whorl section and prorsiradiate primaries of Leanza's *S. araucanus* are, however, all to be found in *Olcostephanus* (*Subastieria*) *nicklesi* Wiedmann & Dieni, and it is to this subgenus that the Argentinian material is best referred. The Argentinian material would seem to comprise some of the few adult examples of this subgenus yet recorded. In maturity, therefore, *Subastieria* should be regarded a close homoeomorph of *Simbirskites*; possibly the latter is descended from the former.

Thieuloy (1977*a*: 432) has recently introduced the new subgenus *Lemurostephanus* within *Olcostephanus* for forms with a very wide umbilicus (40–45% of the diameter), well-developed parabolae and primary ribs terminating in pointed bullae from which arise bundles of 2–4 secondary ribs. Besides the type species, *Holcostephanus madagascariensis* Lemoine (Fig. 14), Thieuloy (1977*a*)

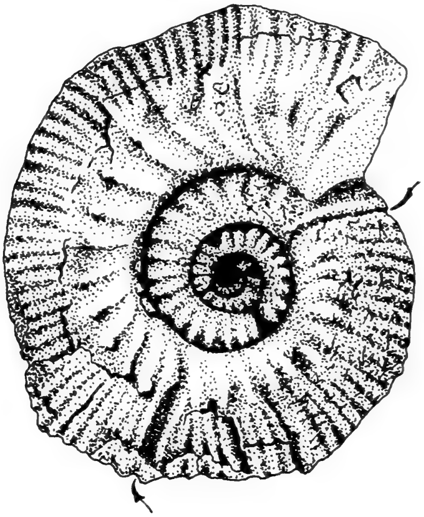

Fig. 14. *Olcostephanus* (*Olcostephanus*) *madagascariensis* (Lemoine). The holotype from the Lower Valanginian of Madagascar (after Collignon 1962). × 1.

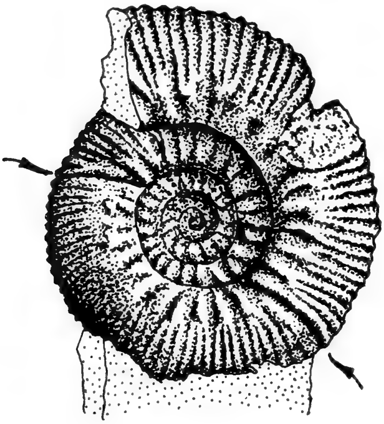

Fig. 15. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny) (♂). The holotype of *Astieria detonii* Rodighiero from Venice (after Rodighiero 1919). × 1.

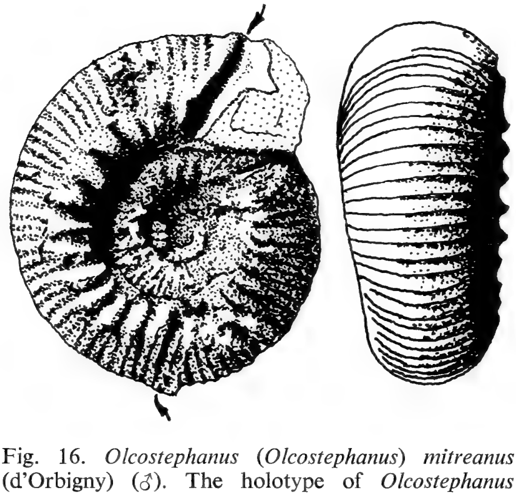

Fig. 16. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny) (♂). The holotype of *Olcostephanus wynnei* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

also included in this subgenus *Spiticeras detonii* Rodighiero (Fig. 15), *Olcostephanus wynnei* Spath (Fig. 16), *Olcostephanus mitreanus* (d'Orbigny) (Fig. 17), *O. sanctifirminensis* Thieuloy, *Holcostephanus chaignoni* Sayn, *Maderia*? *latiumbilicata* Imlay and the species of '*Simbirskites*' described by Leanza (1957) and discussed above. Of these, Leanza's '*Simbirskites*' species together with *H. chaignoni* Sayn, *Maderia*? *latiumbilicata* and *O.* (*L.*) *sanctifirminensis* can adequately be included in the subgenus *Subastieria*, whilst *Spiticeras detonii*, *Olcostephanus wynnei* and *O. mitreanus* are conspecific microconchs whose

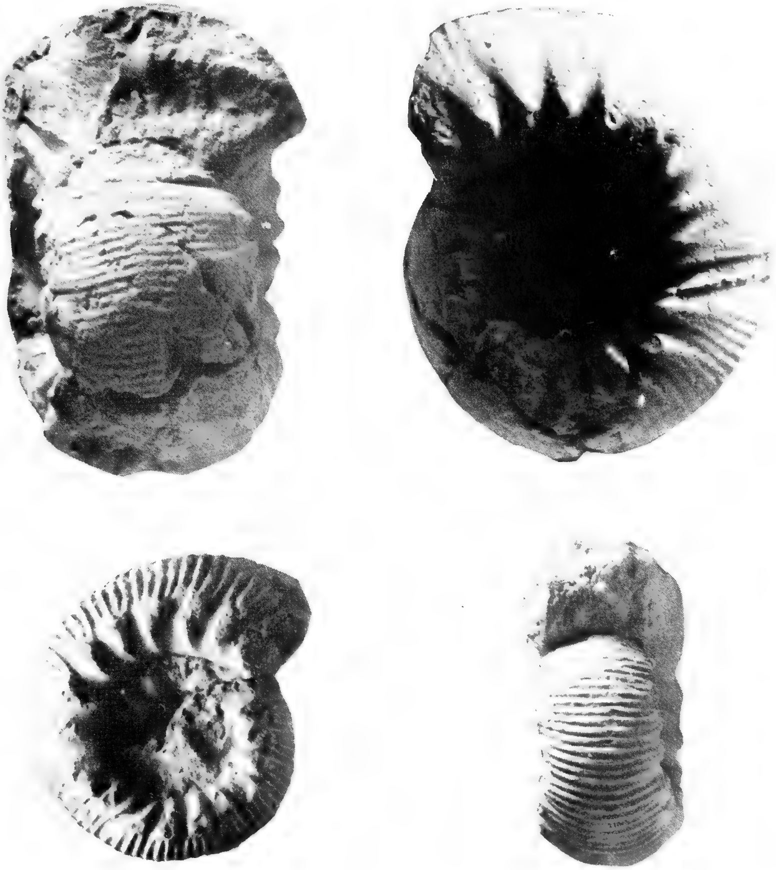

Fig. 17. *Olcostephanus* (*Olcostephanus*) *mitreanus* (d'Orbigny). The syntypes in the Natural History Museum, Paris, R3118 (D'Orbigny Collection No. 4871), of which the smaller (a microconch) has been selected as lectotype (Thieuloy 1977*a*). The paralectotype would seem to be an immature macroconch. × 1.

probable macroconch, *O. collignoni* (Besairie) (Fig. 18), is a typical *Olcostephanus* s.s. In the writer's opinion, the subgenus *Lemurostephanus* comprises an heterogeneous assemblage of *O.* (*Subastieria*) and *O.* (*Olcostephanus*) and is of little taxonomic significance. The author prefers not to use the name.

During the early ontogenetic stages (Fig. 19), the suture line of *Olcostephanus* is relatively simple with long, thin saddles and a trifid first lateral lobe (L). With ontogeny the suture becomes very deeply incised (Fig. 20K) with long, thin folioles and lobules. *Olcostephanus* (*Subastieria*) *hispanicus* (Mallada) (Fig. 20H–I) shows a similar suture line, as does *Dobrodgeiceras broggianum* (Lissón), although in the latter the saddles are broader and shorter (Fig. 20J).

The following subdivisions within the Olcostephaninae are here recognized:

S. (*Saynoceras*). Small, inflated microconchs with trapezoidal whorl sections.

Fig. 18. *Olcostephanus* (*Olcostephanus*) *collignoni* (Besairie) (♀). The holotype from the Upper Valanginian of Ambiky, Madagascar. × 1.

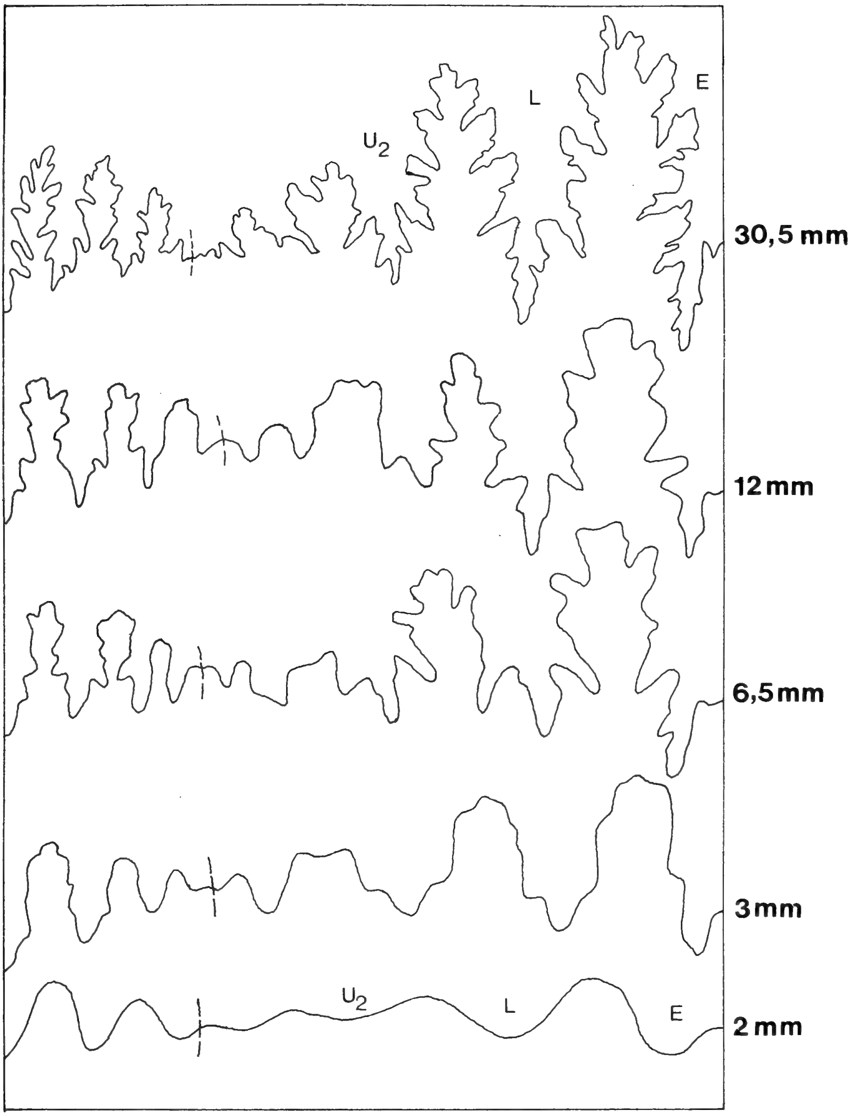

Fig. 19. Sutural ontogeny of *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂) (after Riccardi *et al.* 1971).

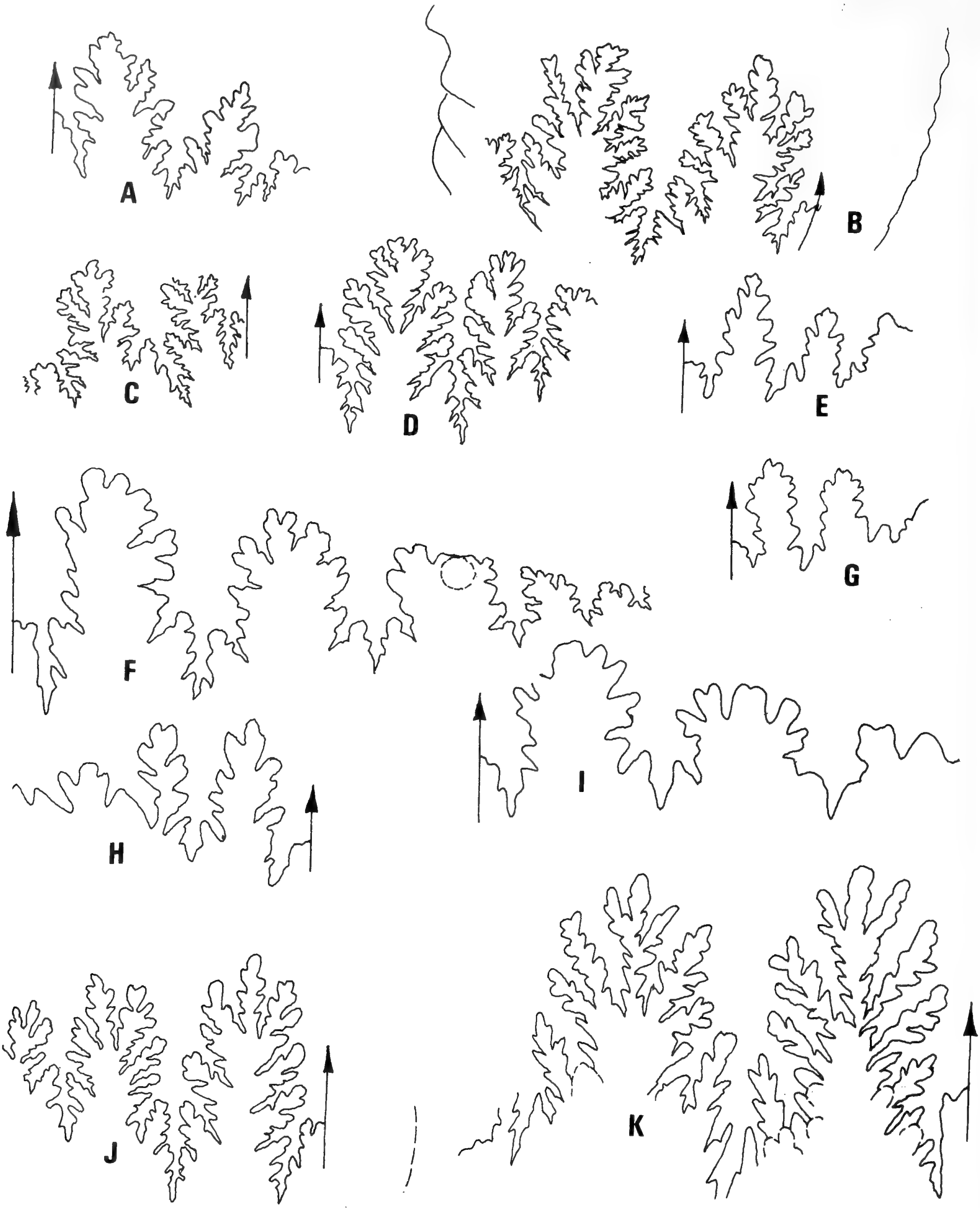

Fig. 20. Olcostephaninid suture lines. A. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian) (after Baumberger 1908). B. *Olcostephanus* (*Olcostephanus*) *imbricatus* (Baumberger) (after Baumberger 1908). C. *Olcostephanus* (*Olcostephanus*) *leptoplanus* (Baumberger) (after Baumberger 1907). D. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen) (after Tzankov 1943). E. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (after Tzankov 1943). F. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (after Pictet & Campiche 1860). G. *Valanginites bachelardi* (Sayn) (after Tzankov 1943). H,J. *Olcostephanus* (*Subastieria*) *hispanicus* (Mallada) (after Tzankov 1943). I. *Dobrodgeiceras broggianum* (Lísson) (after Riccardi & Westerman 1970). K. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath); drawn from the holotype, × 1.

Umbilical tubercles give rise to 1–2 weak ribs leading to ventrolateral tubercles; ribbing normally subordinate to tubercles on outer whorl, but may be sharp at some stages (after Wright *in* Arkell *et al.* 1957). Age: low Upper Valanginian.

S. (*Ceratotuberculus*). Small, inflated, like *Saynoceras*, but with more, 2–4, secondaries per tubercle, and with a smooth ventral furrow. Age: Lower Hauterivian.

O. (*Olcostephanus*). Compressed to inflated forms, usually with primary ribs terminating in tubercles on the umbilical shoulder, from which secondary ribs diverge in fasciculate bundles to pass uninterrupted across the venter. Parabolae may or may not be present. Dimorphic; males small, with lappets, females large and with simple peristomes. Age: Valanginian–Middle Hauterivian.

O. (*Subastieria*). Similar to *O.* (*Olcostephanus*), but with sloping umbilical wall, prorsiradiate primaries and a coronote whorl section throughout ontogeny. Adults homoeomorph *Simbirskites*. Age: Upper Valanginian–Lower Hauterivian.

O. (*Parastieria*). Based upon a lappeted microconch species. Inner whorls with numerous, fine primaries giving rise to 2–3 flexuous secondary ribs with intercalatories between bundles. Body chamber high-whorled, compressed, with slightly sinuous, broad, flat-topped ribs and no umbilical tubercles, Age: Lower Hauterivian.

O. (*Jeannoticeras*). Similar to *O.* (*Parastieria*) from which it is doubtfully separable, but with fine bundled ribbing retained on to the adult body chamber. Dimorphic. Age: Lower Hauterivian.

O. (*Mexicanoceras*). As for *O.* (*Olcostephanus*) but small, with ribs interrupted on outer whorls by a ventral furrow. Age: ?Lower Hauterivian.

Dobrogeiceras. Like *O.* (*Olcostephanus*) but very involute; umbilical tubercles have moved to the ventrolateral position, with a consequent lengthening of the prominent primary ribs. Ventral tubercles (?dimorphic) may be present on the body chamber. Age: Upper Valanginian.

Jeanthieuloyites. Similar to *Olcostephanus*, but with long, radial, nontuberculate primaries extending to mid-flank where they regularly bifurcate. Prominent, oblique parabolae. Age: Upper Valanginian.

Valanginites. Extremely inflated with very narrow umbilicus. Umbilical tubercles weak to absent. Secondary ribbing coarse, simple. Age: Upper Valanginian.

Capeloites. Small, compressed, with lappets (microconch). Inner whorls with prominent umbilical bullae from which pairs of ribs (the adoral one thick and robust and the adapical one fine and delicate) are looped to siphonal clavi. Intercalatories occur. On the body chamber siphonal clavi disappear, umbilical bullae weaken considerably, and all secondaries become fine, sinuous, passing uninterrupted across the venter. Age: Uppermost Valanginian–basal Hauterivian.

SEXUAL DIMORPHISM IN AMMONITES

It has long been noted that many ammonites occur in both large and small forms within the same stratum. Whereas the large forms have simple peristomes, the persitomes of the small forms frequently have various types of apertural adornment, e.g. lateral lappets, ventral rostra, ventral horns, etc. Furthermore, many such pairs were seen to have identical early whorls. This led to the concept of sexual dimorphism and, by analogy with extant invertebrates, the large forms were taken to represent the females and the smaller forms the males. Within recent years much attention has been given to the phenomenon of sexual dimorphism within fossil Cephalopoda (Callomon 1957, 1963; Makowski 1962*a*, 1962*b*; Westermann 1964, 1969; Houša 1965; Lehmann 1966, 1969; Palframann 1966, 1967; Cope 1967; Cobban 1969; Zacharov 1969; Reyment 1971; Riccardi *et al.* 1971; Kennedy & Cobban 1976), and it is now a widely accepted phenomenon.

It has often been noted, and Makowski (1962*a*) in his classical study placed much emphasis on the fact, that the inner whorls of the female are invariably identical to the male dimorph.

Douvillé (1880), in his study of *Morphoceras pseudoanceps*, noted that it had inner whorls identical to those of *M. polymorphus* and suggested that they possibly represented a dimorphic pair. Haug (1893) found that the inner whorls of *Sonninia sowerbyi* and *S. sulcata* were identical, and hence indistinguishable, up to a diameter of 30 mm, after which the later ontogenetic stages differed markedly. Makowski (1962*a*) has provided numerous examples from such widely diversified groups as the haploceratids, stephanoceratids, hildoceratids, cheiloceratids, and the scaphitids, where the inner whorls of the large macroconchs (♀) were identical to the smaller microconchs (♂). Palframann (1966) showed *Creniceras renggeri* (Oppel) and *Taramelliceras richei* (de Lorial) to be identical in every feature up to a diameter of about 8 mm. On the body chamber *T. richei* differed from *C. renggeri* in the development of ventrolateral spines. Furthermore, the peristome of *C. renggeri* was highly ornate, whereas that of *T. richei* was relatively simple. Palframann concluded that *C. renggeri* and *T. richei* were merely male and female of the same species. Similar identity of the early growth stages of *Distichoceras bicostatum* (Stahl) and *Horioceras baugieri* (d'Orbigny) led Palframann (1967) to consider them to represent a sexually dimorphic pair. Sutural approximation within a juvenile macroconch of *D. bicostatum* led Palframann (1967: 73) to suggest '. . . it may be that the specimen in question has changed sex during life as do some living molluscs. The latter explanation is considered unlikely though, as this feature has not been seen in other specimens studied here, the explanation of the phenomenon is itself, no doubt, unusual.'

Cope (1967), in a re-examination of the fauna of the Upper Kimmeridge Clay of Dorset, observed a unique type of dimorphism in the perisphinctid *Pectinatites*, in which the apertural ornament of the microconch is in the form of a ventral horn. As a general rule, he found that in this genus the microconch was usually slightly coarser ribbed than its macroconch at a similar diameter.

Riccardi *et al.* (1971) observed that identity of ornament between *Olcostephanus atherstoni* (Sharpe) dimorphs was restricted to the nucleus under 20 mm in diameter.

It is significant, however, that in all cases where there is identity of early ontogenetic stages in ammonites the change is always from a younger, typically male-type morphology to an older female-type morphology. According to Fretter & Graham (1964: 130) '. . . consecutive hermaphrodites change sex once in their lives, usually from a younger male to an older female phase', whilst Henderson & Henderson (1967: 478) define protandry as the '. . . condition of hermaphrodite plants and animals where male elements mature and are shed before female elements mature'.

A necessary prerequisite for the hypothesis of protandrism is, therefore, that the forms involved are simultaneous hermaphrodites. To prove this it would be necessary to study the soft parts of an ammonite, an obvious impossibility.

Whilst hermaphroditism is virtually unknown among extant Cephalopoda, having been recorded from but a single specimen of *Octopus vulgaris* (Pickford 1947: 522), it is known to occur in many species of Bivalvia and Gastropoda. Indeed, a tendency towards protandrism is frequent in many simultaneous hermaphrodites. Amongst the Bivalvia simultaneous hermaphroditism is known in *Pecten*, *Chlamys*, *Cardium*, *Teredo*, *Poromya*, etc. Not all species of these genera are, however, hermaphroditic. Thus *Cardium edule* is dioecious; whilst in some simultaneous hermaphrodites, e.g. *Teredo diegensis*, a certain number of young males never change sex and must therefore be regarded as true males.

In the Gastropoda simultaneous hermaphroditism is well known amongst the opisthobranchs and the pulmonates, as well as occurring to a limited extent in the prosobranchs, e.g. *Diodora*, *Puncturella*, *Patella*, etc. Whilst *Diodora* is predominantly dioecious, Bacci (1947) has shown about 12 per cent to be protandrous hermaphrodites. Orton (1920) claimed that 90 per cent of a population of *Patella vulgata* changed sex from male to female. Orton *et al.* (1956) found small specimens of *P. vulgata* (16–25 mm shell length) to be 90 per cent males; those with shells 40 mm long were male and female in equal proportions, whilst those with a shell length of 60 mm were 60–70 per cent females. With the exception of the well-known protandrous hermaphroditism of *Crepidula* (Coe 1936), little is known of the conditions in the other hermaphroditic prosobranchs, beyond the fact that most seem to be protandrous consecutive hermaphrodites.

It can be seen, therefore, that protandrous hermaphroditism, and consequently also simultaneous hermaphroditism, are well known in the other molluscan classes and it seems possible that it was at some stage equally common in the Cephalopoda. The fact that extant cephalopods are dioecious is not, therefore, in itself significant since, according to Fretter & Graham (1964: 128), '. . . there is some evidence for regarding the hermaphroditic state as the primitive one, especially in the phylum Mollusca'.

When the literature on sexual dimorphism in ammonites is studied, it is found that the occurrence of rare, aberrant mutants supports the possibility that some ammonites were, in fact, hermaphroditic.

Makowski (1962*a*: 23) considers the genus *Hecticoceras* to exhibit type 'A' dimorphism, i.e. microconchs have 5–6 whorls and macroconchs at least 7, with a morphological hiatus of one whorl between the two dimorphs. However, of the 21 specimens studied, Makowski noted that 3 examples had '. . . 6½ whorls each, their aperture is not quite simple, but is nearing that of the growth stages of large forms and provided with small broad lappets. However, the spiral pattern followed is that of large forms, completely different from the spiral in the small forms. Hence, they should be regarded as large forms whose growth halted at the stage with about 6½ whorls.' Makowski (1962*a*) makes no mention of whether he is dealing with a single species, and thus the true value of the observation is lost. If, however, the *Hecticoceras* in question were all referable to a single species, then this combination of male (lappets) and female (spiral form) characteristics would seem to suggest hermaphroditism.

Cope (1967: 53) recorded 4 specimens of *Pectinatites* (*Virgatosphinctoides*) *reisiformis densicostatus* Cope which he considered to be 'intersexual'. Thus, '. . . one specimen is intermediate in size between macroconch and microconch and has rib density of a typical microconch up to a diameter of 30 mm. Thereafter it becomes more finely ribbed, and is intermediate between macroconch and microconch in rib density'.

'At a diameter of 94 mm a horn is developed, and beyond this there is about three-eights of a whorl of coarsely ribbed shell with sculpture similar to the outer whorls of a macroconch, but bearing four further horns . . . in addition to the above specimen which is absolutely intermediate in character between macroconch and microconch, three other specimens show a slight degree of intersexuality. These three specimens are apparently normal macroconchs to judge by their size, rib density and sculpture. They do, however, develop a type of horn in the later stages of development; this appears at a diameter of 140–150 mm and is unlike the true microconch horn in that it is developed from a single rib, has negligible ventral projection but projects laterally some distance down the whorl side. In addition, the diameter at which these structures are developed is much greater than that at which the true horn of the microconch occurs.'

Whilst the intermediate size of the mutants described by Cope (1967) need not necessarily be significant in view of the possible size overlap between dimorphs, as was noted by Cobban (1969: 9) in his study of *Scaphites leei* and *S. hippocrepis*, the typical female-type ribbing, associated with male-type ornament is, and must surely be, interpreted not as intersexuality but rather as bisexuality.

It is suggested that these rare observations of apparent bisexuality, and thus hermaphroditism, support the evidence provided by the shells of sexually dimorphic ammonites that some ammonites changed sex from a younger male phase to an older female state, and thus provide the first examples of protandrism within the class Cephalopoda. It should be noted, however, that by analogy with extant Mollusca, not all species of even a single genus need be protandrous, nor even hermaphroditic.

Little is known of the exact reasons for protandric changes within those molluscs which are simultantous hermaphrodites. Pellegrini (1948), in his study of *Patella coerulea*, concluded that the change of sex was restricted to the resting period between successive breeding seasons and liable to affect animals of any age. Fretter & Graham (1964) consider the change to take place in such a way as to render the animals one sex early in the breeding season, and of the other sex later, or there may have been a winter pause between the two phases. According to Barnes (1968: 309) the sex of the older individuals is influenced at least partly by the presence or absence of other sexes in teh association. Thus, in *Crepidula* '. . . young specimens are always males. This initial male phase is followed by a period of transition in which the male reproductive tract degenerates; the animal now develops into a female or another male. . . . An older male will remain male as long as it is attached to a female. If such a male is removed or isolated it will develop into a female. The presence of a large number of males influences certain of the males to become females. When the individual once becomes female, it remains in that state.'

The work of Gould (1919, 1947) and Coe (1938*a*, 1938*b*, 1944, 1948) suggests that the transition from male to female occurs at different times in different individuals, indicating sex changes to be influenced by other animals in the chain, and by external stimuli.

When immature limpets are cultured in association with mature females, the great majority assume the functional male phase. Gould (1919, 1952) presented evidence, later supported by Coe (1953), to show that the formation and maintenance of the male phase is influenced by a substance or substances secreted in the water by mature females. Not all young males react in the same way to the mating stimulus.

SEXUAL DIMORPHISM IN *OLCOSTEPHANUS*

Within the Uitenhage olcostephanid fauna, sexual dimorphism is very apparent due to the unusually large size attained by the macroconch forms, some of which exceed 300 mm in diameter, whereas the largest undoubted microconch so far recorded from these beds is only slightly more than 100 mm in diameter, with the average far less. As recognized within many of the European Jurassic faunas, there are two distinct size groups (Fig. 21)—small forms with lappets and large forms with simple peristomes. However, these two distinct size groups comprise three morphological components (see Figs 22–23). There are small forms, both with and without parabolae, which bear lateral lappets and represent microconchs; there are moderately large strongly inflated forms, falling both into the microconch and macroconch size groups, both with and without parabolae and invariably without the peristome preserved; and,

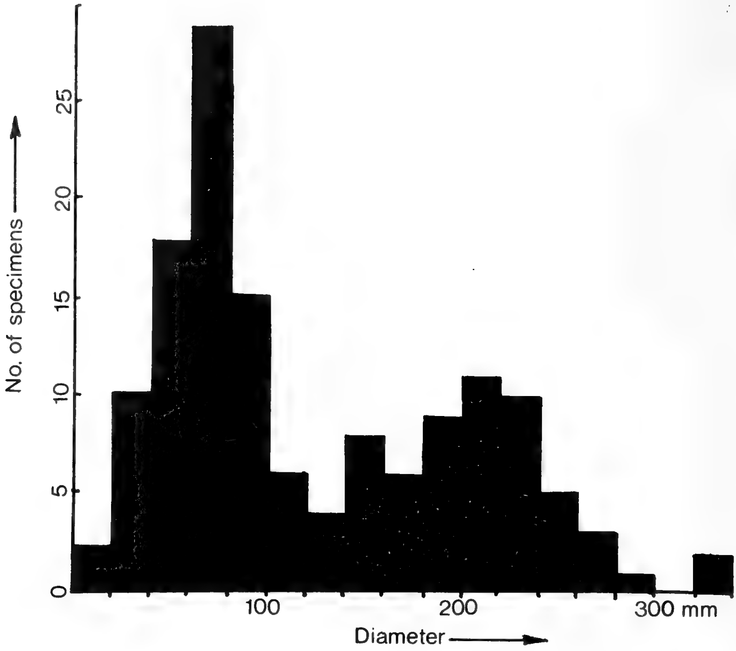

Fig. 21. Size-frequency histogram of the Uitenhage *Olcostephanus* fauna, showing the double peak corresponding to microconch and macroconch dimorphs.

finally, there are gigantic, generally strongly inflated forms lacking parabolae and with simple peristomes representing mature macroconchs. The intermediate groups have one feature in common; they are all inflated beyond the limits of microconchs and hence must be considered immature macroconchs. However, many of them differ from mature macroconchs in possessing parabolae, features which never occur on the outer whorls, except in the form of the simple peristome, of mature female forms. That some macroconchs had parabolae on their earliest whorls is revealed by a gigantic phragmocone of *O. rogersi* (Kitchin) (Fig. 71A–D), corresponding to a diameter of approximately 200 mm, which shows the impression on an inner whorl, corresponding to a diameter of about 60 mm, of a prominent parabola. Parabolae would seem, therefore, to be restricted to the inner whorls of certain macroconchs, and to certain microconchs. Whether parabolae are the product of male genetic control alone, thereby providing evidence of protandry in *Olcostephanus*, is uncertain in view of the slight but significant morphological differences between the inner whorls of macroconch forms and the microconch dimorph beyond a diameter of 20 mm. As concerns *O. baini* (Sharpe) dimorphs, the macroconch is already distinguishable at 30 mm diameter from the microconch by its slightly more numerous secondaries, with invariably 3 secondaries per bulla as against the 2–3 of the microconch. This is in accord with the observations of Cope (1967) on dimor-

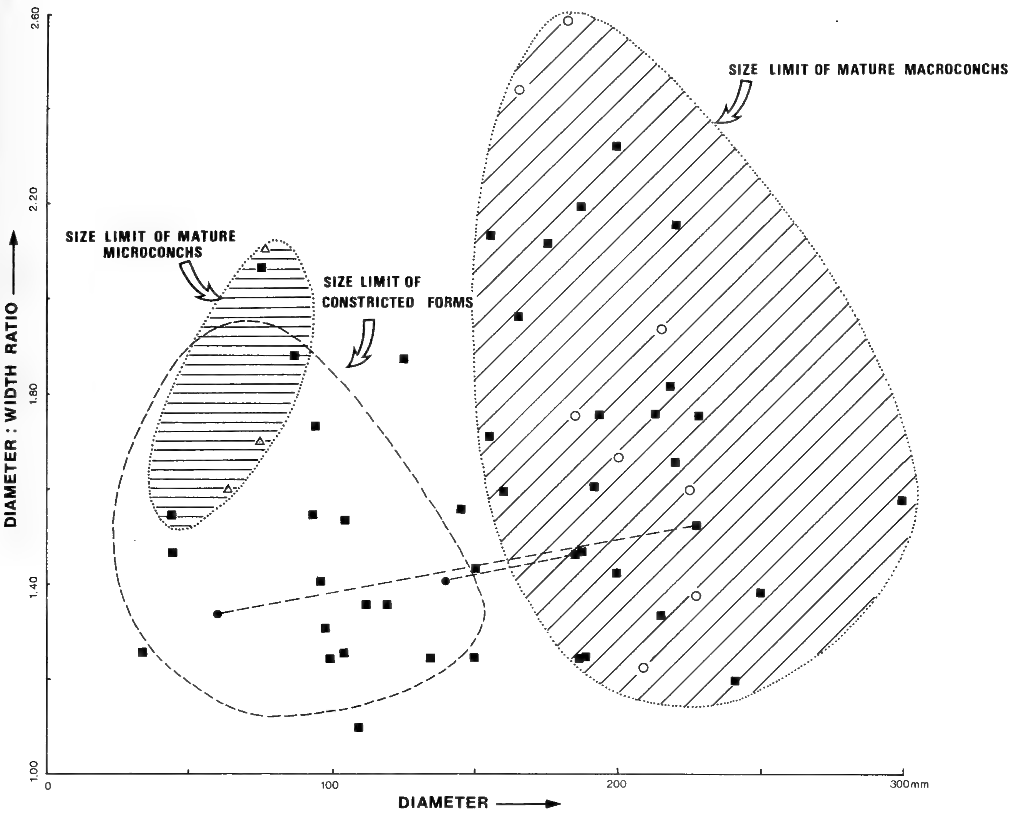

Fig. 22. Diameter/inflation plot for the unconstricted individuals of *Olcostephanus* from the Sundays River Formation. Squares = unconstricted forms; open triangles = unconstricted forms with lappets; circles = unconstricted forms with simple peristome.

phism in the Upper Jurassic genus *Pectinatites*, and also those of Riccardi *et al.* (1971) on *Olcostephanus*, that the inner whorls of the macroconch forms tend to be slightly more densely ribbed than the microconch dimorph.

The largest diameter at which parabolae have been observed is approximately 120 mm diameter, whilst an immature macroconch of *O. baini* (Sharpe), recognizable by its denser ribbing, shows a noticeable increase in inflation immediately after a parabola at 60 mm diameter (Fig. 151B–D).

Within the Uitenhage fauna there is no size overlap between corresponding macroconchs and microconchs.

THE PERISTOME IN *OLCOSTEPHANUS*

The commonest modification to the microconch aperture is the development of lateral lappets although, as already noted, in some ammonites this takes the form of a rostrum, a ventral lappet, or a ventral horn.

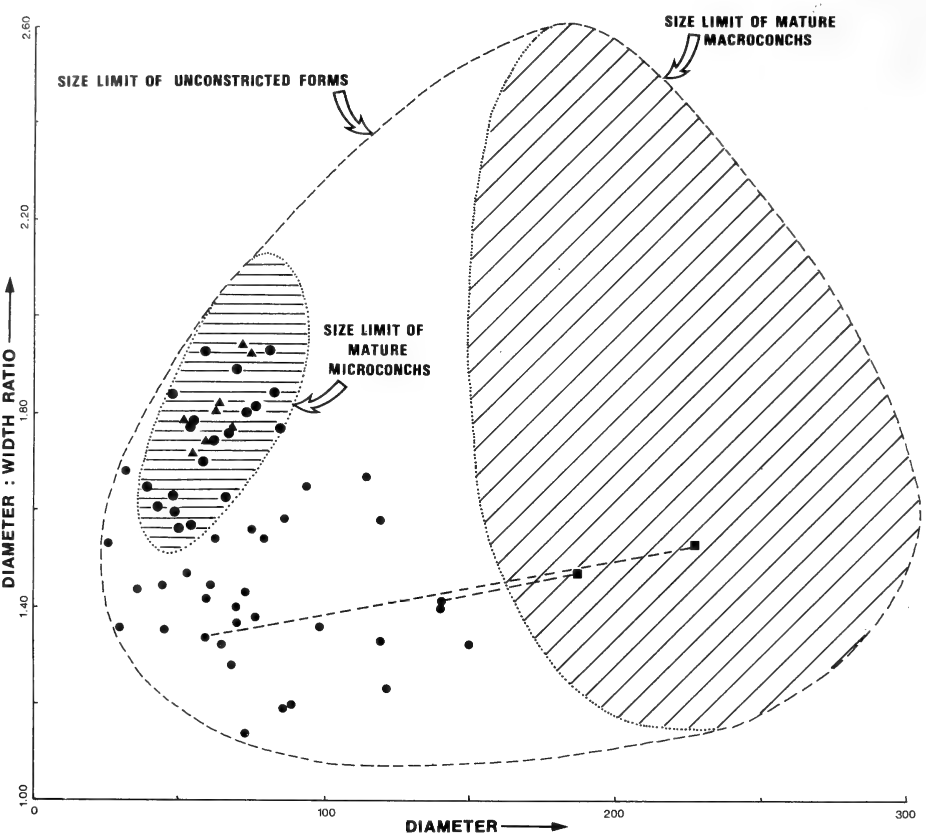

Fig. 23. Diameter/inflation plot for the constricted individuals of *Olcostephanus* from the Sundays River Formation. Dots = constricted forms; closed triangles = constricted forms with lappets.

The function of these apertural extensions has long been a subject of contention. Thus, Cope (1967: 17) considered the ventral horn in *Pectinatites* to possibly have assisted in copulation by housing the spadix. According to Bidder (*in* Westermann 1971), however, such a horn was more likely a median glandular modification equivalent to Van der Hoeven's organ. Lappets have even been compared with the claspers of insects, but according to Arkell (*in* Arkell *et al.* 1957: L92) '. . . their only conceivable function seems to be protective. In planulate and sphaerocone shells Westermann (1954) has noted that the microconchs frequently have exceptionally large, converging, lateral lappets, which caused the aperture to become occluded. According to Westermann (1971) such '. . . occluded apertures are obviously "specialized" features preventing macrophagous predation'. None the less, he was led to conclude that '. . . the function of the diverse apertural shapes, however, remains unknown'. It seems to the writer most reasonable to interpret them as display characters, designed to attract females.

Lateral lappets are preserved in a number of examples of *Olcostephanus* from the Uitenhage Group, usually as internal moulds, although in a single specimen (Fig. 131A–B) the peristome is preserved as recrystallized test. In this microconch the peristome comprises a deep, slightly flexuous constriction, bordered adapically and adorally by prominent parabolic ribs. The adapical rib is prominently flared, whilst the adoral rib is associated with well-developed lateral lappets. On this same specimen, SAM–PCU1527, the outer whorl is seen to bear a parabola which takes the form of a prominent, deep, oblique constriction bordered by strongly developed parabolic ribs, the adapical rib being more strongly flared than that to the anterior. The parabola truncates ribbing adapically, but is parallel to the adoral ribbing. That such parabolae are associated with halts in growth is evidenced by the change in ribbing direction adorally, and often by a distinct change in inflation immediately after such a feature. Such parabolae are thus virtually identical to the peristome and must surely have an identical mode of formation. However, according to Arkell (*in* Arkell *et al.* 1957: L93) '. . . they [parabolae] are not, however, the same as the peristome of the adult shell, for often no such constriction or other features may be found at the end of the adult body chamber'. In *Olcostephanus* this is never the case, and it seems inconceivable that they owe their origins to two unrelated processes. Consequently, parabolae in *Olcostephanus*, at least, are interpreted as relict peristomes.

Accepting parabolae in *Olcostephanus* to represent relict peristomes, it is of interest to note that in many extant gastropods, e.g. *Charonia tritonis tritonis* (Linnaeus), the whorls are ornamented with varices which represent the position of relict apertures developed during halts in growth. They would appear, therefore, to be absolutely analogous to the parabolae occurring in *Olcostephanus*. What is especially interesting is the fact that in extant Gastropoda they are known to be of specific importance.

HOMOEOMORPHY IN *OLCOSTEPHANUS*

A significant feature associated with sexual dimorphism in *Olcostephanus* is a striking degree of convergence in the outer whorls of macroconch forms. This was already noted by Makowski (1962*a*: 21) who wrote '. . . we may note the side by side existence of large forms (macroconchs) whose last whorls and particularly the last body chamber are identical, while their young forms differ in section or in character of ornamentation. These differences, being not very striking, are not taken into account in the specific delimitation of large forms (macroconchs), they are, however, very readily discernible in small forms (microconchs) which repeat the character of the young whorls of large forms (macroconchs).'

It was this pitfall that led Riccardi *et al.* (1971) to regard *O. schenki* (Oppel)

(= *O. baini* ♀), a species with prominent parabolae, as merely the inner whorls of the large *O. atherstoni* macroconch, whilst their microconch forms of *O. atherstoni*, viz. *O. psilostomus* Neumayr & Uhlig, *O. wilmanae* (Kitchin), and *O. midas* (Leanza), do not possess such features.

With regard to convergence within macroconch forms of *Olcostephanus*, Spath (1930: 143) noted that '. . . examples like those figured by Burckhardt or by Böse from Mexico as *Astieria* cfr. *atherstoni* and *A.* ex. aff. *atherstoni* represent the outer whorls of *Olcostephanus* of the *astierianus–filosus* group such as are common in the south of France' and that '. . . it is probable that in each area that had its *Olcostephanus* fauna there were developed "*atherstoni*" forms which thus do not constitute a true species but are merely homoeomorphous local variants of the common root-stock' (Spath 1930: 34).

This convergence is very evident in the macroconch forms of the Uitenhage olcostephanid fauna. Thus, the macroconch forms of *O. atherstoni* (Sharpe) and *O. baini* (Sharpe) differ only in degree of inflation, whilst with a broad specific interpretation it would be possible to group most *Olcostephanus* macroconchs within a single species. By far the most important factor in the matching of sexual dimorphs is a close similarity between the inner whorls of the macroconch and the microconch dimorph. In those forms studied by Makowski (1962*a*) there was complete identity. In *Olcostephanus*, however, as noted by Riccardi *et al.* (1971: 96), identity of ornament is restricted to the nucleus under 20 mm diameter, with the inner whorls of the *O. baini* macroconch being slightly more densely ribbed at 30 mm diameter than the microconch at 50 mm diameter.

The fact that three morphological types, i.e. the microconch, the macroconch, and the inner whorls of the macroconch, may be distinguished within a single species has led to a proliferation of names, the majority endemic, which together with an almost complete disregard for intraspecific variation has led to taxonomic confusion.

DESCRIPTION OF THE SUNDAYS RIVER SPECIES OF *OLCOSTEPHANUS*

Olcostephanus (*Olcostephanus*) *atherstoni* (Sharpe, 1856)

Figs 9, 19, 24–26, 27A–D, 28–43, 55, 118, 143C–D, 151A

Microconch (♂)

Ammonites astieri Pictet & Campiche (*non* d'Orbigny), 1860: 298, pl. 43 (figs 1, 3 only).
Olcostephanus psilostomus Neumayr & Uhlig, 1881: 149, pl. 32 (fig. 2).
Astieria aff. *psilostoma* (Neumayr & Uhlig) von Koenen, 1902: 151, pl. 54 (fig. 21).
Astieria psilostoma (Neumayr & Uhlig) von Koenen, 1902: 151. Baumberger, 1907: 35, pl. 24 (fig. 6), pl. 21 (fig. 4), figs 111–113.
Astieria atherstoni (Sharpe) Baumberger, 1907: 39, pl. 21 (fig. 3), pl. 24 (figs 2, 5 only).
Astieria leptoplana Baumberger, 1908: 9, pl. 28 (fig. 2 only).
Holcostephanus wilmanae Kitchin, 1908: 195, pl. 9 (fig. 1).
Holcostephanus (*Astieria*) *psilostomus* (Neumayr & Uhlig) Wegner, 1909: 85.
Holcostephanus (*Astieria*) *psilostomus* var. *picteti* Wegner, 1909: 85.
Holcostephanus (*Astieria*) *psilostomus* var. *wilmanae* Kitchin, Wegner, 1909: 86.
Holcostephanus (*Astieria*) *psilostomus* var. *koeneni* Wegner, 1909: 86.

Fig. 24. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the holotype, BM–C32202, × 1. Photo W. J. Kennedy.

Fig. 25. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Ventral view of the holotype, BM-C32202. × 1. Photo W. J. Kennedy.

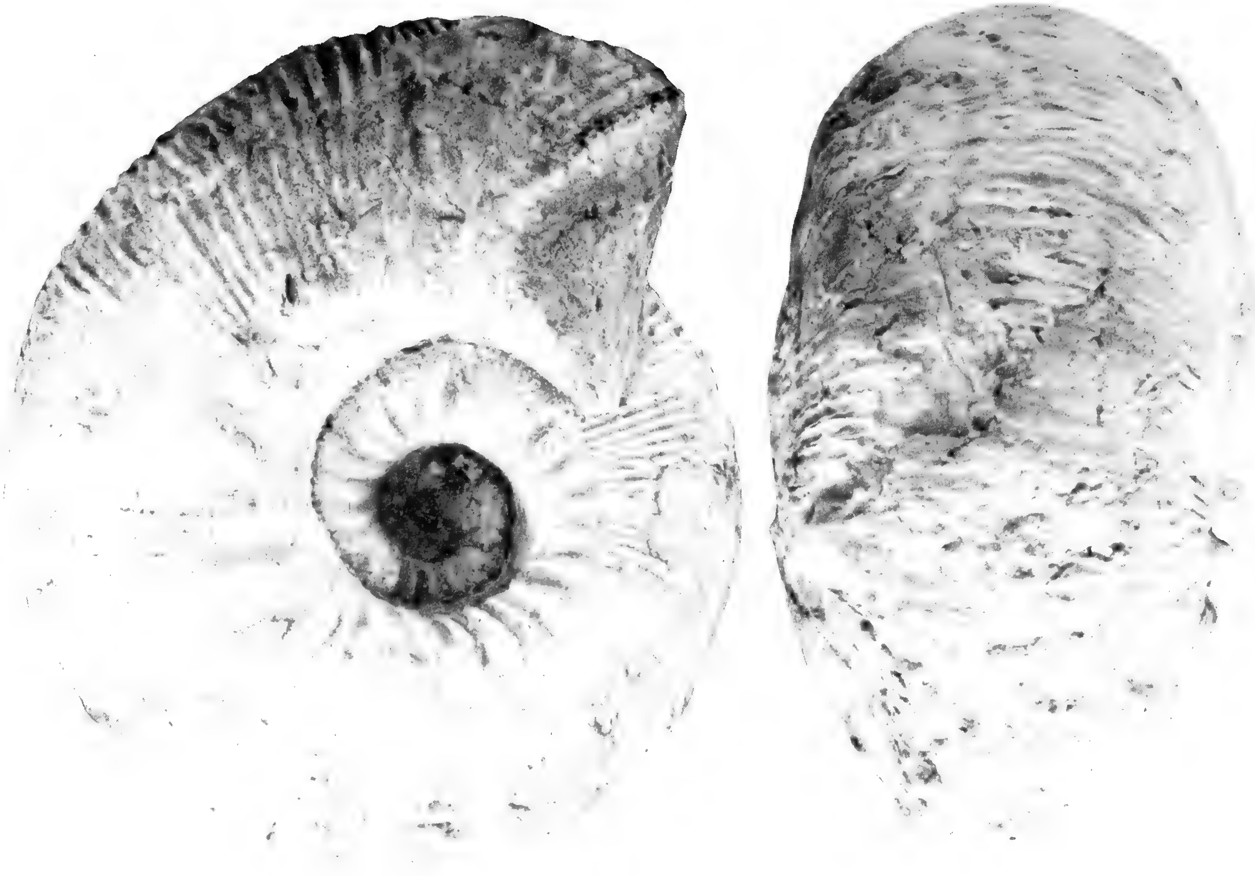

Fig. 26. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral and ventral views of BM–C47128. Note constant rate of inflation and constricted peristome. × 0,44.

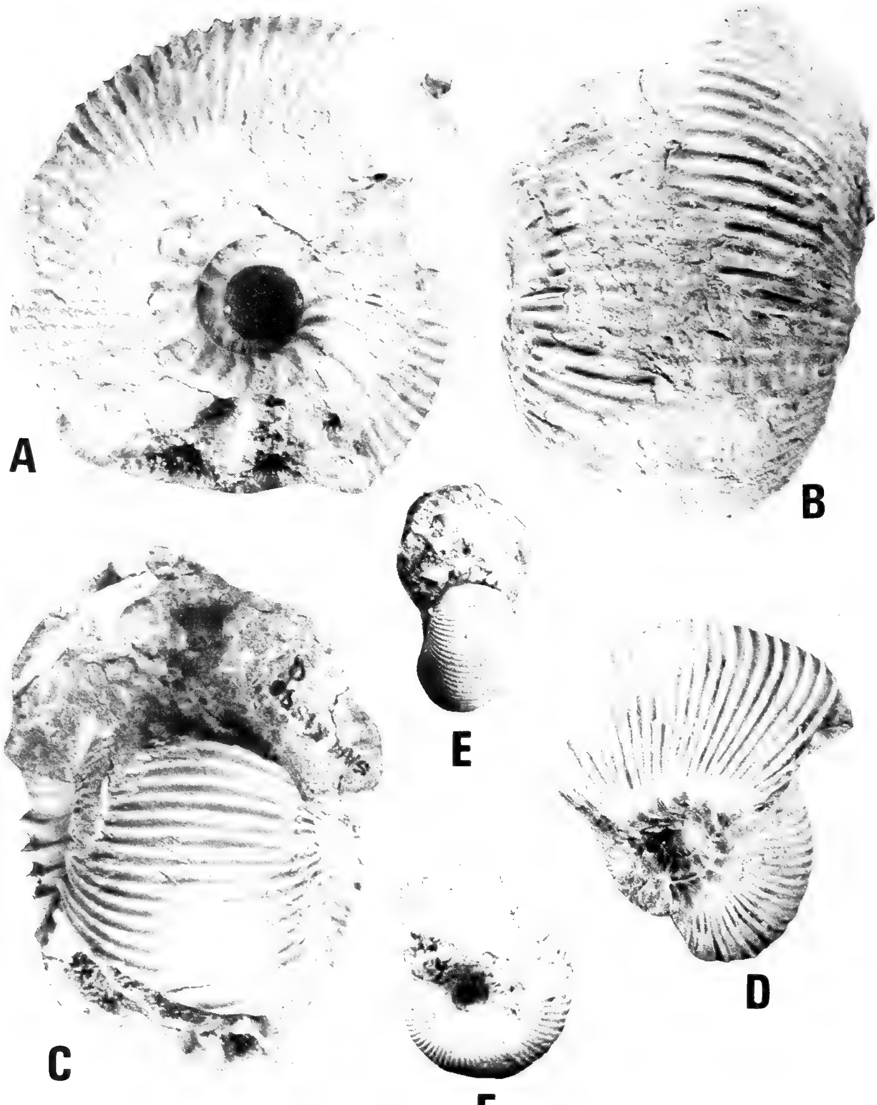

Fig. 27. A–C. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀), × 0,66. Lateral, ventral and front views of SAM–PCU1590. D. Lateral view of a slightly crushed specimen. SAM–PCU1585. E–F. *Olcostephanus* (*Olcostephanus*) ?*densicostatus* (Wegner) sp. juv. Front and lateral views of SAM–PCU1612, × 1.

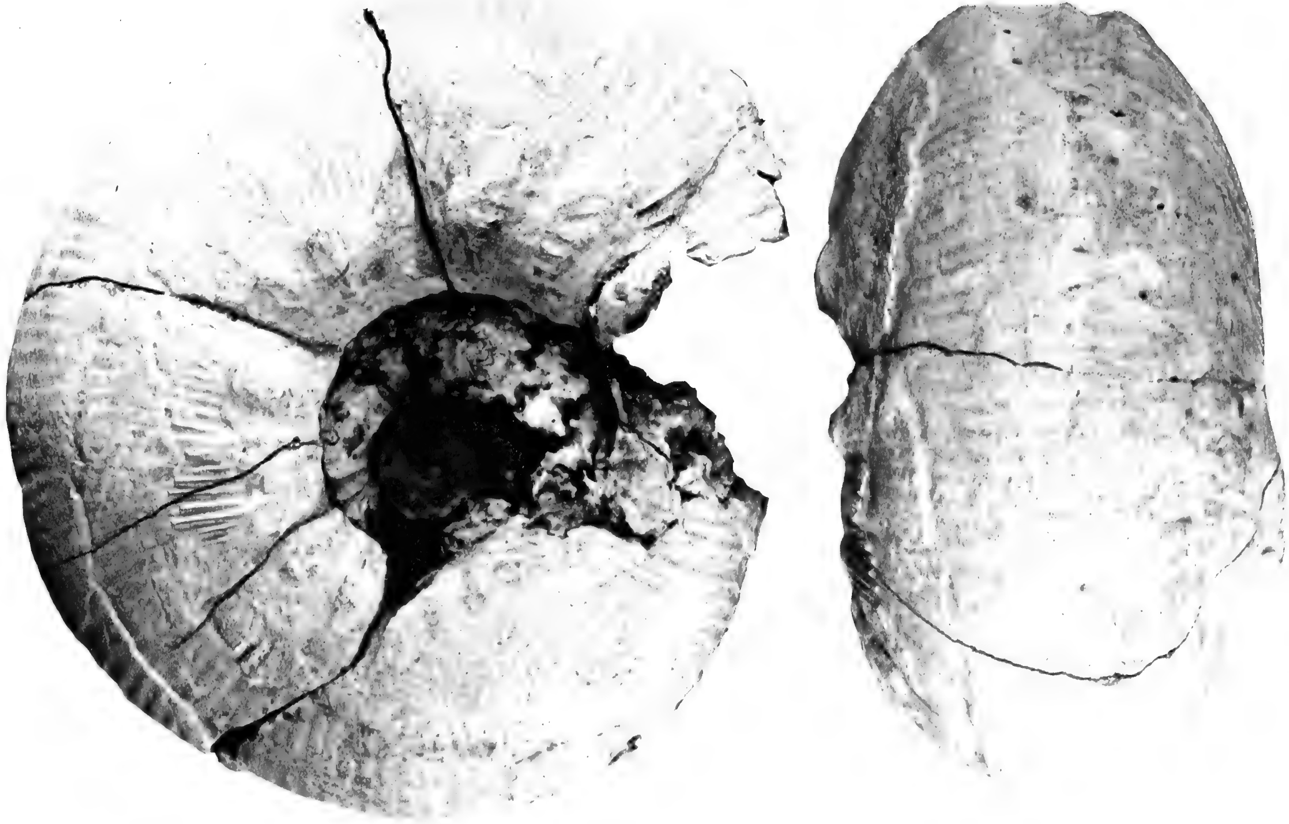

Fig. 28. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). Lateral and ventral views of SAM–315. × 0,44.

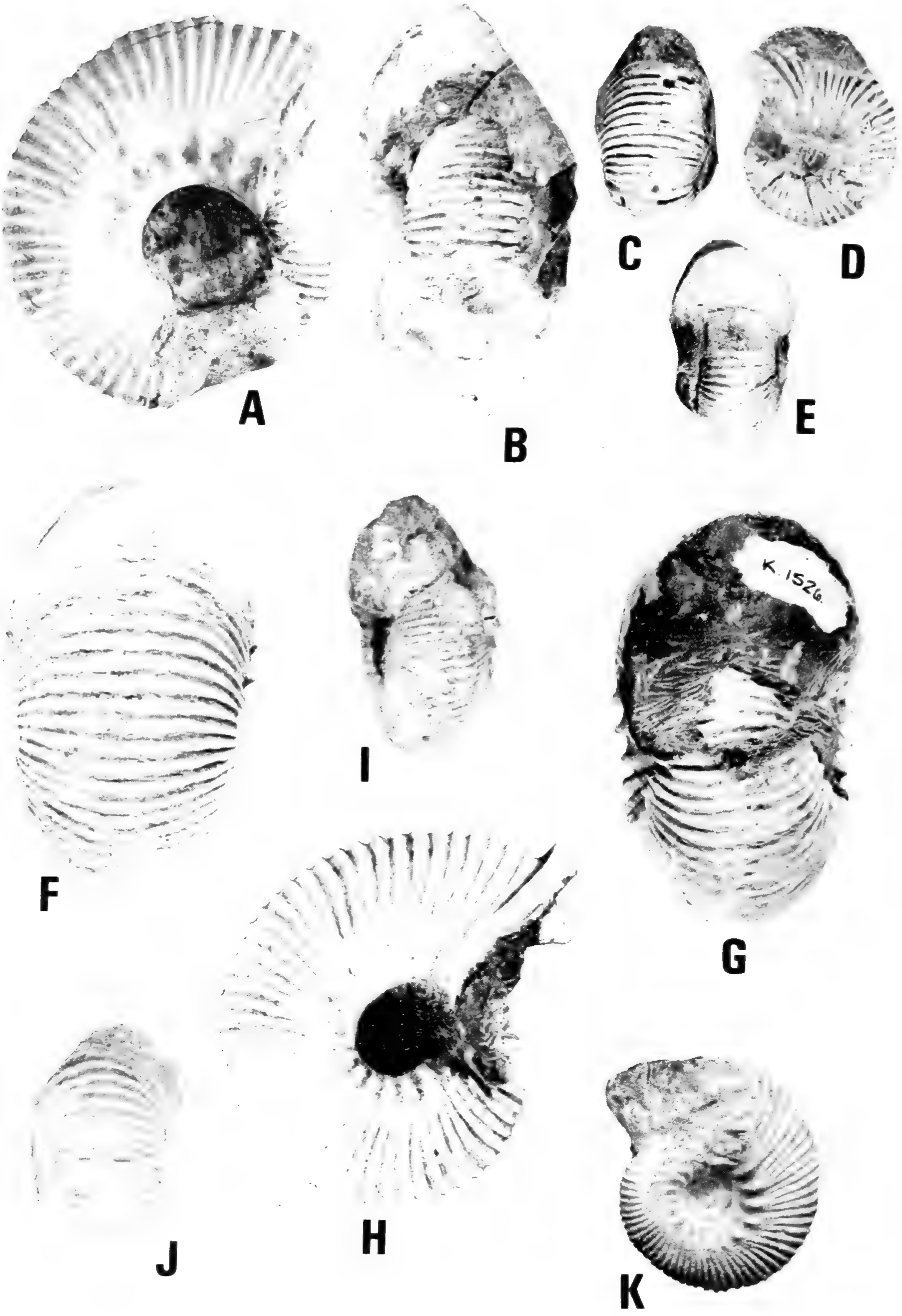

Fig. 29. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). A–B. Lateral and front views of SAM–PCU1532, a microconch, × 0,75. C–E. Ventral, lateral and front views of SAM–PCU1608, a juvenile, × 0,66 F–H. Ventral, lateral and front views of SAM–PCU1526, a microconch, × 0,66. I–K. Front, ventral and lateral views of AM–839, a juvenile, × 0,68.

Fig. 30. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Rogersites otoitoides* Spath, SAM-9242. × 0,75.

Astieria psilostoma var. *veneto* Rodighiero, 1919: 88, pl. 9 (fig. 11).
? *Astieria* aff. *baini* (Sharpe) Böse, 1923: 76, pl. 2 (figs 3–5).
Astieria psilostoma var. *crassa* Roch, 1930: 315.
Astieria psilostoma var. *lateumbilicata* Roch, 1930: 314, pl. 16 (fig. 3).
Rogersites otoitoides Spath, 1930: 149, pl. 14 (fig. 1).
Rogersites wilmanae (Kitchin) Spath, 1930: 145, pl. 13 (fig. 3), pl. 14 (fig. 4), pl. 15 (fig. 2).
Rogersites tenuicostatus Imlay, 1937: 562, pl. 73 (figs 3–9).
Holcostephanus midas Leanza, 1944: 16, pl. 1 (fig. 1).
? *Taraisites bosei* Cantu Chapa, 1966: 16.
Taraisites tenuicostatus (Imlay) Cantu Chapa, 1966: 16.
Olcostephanus atherstoni (Sharpe) (♂), Riccardi *et al.*, 1971: 91, pl. 12 (fig. 4), pl. 13 (figs 2–3).

Macroconch (♀)

Ammonites atherstoni Sharpe, 1856: 196, pl. 23 (fig. 1).
Olcostephanus atherstoni (Sharpe) Holub & Neumayr, 1882: 272. Riccardi *et al.*, 1971: 91, pl. 12 (fig. 3), pl. 13 (figs 1, 4 only).
Non Olcostephanus (*Astieria*) *atherstoni* (Sharpe) Pavlow & Lamplugh, 1892: 495 (= *O.* (*Subastieria*) *decipiens* Spath).
Holcostephanus (*Astieria*) *atherstoni* (Sharpe) Kilian & Leerhardt, 1895: 973. Wegner, 1909: 81. Kilian, 1910: 213.
Non Holcostephanus (*Astieria*) *atherstoni* (Sharpe) Kilian, 1902: 865, pl. 57 (fig. 1) (= ? *O. ventricosus* (von Koenen)).
Holcostephanus atherstoni (Sharpe) Uhlig, 1903: 132. Kitchin, 1908: 185. Collignon, 1962: 38, pl. 188 (fig. 860).
Non Holcostephanus (*Astieria*) cf. *atherstoni* (Sharpe) Karakasch, 1902: 103, pl. 1 (fig. 3) (= *O. sharpei* Karakasch).
Non Holcostephanus atherstoni (Sharpe) Hatch & Corstorphine, 1909: 303, fig. 76a (= *O. baini* (Sharpe)).
? *Astieria* cf. *atherstoni* (Sharpe) Baumberger, 1907: 39, pl. 23 (fig. 1), fig. 114 only.
Non Holcostephanus cf. *atherstoni* (Sharpe) Kitchin, 1908: 193 (= *O. baini* (Sharpe)).

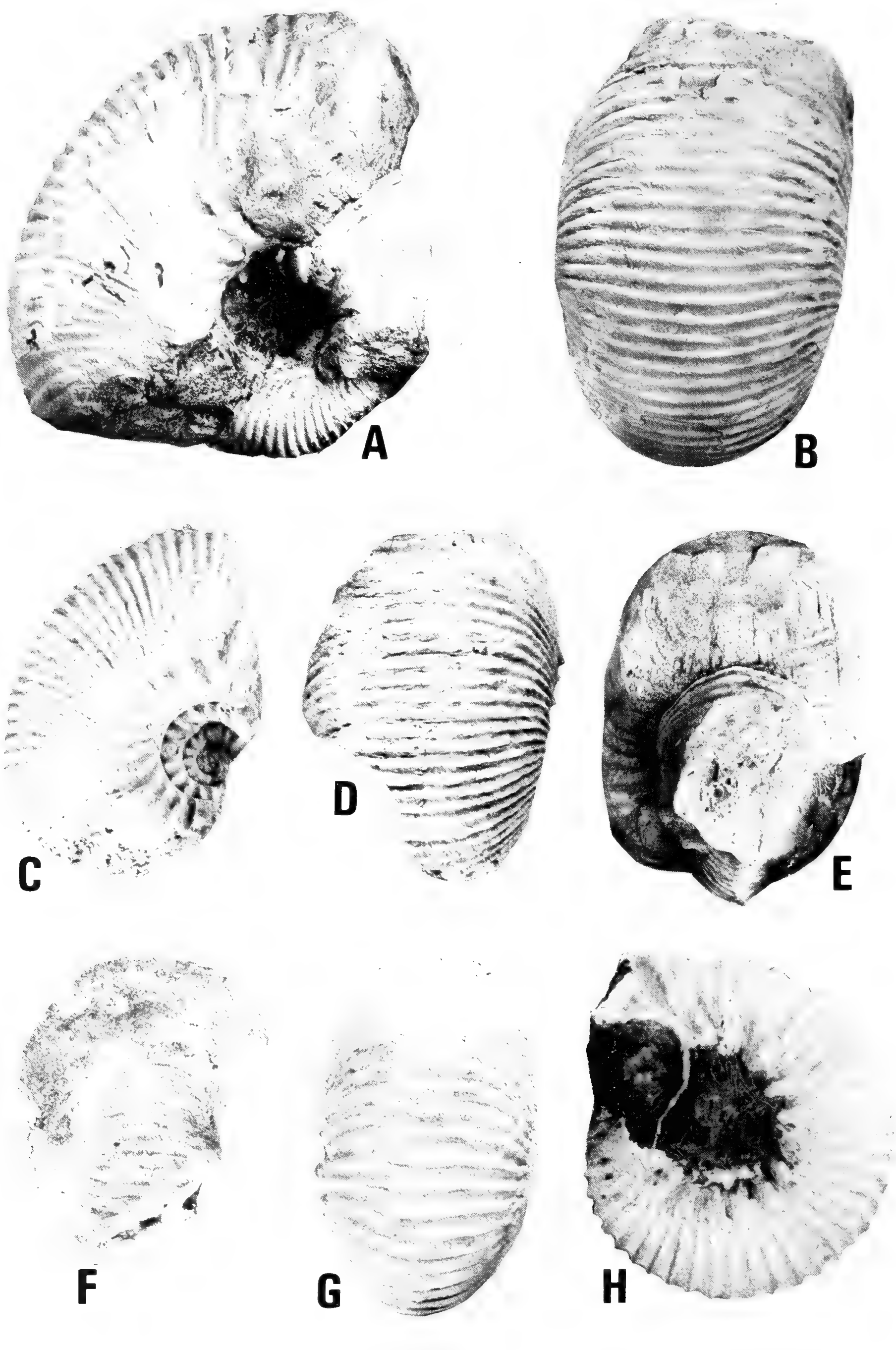

Fig. 31. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). A–B, E. Lateral, ventral and front views of an immature macroconch, AM–4292, × 0,75. C–D, F. Lateral, ventral and front views of an immature macroconch, SAM–PCU1589, × 0,44. G–H. Ventral and lateral views of SAM–PCU1529, a microconch, × 0,66.

Astieria cf. *atherstoni* (Sharpe) Böse, 1923: 77, pl. 3 (figs 1–2).
Rogersites curvicostatus Besairie, 1936: 141, pl. 12 (figs 7, 10), pl. 13 (fig. 8).
? *Astieria* aff. *atherstoni* (Sharpe) Riedel, 1938: 13, pl. 3 (figs 5–6), pl. 12 (fig. 3).
Rogersites prorsiradiatus Imlay, 1937: 561, pl. 17 (figs 1–7).
Taraisites neoleonense Cantu Chapa, 1966: 16.
Olcostephanus (*Rogersites*) *atherstoni* (Sharpe) Spath, 1939: 32, pl. 20 (fig. 4).
? *Non Olcostephanus* (*Rogersites*) cf. *atherstoni* (Sharpe) Spath, 1939: 32, pl. 20 (fig. 3) (= ? *O. baini* (Sharpe)).
Rogersites atherstoni (Sharpe) Tzankov, 1943: 196, pl. 8 (figs 1–2, 4 only).
Non Olcostephanus cf. *O. atherstoni* Baumberger (*non* Sharpe), Imlay & Jones, 1970: B38, pl. 9 (figs 1–3, 6–10).

Material

18 specimens; 8 microconchs (SAM–PCU1526, 1529, SAM–9242, BM–C32199, 32204), 7 macroconchs (SAM–PCU1585, 1589–90, 1604, AM–4292, BM–C32202, 47128), and 3 juveniles (SAM–PCU1608, AM–839, 4293).

Holotype

By monotypy, the original of the specimen of *Ammonites atherstoni* figured by Sharpe (1856: 196, pl. 21 (fig. 1)) from the Sundays River, now in the British Museum, BM–C32202.

Diagnosis

Dimorphic. Microconch fairly small (60–100 mm in diameter), with peristome bearing lateral lappets. Primary ribs rursiradiate, terminating in about 18 bullae on the final whorl from which arise bundles of 3 prorsiradiate

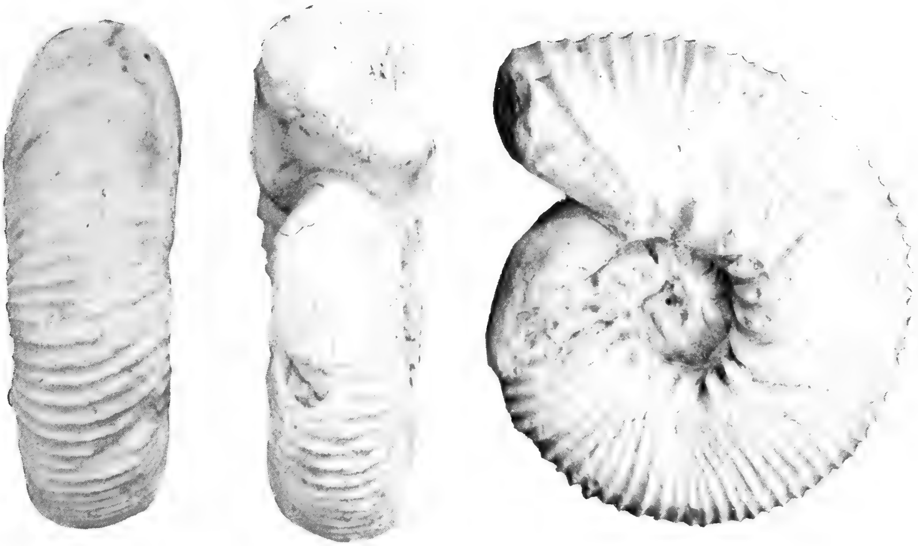

Fig. 32. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Holcostephanus wilmanae* Kitchin, BM–C32199, a laterally crushed microconch. × 0,75.

secondaries. There are 25–37 ribs per half-whorl. Parabolae lacking. Whorl section apparently variable. Macroconch large (+ 200 mm in diameter), strongly inflated, with well-rounded venter and depressed, semicircular whorl section. Primary ribs rursiradiate, terminating in 17–25 bullae at the umbilical shoulder from which arise bundles of 3–4 secondaries, with 1–2 intercalatories between bundles. There are 40–50 secondary ribs per half whorl. Parabolae absent at all growth stages. Peristome simple.

Description

Microconch (♂): the shell is rather small, with lappets present at diameters from 60–100 mm, and comprises somewhat inflated to rather compressed cadicones, involute up to the umbilical bullae so that about 75 per cent of the previous whorl is covered. The shell becomes slightly more evolute as the umbilical seam egresses on the adoral portion of the body chamber. About 18 rursiradiate primary ribs terminate in prominent bullae on the umbilical shoulder of the final whorl, from which fasciculate bundles of commonly three, rarely only two, secondary ribs arise, generally with an intercalated rib between bundles. The coarse secondaries are prorsiradiate, recurving slightly so as to cross the venter transversely. There may be a slight inflexion of the secondaries as they cross the siphonal line. The umbilical wall is steep, with a subrounded umbilical shoulder. The whorl section is rather variable. Whilst parabolae are lacking on the phragmocone, the peristome is provided with a typical parabola, viz. a deep, oblique constriction bordered both adorally and adapically by prominent ribs, the adapical one of which is prominently flared. The adoral rib is provided with well-developed, slightly converging lateral lappets. There are between 8–10 secondaries per 3 bullae on the final whorl with between 7 and 9 secondaries within a 30 mm distance along the venter.

Macroconch (♀): shell large, with peristome preserved at 200 mm diameter; strongly inflated, cadicone, involute up to the umbilical bullae on the inner whorls, with about 80 per cent of the preceding whorl being covered, but becoming slightly evolute on the final whorl as the umbilical seam egresses, so as to make a short distance of secondary ribbing visible below the umbilical seam. Prominent primary ribs begin at, or close to, the umbilical seam and curve backwards (virguliform) to terminate in 17–25 prominent bullae on the umbilical shoulder. Each bulla gives rise to bundles of 3–5 prorsiradiate secondaries, generally with 1–2 intercalated ribs between bundles, so that there are between 10 and 17 secondaries per 3 bullae. The secondaries recurve slightly so as to cross the venter transversely. At diameters greater than 90 mm there are almost invariably 4 secondaries per bulla. At 75 mm diameter there are 10 ribs per 3 bullae, with a rib spacing across the venter of 3–4 mm. The whorl section is semicircular and rather depressed, with a broad, evenly-rounded venter. Parabolae are lacking at all growth stages. The peristome is seen to be preserved in a single specimen, BM–C47128, and is simple. The whorls of the macroconch show a steady rate of inflation. SAM–PCU1604 is preserved as an internal

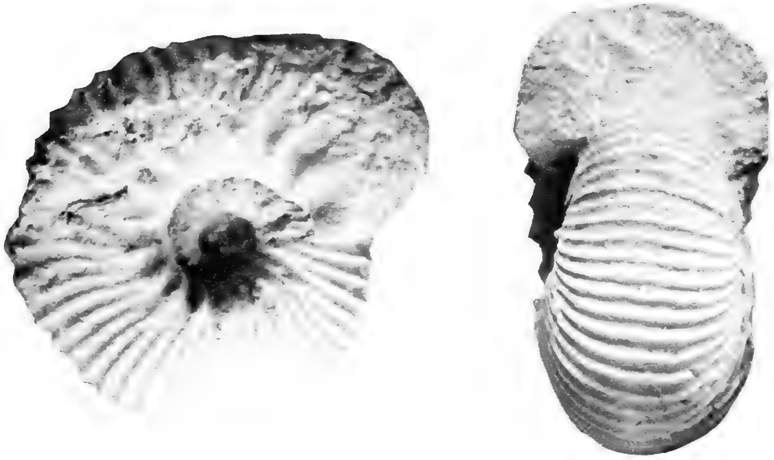

Fig. 33. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* (Kitchin), BM–C32204, a probable microconch. × 1.

mould. It is moderately large and somewhat inflated, with a rather narrow umbilicus, and steep umbilical walls. Well-developed primaries terminate in small but distinct bullae on the umbilical shoulder, from which arise bundles of fine, prorsiradiate secondaries which very occasionally bifurcate at about mid-flank, with 1–2 intercalated ribs between bundles. There are 20 umbilical bullae on the outer whorl. Parabolae are lacking.

The following description of the holotype of *O. atherstoni* is based on a plastotype supplied by M. K. Howarth: the specimen is moderately large, and somewhat inflated, and appears to have much of the shell material preserved. The umbilicus is narrow and deep, with convex umbilical walls and a subrounded umbilical shoulder. Primary ribs begin at, or close to, the umbilical seam and pass strongly backwards (rursiradiate) to the umbilical shoulder where they terminate in small but prominent umbilical bullae, of which there are about 20 on the outer whorl. There are fewer umbilical bullae on the earlier whorls. From the umbilical bullae arise bundles of usually 4 fine secondary ribs, rarely 3 or 5, with commonly 2 intercalated ribs between bundles, although there may occasionally be one only. Thus, on the adoral portion of the outer whorl there are 37 secondaries per 7 bullae, with 26 ribs within a 100 mm distance along the venter. The outer whorl is not complete, but there were probably in all about 100 secondaries. Portion of an earlier whorl, evident in the broken umbilicus, shows ribbing to have been coarser at earlier growth stages, with secondaries generally arising in bundles of 3, with an intercalated rib between bundles. The whorl section is semicircular and depressed, with an evenly rounded venter. The whorls show a constant rate of inflation. Although the specimen is entirely septate, matrix on the outer whorl shows that the umbilical seam of the following whorl egressed markedly, and that it represented the body whorl. There is no evidence for parabolae at any growth stage.

Specimen AM–4293 represents a typical juvenile. In this example, there are 17 bullae on the outer whorl, from which arise bundles of 2–3 prorsiradiate secondaries with an intercalated rib between bundles. There are 10 ribs per 3 bullae, with 13 secondaries within a 20 mm distance along the venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C47128	197	81	*c.* 95	1,17	95	61 (31)
,,	*c.* 130	56	?	?	52	34 (26) (♀)
SAM–PCU1590	102	49	75	1,53	45	25 (25)
,,	80	34	52	1,53	29	16 (20) (♀)
SAM–PCU1604	98	48	67	1,40	35	*c.* 21 (21) (♀)
PEM–1468/74	72	33	36	1,09	30	21 (29) (♂)
SAM–PCU1529	58	*c.* 22	?	?	28	? ? (♂)
SAM–PCU1598	66	28	?	?	32	19 (29) (♂)
SAM–PCU1526	72	31	41	1,32	30	17 (24) (♂)
SAM–9242†	94	36	47	1,31	42	26 (28) (♂)
BM–C32202*	134	61	80	1,31	48	27 (20) (♀)
,,	106	51	66	1,29	36	23 (22)
,,	*c.* 80	40	53	1,32	28	17 (21)
BM–C32204‡	44	19	24	1,26	17	10 (23) (♂)

† The holotype of *Rogersites otoitoides* Spath.
* Plastotype of *O. atherstoni* (Sharpe).
‡ Specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* Kitchin.

Discussion

It is hardly necessary to point out the confusion that has surrounded Sharpe's species since its inception in 1856. This has been due to a number of factors. First and foremost is the marked homoeomorphy between *O. atherstoni* (♀) and macroconchs of other species. This, together with the comparison of different growth stages, the failure to recognize sexual dimorphism, and the placing of constricted forms within this species have all added to the confusion. Thus, this name has been used for species from the Crimea (Karakasch 1902), England (Pavlow *in* Pavlow & Lamplugh 1892), Mexico (Burckhardt 1906; Böse 1923), the Swiss Jura (Baumberger 1907), Pakistan (Spath 1939), South Africa (Kitchin 1908; Spath 1930), France (Collignon 1962), and Argentina (Riccardi *et al.* 1971).

Riccardi *et al.* (1971), in describing forms of *Olcostephanus* from the Lower. Cretaceous of west-central Argentina, assigned their entire olcostephanid fauna '. . . to the almost cosmopolitan *Olcostephanus atherstoni* (Sharpe)'. They place into synonymy with Sharpe's holotype, which they take to represent a macroconch, the following species: *O. schenki* (Oppel), *O. sudandina* (Windhausen),

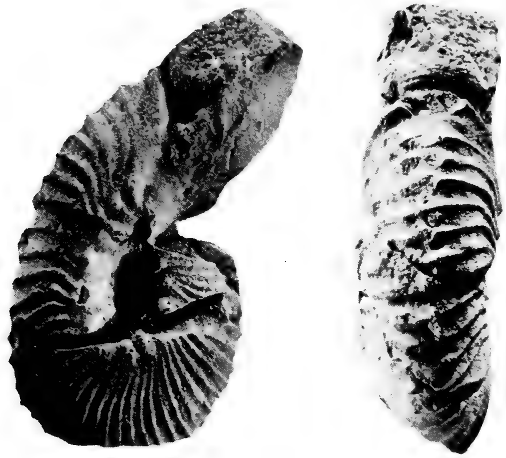

Fig. 34. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Rogersites tenuicostatus* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

and with reservation *O. curacoensis* (Weaver) and *O. sublaevis* Spath. The microconch is taken to be represented by the synonymous species *O. psilostomus* Neumayr & Uhlig, *O. wilmanae* (Kitchin), and *O. midas* (Leanza). Moreover, these authors hint that *O. otoitoides* (Spath), *O. wynnei* Spath, *O. baini* (Sharpe), *O. baini* var. *ambikyi* (Besairie), *O. auritus* (Leanza), *O. salinarius* Spath, *O. sphaeroidalis* (Spath), *O. glaucus* Spath, *O. rigidus* (Baumberger), *O. leptoplanus* (Baumberger), *O. imbricatus* (Baumberger), and *O. modderensis* (Kitchin) were a group of doubtfully distinct species over which *O. atherstoni* had priority.

These authors have, however, been misled both by the convergence between macroconch forms, and in neglecting the specific importance of parabolic constrictions.

The microconch is represented, amongst South African material, by *O. otoitoides* (Spath) (Fig. 30), the crushed *O. wilmanae* (Kitchin) (Fig. 32) and the specimen figured by Spath (1930) as *Rogersites* aff. *wilmanae* (Fig. 33). Other synonyms certainly include *O. tenuicostatus* (Imlay) (Fig. 34), *O. prorsiradiatus* (Imlay) (Fig. 35), and *O. neoleonensis* (Cantu Chapa) (Fig. 36), the latter species based upon the inner whorls of *O. prorsiradiatus*, as well as *O. psilostomus* (Pictet) (Fig. 37), *O. midas* (Leanza) (Fig. 38), *O. leptoplanus* (Baumberger) (Fig. 39), of which *Astieria psilostoma* var. *picteti* Wegner (1909) is a junior objective synonym, and possibly *O. curacoensis* (Weaver) (Fig. 40).

Astieria sudandina Windhausen (1931) (Fig. 41) was based upon a specimen illustrated only in lateral view, without scale, description or locality, and is thus a *nomen nudum*. According to Riccardi *et al.* (1971), it is a synonym of *O. atherstoni*.

Maderia altiumbilicata Imlay (1938) was based upon a strongly inflated, globose, pyritic nucleus with a strongly depressed, semilunate whorl section.

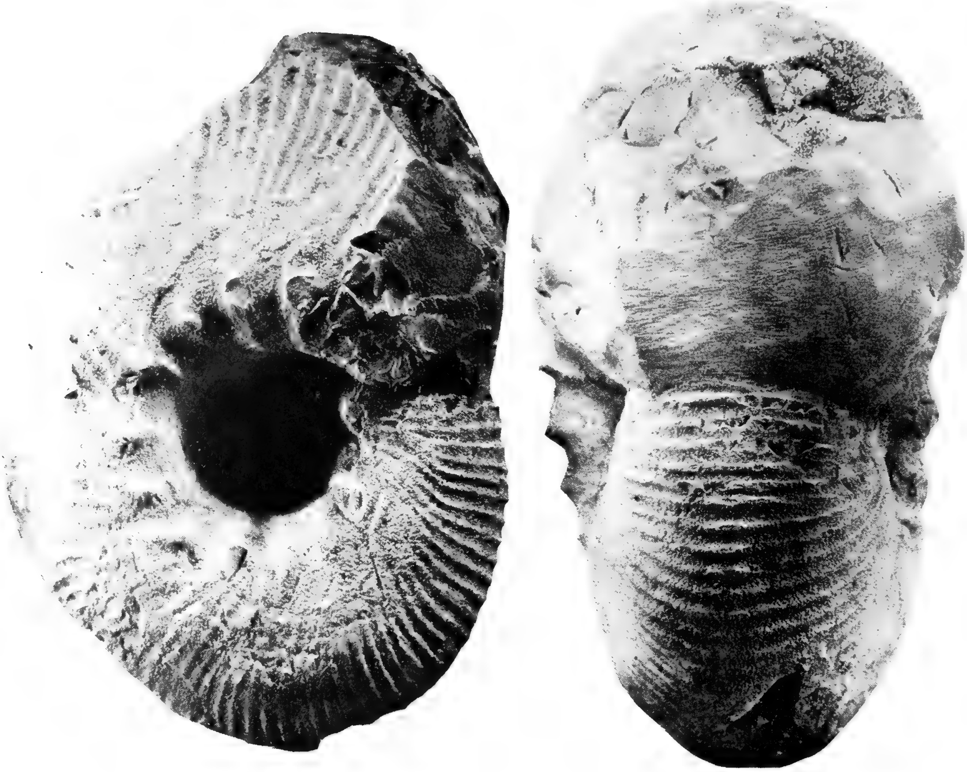

Fig. 35. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). The holotype of ***Rogersites prorsiradiatus*** Imlay from the Upper Valanginian of the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Fig. 36. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe). The holotype of *Taraisites neoleonense* Cantu Chapa from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

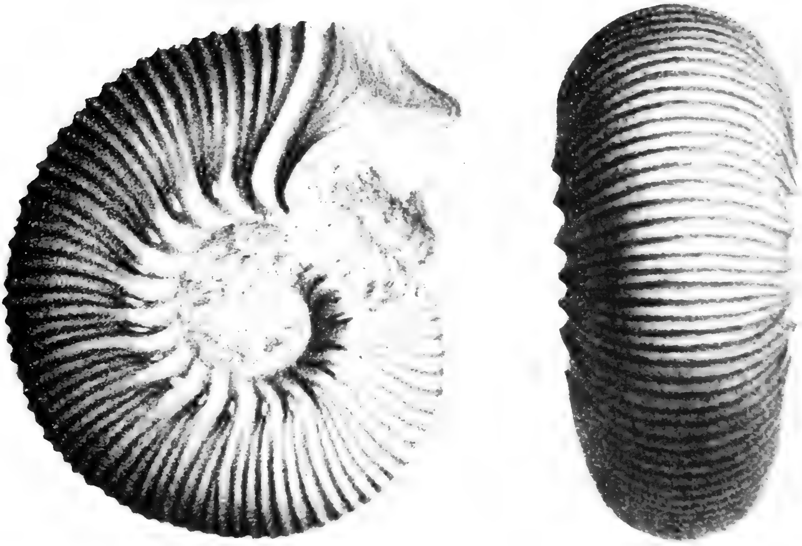

Fig. 37. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Olcostephanus psilostomus* Neumayr & Uhlig from northern Germany (after Neumayr & Uhlig 1881). × 1.

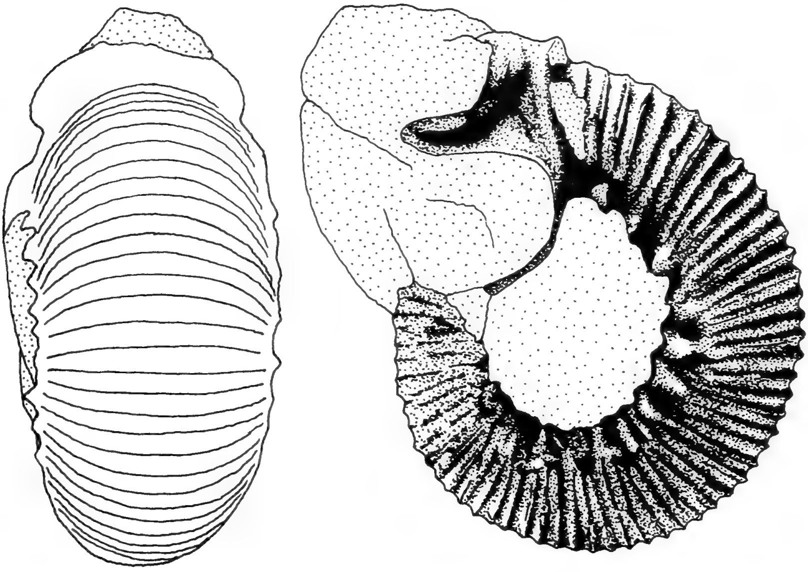

Fig. 38. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The holotype of *Holcostephanus midas* Leanza from the Upper Valanginian of Neuquén, Argentina (after Leanza 1944). × 1.

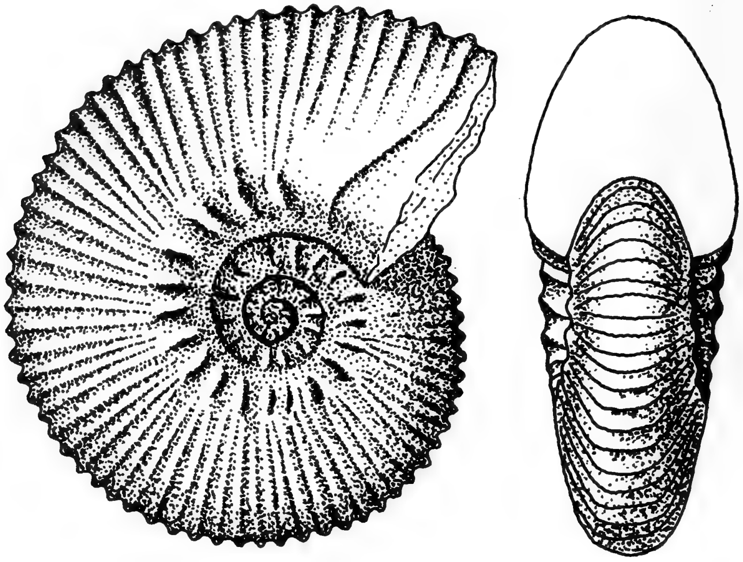

Fig. 39. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♂). The original of this specimen is the type of *Holcostephanus leptoplanus* Baumberger, by lectotype designation herein, and also of *Holcostephanus* (*Astieria*) *psilostomus* var. *picteti* Wegner (after Pictet & Campiche 1858). × 1.

Ornament comprises 16–17 primary ribs which terminate in bullae on the umbilical shoulder from which arise bundles of three prorsiradiate secondaries. Parabolae are lacking, and the writer believes this species to be based upon a nucleus of *O. atherstoni*.

As can be seen from Figures 42–43, *Rogersites curvicostatus* Besairie (1936) is merely based upon a macroconch of *O. atherstoni* whilst, according to Thieuloy (1977*b*: 126), *Astieria carpathica* Jekelius (1913) is also a synonym of Sharpe's species.

Taraisites bosei Cantu Chapa (Fig. 9) was erected for the poorly preserved specimen figured by Böse (1923: 76, pl. 2, figs 3–5) as *Astieria* aff. *baini*, and made the type of the genus *Taraisites*. This fragment appears to be specifically indeterminate; it may be either *O. baini* or a juvenile *O. atherstoni*. It is best regarded as a *nomen dubium*, not to be used.

Olcostephanus actinotus (Baumberger) (Fig. 44) is a rather large species, probably an immature macroconch, with a deep umbilicus and steep walls ornamented with 17–18 slender, rursiradiate primaries terminating in bullae. From these commonly arise 4, occasionally 3 or 5, secondaries with 1–2 intercalated ribs between bundles. Parabolae are lacking. This species seems to differ from *O. atherstoni* in its more compressed form with a subtrigonal whorl section, and in its straight not sinuous secondary ribs.

Olcostephanus andartae Thieuloy (1972) (Fig. 45) has a depressed whorl section with steep umbilical walls. On the outer whorl, 14–15 primary ribs

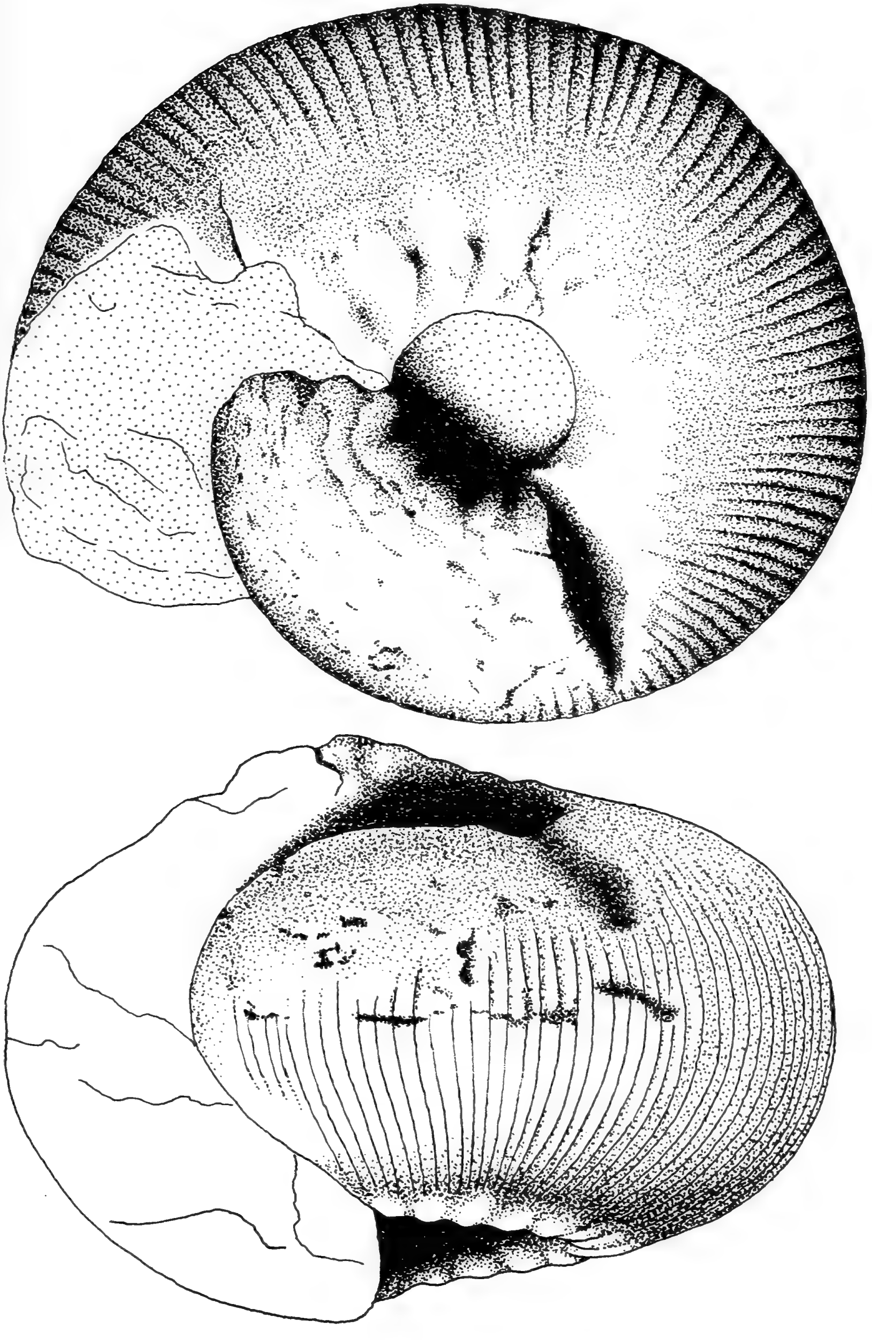

Fig. 40. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). The holotype of *Astieria curacoensis* Weaver from Neuquén, Argentina (after Weaver 1931). × 1.

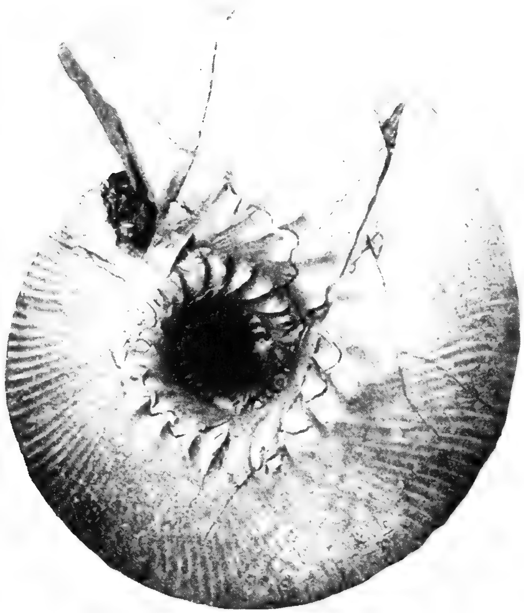

Fig. 41. *Olcostephanus* (*Olcostephanus*) cf. *atherstoni* (Sharpe) (♀). The holotype, by monotypy, of *Astieria sudandina* Windhausen, a *nomen nudem* since it was not described, whilst the scale and locality are also unknown (after Windhausen 1931). × 1.

terminate in prominent rounded tubercles on the umbilical shoulder and give rise to bundles of 3–4 coarse, prorsiradiate secondaries characterized by frequent bifurcation at midflank. Parabolae are lacking. This species differs from *O. atherstoni* in its coarser, more distant ribbing with frequent bifurcation and in possessing swollen, rounded umbilical tubercles. *Olcostephanus bossingaulti* (d'Orbigny) (Fig. 46), of which *O. laticosta* (Gerth) (Fig. 47) is merely based upon a juvenile, is an Hauterivian species which is very close to *O. andartae*, but seems to lack bifurcating secondaries.

'*Simbirskites*' *araucanus* Leanza (1957) is a moderately large, fairly evolute species of *Olcostephanus*, with inclined umbilical walls ornamented with about 20–23 prorsiradiate primaries per whorl. These terminate in prominent umbilical bullae which generally give rise to three radial, to slightly prorsiradiate secondaries, frequently with an intercalated rib between bundles. There are about seventy secondary ribs per whorl, a short distance of which are exposed in the umbilicus, beneath the umbilical seam. Parabolae lacking. This species differs from the microconch of *O. atherstoni* in its more evolute form, with sloping umbilical walls and prorsiradiate primaries, and should be assigned to the subgenus *Subastieria*. It seems likely that the Sardinian *O.* (*Subastieria*) *nicklesi* Wiedmann & Dieni (Fig. 48) is merely based upon juveniles of this species.

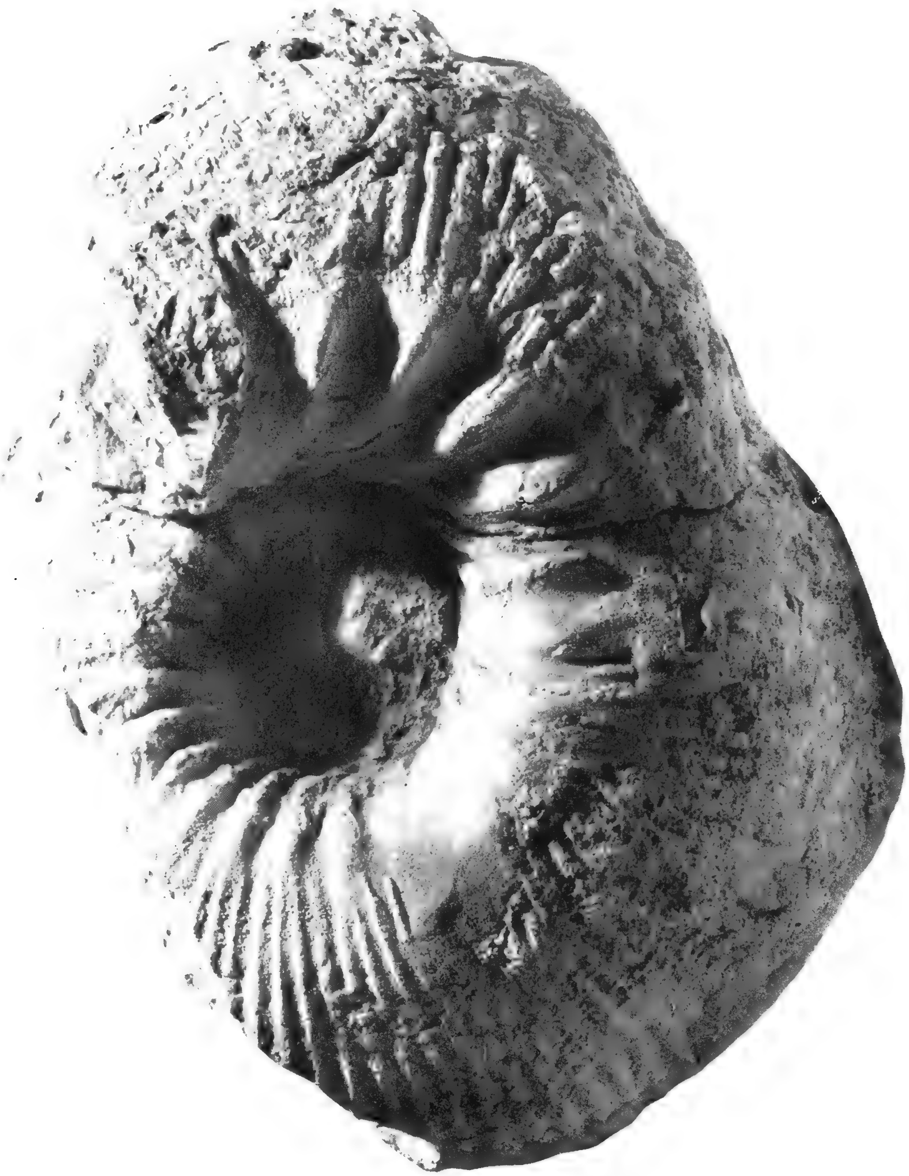

Fig. 42. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the holotype of *Rogersites curvicostatus* Besairie, in the collections of the University of Paris. × 1.

Fig. 43. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Front view of the holotype of *Rogersites curvicostatus* Besairie, in the collections of the University of Paris. × 1.

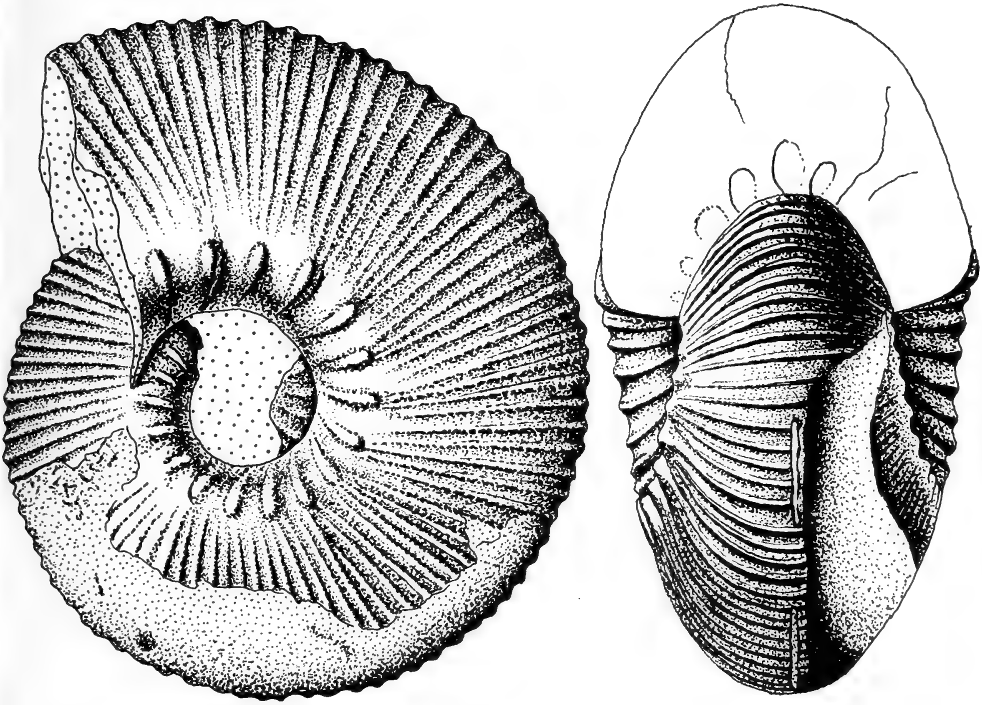

Fig. 44. *Olcostephanus* (*Olcostephanus*) *actinotus* (Baumberger) (♀), from the Swiss Jura (after Baumberger, 1908). × 1.

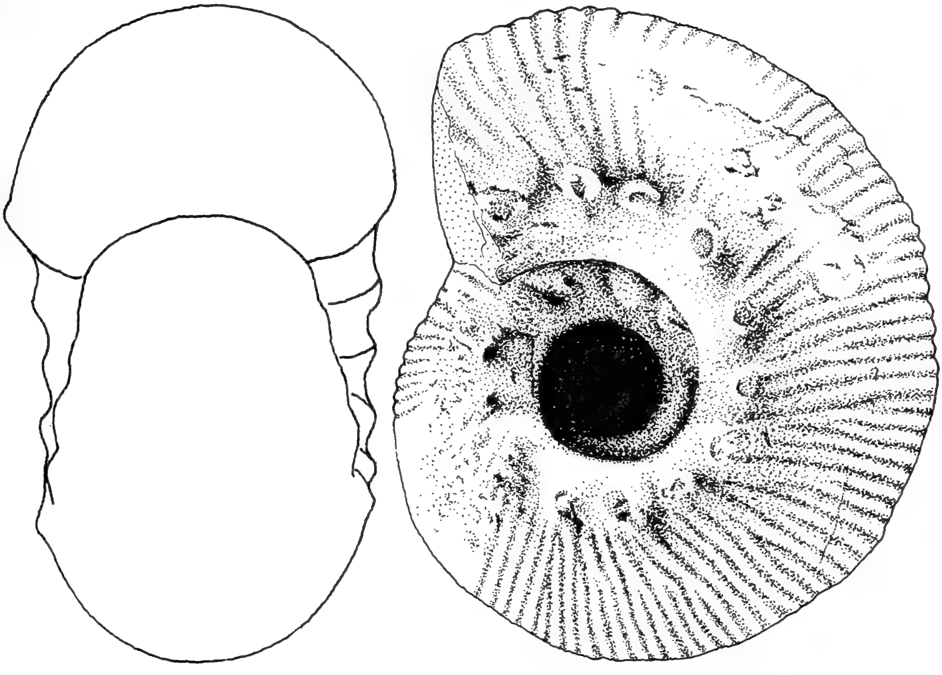

Fig. 45. *Olcostephanus* (*Olcostephanus*) *andartae* Thieuloy. The paratype, possibly a macroconch, from the Lower Hauterivian of Rottier (Drôme) (after Thieuloy 1972). × 1.

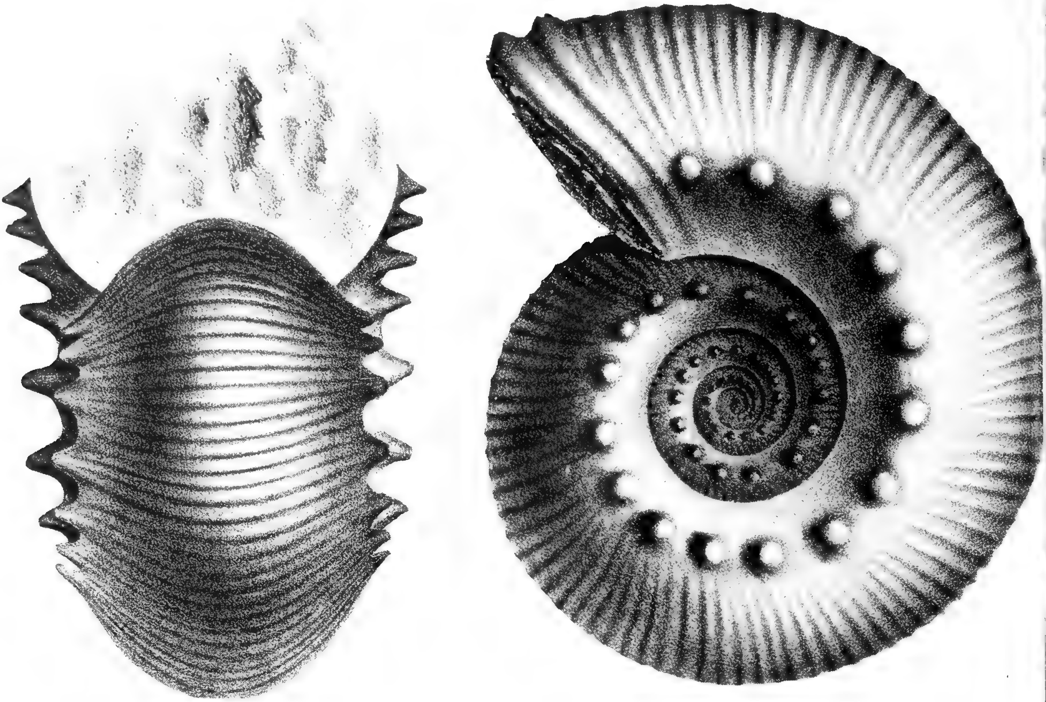

Fig. 46. *Olcostephanus* (*Olcostephanus*) *bossingaulti* (d'Orbigny) (♀). The holotype, by monotypy, from Colombia (after d'Orbigny 1842*b*). × 1.

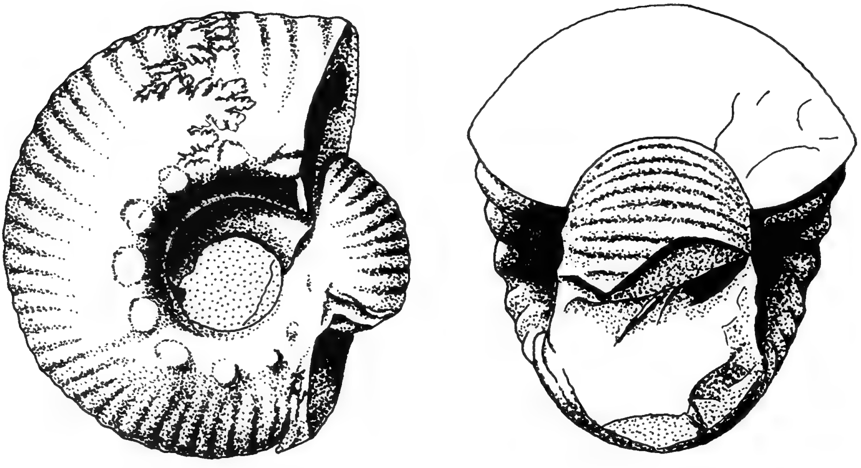

Fig. 47. *Olcostephanus* (*Olcostephanus*) *bossingaulti* (d'Orbigny). The holotype of *Astieria laticosta* Gerth from Neuquén, Argentina (after Gerth 1925). × 1.

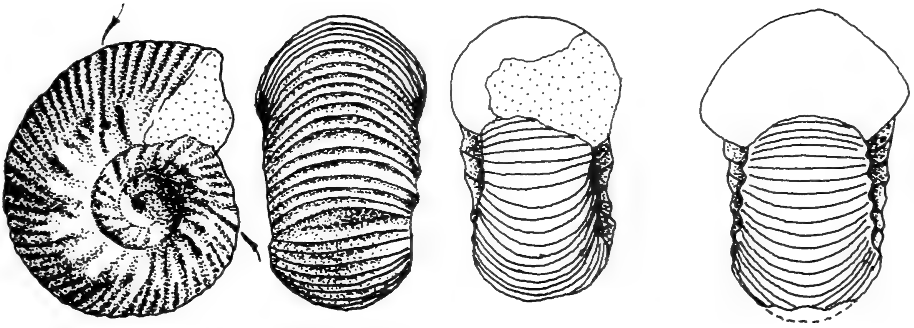

Fig. 48. *Olcostephanus* (*Subastieria*) *nicklesi* Wiedmann & Dieni. The holotype and front view of a paratype from the Upper Valanginian of Sardinia (after Wiedmann & Dieni 1968). × 1.

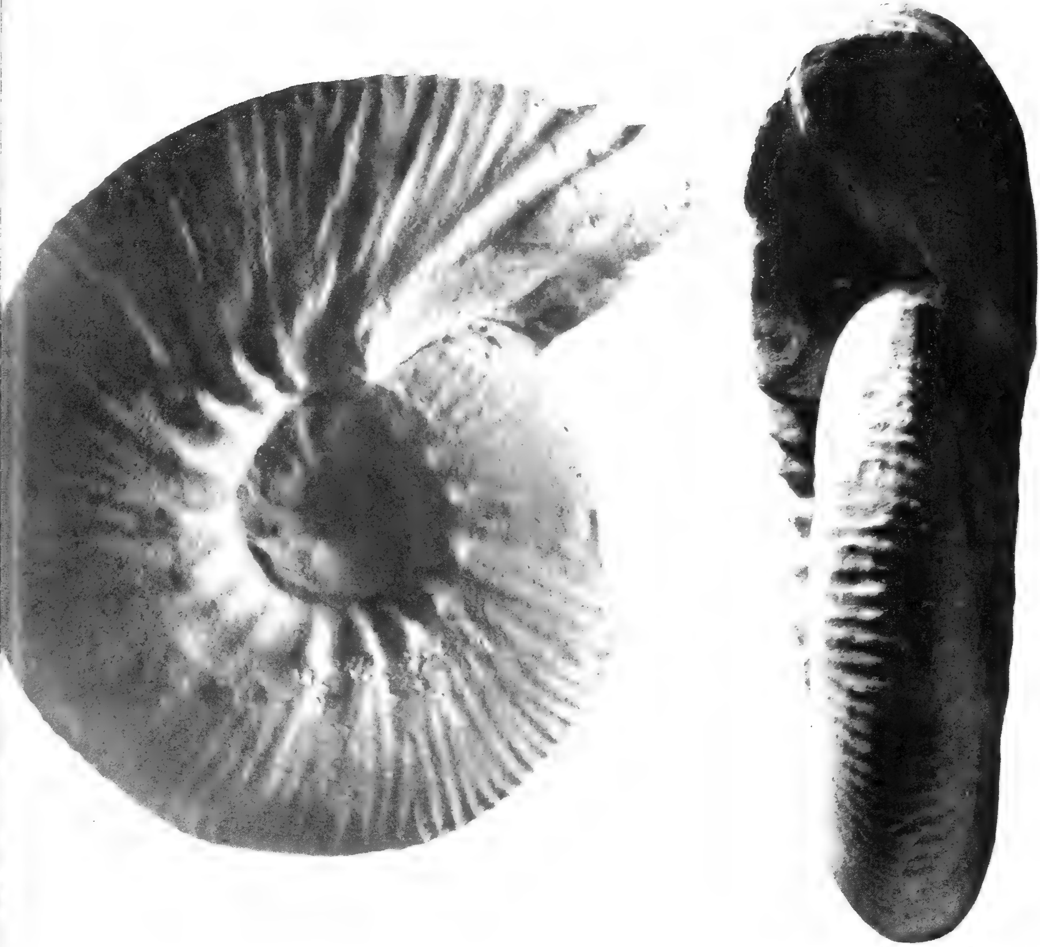

Fig. 49. *Olcostephanus* (*Olcostephanus*) *bernardensis* (Lory) (♀). A cast of the holotype MNHP–R3111, from the Middle Hauterivian of the Hautes-Alpes. × 1.

A cast of the holotype of *Olcostephanus bernardensis* (Lory) (Fig. 49)* in the Natural History Museum, Paris, with the number MNHP–R3111, shows this species to be moderately involute (umbilicus 28% of the diameter), with a strongly compressed whorl section (W/H = 0,75). On the outer whorl, nineteen rursiradiate primaries terminate in bullae which give rise to bundles of prorsiradiate secondary ribs. The secondaries sometimes bifurcate on the flanks so that there are about 115 ribs across the venter of the final whorl. Parabolae are lacking and the peristome appears to be simple. This species seems to differ from the *O. atherstoni* macroconch in being somewhat more densely ribbed, with more frequent bifurcation of secondaries.

'*Maderia*' *cupidinensis* Imlay (1938) was based upon a pyritic nucleus with a strongly depressed, semilunate whorl section. Between 20 and 22 primary ribs terminate in umbilical bullae from which arise 2–3 slightly prorsiradiate secondaries. Parabolae are lacking. This species seems to differ from *O. atherstoni* in the shape of the whorl section, and in being less inflated. It closely approaches *O. andartae* Thieuloy.

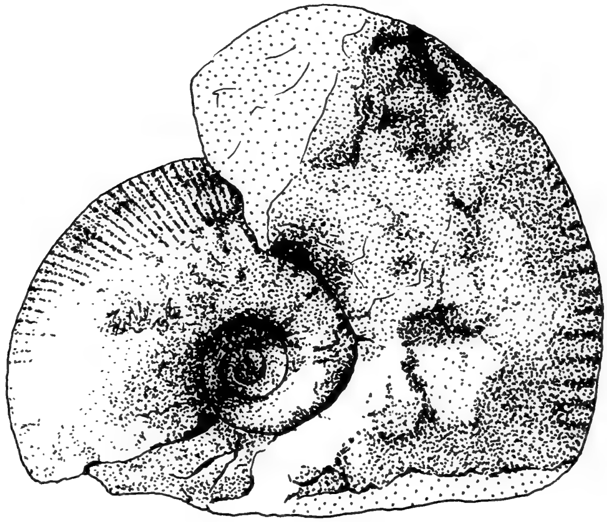

Fig. 50. *Olcostephanus* (*Olcostephanus*) *crassus* (Zwierzycki) (♀). The holotype, by monotypy, from the Tendaguru Formation of Tanzania (after Zwierzycki 1914). × 1.

Olcostephanus crassus (Zwierzycki) (Fig. 50) is based upon a poorly preserved macroconch which approaches *O. atherstoni*, but should be regarded as specifically indeterminate, a *nomen dubium*.

Olcostephanus discoideus Imlay (Fig. 51) is a probable macroconch with a compressed ovate whorl section, the compression seemingly enhanced by crushing. About 20 primaries terminate in small bullae on the umbilical shoulder from which arise 3, rarely 2 or 4, radial secondaries with 1–2 intercalated ribs

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* This figure and various others are not up to our usual standard; some are from published illustrations and others cannot be replaced—Ione Rudner, Editor.

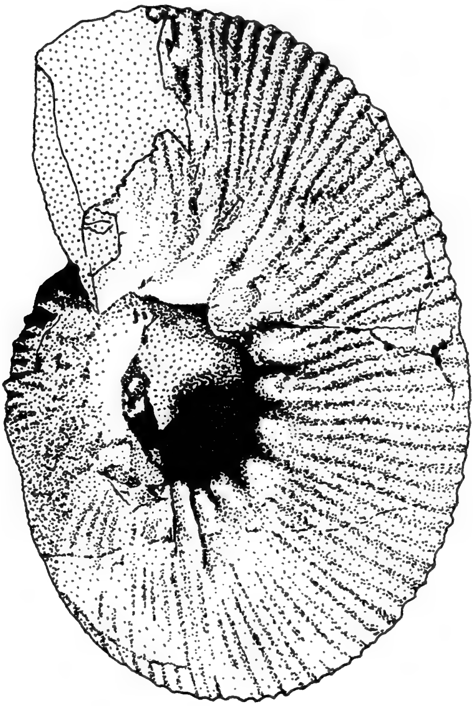

Fig. 51 *Olcostephanus* (*Olcostephanus*) *discoideus* Imlay (♀). The holotype from the Taraises Formation of northern Mexico. (after Imlay 1938). × 1.

between bundles. On the adoral three-quarters of the outer whorl, the adapical rib of most bundles bifurcates. Its strongly compressed form separates Imlay's (1938) species from *O. atherstoni.*

Olcostephanus irregularis (Wegner) (Fig. 52) is a strongly compressed (?crushed), moderately evolute form with steep umbilical walls. About fifteen umbilical bullae per half whorl give rise to bundles of commonly three, slightly prorsiradiate secondaries which frequently bifurcate near midflank. There are occasional intercalatories between bundles. Parabolae lacking. This species differs from *O. atherstoni* in its more compressed form, more numerous umbilical bullae and frequent bifurcation of secondaries.

A cast of *Olcostephanus lamberti* (Kilian) (Fig. 53), MNHP–R3110, shows the original to have been somewhat eroded and slightly distorted. The whorl section is distinctly compressed, elliptical, and the umbilicus fairly wide with convex, rather sloping, umbilical walls. There are thirteen slightly rursiradiate, almost radial, primary ribs per whorl which terminate in rather prominent bullae at the umbilical shoulder. From these arise bundles of 3–4 rather coarse, prorsiradiate secondaries with intercalated ribs between bundles. The secondary ribs are about as wide as the interspaces and there are 65–70 on the outer whorl.

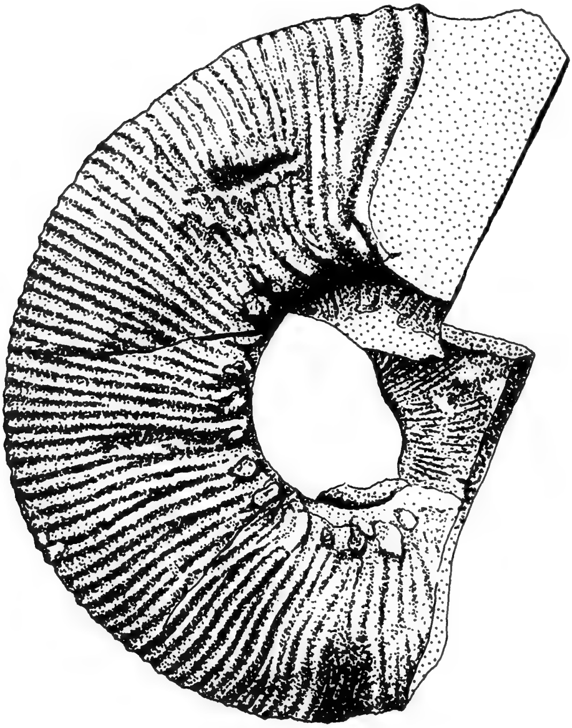

Fig. 52. *Olcostephanus* (*Olcostephanus*) *irregularis* (Wegner) (♀). The holotype, by monotypy, from the Lower Hauterivian of Marignac (Drôme) (after Wegner 1909). × 1.

Parabolae are lacking but there is a prominent apertural constriction. This species resembles *O. atherstoni* but may be distinguished by its more compressed form, fewer umbilical bullae and its younger (mid-Hauterivian) age.

Olcostephanus fascigerus Spath (Figs 92–97) differs from *O. atherstoni* in its finer, thread-like secondary ribs with more intercalatories between bundles, its more prominent bullae, and its constant rate of inflation which gives Spath's (1939) species a cylindrical aspect in ventral view.

The microconch of *O. baini baini* (Sharpe) (Fig. 114) differs from that of *O. atherstoni* in being smaller with somewhat fewer secondary ribs per whorl, and in possessing parabolae. The *O. baini* var. *sphaeroidalis* (Spath) microconch (Figs 145–146, 149) differs from *O. atherstoni* (♂) in possessing parabolae.

Within the Uitenhage fauna, *O. atherstoni* macroconchs are rather rare and only five further specimens, one of which is fragmentary, are without hesitation assigned to Sharpe's species. However, very common are large macroconchs which differ from the holotype of *O. atherstoni* in the greater inflation of their middle whorls and their more depressed whorl section (Fig. 118). Whilst the differences may appear slight, the holotype of *O. baini*

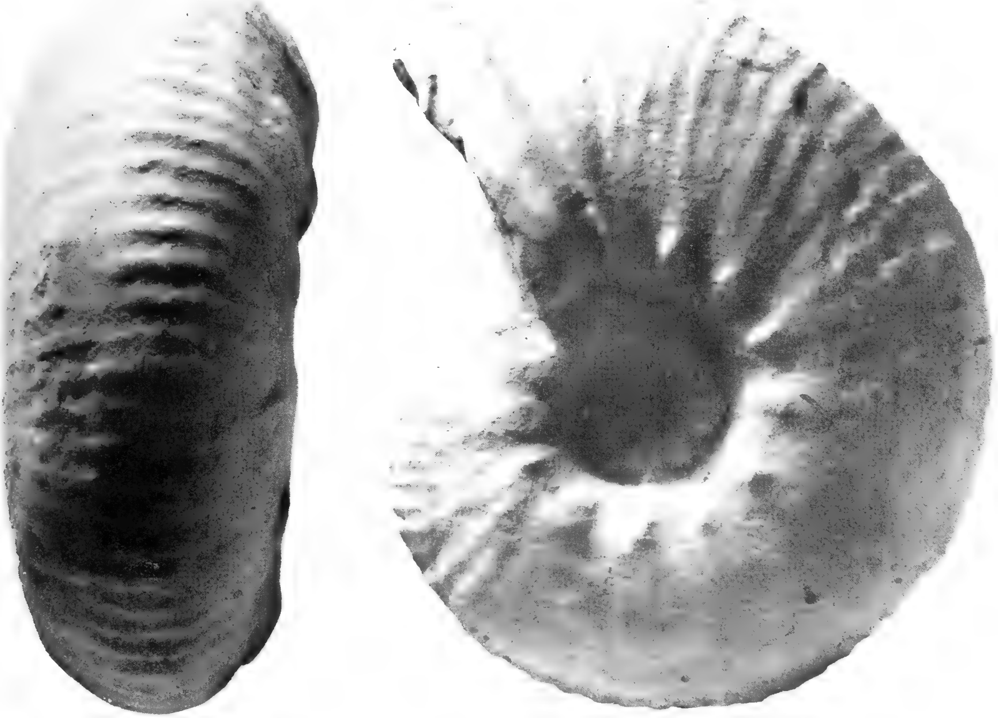

Fig. 53. *Olcostephanus* (*Olcostephanus*) *lamberti* (Kilian). A cast of the holotype, MNHP–R3110, from the Middle Hauterivian of Montbrand, Hautes-Alpes. × 1.

var. *sphaeroidalis* (Spath) shows that in addition the inner whorls of these more inflated forms bear parabolae. As such, the similarities merely provide further evidence of the perturbing homoeomorphy between adult macroconchs of *Olcostephanus*.

Occurrence

Olcostephanus atherstoni is a widely distributed species which is at present recorded from South Africa, Madagascar, Argentina, northern Mexico, Morocco, France, Austria, Switzerland and Germany but, rather curiously, not yet from Pakistan.

Olcostephanus (*Olcostephanus*) *densicostatus* (Wegner, 1909)

Figs 27E–F, 54–55

Microconch (♂)

? *Olcostephanus salinarius* Spath, 1939: 13, pl. 1 (figs 1–3, 6–7 only), pl. 2 (fig. 5), pl. 19 (fig. 4), pl. 20 (fig. 2). Fatmi, 1977: 266, pl. 1 (figs 5–6), pl. 2 (fig. 4), pl. 3 (fig. 1).

? *Holcostephanus auritus* Leanza, 1944: 18, pl. 2 (fig. 1).

? *Holcostephanus busnardoi* Collignon, 1962: 43, pl. 191 (fig. 868).

Macroconch (♀)

Non Holcostephanus atherstoni Sharpe var. nov., Kilian, 1902: 865, pl. 57 (fig. 1) (= ? *O. ventricosus* (von Koenen)).
Holcostephanus (*Astieria*) *atherstoni* var. *densicostata* Wegner, 1909: 82, pl. 16 (fig. 3).
? *Astieria multistriata* Zwierzycki, 1914: 53, pl. 6 (figs 6–9, 16).
? *Rogersites sakalavensis* Besairie, 1936: 139, pl. 13 (figs 10–12).
? *Rogersites spathi* Besairie, 1936: 140, pl. 12 (figs 1–2).
? *Rogersites filifer* Imlay, 1937: 559, pl. 73 (figs 1–2), pl. 74 (figs 4–5).
Olcostephanus densicostatus (Wegner) Spath, 1939: 27.
Rogersites atherstoni var. *densicostatus* (Wegner) Tzankov, 1943: 197, pl. 9 (figs 1–3).

Material

A single juvenile, SAM–PCU1612, without locality data but presumably from the Sundays River Formation.

Holotype

By lectotype designation herein, the original of the specimen of *Holcostephanus* (*Astieria*) *atherstoni* var. *densicostata* figured by Wegner (1909: 82, pl. 16 (fig. 3)) (Fig. 54) from Escragnolles (Alpes Maritimes).

Diagnosis

A species resembling *O. atherstoni* (Sharpe) but with finer, more numerous secondaries (Fig. 55). In the presumed microconch there are between 54 and 75 secondaries per half whorl, with well in excess of 60 per half whorl in the macroconch.

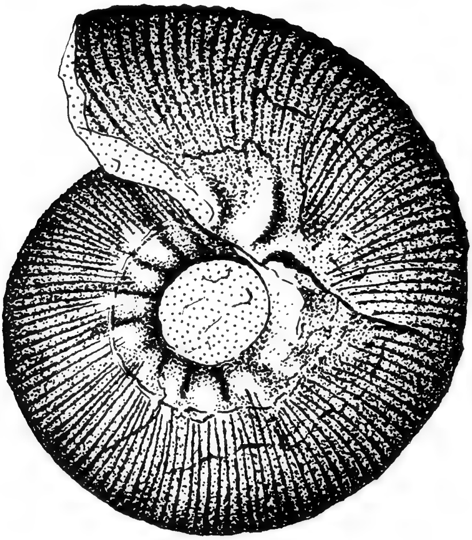

Fig. 54. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner). The holotype, by lectotype designation herein, from the Lower Hauterivian of Escragnolles (after Wegner 1909). × 1.

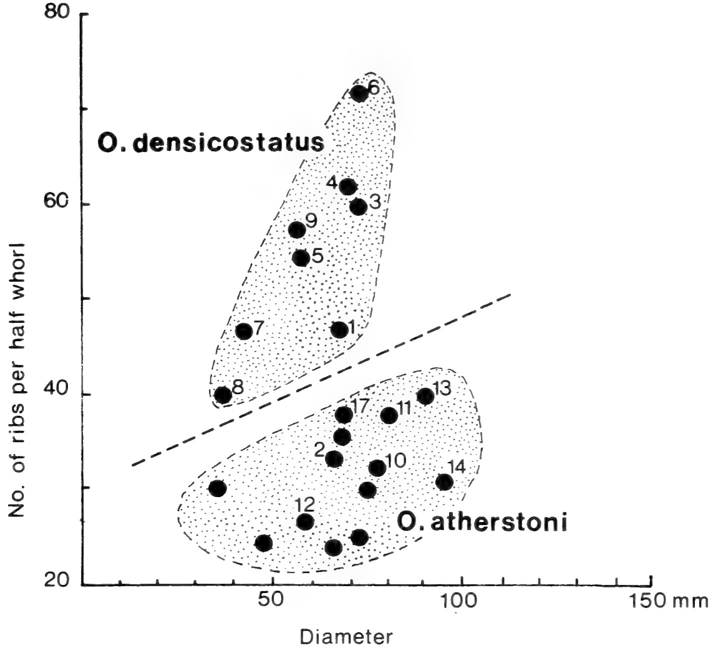

Fig. 55. Plot of rib density versus diameter for microconchs of *O. atherstoni* and the *O. densicostatus* plexus. 1 = *O. salinarius* var. *crassa* Spath, 2 = *O. midas* (Leanza), 3 = *O. densicostatus* (a probable macroconch), 4 = *O. salinarius* Spath (the holotype), 5 = *O. salinarius* var. *involuta* Spath, 6 = *O. salinarius* var. *obesa* Spath, 7 = *O. salinarius* sp. juv. (in Spath 1939), 8 = *O. salinarius* sp. juv. (in Spath 1939), 9 = *O. auritus* (Leanza), 10 = *O. atherstoni* (♂) (in Riccardi *et al.* 1971), 11 = *O.* aff. *wilmanae* (in Spath 1930), 12 = SAM–PCU1526, 13 = *O. wilmanae* (Kitchin), 14 = *O. otoitoides* (Spath), 15 = *O. tenuicostatus* (Imlay), 16 = *O. prorsiradiatus* sp. juv. (in Imlay 1937), 17 = *O. leptoplanus* (in Pictet & Campiche 1860).

Description

A single juvenile (Fig. 27E–F), preserved as a ferruginous internal mould, is referred, with reservations, to this species. The umbilicus is rather narrow and ornamented with about 18 bullae on the outer whorl. There are about 70 fine secondary ribs on the outer whorl (at a comparable diameter a juvenile *O. atherstoni* has only 60) but their connections with the umbilical bullae are indistinct. The whorl section is semicircular.

Discussion

The widespread occurrence of forms closely resembling *O. atherstoni* (Sharpe) but differing in the possession of denser secondary ribbing would seem to justify Spath's (1939: 27) elevation of Wegner's (1909) variety to specific rank. In his original description, Wegner also included the juvenile figured by Kilian (1902, pl. 57 (fig. 1)) into this species but Kilian's specimen shows a prominent parabola and is excluded from *O. densicostatus* as herein interpreted.

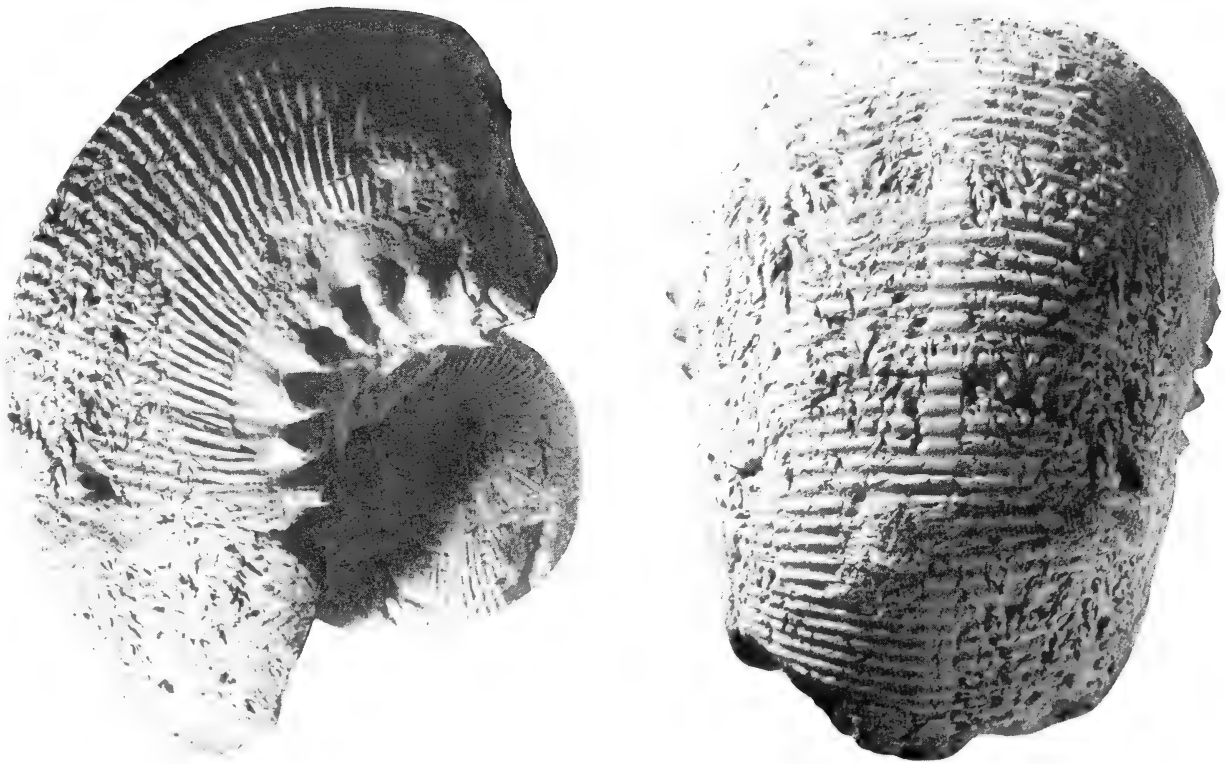

Fig. 56. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie) (♀). The holotype in the collections of the University of Paris, from the Upper Valanginian of Ambiky, Madagascar. × 1.

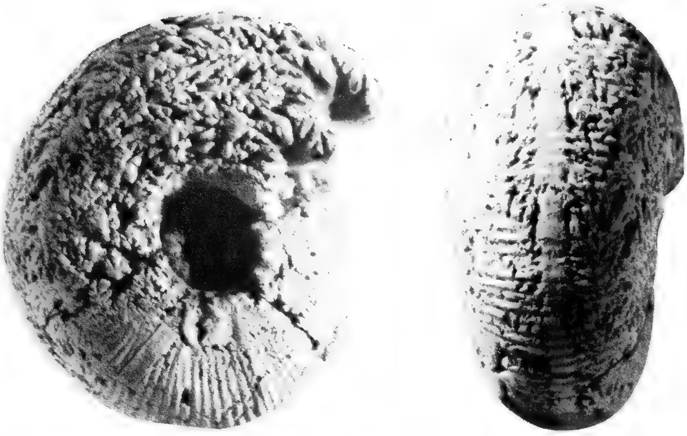

Fig. 57. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie). A hypotype in the collections of the University of Paris, from Ambiky, Madagascar. × 1.

Olcostephanus sakalavensis (Besairie) (Figs 56–57) is a strongly inflated macroconch species with a very depressed whorl section. The steep umbilical walls are ornamented with about 12 rursiradiate primaries per half whorl which terminate in bullae on the umbilical shoulder. From these arise bundles of 4–6, fine, prorsiradiate secondaries with intercalated ribs between bundles, so that there are 36 secondaries across the venter per 7 umbilical bullae on the outer whorl of the holotype. Parabolae are lacking at all growth stages. Modern revision of the European material will probably show that *O. sakalavensis* is a synonym of *O. densicostatus.*

Olcostephanus filifer (Imlay) (Fig. 58) was created for a large, strongly inflated macroconch with a broadly convex venter. The umbilicus of this species is narrow and deep, with vertical walls ornamented by 20 weak, rursiradiate primaries which terminate in rather weak tubercles at the umbilical shoulder. Each tubercle gives rise to 4–5 fine, prorsiradiate secondary ribs with 1–2 intercalated ribs between bundles. Parabolae are lacking. This species was said to differ from *O. densicostatus* in its finer ribbing and more numerous umbilical tubercles, but the differences are slight and probably do not warrant specific separation. *Olcostephanus filifer* is certainly a synonym of *O. sakalavensis.*

Olcostephanus spathi (Besairie) (Fig. 59) is based upon the inner whorls of a macroconch. It is a moderately inflated species with a semilunate, depressed whorl section. The umbilical walls are strongly convex and ornamented with 25 rursiradiate primaries which terminate in rather small umbilical bullae. From these arise bundles of slightly prorsiradiate, almost rectiradiate, secondaries whose connections with the umbilical bullae are indistinct. Between bundles there are several intercalated ribs, so that there are 33 secondaries across

Fig. 58. *Olcostephanus (Olcostephanus) filifer* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

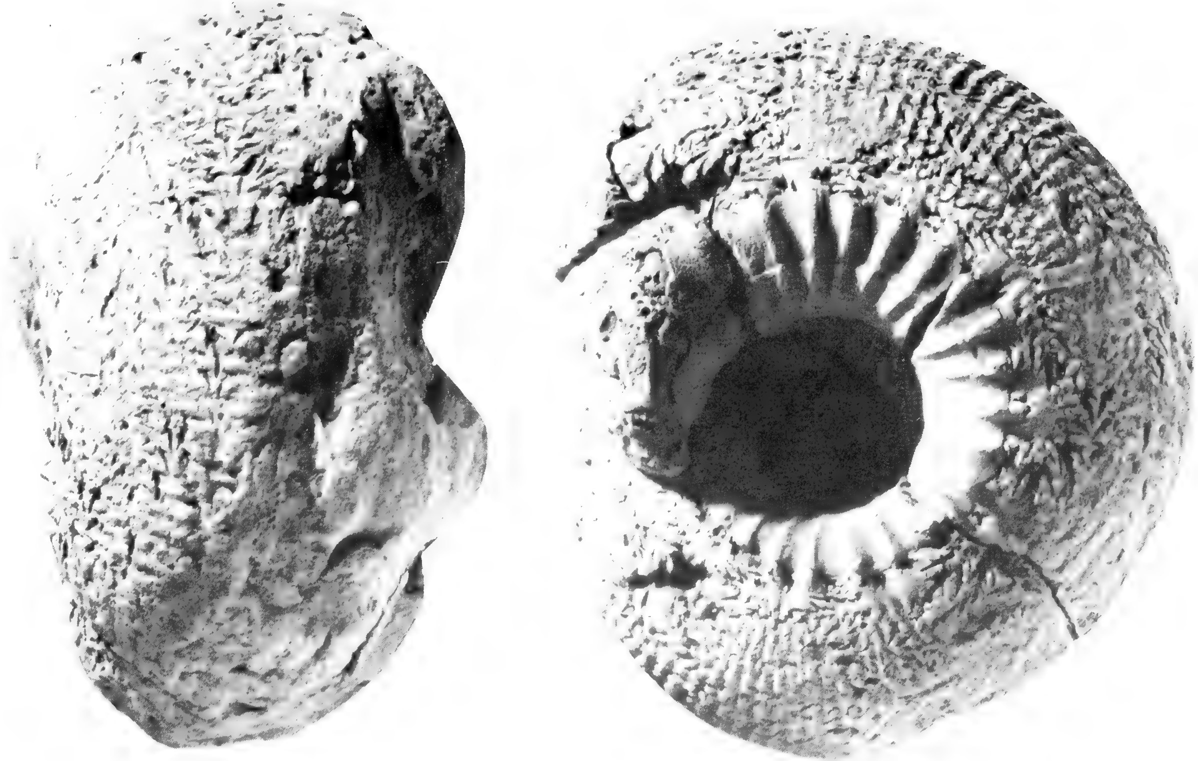

Fig. 59. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie) (♀). The holotype of *Rogersites spathi* Besairie from the Upper Valanginian of Ambiky, Madagascar. × 1.

the venter per 8 umbilical bullae on the outer whorl of the holotype. Parabolae are lacking. This species is based upon the inner whorls of *O. sakalavensis* and is probably, therefore, a junior subjective synonym of *O. densicostatus*.

The holotype of *O. salinarius* Spath (Fig. 60) is a microconch, somewhat inflated and with a rather wide umbilicus. Rursiradiate primaries terminate in 20–24 umbilical bullae from which arise bundles of 4–5 fine, prorsiradiate secondaries. Parabolae are lacking. In view of the side-by-side occurrence of this species with *O. sakalavensis* in the Spiti Shales (Fatmi 1977) they are herein regarded as sexual dimorphs and *O. salinarius* is likely to become a junior subjective synonym of *O. densicostatus*. According to Fatmi (1977), *O. geei* Spath (Fig. 61) is a synonym of *O. sakalavensis*. As can be seen from Figure 62, *Holcostephanus auritus* Leanza is undoubtedly a synonym of *O. salinarius* and hence also probably based upon the microconch of *O. densicostatus*.

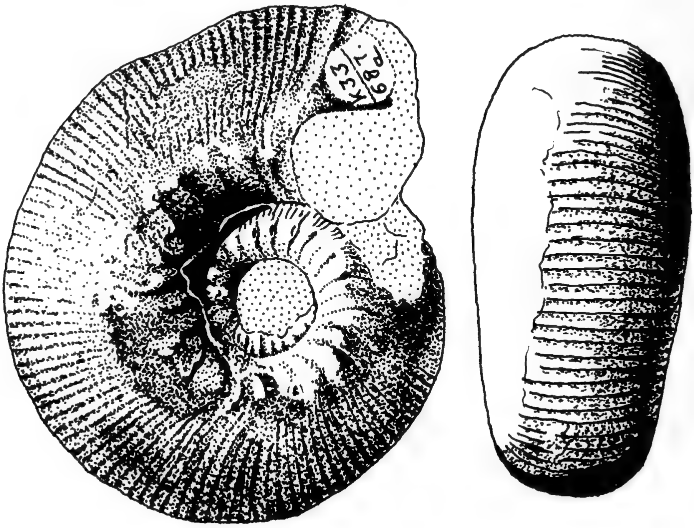

Fig. 60. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner) (♂). The holotype of *Olcostephanus salinarius* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Olcostephanus bakeri (Imlay) (Fig. 63) is based upon an inflated macroconch with a semicircular whorl section and rursiradiate primary ribs which terminate in 11–12 small, pointed umbilical bullae per whorl. From these arise bundles of 4–5 secondaries which frequently bifurcate on the lower part of the flanks and with 1–2 intercalated ribs between bundles. Thus, there are about 120 ribs across the venter of the outer whorl. Parabolae are lacking. This species differs from *O. densicostatus* in possessing far fewer umbilical bullae and by showing more frequent bifurcation of the secondary ribs.

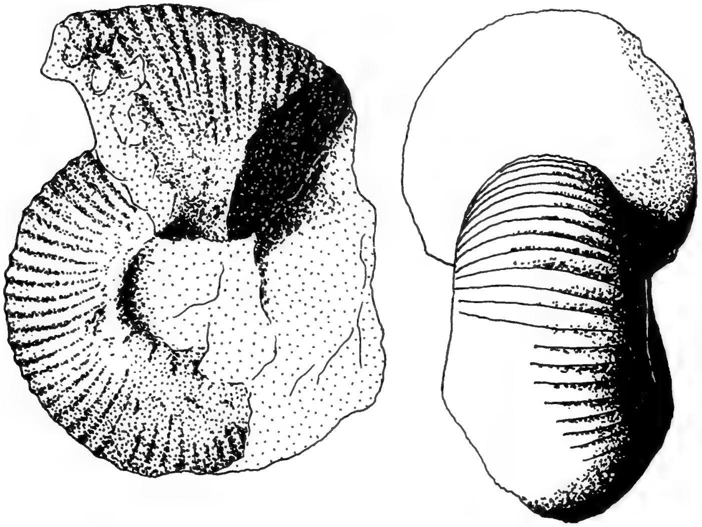

Fig. 61. *Olcostephanus* (*Olcostephanus*) *sakalavensis* (Besairie). The holotype of *Olcostephanus geei* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

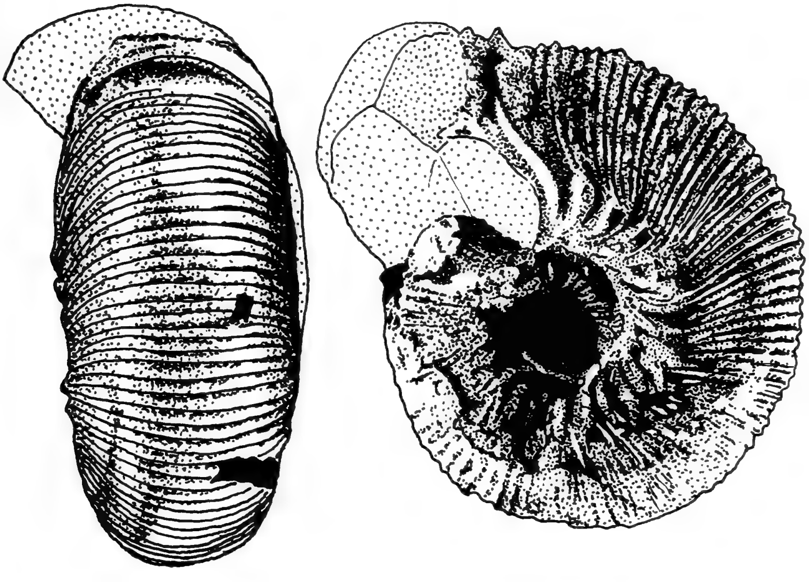

Fig. 62. *Olcostephanus* (*Olcostephanus*) *densicostatus* (Wegner) (♂). The holotype of *Holcostephanus auritus* Leanza, from the Lower Hauterivian of Argentina (after Leanza 1944). × 1.

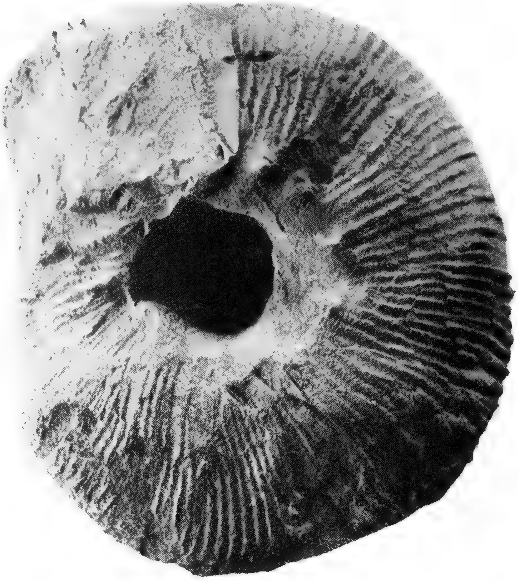

Fig. 63. *Olcostephanus* (*Olcostephanus*) *bakeri* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

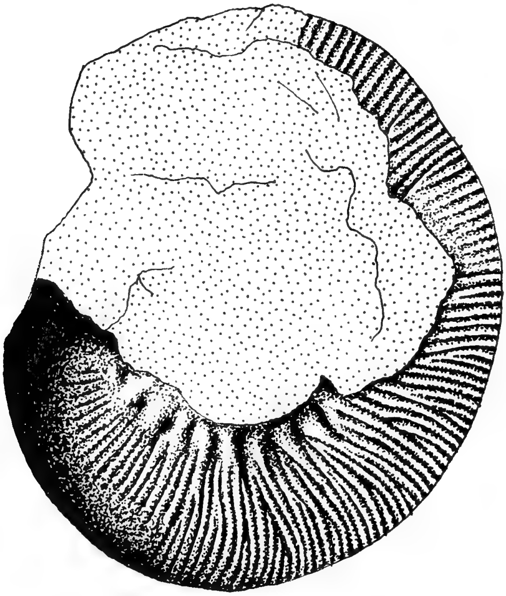

Fig. 64. *Spiticeras*? *balestrai* (Rodighiero). The holotype of *Astieria balestrai* Rodighiero, from Venice (after Rodighiero 1919). × 1.

'Astieria' balestrai Rodighiero (Fig. 64) resembles the presumed microconchs of *O. densicostatus* but frequent trifurcation of the secondary ribs suggests it is better referred to the genus *Spiticeras*.

Olcostephanus busnardoi (Collignon 1962) is based upon what appears to be a microconch showing a wide, deep umbilicus with vertical walls. Small rounded tubercles on the umbilical shoulder give rise to bundles of 3–5 slightly prorsiradiate ribs, with intercalatories between bundles. Parabolae are lacking. It is doubtful whether this species can be satisfactorily distinguished from the suspected microconchs of *O. densicostatus*.

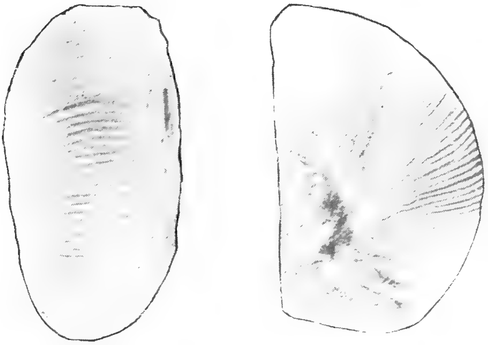

Fig. 65. *Olcostephanus delicatecostatus* Haas. The holotype from Colombia (after Haas 1960). × 1.

Olcostephanus delicatecostatus Haas (Fig. 65) from the Upper Valanginian of Colombia is characterized by '. . . the fineness and density of costation, there being nearly 25 ribs on a quarter whorl. . . . Some ribs bifurcate at about mid-flank. In one individual only 3 circumumbilical tubercles of medium strength are present. In the holotype . . . one or two narrow, extremely shallow constrictions are recognizable' (Haas 1960: 9). The density of ribbing in Haas's species is comparable to that of *O. densicostatus* but it can be distinguished by the irregular (?pathological) development of umbilical tubercles. What Haas (1960) refers to as constrictions in *O. delicatecostatus* do not seem to be parabolae but merely irregularities in growth.

Olcostephanus latiflexus (Baumberger 1908) (Fig. 66) is a moderately large, compressed form, with a wide rather shallow umbilicus and a very depressed whorl section. About 21 rursiradiate primaries on the outer whorl terminate in bullae from which arise 4–5 prorsiradiate secondaries with intercalated ribs between bundles. Parabolae appear to be lacking. This species is disturbingly close to *O. salinarius* and the other suspected microconchs of *O. densicostatus* and, as it has priority over Wegner's (1909) species, its affinities warrant closer scrutiny.

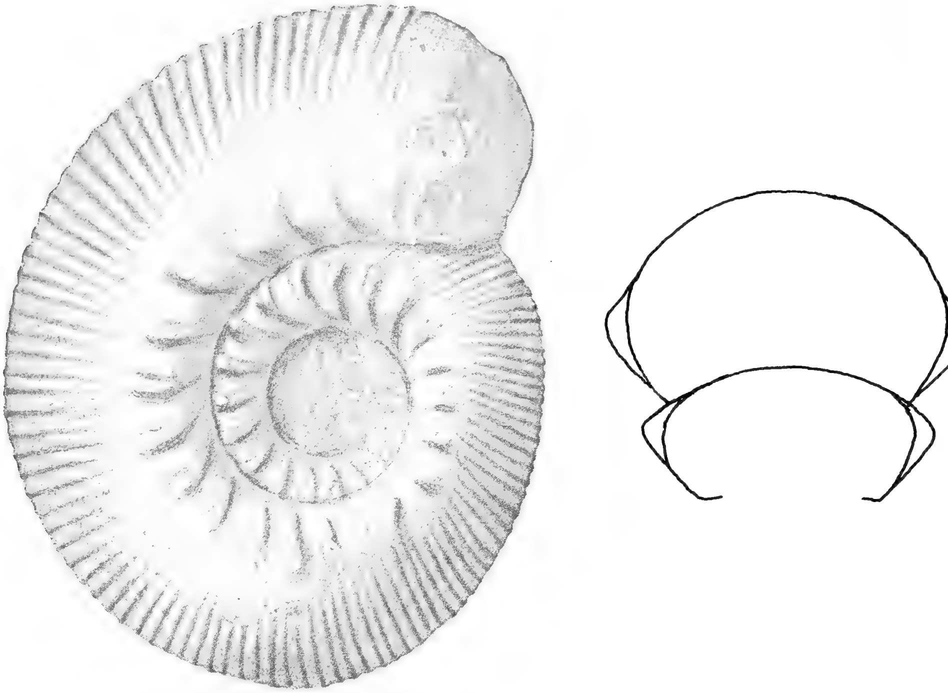

Fig. 66. *Olcostephanus* (*Olcostephanus*) *latiflexus* (Baumberger), (♂). The holotype, by lectotype designation herein, from the Swiss Jura (after Baumberger 1908). × 1.

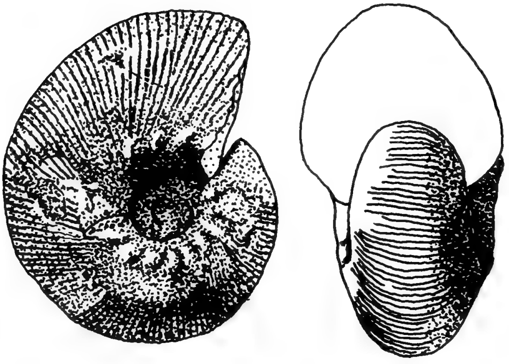

Fig. 67. *Olcostephanus* (*Olcostephanus*) *multistriatus* (Zwierzycki). The holotype, by lectotype designation herein, from the Lower Hauterivian of Tanzania (after Zwierzycki 1914). × 1.

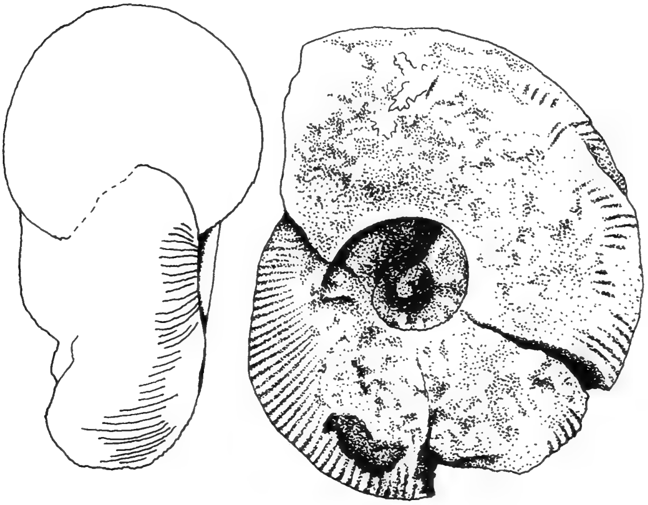

Fig. 68. *Olcostephanus* (*Olcostephanus*) *rebillyi* (Collignon). The holotype from the Lower Valanginian of Madagascar. (after Collignon 1962). × 1.

Olcostephanus multistriatus (Zwierzycki) (Fig. 67) is based upon a juvenile which does not seem to warrant specific separation from *O. densicostatus*.

Olcostephanus rebillyi (Collignon) (Fig. 68) is a species, allegedly from the Lower Valanginian, which is characterized by its rounded whorl section, relatively flat inner flanks, and by the fineness of its ornament which consists of extremely small tubercles from which arise bundles of very fine, prorsiradiate secondaries. Parabolae are apparently lacking. It was said to differ from *O. salinarius* in its narrower umbilicus, less inflated form and more flexuous ribs, but the differences are slight. In view of its age, however, Collignon's (1962) species is for the present maintained as distinct.

Olcostephanus rabei (Besairie) (Fig. 69) shows few features to distinguish it from *O. sakalavensis* and may also prove to a synonym of *O. densicostatus*.

Occurrence

Olcostephanus densicostatus is present in the Swiss Jura and perhaps Pakistan, Madagascar, Tanzania, South Africa, and Mexico.

Olcostephanus (*Olcostephanus*) *rogersi* (Kitchin, 1908)

Figs 70–73, 74A–B, 75A–B, 76, 80, 150E–G

Microconch (♂)

Holcostephanus rogersi Kitchin, 1908: 201, pl. 9 (fig. 1), pl. 10 (fig. 3). Hatch & Corstorphine, 1909: 303, fig. 76c. Giovine, 1950: 39.

Holcostephanus (*Astieria*) *rogersi* Kitchin, Wegner, 1909: 88.

Rogersites rogersi (Kitchen) Spath, 1930: 147. Besairie, 1936: 141.

Rogersites crassicostatus Spath, 1930: 199.

Olcostephanus (*Olcostephanus*) *madagascariensis* (Lemoine) Fatmi, 1977: 271, pl. 5 (fig. 4).

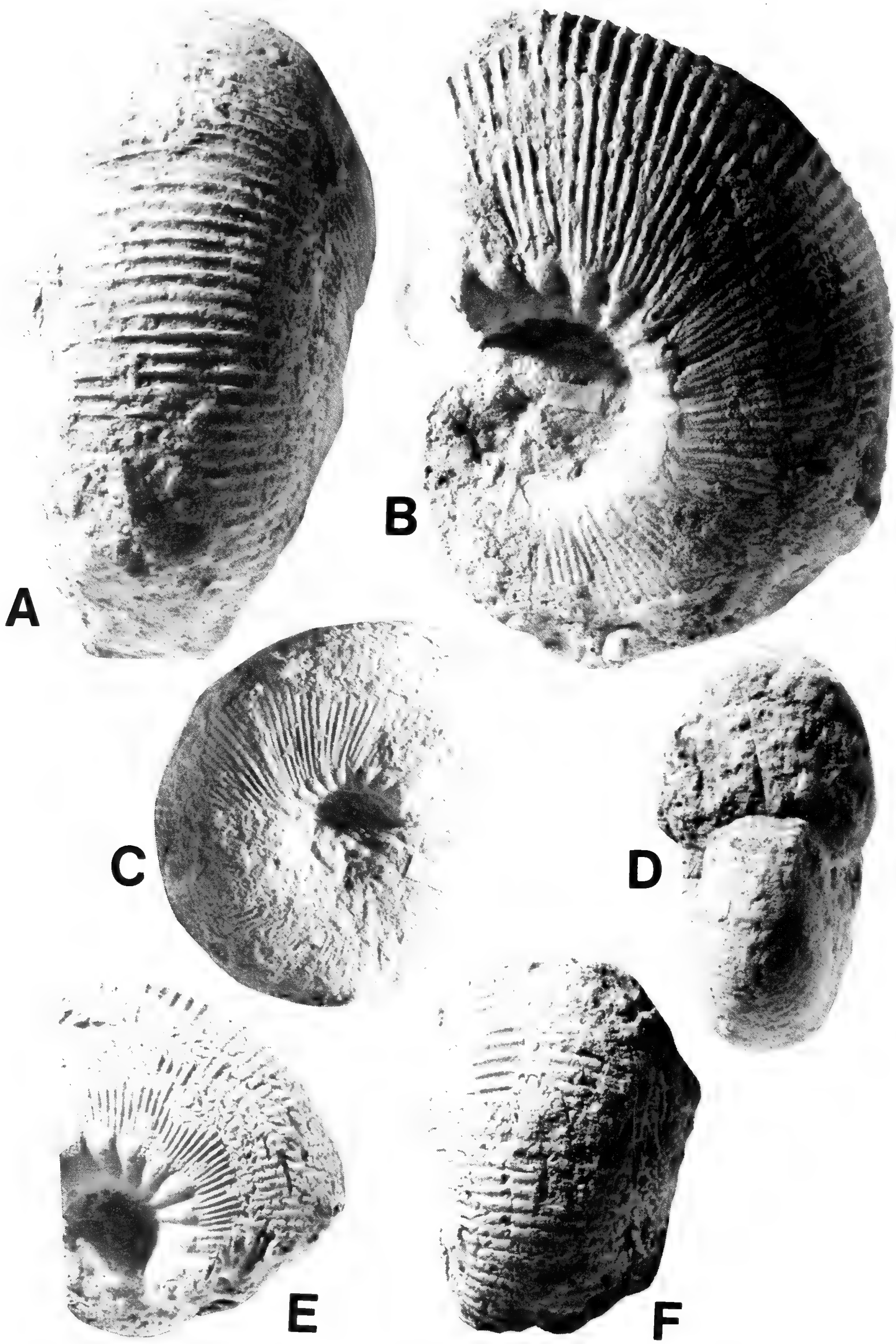

Fig. 69. *Olcostephanus* (*Olcostephanus*) *rabei* (Besairie), × 1. A–B. The holotype. C–F. Paratypes. From the Upper Valanginian of Madagascar.

Macroconch (♀)

Holcostephanus modderensis Kitchin, 1908: 202, pl. 10 (fig. 3). Giovine 1950: 39.
? *Astieria imbricata* Baumberger, 1908: 14, figs 123–125, pl. 26 (figs 2–3).
Holcostephanus (*Astieria*) *modderensis* Kitchin, Wegner, 1909: 89. Kilian 1910: 214.
Rogersites modderensis (Kitchin) Spath, 1924: 86. Spath, 1930: 148.
? *Holcostephanus* (*Rogersites*) *leanzai* Giovine, 1950: 38, pl. 2 (figs 1–3).
Rogersites kitchini Spath, 1930: 148, pl. 15 (fig. 4).
Olcostephanus modderensis (Kitchin) Riccardi *et al.*, 1971: 90.
Olcostephanus kitchini (Spath) Riccardi *et al.*, 1971: 90.

Material

14 specimens; 6 microconchs (SAM–4698, 5071, 11004, SAM–PCU1527, LJE–989b, PEM–1468/42), 7 macroconchs (SAM–PCU1542, 1566, LJE–989e, AAS–370, PEM–1465/81, BM–C47127, SAM–5070), and 1 juvenile (AM–4028).

Holotype

By monotypy, the original of *Holcostephanus rogersi*, SAM–5071 (Fig. 70D–G), figured by Kitchin (1908: 201, pl. 9 (fig. 2)) from the Sundays River Formation.

Diagnosis

Dimorphic. Microconch small (about 70 mm diameter), with 16 rursiradiate primaries per whorl, terminating in prominent umbilical bullae, from which arise invariably 3 coarse, radial secondaries, usually with an intercalated rib between bundles. Parabolae prominent. Macroconch large (300+ mm diameter), extremely inflated, globose. Inner whorls only with parabolae. About 18 very prominent umbilical tubercles on the outer whorls give rise to very coarse, radial secondaries, 3–4 per bulla, with 1–2 intercalated ribs between bundles.

Description

Microconch (♂): Kitchin's holotype, which is taken to represent a microconch, is a poorly preserved internal mould, with odd patches of recrystallized shell. Moreover, it has been slightly crushed, thereby leading Kitchin (1908) to believe the secondary ribbing to be rursiradiate. A near perfect example of this dimorph, LJE–989e, with the lappets preserved, shows, however, the true characters. In this latter specimen, the whorl section is rather depressed, with a fairly broad, evenly rounded venter, as in the holotype. The whorls are involute up to the umbilical bullae, except on the anterior portion of the body chamber when the umbilical seam egresses slightly to reveal a short distance of secondary ribbing of the penultimate whorl. The umbilicus is moderately wide and deep, with steep umbilical walls. The slope of the latter decreases slightly as the umbilical seam egresses.

The primary ribs begin at the umbilical seam and are prominently developed, curving backwards (rursiradiate) to sharp, prominent bullae on the umbilical shoulder. With the egression of the umbilical seam the primary

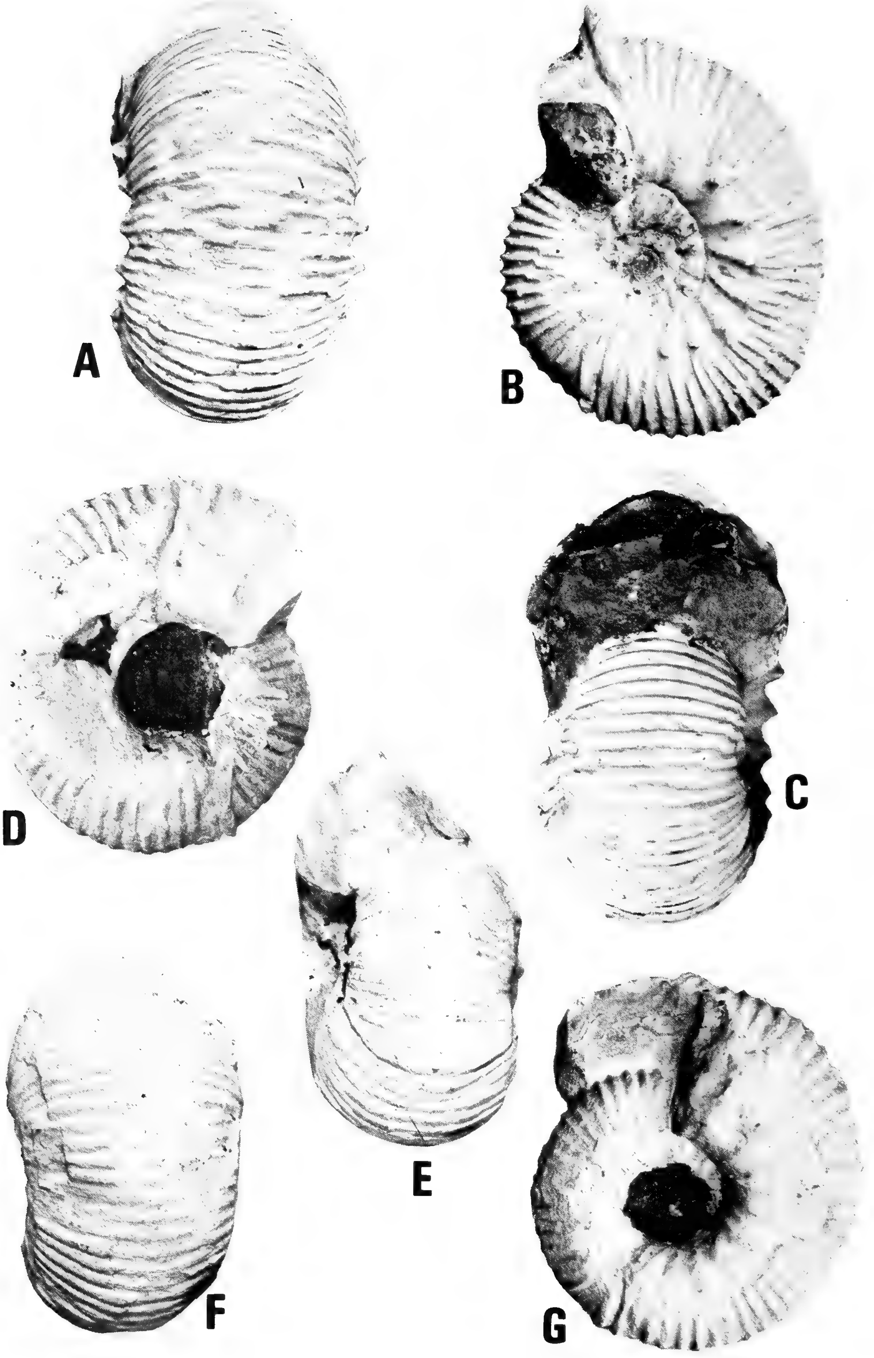

Fig. 70. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂), × 0,75. A–C. Ventral, lateral and front views of LJE–989*b*, with recrystallized test preserved, showing prominent umbilical bullae, radial secondaries, parabolae and lappets. D–G. Right lateral, front, ventral and left lateral views of the holotype, by monotypy, SAM–5071, based upon a poorly preserved internal mould.

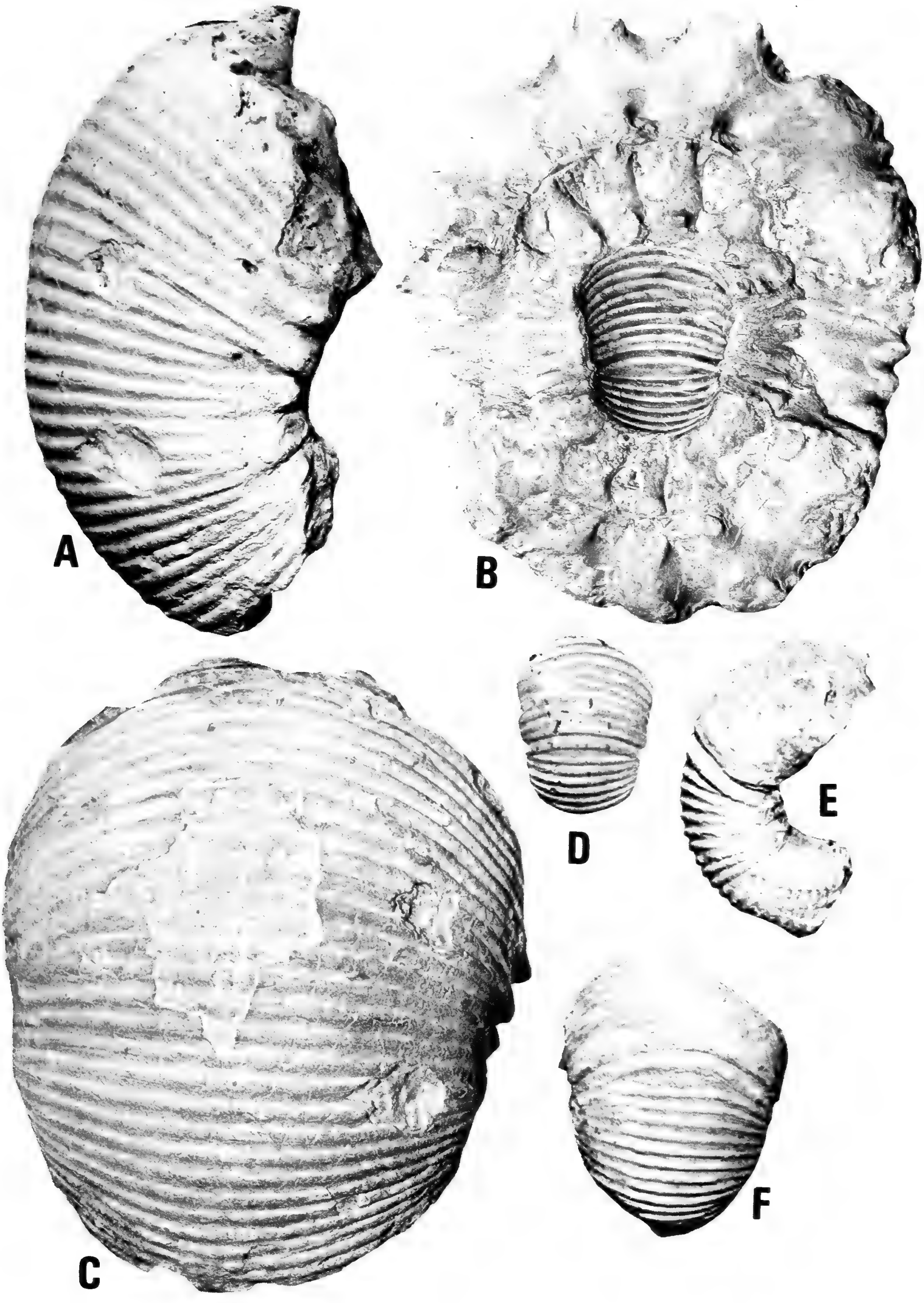

Fig. 71. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀), × 0,44. A–D. Lateral, dorsal, and ventral views, and ventral view of a plasticine mould of the internal whorls of SAM–PCU1542. E–F. Lateral and ventral views of PEM–1468/81, an immature macroconch.

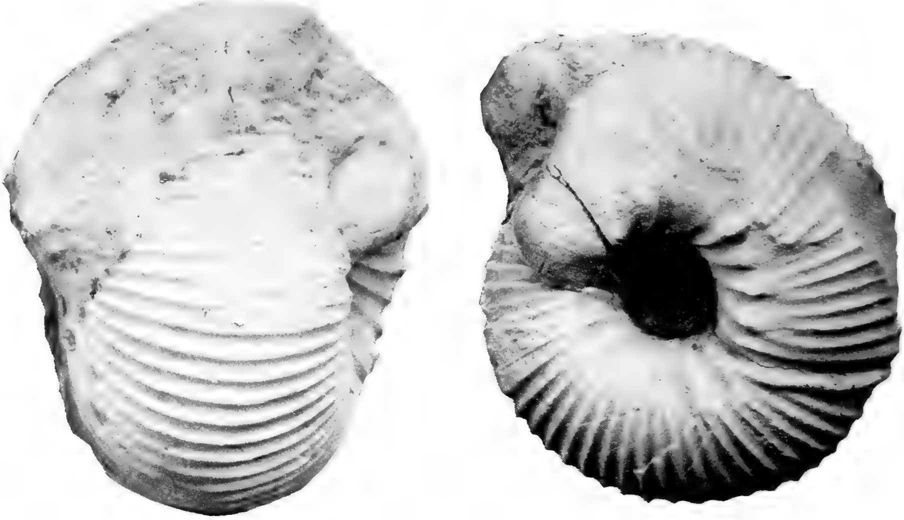

Fig. 72. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). The holotype of *Rogersites modderensis* (Kitchin), BM–C32201. × 0,75.

ribs become almost radial. From the umbilical bullae, bundles of three, very rarely only two, radial secondaries pass straight across the venter, although on the adoral portion of the body chamber, i.e. with the egression of the umbilical seam, they become distinctly prorsiradiate. There is a deep oblique parabola about 180° from the peristome, the adapical rib of which is prominently flared. The peristome is virtually identical to this parabola except that the posterior margin is even more prominently flared, while the adoral rib bears well-preserved lateral lappets which have a subhorizontal twist to them.

Macroconch (♀): in the slightly crushed holotype of *O. modderensis* (Kitchin) (Fig. 72), which represents merely the inner whorls of the macroconch of this species, well-developed rursiradiate primary ribs terminate in about 16 sharp umbilical bullae on the outer whorl. These give rise to bundles of commonly 3, occasionally 4, very coarse, radial secondaries, generally with an intercalated rib between bundles. The secondary ribbing may become slightly prorsiradiate as a parabola is approached. There is a very prominent, deep, oblique parabola on the outer whorl.

The following is a description of the holotype of *O. kitchini* (Spath) based on a plastotype supplied by M. K. Howarth: the shell is gigantic, extremely inflated, with a very depressed whorl section. The umbilical seam of the outer whorl has already begun to egress, showing it to represent part of the body chamber. The umbilicus is narrow and very deep. The umbilical walls of the penultimate whorl are very steep, convex, and ornamented with 17 prominent rursiradiate primaries which begin at, or close to, the umbilical seam and terminate in prominent bullae on the umbilical shoulder. On the final whorl

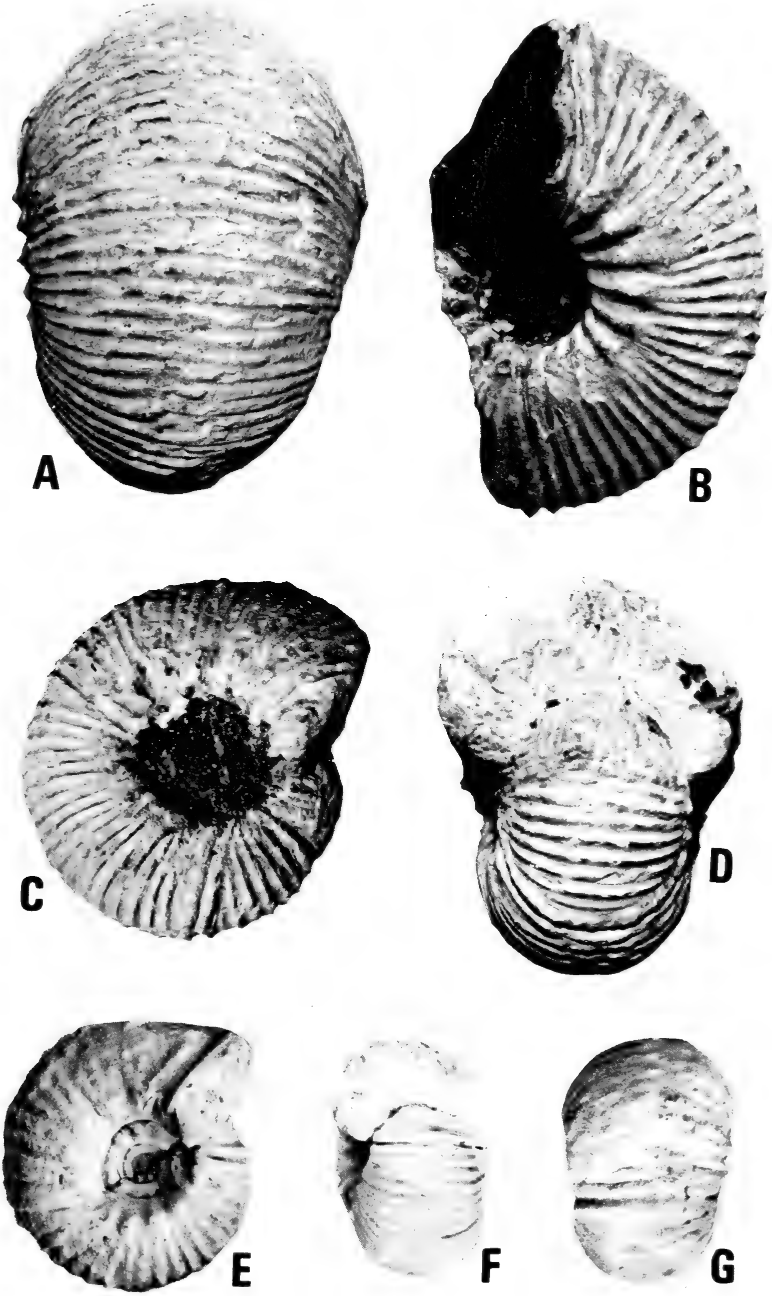

Fig. 73. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). A–B. Ventral and lateral views of AAS–989e, × 0,75. C–D. Lateral and front views of AAS–370, a specimen which is only tentatively included here, × 0,75. E–G. Lateral, front and ventral views of a juvenile in the Albany Museum, × 1.

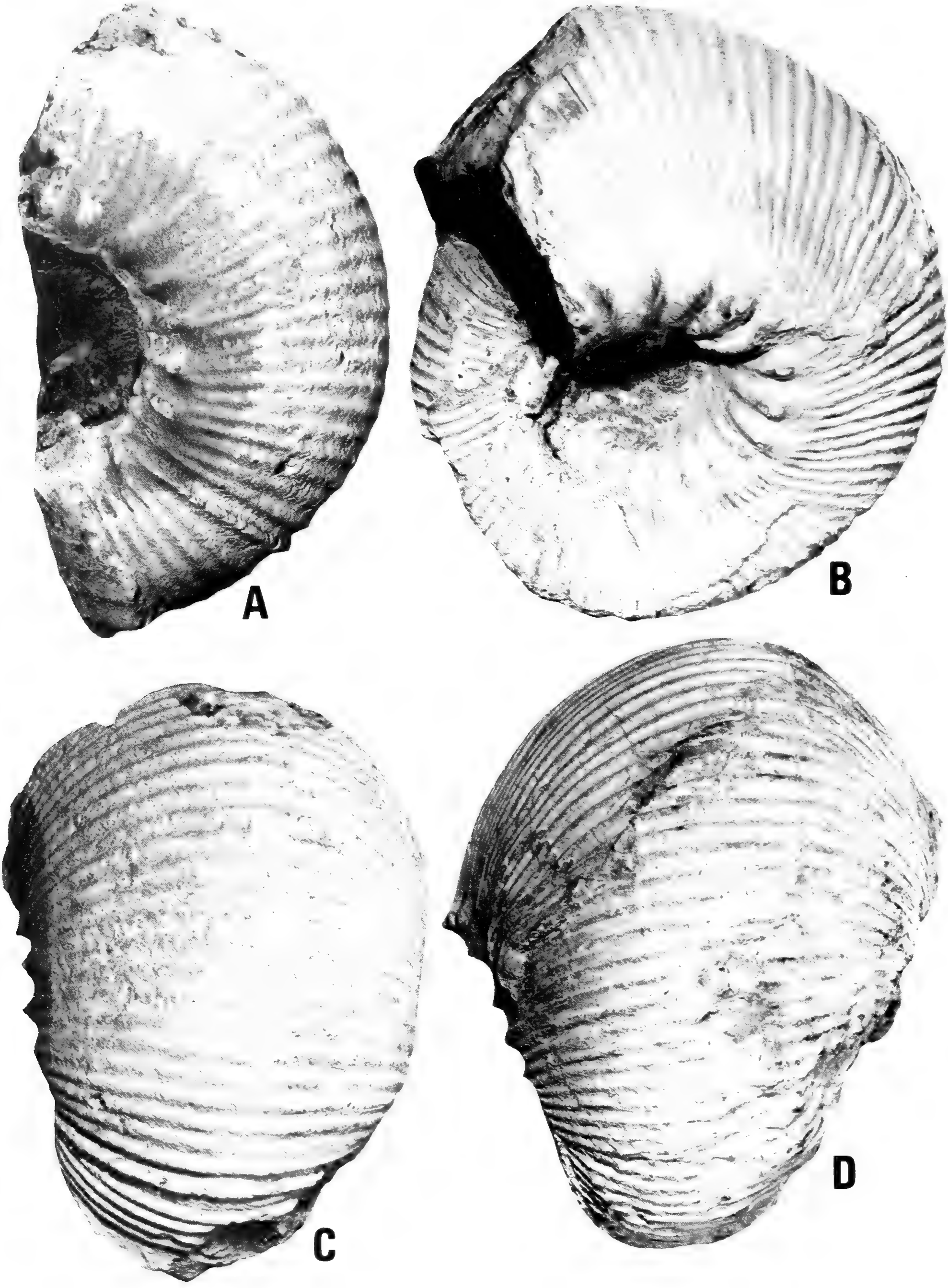

Fig. 74. A, C. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). Lateral and ventral views of SAM–5070, × 0,44. B, D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Lateral and ventral views of PEM–1463/41. Note the rapid rate of inflation, × 0,44.

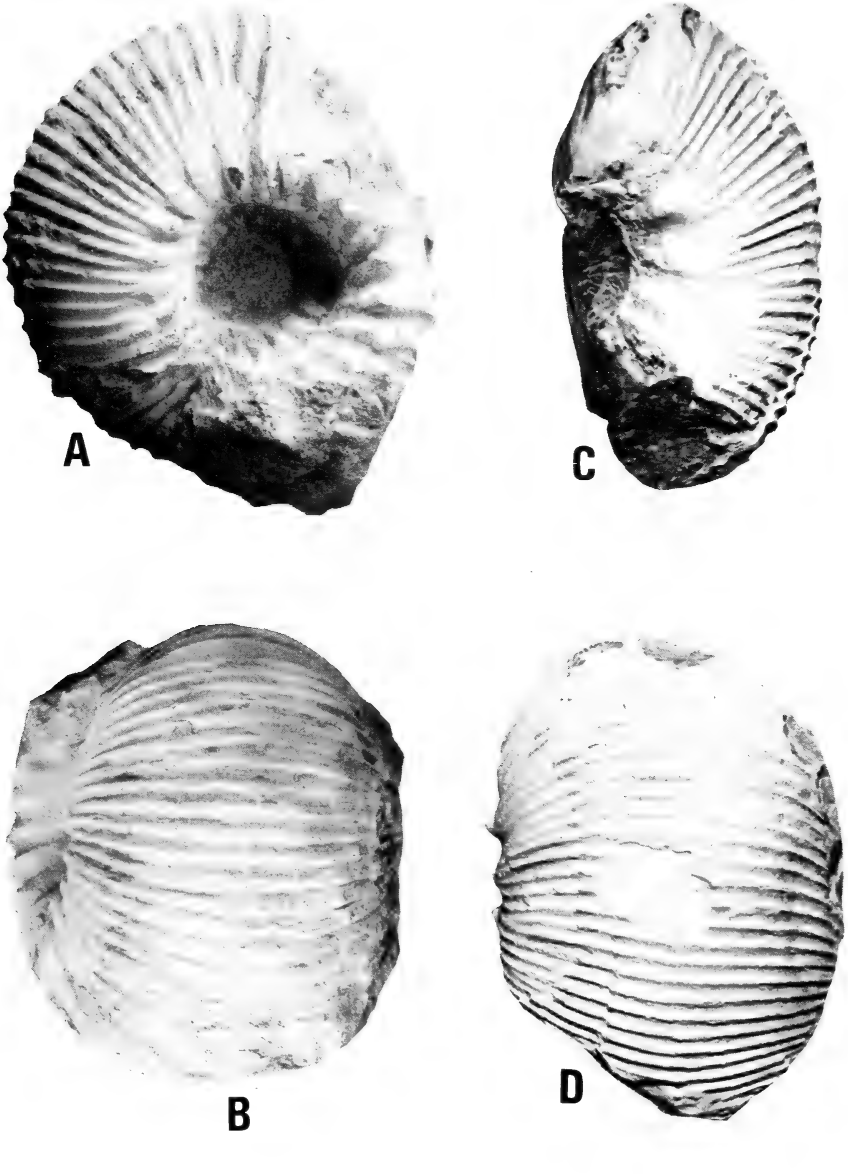

Fig. 75. A–B. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♀). Lateral and ventral views of a specimen in the Geological Survey, Pretoria, × 0,75. C–D. *Olcostephanus* sp. Lateral and ventral views of a macroconch fragment which approaches *O. saintoursi* (Collignon), but appears to lack constrictions, SAM–PCU1562. × 0,44.

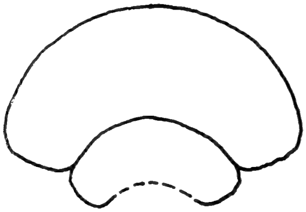

Fig. 76. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂). Whorl section of the holotype. × 1.

the bullae become rounded and swollen, and very prominent, while the primaries weaken considerably on the umbilical wall, being almost entirely effaced on the adoral portion of the outer whorl. Extremely coarse secondaries arise from the umbilical tubercles and vary from almost radial to slightly prorsiradiate in direction. There are commonly 3 secondary ribs per tubercle, with an intercalated rib between bundles, although on the adoral portion of the outer whorl there are commonly 4 ribs per bundle. There is not the slightest doubt that this species merely represents a mature growth stage of *O. modderensis*.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
PEM–1468/81	85	32	?	?	41	28 (33) (♀)
,,	75	28	55	1,96	29	?
,,	55	23	37	1,61	21	8 (15)
Plastotype of *O. modderensis*	77	38	59	1,55	25	? (♀)
	65	28	50	1,79	21	10 (15)
SAM–PCU1542	*c.* 220	75	155	2,06	?	? (♀)
,,	*c.* 125	?	84	?	?	?
,,	*c.* 60	?	45	?	?	?
SAM–5070	*c.* 170	77	119	1,55	85	45 (26) (♀)
,,	*c.* 140	60	?	?	65	?
LJE–989e	75	28	48	1,71	27	13 (17) (♀)
,,	54	33	35	1,52	20	12 (22)
SAM–5071	58	24	35	1,46	26	16 (28) (♂)
,,	46	26	30	1,50	21	11 (24)
,,	35	15	24	1,60	18	?
LJE–989b	59	17	30	1,76	27	16 (27) (♂)
,,	47	15	29	1,93	19	11 (23)
,,	33	11	22	2,00	15	7 (21)
Plastotype of *O. kitchini*	235	90	*c.*195	2,17	95	69 (29) (♀)

Discussion

The only significant difference between the holotypes of *O. modderensis* and *O. rogersi* is the extreme inflation of the former and consequently they are regarded as sexual dimorphs.

In 1930, Spath, when describing *Rogersites kitchini*, referred to a large but fragmentary specimen which he considered '. . . closer to the present species (*R. kitchini*) than to any other described form of *Rogersites*', while considering it to have '. . . the general appearance of what a gigantic *R. schenki* may be supposed to be like' (Spath 1930: 149). This specimen, SAM–5070, is here figured (Fig. 74A, C) and can be seen to show all the characteristics of *O. rogersi* (♀). It is still septate at a diameter of 175 mm and thus represents merely the inner whorls of a much larger specimen. It has rursiradiate primary ribs terminating in umbilical bullae on the umbilical shoulder, from which arise 3–4 radial secondaries. At this diameter there are 14 secondary ribs per 4 bullae. A prominent deep parabola is evident at a diameter corresponding to about 130 mm. There seems little doubt that this example represents merely a larger growth stage than that represented by the holotype of *O. modderensis.*

Another gigantic phragmocone (Fig. 71A–C), approximately 220 mm in diameter, shows an even later growth stage in the ontogeny of this species. The secondary ribbing is still remarkably coarse, with 3–4 radial secondaries arising from each umbilical bulla and 17 secondaries per 4 bullae on the outer whorl. The umbilicus is narrow and very deep, with broad, almost vertical, slightly convex umbilical walls ornamented with prominent rursiradiate primaries. Whilst the outer whorl, admittedly not complete, shows no sign of parabolae, an impression of an inner whorl corresponding to a diameter of about 60 mm shows a deep, oblique parabola, and at this growth stage would appear to be almost identical to the holotype of *O. modderensis.* On the adoral portion of the outer whorl of this specimen the umbilical bullae are seen to become more prominent, a trend which is continued in the even larger, approximately 300 mm diameter, holotype of *O. kitchini* (Spath), a species which is undoubtedly conspecific with the present form.

Kitchin (1908) noted a slight forward inclination of the secondary ribbing on the adoral portion of the outer whorl of *O. modderensis*, but thought it might have been due to crushing. However, the habit of the ribbing becoming prorsiradiate as it approaches the peristome, and thus also parabolae (which are interpreted as relict peristomes), is common to many species of *Olcostephanus.* Indeed, *O. tenuicostatus* Imlay, a synonym of *O. atherstoni*, was distinguished by '. . . the forward inclination of the ribs near the aperture' (Imlay 1937: 562).

Olcostephanus rogersi is undoubtedly closely related to *O. baini* (Sharpe), as is evidenced by the close similarity of the microconchs. *Olcostephanus baini* (♂) differs from *O. rogersi* (♂) in having slightly fewer secondaries per bulla, while the direction of ribbing is prorsiradiate and not radial as in *O. rogersi.* A subtle, but distinctive difference is also seen in the nature of the whorl sections, that of *O. rogersi* (♂) being more depressed, with a broader, flatter

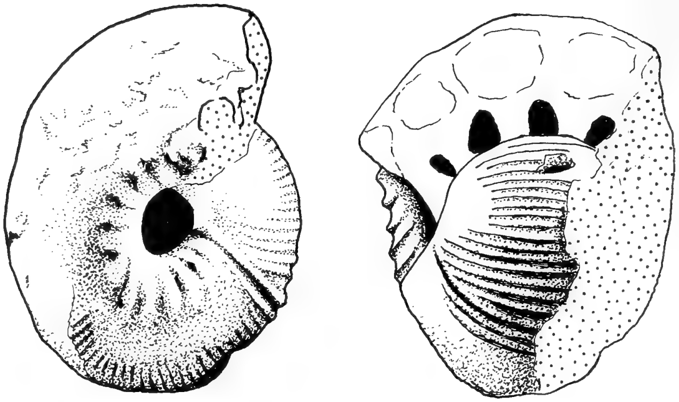

Fig. 77. *Olcostephanus* (*Olcostephanus*) *angusticoronatus* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

venter, whereas the whorl section of *O. baini baini* (♂) is almost semicircular. Kitchin (1908) considered the weak umbilical tubercles of *O. rogersi* important in the separation of this species from *O. baini* but this feature is due to the fact that the holotype is an internal mould.

Olcostephanus baini var. *sphaeroidalis* (Spath) (♂) has a less inflated form while the secondary ribbing is also prorsiradiate. Whilst the differences between *O. rogersi* and *O. baini* may seem slight, the very marked differences between the macroconch forms of these two species suggests that the separation is a valid one.

In describing the ammonite fauna of the Taraises Formation of northern Mexico, Imlay (1938) created the new species *Valanginites angusticoronatus* (Fig. 77) for very involute, globose forms with rursiradiate primary ribs terminating in 16 umbilical bullae from which radiate bundles of 3–4 ribs. There are two prominent parabolae per whorl. This species is very close to the inner whorls of *O. rogersi* macroconch from which it appears to differ in being somewhat more involute and more finely ribbed.

Although originally assigned to the genus *Holcostephanus*, '*H.*' *bachelardi* Sayn (Fig. 78) has recently been included in the synonymy of *Valanginites psaephoides* (Mayer–Eymar) (Thieuloy 1977*a*).

Olcostephanus imbricatus (Baumberger) (Fig. 79) is a strongly inflated, globose species with coarse almost radial secondary ribs which arise from 19–20 umbilical bullae. According to Baumberger (1908: 17), the secondaries arise in pairs from the bullae but quickly bifurcate so that 4 ribs from each bulla cross the venter. There are prominent parabolae on the inner whorls. This species is very close to the macroconch of *O. rogersi* and this relationship bears closer scrutiny.

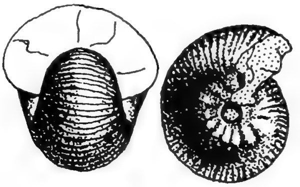

Fig. 78. *Valanginites psaephoides* (Mayer-Eymar). The holotype, by monotypy, of *Holcostephanus bachelardi* Sayn allegedly from the Barremian of France (after Sayn 1889). × 1.

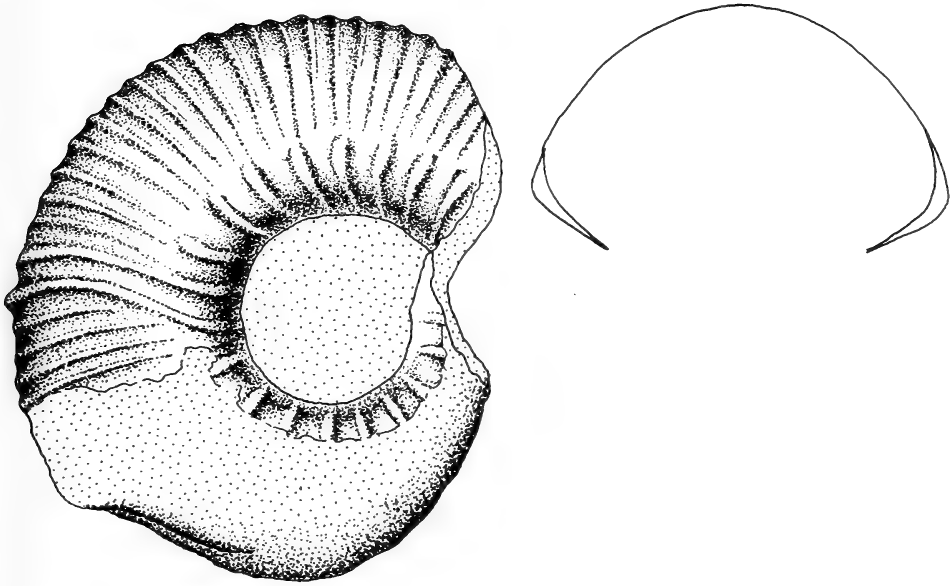

Fig. 79. *Olcostephanus* (*Olcostephanus*) *imbricatus* (Baumberger) (♀). A hypotype from the Swiss Jura (after Baumberger 1908). × 1.

The resemblance between *O. crassicostatus* (Spath) (Fig. 80) and the *O. baini* microconch was first noted by Kitchin (1908) when he described the former as *Holcostephanus* cf. *baini* (Sharpe). The large number of *O. baini* microconchs now available allows a better judgement of the intraspecific variation within this dimorph, and hence a closer comparison with *O. crassicostatus*. The latter species differs from *O. baini* (♂) in its larger adult size, generally radial secondary ribbing although, as in most species of *Olcostephanus*, this tends to become prorsiradiate near the aperture, and in commonly having three secondary ribs arising from each bulla. In addition, the whorl section of *O. crassicostatus* is strongly depressed and with a broad, flattish, gently rounded venter. The features which separate *O. crassicostatus* from *O. baini* are all characters typical of the *O. rogersi* microconch and hence *O. crassicostatus*

Fig. 80. *Olcostephanus* (*Olcostephanus*) *rogersi* (Kitchin) (♂). The holotype of *Rogersites crassicostatus* Spath, SAM–4698, a gerontic microconch. × 1.

is considered to be based upon a gerontic individual of *O. rogersi* (♂). Two other individuals, SAM–PCU1527 and PEM–1463/42, show these same features, the former at 72 mm diameter and with the peristome and lappets preserved and the latter preserved as an internal mould.

'*Subastieria*' *chanchelula* (Anderson 1938) shows a depressed reniform whorl section, with a deep, narrow umbilicus and steep umbilical walls. Prorsiradiate primaries terminate in bullae on the umbilical shoulder from which arise 2–3 rectiradiate secondaries with an occasional intercalated rib between bundles. Parabolae appear to be lacking. The absence of parabolae and the prorsiradiate primary ribs serve to distinguish this species from *O. rogersi*. According to Imlay (1960) it may be a juvenile *Simbirskites*.

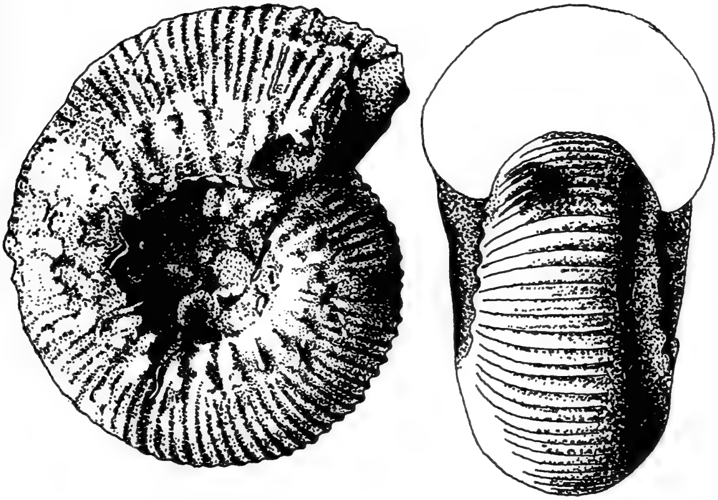

Fig. 81. *Olcostephanus* (*Olcostephanus*) *radiatus* Spath. The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Olcostephanus radiatus Spath (Fig. 81) is very close to *O. rogersi* (♂) but differs in having more umbilical bullae (twenty-four) and, in the holotype, by the absence of parabolae.

Olcostephanus madagascariensis (Lemoine) (Fig. 14), the type of the subgenus *Lemurostephanus*, resembles the *O. rogersi* microconch but can be distinguished by having distinctly sloping umbilical walls and more numerous bullae. The specimen figured by Fatmi (1977: 271, pl. 5 (fig. 4)) is indistinguishable from the present material of *O. rogersi* (compare Fatmi's specimen with Figure 70A–C), and is included in the synonymy of the latter species. *Olcostephanus mitreanus* (d'Orbigny) (Fig. 17), which includes amongst its synonyms *O. detonii* (Rodighiero) (Fig. 15), *O. wynnei* Spath (Fig. 16), and possibly the specimen figured by Thieuloy (1977*a*, pl. 9, fig. 27) as *O.* (*Lemurostephanus*) aff. *sanctifirminensis* Thieuloy, differs from *O. rogersi* (♂) in being more evolute.

Fig. 82. *Olcostephanus* (*Olcostephanus*) *leanzai* (Giovine) (♀). The holotype from the Lower Hauterivian of Neuquén, Argentina (after Giovine 1950). × 0,66.

'*Maderia*' *multituberculata* Imlay (1938) is based upon an inflated, globose, pyritic nucleus with a strongly depressed, semilunate whorl section. About 26 rursiradiate primary ribs terminate in bullae on the umbilical wall and give rise to 2–3 prorsiradiate secondary ribs. Parabolae are prominent and thinning of the ribs across the siphonal line is insignificant. This species differs from *O. rogersi* in its more numerous primary ribs and prorsiradiate secondaries. It is probably based upon the innermost whorls of *O. globosus* Spath.

Olcostephanus leanzai (Giovine) (Fig. 82) is a coarsely ribbed, globose species which was compared with *O. rogersi* and *O. modderensis*. It is unknown whether the inner whorls of this species bear parabolae. So far as can be judged, it differs from the *O. rogersi* macroconch only in the possession of more numerous umbilical bullae but the differences are slight.

Olcostephanus saintoursi (Collignon) (Fig. 83) is too fragmentary to allow a proper comparison, but has finer, more numerous secondaries and is apparently from Lower Valanginian strata. The large size and strong inflation

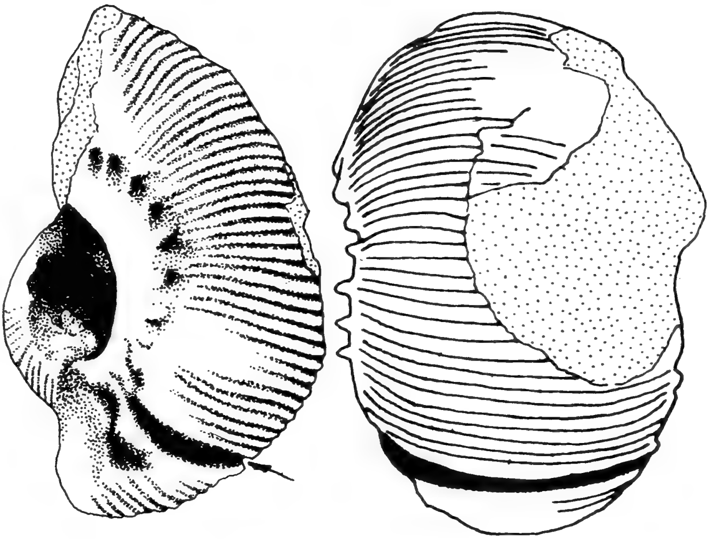

Fig. 83. *Olcostephanus* (*Olcostephanus*) *saintoursi* (Collignon) (♀). The holotype from the Upper Valanginian of Madagascar (after Collignon 1962). × 1.

of this species clearly indicate it to be an immature macroconch but topotype material is necessary to prove its validity.

Dobrodgeiceras wilfridi (Karakasch) (Fig. 12) is another strongly inflated form but differs from the *O. rogersi* macroconch in its small adult size, extremely narrow umbilicus, and the shifting of the umbilical tubercles to a ventrolateral position with a consequent lengthening of the primaries.

Olcostephanus laticostus (Gerth) (Fig. 47) has swollen umbilical tubercles and lacks parabolae and hence cannot be confused with *O. rogersi*. It is, how-

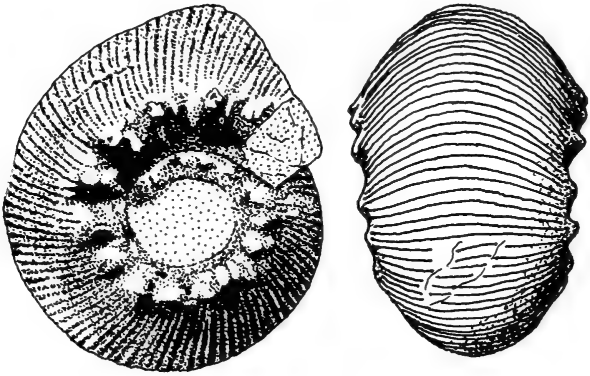

Fig. 84. *Olcostephanus* (*Olcostephanus*) *singularis* (Baumberger). The holotype, by monotypy, of *Holcostephanus klaatschi* Wegner, from the Lower Hauterivian of Basses-Alpes, France (after Wegner 1909). × 1.

ever, close to *O. klaatschi* (Wegner) (Fig. 84) from which it differs in the possession of much coarser ribbing. Wegner's (1909) species differs from *O. rogersi* in being more finely and densely ribbed, lacking parabolae, and with swollen umbilical tubercles at early growth stages. It is almost certainly merely based upon the inner whorls of *O. singularis* (Baumberger).

Astieria dolioliformis Roch (Fig. 13) was erected for extremely inflated, globose forms with a very narrow umbilicus ornamented with nineteen primaries, each terminating in a small umbilical tubercle. Each bulla gives rise to two secondary ribs separated by an intercalatory. As suggested by Spath (1939: 25), this species is best assigned to the genus *Valanginites*.

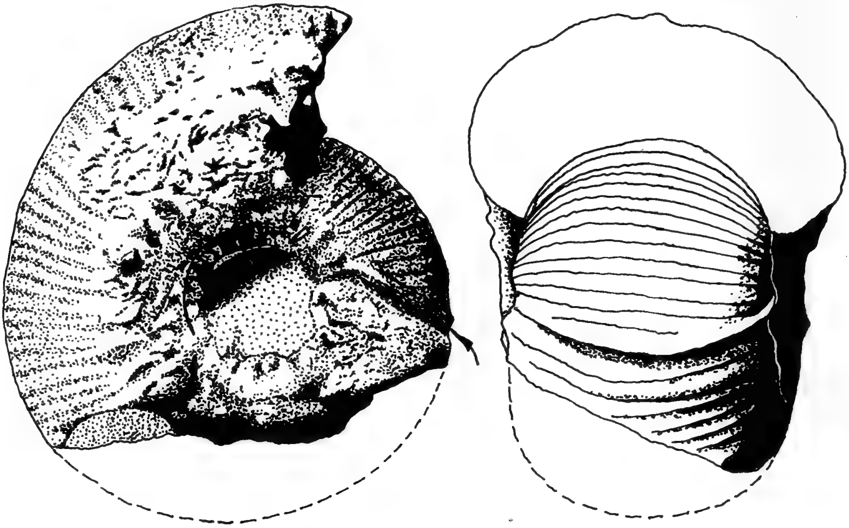

Fig. 85. *Olcostephanus* (*Olcostephanus*) *globosus* Spath (♀). The holotype of *Olcostephanus pachycyclus* Spath from the Spiti Shales of Pakistan (after Spath 1939). × 1.

Olcostephanus pachycyclus (Folgner MS) Spath (Fig. 85) is very close to the holotype of *O. modderensis*, i.e. the *O. rogersi* macroconch, from which it differs only in the possession of far more umbilical bullae (twenty-three at 70 mm diameter). Fatmi (1977) has included this species in the synonymy of *O. globosus* Spath (Fig. 86).

Olcostephanus drumensis (Sayn MS) (Kilian) (Fig. 87) differs from *O. rogersi* in the possession of more numerous umbilical tubercles and in its denser, finer secondary ribbing.

Olcostephanus psilostomus quadricostatus (Tzankov) (Fig. 88) was based upon two individuals, a macroconch and a microconch. The latter is herein selected as lectotype and seems very close to *O. mitreanus* (♂), although it is unclear from Tzankov's (1943) figure if the Bulgarian form has parabolae. It differs from the *O. rogersi* microconch in its smaller adult size, wider umbilicus

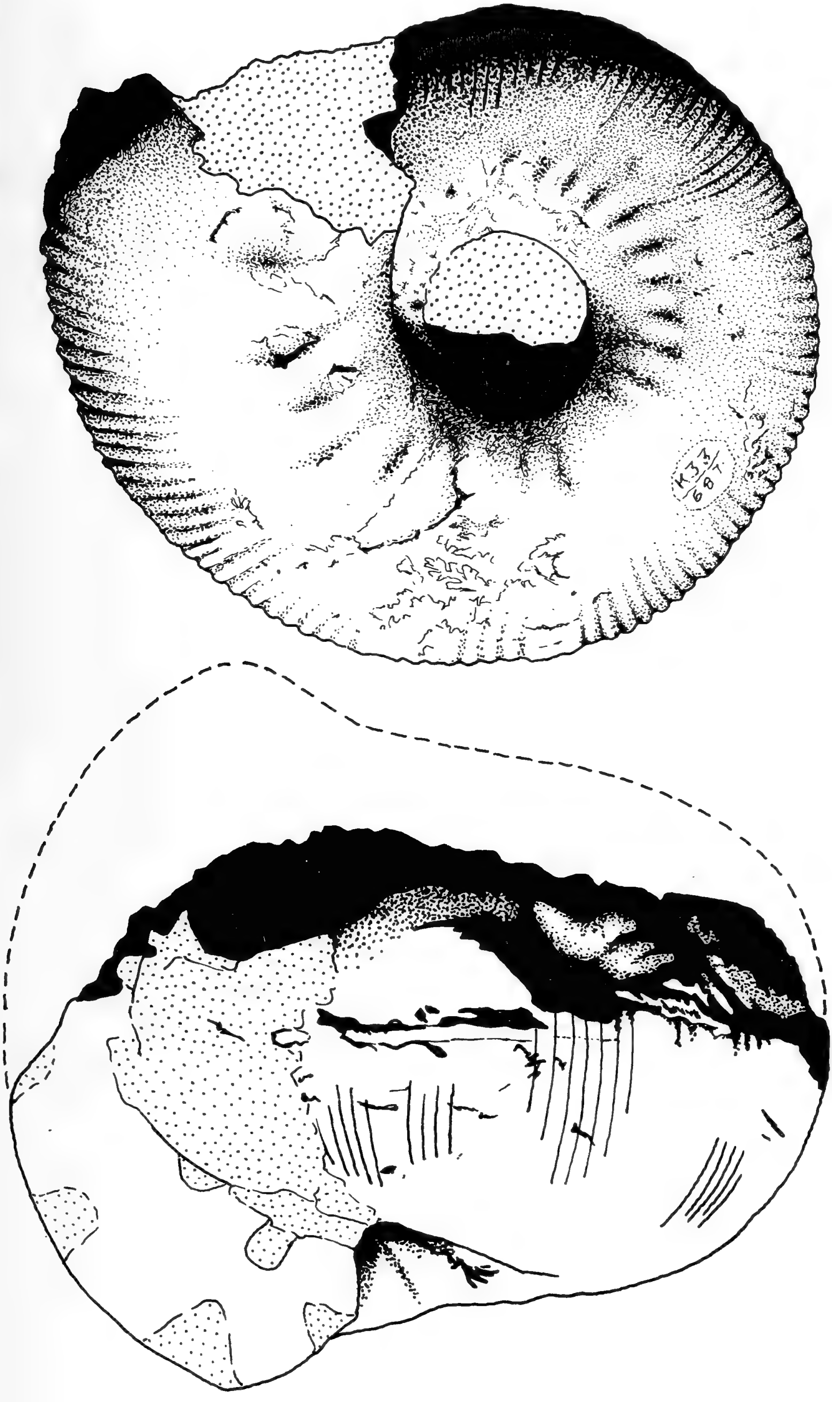

Fig. 86. *Olcostephanus* (*Olcostephanus*) *globosus* Spath (♀). The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

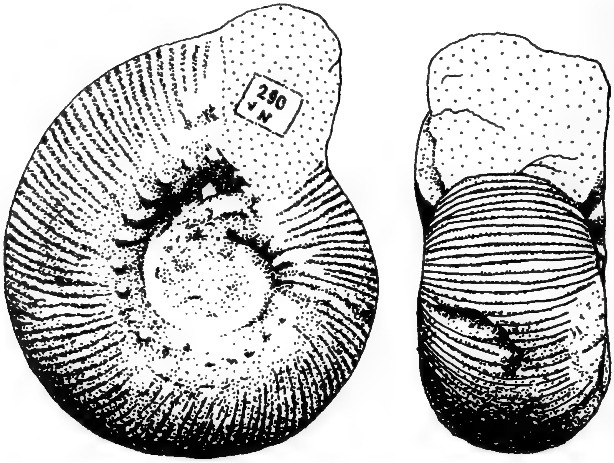

Fig. 87. *Olcostephanus* (*Olcostephanus*) *drumensis* (Sayn MS) Kilian. The holotype, by monotypy, from the Middle Valanginian of Fontanil, France (after Kilian 1910). × 1.

and apparent lack of parabolae. It still remains to be demonstrated that the macroconch which forms part of the syntype series is, in fact, conspecific with the microconch. Since the Bulgarian microconch is certainly specifically distinct from '*O. psilostomus*', the writer would suggest elevating Tzankov's (1943) trivial name to full specific status, i.e. *O. quadricostatus* (Tzankov).

Occurrence

This species is known with certainty only from South Africa and Pakistan, but may also be present in the Swiss Jura and Argentina.

Olcostephanus (*Olcostephanus*) *victoris* Spath, 1939 (♀)

Figs 89–90

Olcostephanus victoris Spath, 1939: 20, pl. 19 (fig. 7a–b). Fatmi, 1977: 268.

Material

A single specimen, LJE–991, from Addo Drift East B farm in the Uitenhage district.

Holotype

The original of *Olcostephanus victoris* figured by Spath (1939: 20, pl. 19 (fig. 7a only)) (Fig. 89) from the Chichali Pass of Pakistan.

Diagnosis

A rather evolute species of *Olcostephanus*, probably representing the inner whorls of a larger macroconch, with a somewhat compressed form. Primary

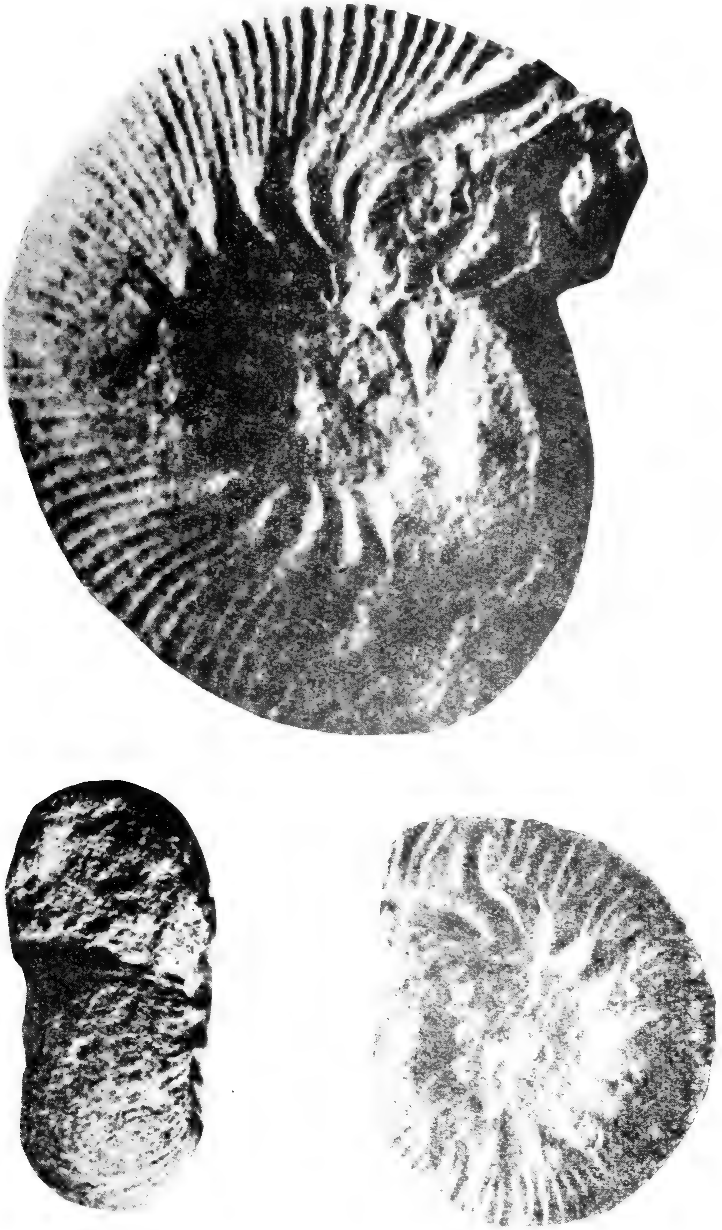

Fig. 88. *Olcostephanus* (*Olcostephanus*) *quadricostatus* (Tzankov). The syntypes from Bulgaria, of which the smaller specimen, a microconch, is selected as lectotype (after Tzankov 1943). × 1.

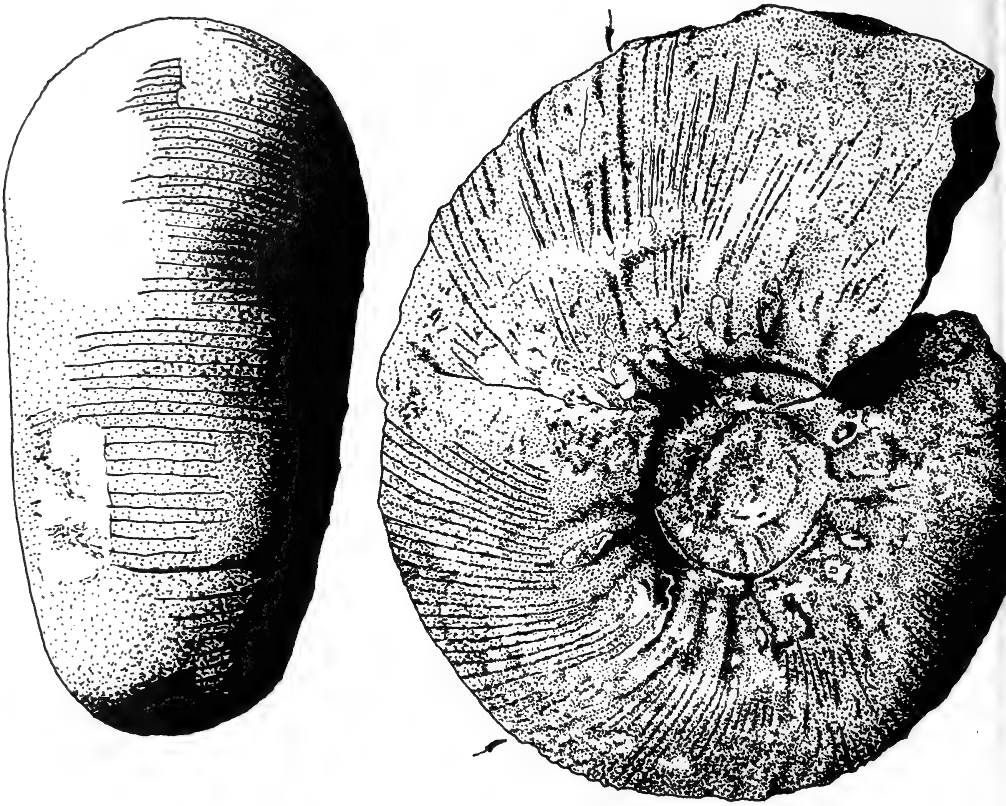

Fig. 89. *Olcostephanus* (*Olcostephanus*) *victoris* Spath (♀). Lateral view of the holotype and ventral view of a paratype, from the Spiti Shales of Pakistan (after Spath 1939). × 1.

ribs rursiradiate, terminating in about 28 umbilical bullae on the outer whorl, from which arise bundles of 3–4 fine, prorsiradiate secondaries. Whorl section suboval, depressed. Parabolae present. Umbilical shoulder rounded, with maximum width some way above the umbilical shoulder.

Description

A single entirely septate specimen (Fig. 90) from the Sundays River is assignable to Spath's species.

This example, LJE–991, has recrystallized test preserved. The shell is somewhat inflated and rather evolute, with a strongly depressed whorl section. At 120 mm diameter the specimen is entirely septate and thus almost certainly represents the inner whorls of a larger probably compressed macroconch. The umbilicus is rather wide and moderately deep, with steep umbilical walls and a well-rounded umbilical shoulder. The venter is rather broad and flattish, but evenly rounded.

On the adoral one-quarter of the outer whorl there is already a distinct egression of the umbilical seam, so that a short distance of secondary ribbing is visible on at least the penultimate whorl. Primary ribs begin at the umbilical seam and pass backwards (rursiradiate) to 26 rather inconspicuous bullae on the umbilical shoulder. These in turn give rise to bundles of 3–4 fine, prorsiradiate secondaries, commonly with an intercalated rib between bundles. The secondaries recurve slightly so as to cross the venter transversely. There are 25 secondaries per 6 bullae on the outer whorl, with 15 ribs within a 50 mm distance along the venter. Maximum width is some way above the umbilical bullae. There are two prominent parabolae on the outer whorl, with a third partially hidden by the adoral portion of the outer whorl.

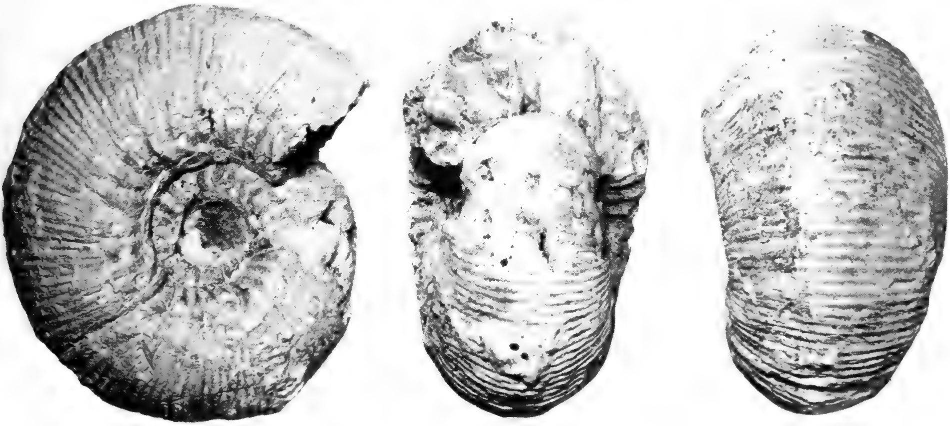

Fig. 90. *Olcostephanus victoris* Spath (♀). Lateral, front and ventral views of LJE–991. Note the convex flanks and the egression of the umbilical seam at a stage when the shell is still entirely septate. × 0,44.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
LJE–991	115	41	69	1,68	51	30 (26)
,,	95	38	56	1,47	42	23 (24)
,,	64	30	37	1,23	26	16 (25)

Discussion

The Uitenhage example closely resembles Spath's holotype. The latter does not, however, show the characteristic egression of the umbilical seam on the outer whorls. None the less, it represents an earlier growth stage than the present specimen and thus may well have become more evolute with ontogeny. Fatmi (1977) considered *O. victoris* a synonym of *O. sakalavensis* Besairie but it differs from that species in being somewhat more evolute, with maximum width somewhat above the umbilical tubercles and in possessing constrictions.

Olcostephanus uitenhagensis (Kitchin) also becomes markedly evolute on the final whorl, hence at a much later stage than *O. victoris*, whilst its inner whorls are more compressed, with broader, flatter flanks. It is unknown whether the inner whorls of *O. uitenhagensis* bear parabolae.

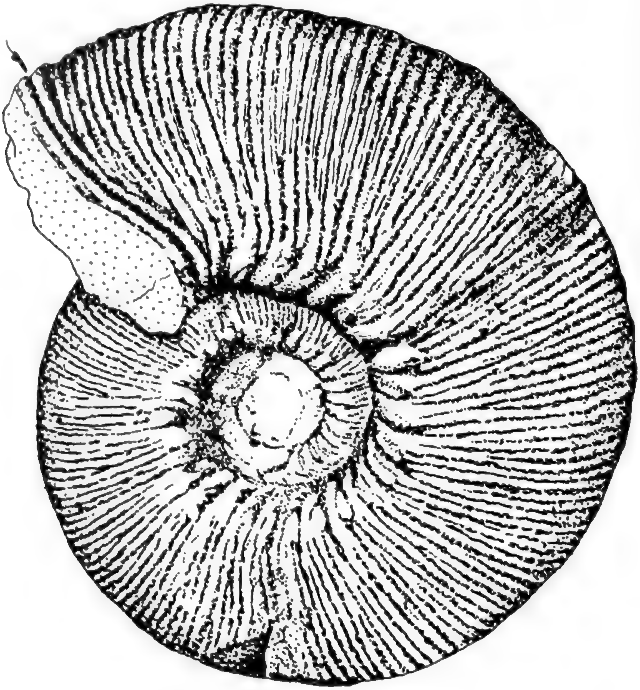

Fig. 91. *Olcostephanus* (*Olcostephanus*) *schafarziki* (Somogyi) (♀). The holotype from Martonkút (after Somogyi 1916). × 1.

Olcostephanus schafarziki (Somogyi) (Fig. 91) would also appear to be rather evolute at moderate diameters but differs from *O. victoris* in lacking parabolae and in the frequent bifurcation of secondaries. In this respect it closely resembles *O. irregularis* (Wegner), with which it may well be conspecific.

Occurrence

This species is currently known only from the Sundays River Formation and the Spiti Shales of Pakistan.

Olcostephanus (*Olcostephanus*) *fascigerus* Spath, 1939 (♀)

Figs 92–97

Holcostephanus (*Astieria*) cf. *convoluta* von Koenen, Uhlig, 1903: 394, pl. 78 (fig. 1).
Olcostephanus fascigerus Spath, 1939: 18, pl. 4 (figs 1–3). Fatmi, 1977: 268, pl. 3 (fig. 3).
Holcostephanus uhligi Collignon, 1962: 23, fig. 827.

Material

Four adult macroconchs, SAM–PCU1568, 1611, SAM–5074, BM–C7126.

Holotype

The original of the specimen figured by Spath (1939: 18, pl. 14 (figs 1–3)) and here refigured (Fig. 92) from the top bed of the middle member of the Chichali Formation of northern Pakistan.

Diagnosis

Large inflated cadicone macroconchs (+ 150 mm diameter), with a depressed whorl section and evenly rounded venter. Between 18 and 22 prominent umbilical bullae on the final whorl give rise to 4–5 radial to prorsiradiate, fine, flexuous, secondary ribs, occasionally bifurcating or with intercalatories, and with 2–5 intercalated ribs between bundles. Parabolae lacking at all growth stages and with a simple peristome in maturity.

Description

The material assigned to this species comprises large, inflated cadicones with depressed whorls and subquadratic whorl sections. Characteristic are the distinct flanks which merge into the broad, evenly rounded venter and provide the whorl section with its subquadrate appearance. The rursiradiate primaries terminate on the umbilical shoulder in about 20–22 somewhat bullate, very prominent tubercles which generally give rise to 5, less commonly 4 or 6, almost radial (SAM–PCU1611) to prorsiradiate (BM–C47126) fine secondaries, usually with 3 intercalatories between bundles. Another feature which distinguishes this species from all other macroconchs from the Uitenhage Group is the almost constant width of the final whorl, which tends to give the shell a cylindrical aspect when viewed ventrally.

In a second specimen, SAM–5074 which shows the same prominent umbilical bullae and cylindrical form as SAM–PCU1611, the secondary ribbing on the adoral portion of the body chamber is very fine and thread-like, with fine secondaries occurring intercalated high up on the flanks.

On SAM–PCU1611 there are 23 secondaries per 3 bullae on the outer whorl, with 18 secondaries within a 100 mm distance along the venter. On the adoral portion of the body chamber the secondary ribbing becomes distinctly prorsiradiate.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1611	226	70	111	1,59	115	?
SAM–5074	235	78	110	1,41	85	?
,,	165	75	100	1,33	65	?
BM–C47126	215	100	121	1,21	88	62 (29)

Fig. 92. *Olcostephanus* (*Olcostephanus*) *fascigerus* (Spath) (♀). The holotype from the Upper Valanginian Spiti Shales of Pakistan (after Spath 1939). × 1.

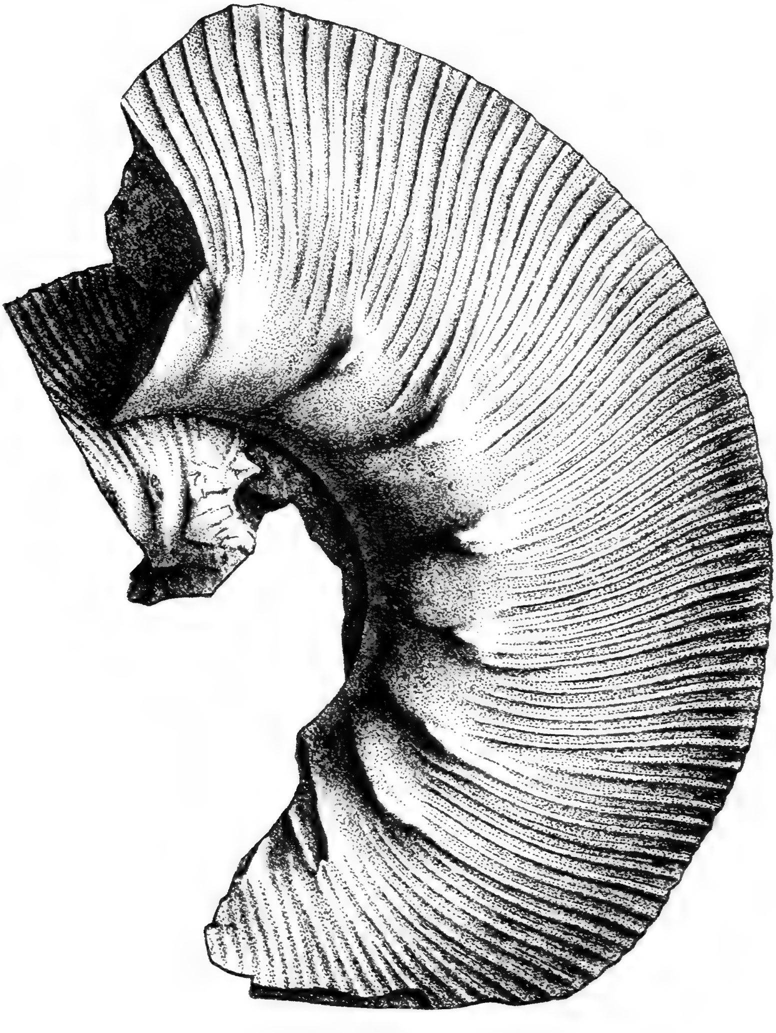

Fig. 93. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Lateral view of the holotype of *Holcostephanus uhligi* Collignon (after Uhlig 1903). × 1.

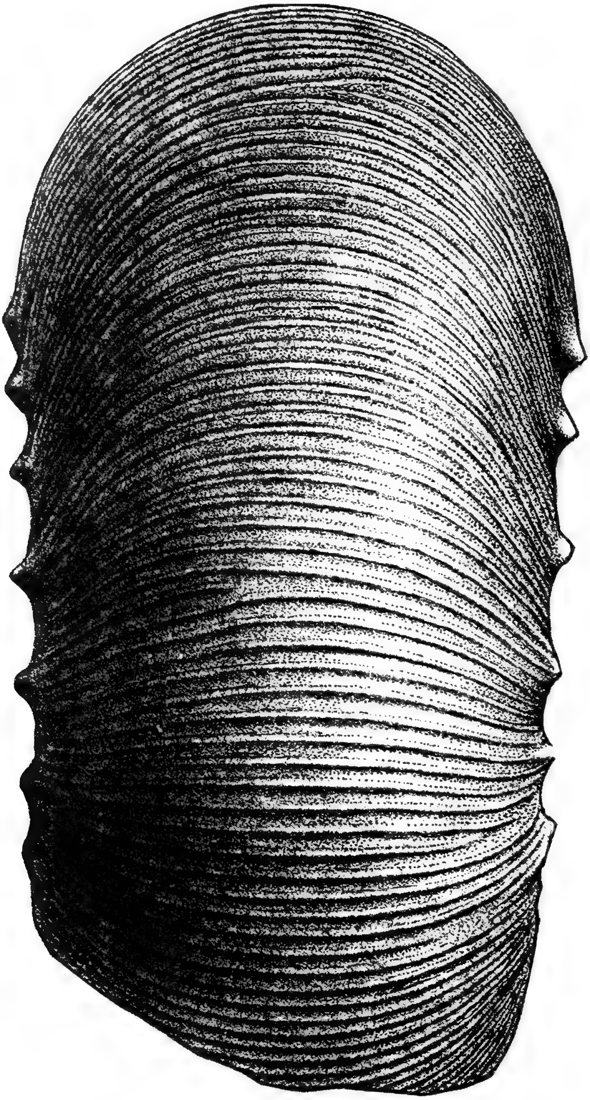

Fig. 94. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral view of the holotype of *Holcostephanus uhligi* Collignon (after Uhlig 1903). × 1.

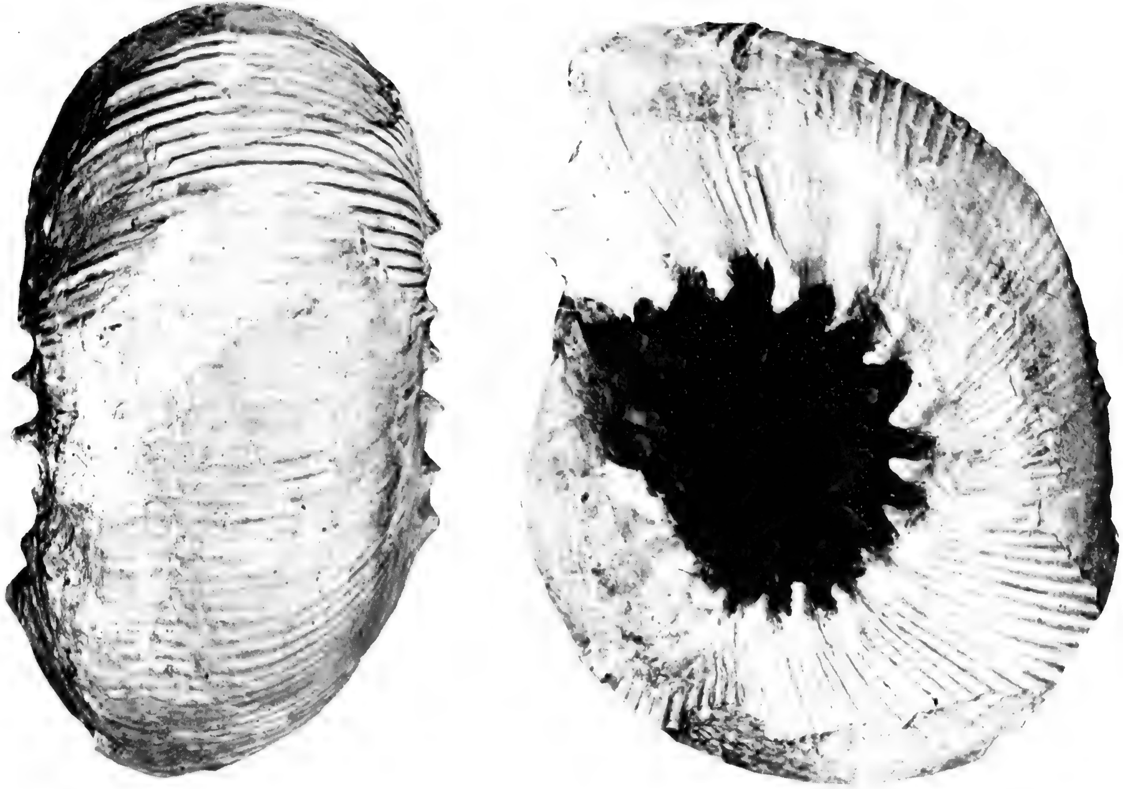

Fig. 95. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral and lateral views of SAM–PCU1611. Note fine secondaries, prominent bullae and constant rate of inflation. × 0,44.

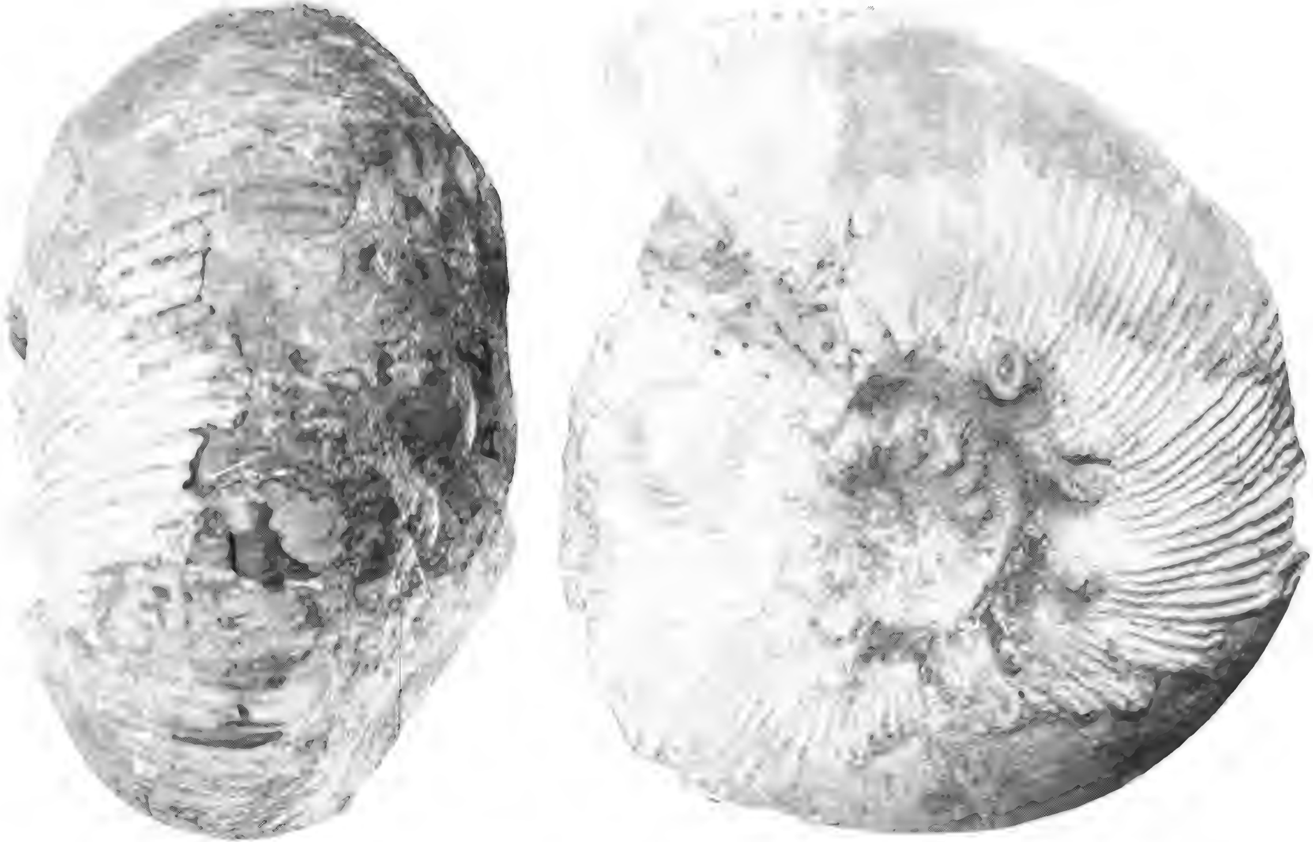

Fig. 96. *Olcostephanus* (*Olcostephanus*) *fascigerus* Spath (♀). Ventral and lateral views of BM–C47126, a specimen with fewer umbilical bullae than the holotype. × 0,44.

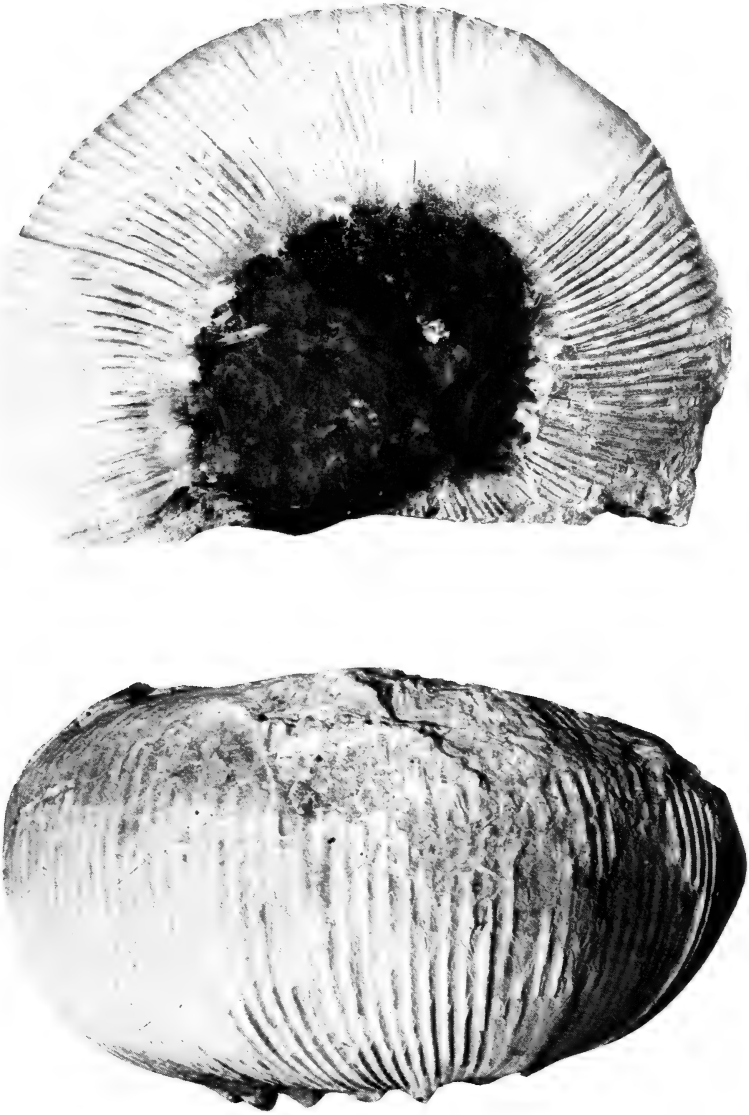

Fig. 97. *Olcostephanus (Olcostephanus) fascigerus* Spath (♀). Ventral and lateral views of SAM–PCU1611. × 0,44.

Discussion

The writer would agree with Spath (1939: 19) that this species should include the adult figured by Uhlig (1903: 394, pl. 78 (fig. 1)) as *Holcostephanus* (*Astieria*) cf. *convoluta* von Koenen (Figs 93–94). Since, however, Uhlig's specimen was subsequently made the type of the new species *H. uhligi* Collignon, the latter name becomes a junior subjective synonym of *O. fascigerus.*

Although Spath (1939) and Fatmi (1977) mention constrictions in their discussions of *O. fascigerus*, none of the figured material shows parabolae and it is herein assumed that parabolae are lacking in the present interpretation of this species.

Olcostephanus fascigerus can be distinguished from all other macroconch dimorphs occurring in the Sundays River Formation by the weak inflation of the whorls which provides it with a cylindrical aspect in ventral view, its prominent umbilical bullae and its fine, irregular secondary ribbing.

Occurrence

This species is at present recorded only from northern Pakistan, Madagascar, and South Africa.

Olcostephanus (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂)
Figs 99–100

Hoplites symonensis Böse, 1923: 96, pl. 5 (figs 5–16).
Taraisites durangense Cantu Chapa, 1966: 16.

Material

Two microconchs, SAM–PCU1547, 1549, collected in the Algoa Brick & Tile quarries at Coega (see Fig. 1).

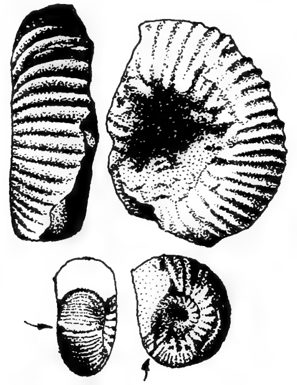

Fig. 98. *Olcostephanus* (*Olcostephanus*) *durangensis* (Cantu Chapa). The syntypes from the Taraises Formation of northern Mexico, of which the smaller specimen is herein selected as lectotype (after Böse 1923). × 1.

Holotype

By lectotype designation herein, the smaller and more complete of the two individuals figured by Böse (1923) and here refigured (Fig. 98) from northern Mexico.

Description

In the only complete example, SAM–PCU1549, which has recrystallized test preserved, the shell is moderately inflated and involute up to the umbilical bullae, with about 80 per cent of the preceding whorl covered. However, the umbilical seam egresses noticeably on the final whorl. The umbilicus is rather wide and moderately deep, with a steep umbilical wall which becomes somewhat inclined with the egression of the umbilical seam. The umbilical shoulder is subrounded. The whorl section is semicircular, with a broadly rounded venter.

The primary ribs begin at the umbilical seam and pass strongly backwards (rursiradiate) to nineteen prominent bullae on the umbilical shoulder of the final whorl. These bullae give rise to thick, robust secondaries, almost invariably in pairs, although very occasionally there is only a single secondary rib arising from a bulla. The rib direction changes significantly on the final whorl. On the adapical portion of the outer whorl the secondaries are very slightly rursiradiate. Half-way round the final whorl the secondary ribbing has become radial, while at the peristome it is distinctly prorsiradiate. This latter feature is not, however, considered characteristic since most olcostephanids show the same tendency for the secondary ribbing to become more inclined near the peristome. There is an occasional intercalated rib between bullae. A rib which occurs intercalated on the one flank is frequently seen to arise from a bulla on the other side.

There are 15 secondaries per 6 bullae on the adoral portion of the body chamber, with 10 ribs within a 40 mm distance along the venter. Prior to the deep parabola on the outer whorl the ribbing is somewhat closer, with 6 secondaries within a 20 mm distance along the venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–K1549	65	26	36	1,38	30	20 (31)
,,	49	21	32	1,52	23	14 (29)
SAM–K1547	45	16	25	1,56	19	12 (27)
,,	35	14	?	?	17	10 (29)

Discussion

The two Uitenhage examples are characterized by robust, distant, predominantly radial secondaries, numerous umbilical bullae, paired secondaries and semicircular whorl sections. The robust nature of the ribbing together with the prominent umbilical bullae suggests better reference to *Olcostephanus* s.s. rather than to the subgenus *Jeannoticeras* which lacks bullae and has finer, more delicate secondaries.

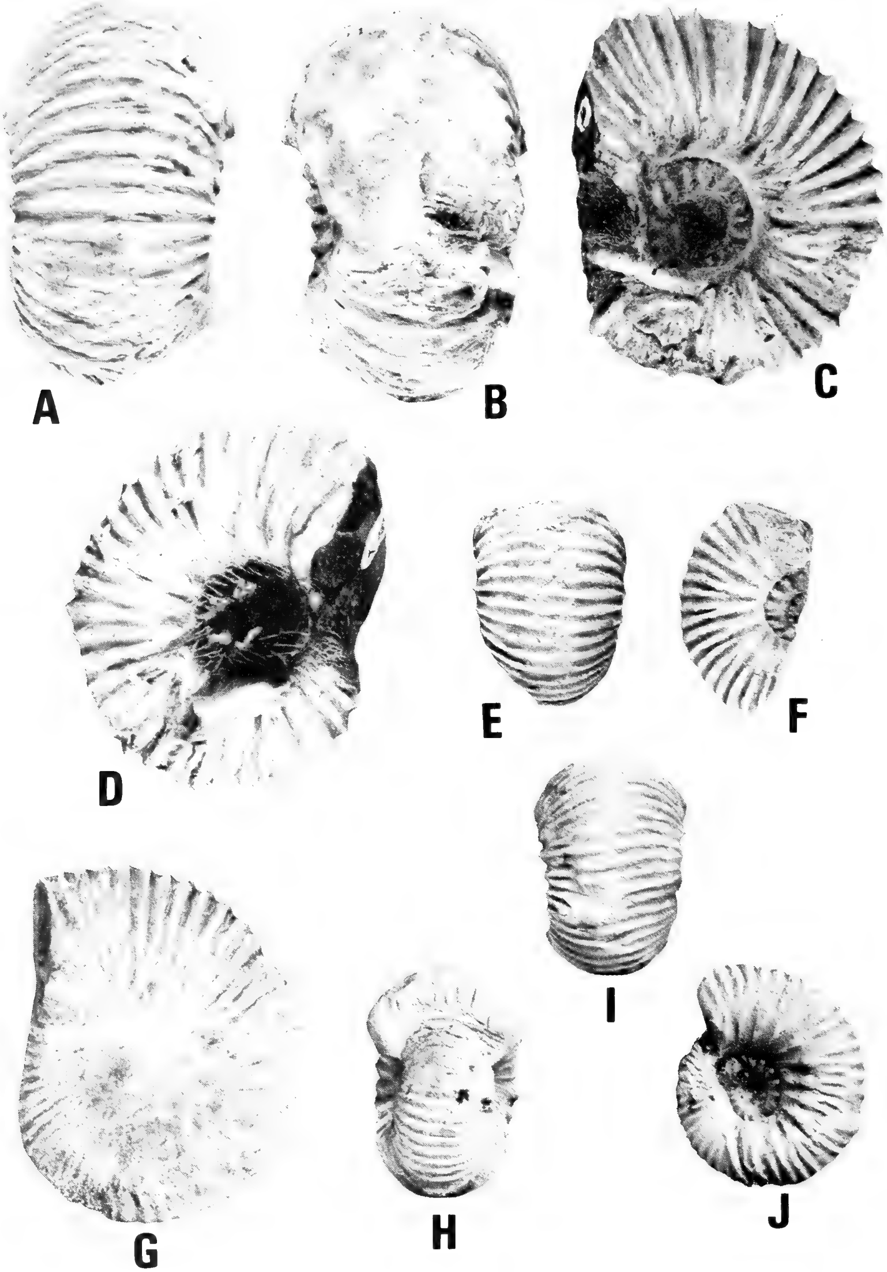

Fig. 99. *Olcostephanus* (*Olcostephanus*) aff. *durangensis* (Cantu Chapa). A–D. Ventral, front, left lateral, and right lateral views of SAM–PCU1459, a microconch, × 0,66. E–F. Ventral and lateral views of SAM–PCU1547, × 0,75. G. Lateral view of a badly crushed individual, AAS–381, × 0,66. H–J. Front, ventral and lateral views of a juvenile in the Albany Museum which may belong here, × 0,75.

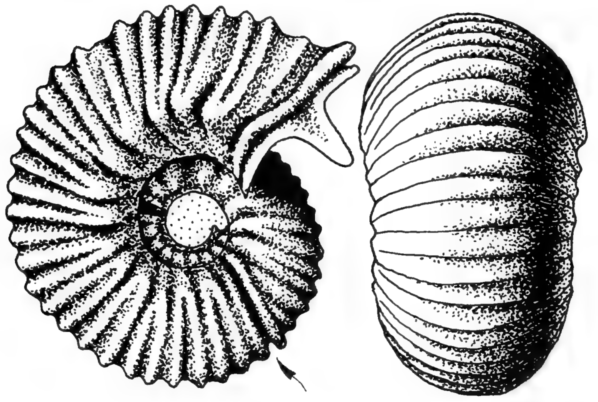

Fig. 100. *Olcostephanus* (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂). A reconstruction based upon SAM–PCU1549. × 1.

Olcostephanus crassicostatus (Spath) is similar, but has fewer umbilical bullae and commonly three secondaries per bulla, while *O. rogersi* (♂) has fewer, more prominent bullae, a more depressed whorl section and characteristically three secondaries per bulla.

Olcostephanus durangensis (Cantu Chapa) (Fig. 98), erected for the *Hoplites symonensis* described by Böse (1923) is very similar, but as the largest specimen is only 16,2 mm in diameter comparison is rather difficult. The Mexican species shows the characteristic radial bifurcation of coarse secondaries from the umbilical bullae, of which there are about 24 per whorl (at 16 mm diameter), but the umbilical walls of the Mexican form slope more. *Olcostephanus baini baini* (♂) has fewer umbilical bullae, from which arise 2–3 prorsiradiate secondaries.

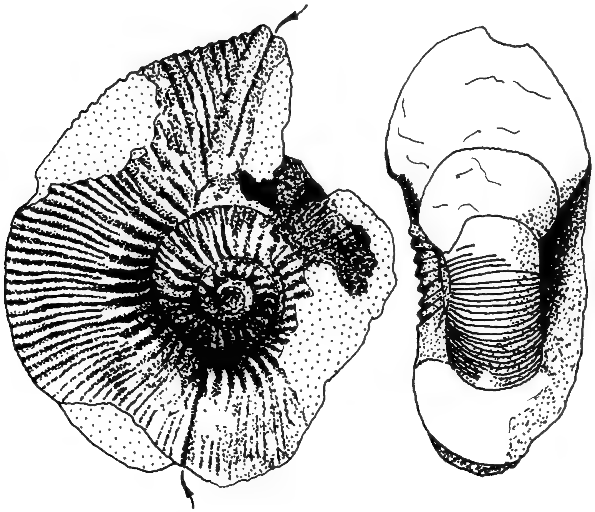

Fig. 101. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♀). The holotype from the *Rutitrigonia schwarzi* Beds of Tanzania (after Zwierzycki 1914). × 1.

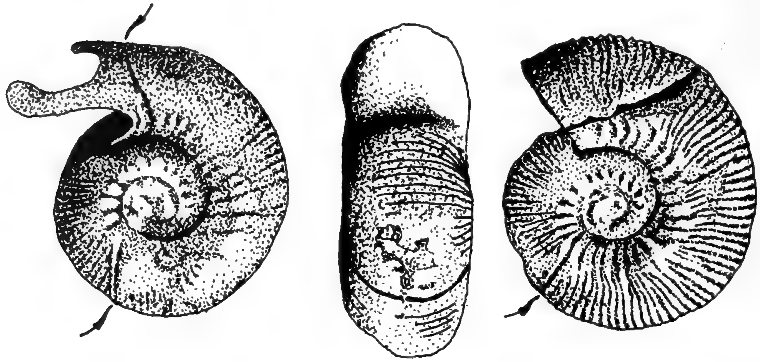

Fig. 102. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♂). Two of the syntypes of *Astieria auriculatus* Zwierzycki from Tanzania, of which the right-hand specimen is herein selected as the lectotype (after Zwierzycki 1914). × 1.

Olcostephanus frequens (Zwierzycki) (Fig. 101), *O. auriculatus* (Zwierzycki) (Fig. 102), *O. pecki* Imlay (Fig. 103), and *O. popenoei* Imlay (Fig. 104) are all characterized by abundant primary ribs from which the secondaries commonly bifurcate and should, therefore, be included in the subgenus *Jeannoticeras*, as should *O. colorinensis* Imlay (Fig. 105). It is doubtful whether more than one species is involved in the above list.

Böse (1923) created *Hoplites aquilerae* for a juvenile form with a rather narrow umbilicus and a depressed, almost semicircular whorl section. On the outer whorl, between 27 and 28 primary ribs terminate in weak bullae on the umbilical shoulder and generally give rise to 2 prorsiradiate secondaries, with occasional intercalatories between bundles. Parabolae are apparently lacking. This species clearly belongs to the subgenus *Jeannoticeras* and differs from the present material in its much finer ribbing, more numerous umbilical bullae and the absence of parabolae.

Whiteaves (1893) introduced the species *Olcostephanus* (*Astieria*) *deansii* (Fig. 106) for a compressed form lacking parabolae and with flexuous secondary ribs which bifurcate just above the umbilical shoulder. This form is perhaps better assigned to the genus *Homolsomites*.

Olcostephanus huizachensis (Cantu Chapa) (Fig. 107) is a small, somewhat compressed species with an oval whorl section. Fifteen primaries terminate in bullae from the umbilical shoulder from which secondary ribs arise in pairs, so that there are thirty distant secondaries across the venter of the outer whorl. This species is close to the present material from which it differs in lacking parabolae and in having more distant secondaries. It is probably the microconch of *O. raricostatus* (Böse).

'*Astieria*' *neohispanica* (Böse 1923) is a very involute, compressed form with about one-quarter of the penultimate whorl visible in the umbilicus. There are about 30–35 primary ribs which seem to lack umbilical tubercles. The lower part of the flanks, immediately above the umbilical shoulder, are smooth.

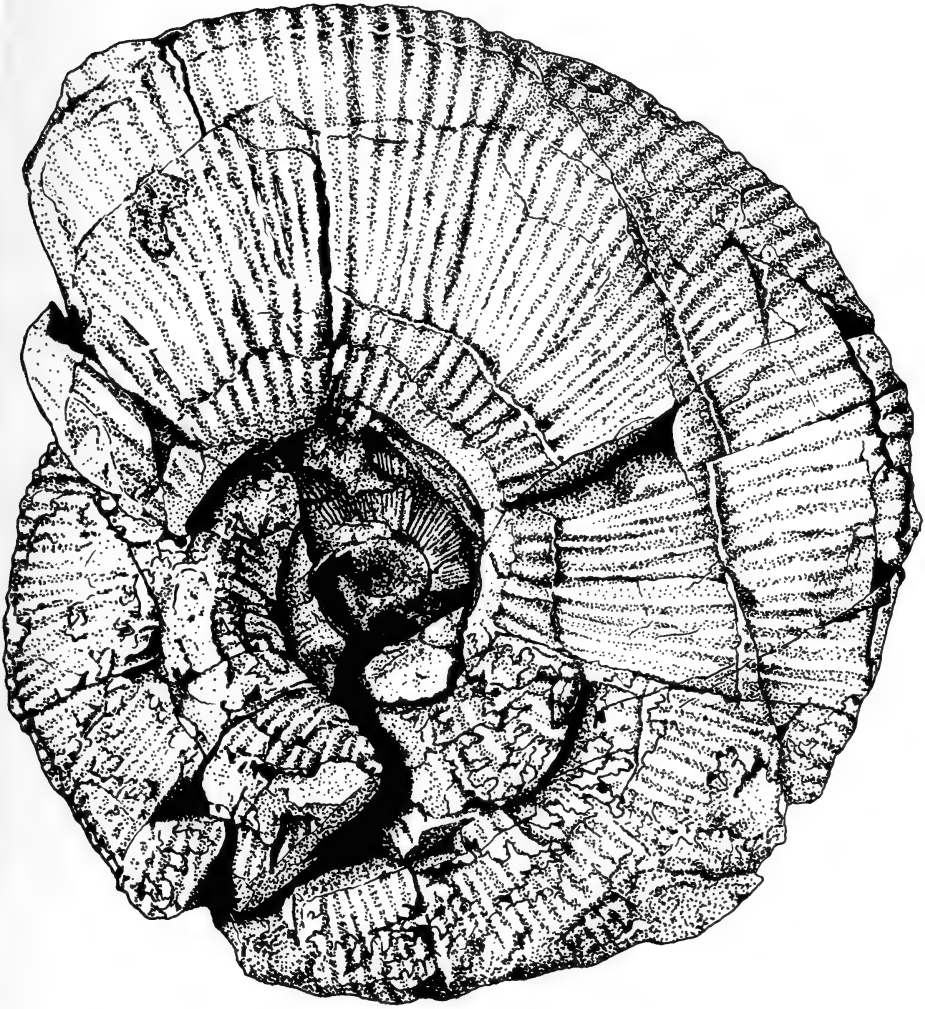

Fig. 103. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♀). The holotype of *Olcostephanus pecki* Imlay from the Upper Valanginian of Oregon (after Imlay 1960). × 1.

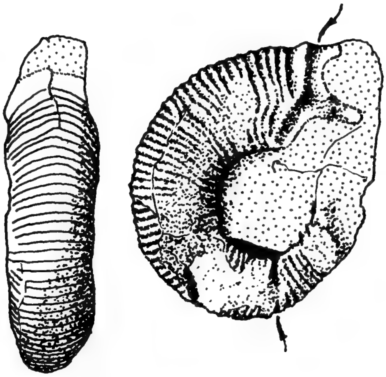

Fig. 104. *Olcostephanus* (*Jeannoticeras*) *frequens* (Zwierzycki) (♂). The holotype of *Olcostephanus popenoei* Imlay from the Upper Valanginian of Oregon (after Imlay 1960). × 1.

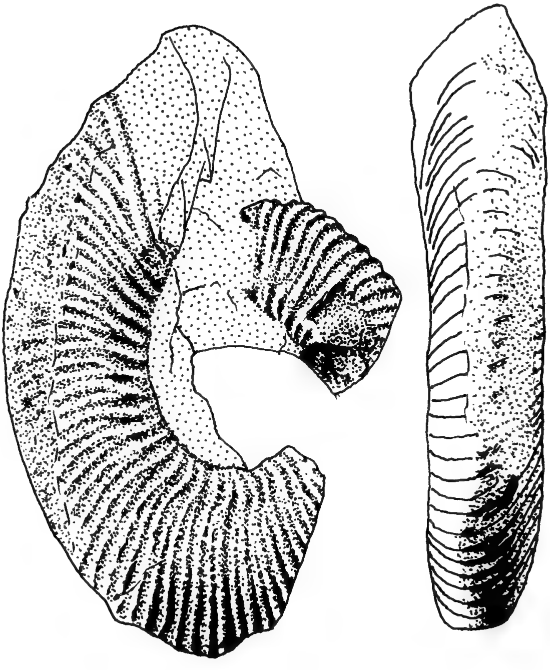

Fig. 105. *Olcostephanus* (*Jeannoticeras*) *colorinensis* Imlay (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

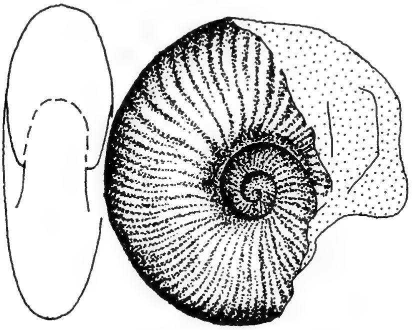

Fig. 106. *Homolsomites*? *deansii* (Whiteaves). The holotype, by monotypy, of *Olcostephanus* (*Astieria*) *deansii* Whiteaves from Queen Charlotte Island, British Columbia (after Whiteaves 1893). × 1.

Fig. 107. *Olcostephanus* (*Olcostephanus*) *huizachensis* (Cantu Chapa) (♂). The holotype from the Taraises Formation of northern Mexico (after Cantu Chapa 1966). × 1.

Above this smooth 'periumbilical band' fine secondaries arise and occasionally bifurcate. Parabolae are lacking. In the writer's opinion, this is a species of *O.* (*Jeannoticeras*) which differs from the Uitenhage material in its much finer ribbing.

Olcostephanus elegans (Karakasch) (Fig. 108) has an inflated shell with a strongly depressed whorl section and well-rounded venter. The umbilicus is fairly wide, with sloping walls and well-rounded shoulders. There are about thirty long primaries on the outer whorl which give rise to pairs of radial secondaries with occasional intercalated ribs. This species is more finely ribbed than

Fig. 108. *Olcostephanus* (?*Jeannoticeras*) *elegans* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

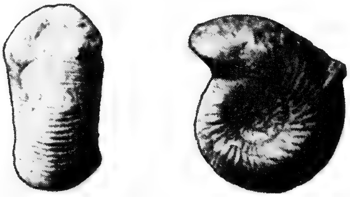

Fig. 109. *Olcostephanus*? *cadoceroides* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of Crimea (after Karakasch 1907). × 1.

the present material and lacks parabolae and is undoubtedly closely related to '*Astieria*' *cadoceroides* Karakasch (Fig. 109) which seems to differ only in the presence of a thick parabolic rib on the outer whorl which is said to form two low tubercles on the venter. Whilst both these species show features of *O.* (*Jeannoticeras*), the sloping umbilical walls with prorsiradiate primaries are features of *O.* (*Subastieria*). However, the alleged ventral tubercles are not a feature of *Olcostephanus* and hence the generic classification of these two forms is uncertain.

The holotype of '*Rogersites*' *quinquestriatus* Besairie (Fig. 110) shows a subcoronate, depressed whorl section and a rather narrow umbilicus. The umbilical shoulders appear evenly rounded and seem to lack umbilical bullae. Simple rectiradiate ribs, about as wide as the interspaces, arise from the umbilical shoulder (the umbilicus is plugged with matrix) and almost invariably bifurcate above midflank, although the occasional rib remains single. There are five prominent oblique parabolae on the outer whorl. This species differs so markedly from the rather consistent characters shown by the genus *Olcostephanus* that it warrants a new generic name. In consequence, the new generic name *Jeanthieuloyites*, for Dr J. P. Thieuloy of the University of Grenoble, is proposed, with '*R.*' *quinquestriatus* Besairie (Fig. 110) as type species.

Olcostephanus bangei (Böse) (Fig. 111) is a very involute species with a narrow umbilicus and steep umbilical walls. Prominent radial primaries terminate in about 10 tubercles on the outer whorl from which arise bundles of 3–4

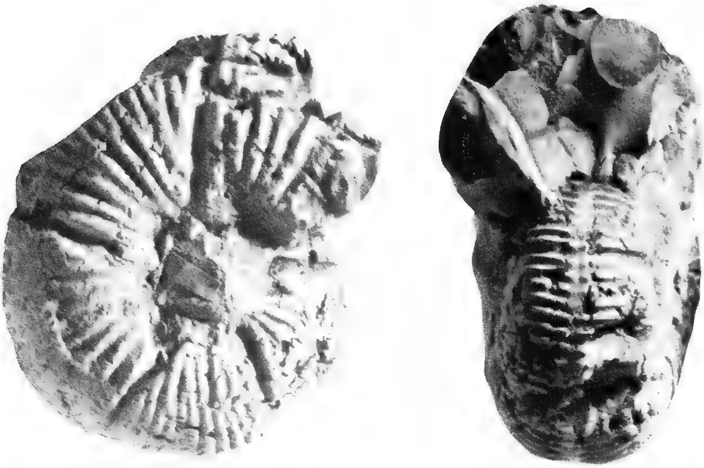

Fig. 110. *Jeanthieuloyites quinquestriatus* (Besairie). The holotype in the collections of the University of Paris, from the Upper Valanginian of Ambiky, Malagasy Republic. × 1.

prorsiradiate secondaries, commonly with an intercalated rib between bundles. There are 45 ribs across the venter of the outer whorl. This species differs from the present material in lacking parabolae, and in having fewer primary and secondary ribs. '*Taraisites*' *carillense* Cantu Chapa (Fig. 112) and '*Rogersites*' *paucicostatus* Imlay (Fig. 113) merely seem to be based upon different growth stages of Böse's (1923) species.

Occurrence

Olcostephanus durangensis is known with certainty only from Mexico, though it may also be present in South Africa.

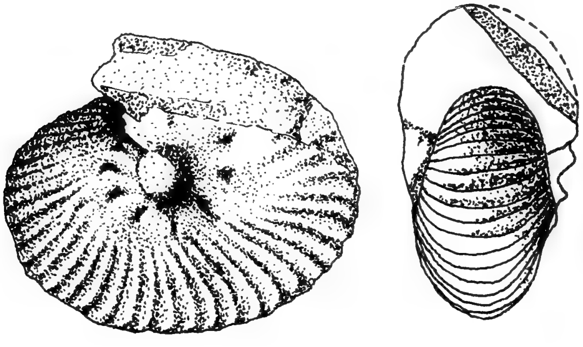

Fig. 111. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse). The holotype, by monotypy, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

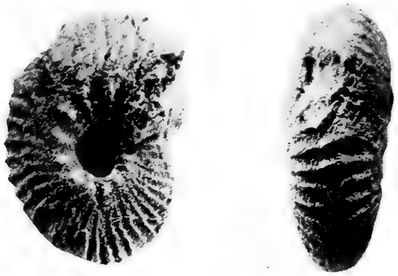

Fig. 112. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse). The holotype of *Taraisites carillensis* Cantu Chapa from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Fig. 113. *Olcostephanus* (*Olcostephanus*) *bangei* (Böse) (♀). The holotype of *Rogersites paucicostatus* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

Olcostephanus (*Olcostephanus*) *baini baini* (Sharpe, 1856)

Figs 114–129, 130A–B, 131C–J, 132–136, 143A–B, 144A–D, 148, 150C–D, 151B–D

Microconch (♂)

Ammonites baini Sharpe, 1856: 197, pl. 23 (fig. 2a–b).
Astieria baini (Sharpe) Kilian, 1902: 866.
Holcostephanus baini (Sharpe) Kitchin, 1908: 187.
? *non Astieria* aff. *baini* (Sharpe) Böse, 1923: 76, pl. 2 (figs 3–5) (= ? *O. atherstoni*).
Rogersites baini (Sharpe) Spath, 1930: 146.
Taraisites baini (Sharpe) Cantu Chapa, 1966: 16.
Olcostephanus baini (Sharpe) Neumayr & Uhlig, 1881: 156; Riccardi *et al.*, 1971: 100.
Olcostephanus (*Rogersites*) *schenki* (Oppel) Fatmi, 1977: 270, pl. 5 (fig. 1).

Macroconch (♀)

Ammonites schenki Oppel, 1863: 286, pl. 81 (fig. 4a–c).
Astieria schenki (Oppel) Pavlow (*in* Pavlow & Lamplugh), 1892: 493.
Holcostephanus (*Astieria*) *schenki* (Oppel) Uhlig, 1903: 130, pl. 18 (fig. 2a–c only).
Astieria atherstoni (Sharpe) Baumberger, 1907: 39, figs 115–116 only.
Holcostephanus schenki (Oppel) Kitchin, 1908: 193, 198, 202–204. Kilian, 1910: 177. Spath, 1930: 150. Besairie, 1930: 629, pl. 64 (fig. 1–1a).
Holcostephanus cf. *atherstoni* (Sharpe) Kitchin, 1908: 193.
Rogersites douvillei Besairie, 1932: 44, pl. 5 (fig. 9–9a), fig. 2; 1936: 138, fig. 9 no. 2.
Rogersites baini var. *ambikyi* Besairie, 1936: 138, pl. 13 (fig. 5), fig. 9 no. 3.
Olcostephanus (*Rogersites*) *schenki* (Oppel) Spath, 1939: 30, pl. 2 (? fig. 6), pl. 18 (figs 9–10).
? *Olcostephanus sublaevis* Spath, 1939: 21, pl. 3 (figs 1–3), pl. 19 (fig. 2).
Holcostephanus douvillei (Besairie) Collignon, 1962: 43, fig. 869.
Olcostephanus atherstoni (Sharpe) Riccardi *et al.*, 1971, pl. 13 (fig. 5a–c only).
Olcostephanus schenki (Oppel) Riccardi *et al.*, 1971: 91, 97.

Material

42 specimens; 16 microconchs (PEM–1463/40a, b, 1462/76, SAM–PCU1528, 1530, 1535, 1540, 1548, AM–429c, BM–C52052, AAS–369a, SAM–525, 581, 583), 23 macroconchs (SAM–316, 1579, 5072, 6157, LJE–989d, PEM–1463/41, 1468/79, 1468/89, SAM–PCU1533, 1538, 1546, 1565, 1570, 1591, 1600, 1602, 1609, AAS–369b, 370, BM–C47122, AM–2345, 2346), and 3 juveniles (SAM–PCU1536, 1579, LJE–989f).

Holotype

By monotypy, the original of *Ammonites baini* figured by Sharpe (1856: 197, pl. 23 (fig. 2a–b)) (Fig. 114) from the Sundays River.

Diagnosis

Dimorphic. Microconch small (about 50 mm diameter), rather inflated. Primary ribs rursiradiate, terminating in 14–18 sharp umbilical bullae, from which arise 2–3 coarse, prorsiradiate secondaries, often with an intercalated rib between bundles. Usually two prominent parabolae per whorl. Peristome with lateral lappets. Macroconch very large (about 250 mm diameter), very strongly inflated, with a greatly depressed whorl section. Primary ribs rursi-

Fig. 114. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). **The holotype, in the British Museum (Natural History). × 1. Photo: W. J. Kennedy.**

radiate, terminating in 17–22 bullae on the body chamber, from which arise bundles of 3–5 prorsiradiate secondaries, with 1–2 intercalatories between bundles. Parabolae present on inner whorls only. Inflation decreases on adoral portion of the body chamber.

Description

Microconch (♂): the shell is small, rarely larger than 60 mm diameter, and involute up to the umbilical bullae on the inner whorls, so that about 80 per cent of the preceding whorl is covered, but becoming slightly more evolute as the umbilical seam egresses on the adoral portion of the body chamber. Consequently, a short distance of the secondary ribbing of the penultimate whorl is visible below the umbilical seam at this stage. The whorls are rather inflated, with a depressed whorl section, the latter tending to become coronate as the umbilical seam egresses. Prominent primary ribs begin at the umbilical seam and curve backwards (rursiradiate) to distinct, sharp umbilical bullae on the umbilical shoulder. Each bulla gives rise to two or three coarse, prorsiradiate secondaries, frequently with an intercalated rib between bundles. Where there are three secondaries per bundle the intercalated rib is usually absent. Often a rib which is seen to arise from a bulla on the one flank is found to be intercalated on the other side. The secondaries recurve slightly so as to cross the venter transversely. In some specimens there may be a slight concave inflexion of the secondaries along the siphonal line. There are 14–18 bullae on the final whorl, with 17–18 secondaries per 6 bullae. The umbilicus is rather narrow and moderately deep, with steep umbilical walls and a subrounded shoulder. The slope of the umbilical wall lessens as the umbilical seam egresses. There are usually two deep parabolae per whorl, commonly about 180° apart. As is characteristic of parabolae, they truncate the ribbing adapically, and are parallel to the adoral ribs. The peristome is virtually identical to these para-

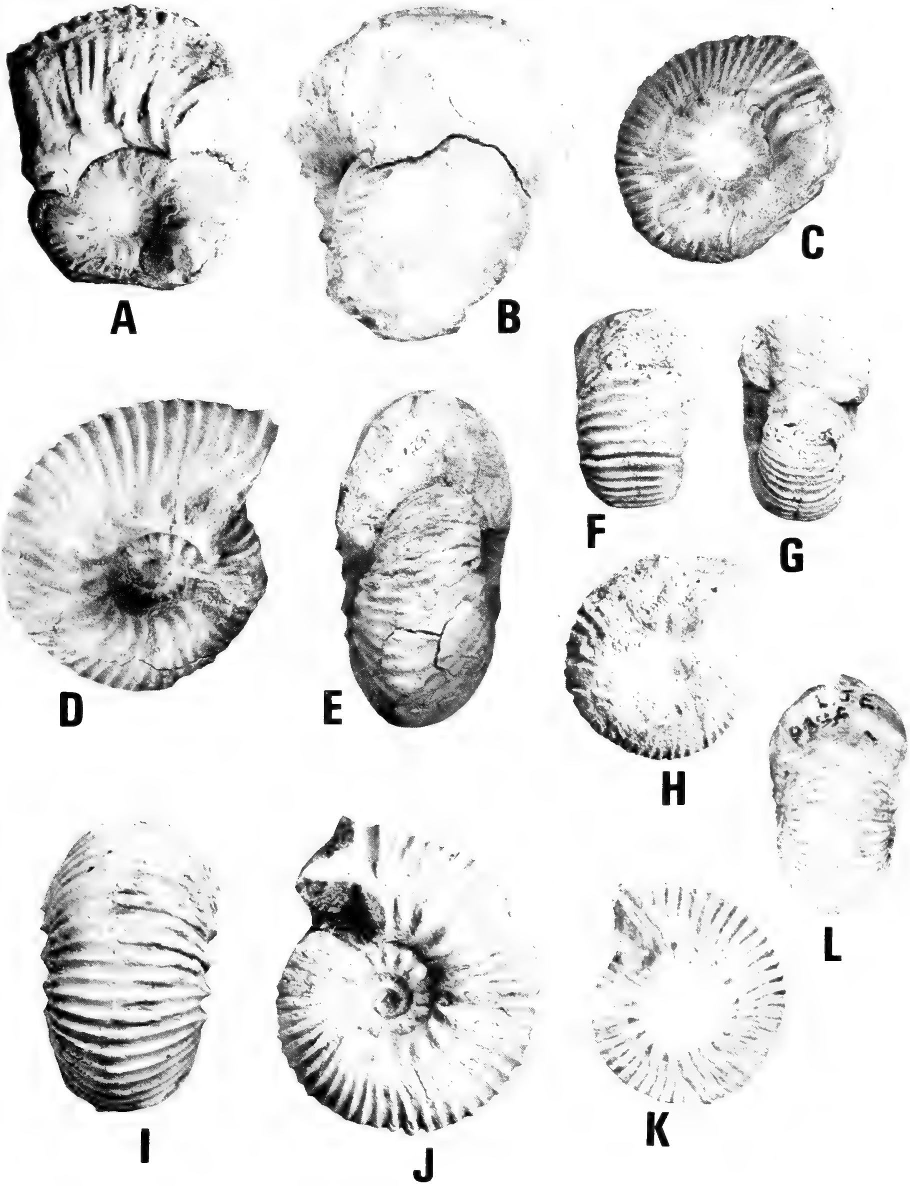

Fig. 115. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A–C. Lateral, front and lateral views of the inner whorls of AM–2346, an immature macroconch, × 075. D–E. Lateral and front views of AM–4292*c*, a microconch, × 0,75. F–H. Ventral, front and lateral views of a juvenile, SAM–PCU1536, doubtfully included here. Note the flattened venter and quadrate whorl section, × 1. I–J. Ventral and lateral views of a microconch in the Albany Museum, × 1. K–L. Lateral and front views of LJE–989f, × 0,75.

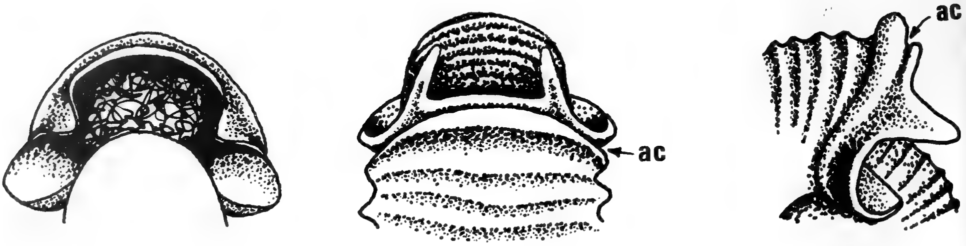

Fig. 116. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). Reconstruction of the peristome of the microconch. × 1.

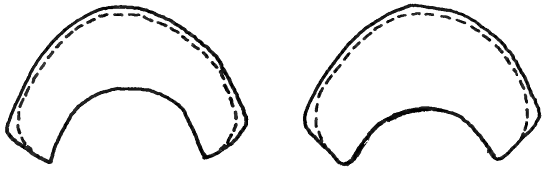

Fig. 117. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). Whorl sections of SAM–PCU1528 (left), PEM–1462/76 (right). × 1.

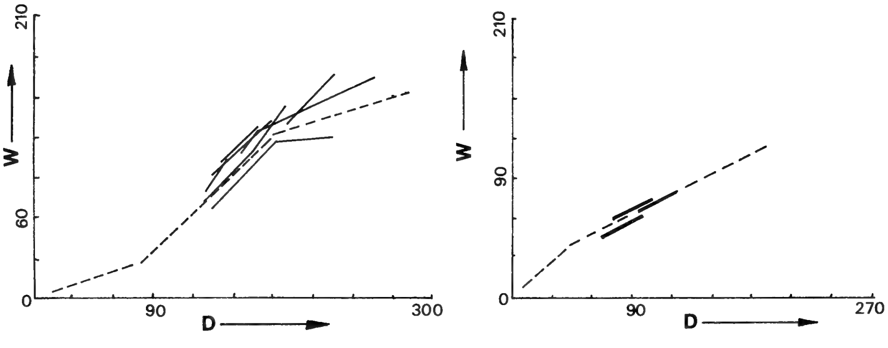

Fig. 118. Plot showing the differing rates of inflation for macroconchs of *O. baini* (left) and *O. atherstoni* (right). Note increased rate of inflation in middle whorls of *O. baini*.

bolae but, when preserved, the adoral margin is seen to bear slightly converging lateral lappets. The whorl section varies somewhat, from almost semicircular to coronate, with a well-rounded venter. The suture line is unknown. As in other olcostephanids the body chamber is almost a full whorl in length.

Macroconch (♀): The shell is very large, commonly around 250 mm diameter, and extremely inflated, with a strongly depressed whorl section. The earliest whorls are only moderately inflated and up to a diameter of about 60 mm closely resemble the microconch, from which they differ only in being slightly more inflated and in having invariably three secondaries per bulla,

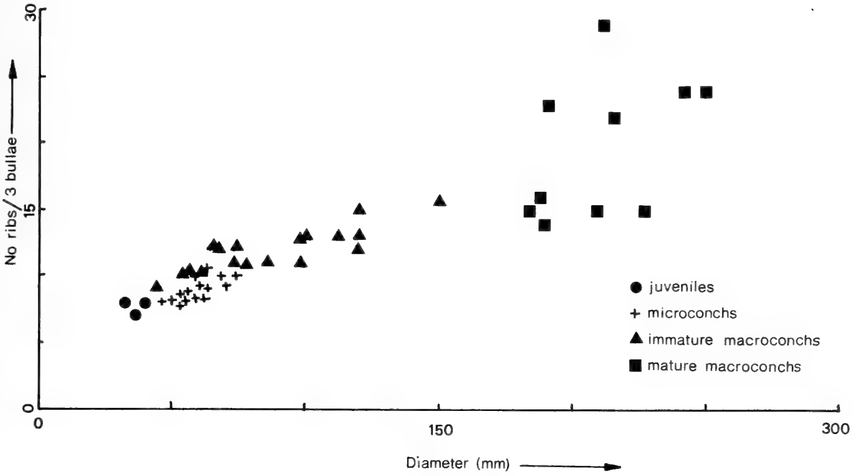

Fig. 119. Plot showing increase in rib density with ontogeny, and between dimorphs, in *O. b. baini* (Sharpe).

commonly with an intercalated rib between bundles. At this stage, the macroconch is, therefore, slightly more densely ribbed than the microconch. After about 60 mm diameter the whorl section rapidly becomes extremely inflated, reaching a maximum about one-third of a whorl behind the peristome. The umbilicus is very narrow and deep, with a vertical umbilical wall and acute shoulder. The slope of the umbilical wall becomes less steep with the egression of the umbilical seam while the umbilical shoulder also becomes distinctly rounded at this growth stage. Prominent primary ribs begin at the umbilical seam and curve backwards (rursiradiate) to terminate in 19–22 bullae on the final whorl. One specimen, SAM–PCU1591, has only 14 bullae on the outer whorl, which become extremely swollen and large near the peristome, and is with reservations referred to this species. Each bulla gives rise to bundles of usually 3–4 coarse prorsiradiate secondaries, rarely 5, with 1–2 intercalated ribs between bundles. There are between 23 and 28 secondaries per 5 bullae on the adoral portion of the body chamber, with generally fewer at earlier growth stages. The secondary ribbing is slightly flexuous, recurving on the flanks so as to cross the venter transversely. At 155 mm diameter (PEM–1468/79) there are 24 secondaries per 6 bullae, and 9 ribs within a 50 mm distance along the venter. In the same specimen at 210 mm diameter there are 21 secondaries per 4 bullae, with a rib spacing of 7 mm. The inner whorls of macroconch dimorphs of *O. baini* have prominent, deep parabolae, the largest diameter at which they are seen to occur being 130 mm. However, in some examples taken to belong to this dimorph by virtue of their very strong inflation, there is no sign of parabolae at smaller diameters. This would seem to suggest that the growth stage at which parabolae ceased to be produced varies from individual to individual, although it would generally seem to be at about 90–120 mm

Fig. 120. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Front and lateral views of SAM–5072. Note homoeomorphic resemblance to *O. atherstoni*. × 0,44.

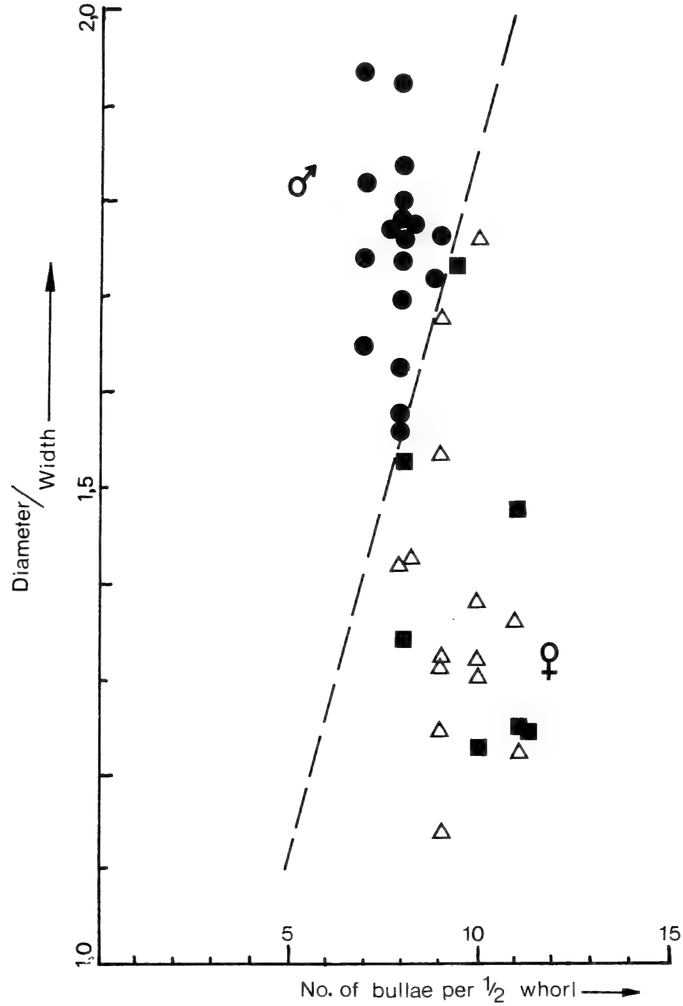

Fig. 121. Plot showing the relationship between inflation (Diameter/Width) and number of umbilical bullae per half whorl in *O. b. baini* dimorphs. Dots = microconchs, triangles = immature macroconchs, squares = mature macroconchs.

diameter. Parabolae never occur on the outer whorls of macroconch forms, although the peristome takes the form of a parabola.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
AM–2344	50	21	31	1,48	17	9 (18)
AM–2345	68	26	46	1,77	25	13 (19) (♀)
,,	56	22	32	1,45	18	10 (18)

Fig. 122. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe) (♀). Ventral and lateral views of a specimen in the British Museum (Natural History). × 0,66.

No.	D	H	Wi	W/H	Uo	Ui
PEM–1468/73	180	82	135	1,65	70	44 (24) (♀)
,,	135	62	90	1,45	50	27 (20)
SAM–PCU1591	255	115	166	1,44	90	52 (20) (♀)
,,	174	85	150	1,76	69	?
PEM–1468/89	250	92	155	1,68	110	82 (33) (♀)
,,	167	83	126	1,52	65	43 (26)
PEM–1468/79	225	87	122	1,40	83	46 (20) (♀)
,,	184	79	120	1,52	56	31 (17)
SAM–316	208	93	138	1,48	78	47 (22) (♀)
,,	145	60	100	1,67	55	?
PEM–1468/80	170	100	?		?	? (♀)
,,	140	75	?		?	?
AM–2346	55	23	37	1,61	27	17 (31) (♀)
,,	38	13	21	1,61	13	7 (18)
,,	24	11	17	1,55	10	4 (17)
SAM–PCU1546	226	108	170	1,57	55	43 (19) (♀)
,,	190	85	132	1,55	?	?

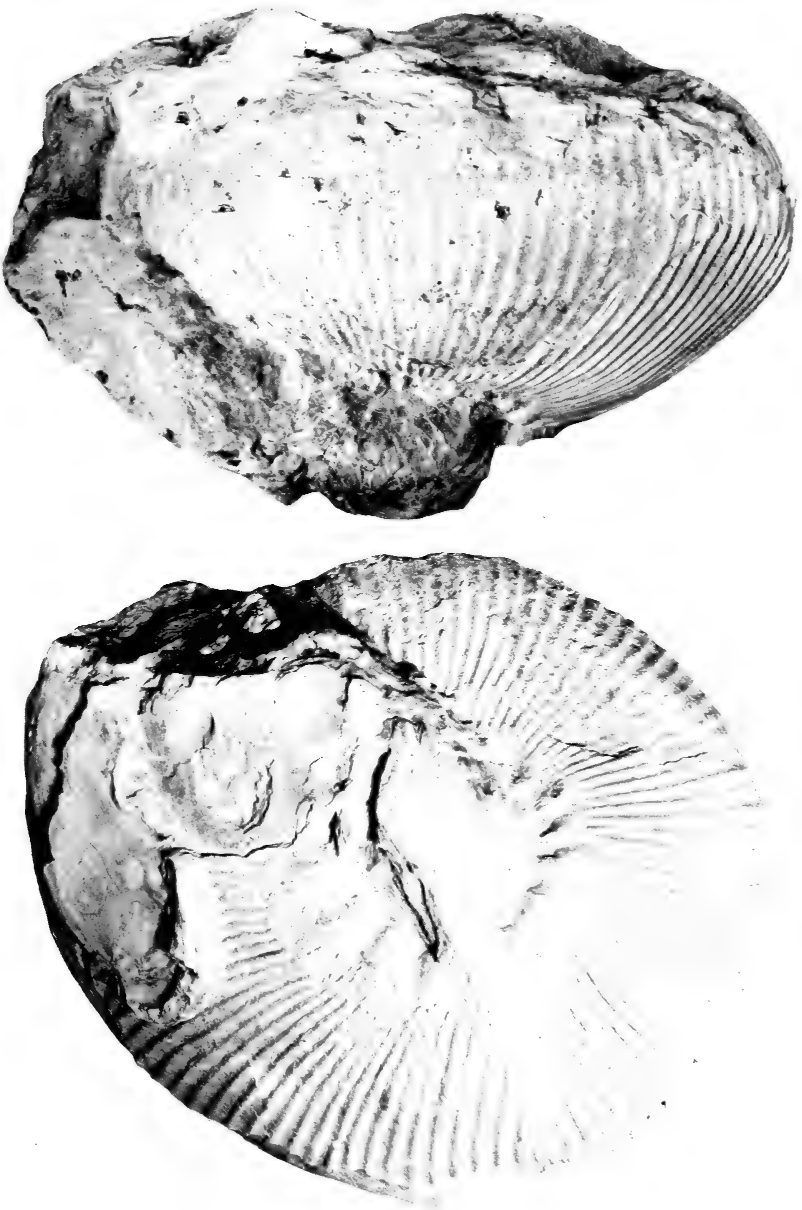

Fig. 123. *Olcostephanus (Olcostephanus) baini* (Sharpe) (♀). Lateral and front views of SAM–PCU1546. Note encrusting oysters, one of which fills the umbilicus. × 0,44.

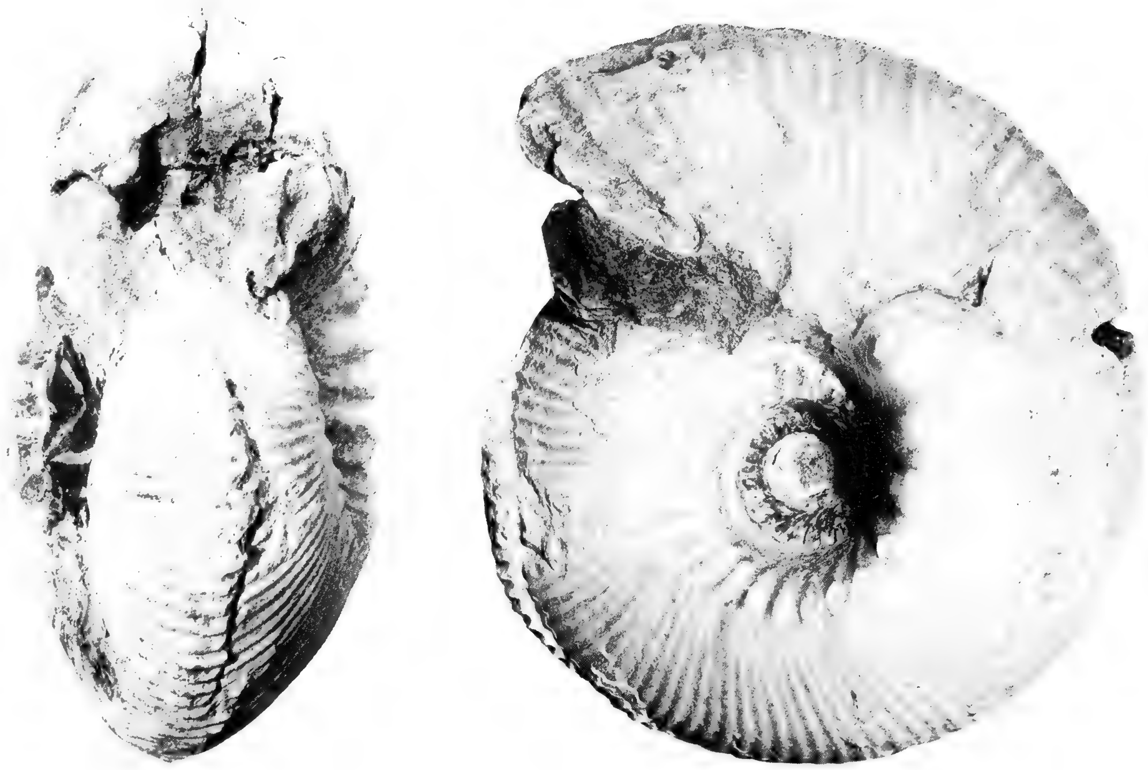

Fig. 124. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Front and lateral views of PEM–1468/79, showing maximum inflation about one-third of a whorl behind the peristome. × 0,44.

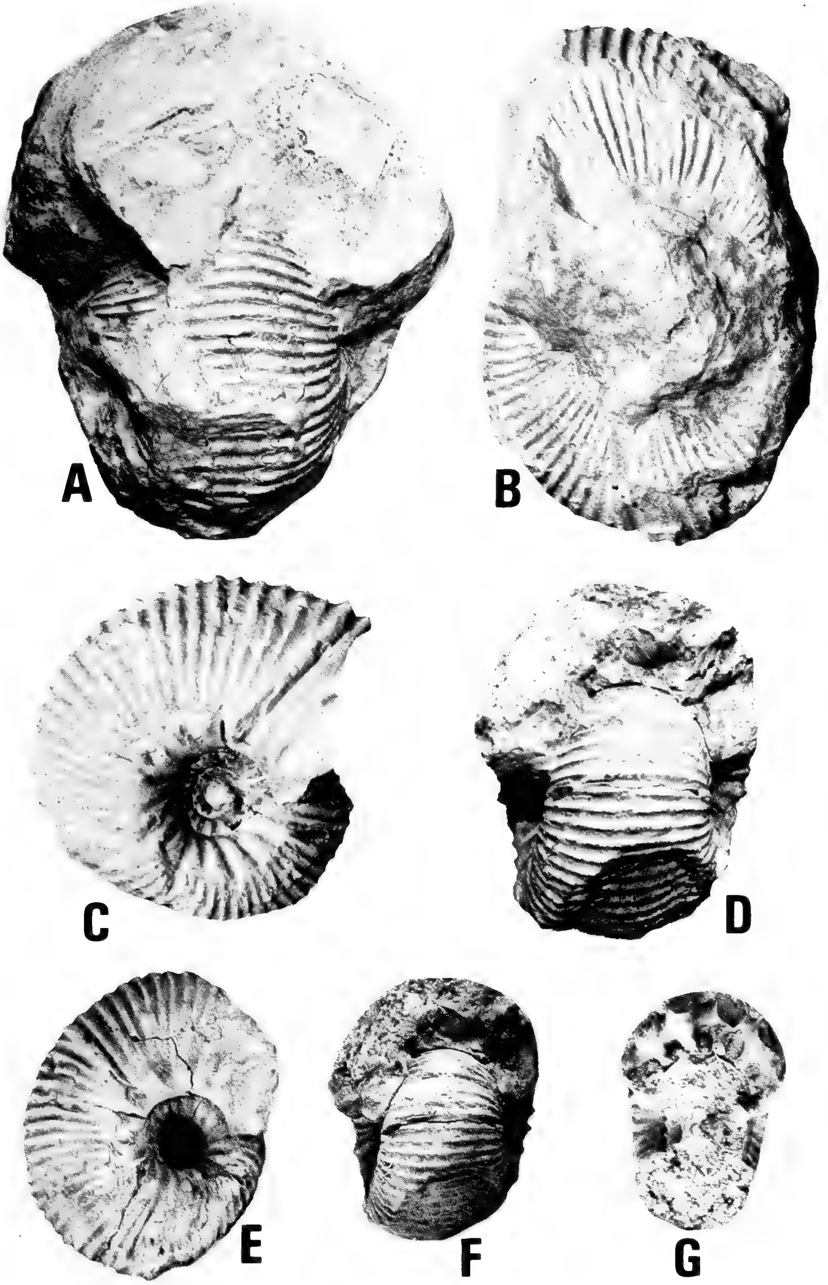

Fig. 125. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). A–B. Front and lateral views of a specimen in the South African Museum, × 0,44. C–D. Lateral and front views of SAM–PCU1533, an immature macroconch, × 0,75. E–G. Lateral, front and cross-sectional views of inner whorls of SAM–PCU1533, × 0,75.

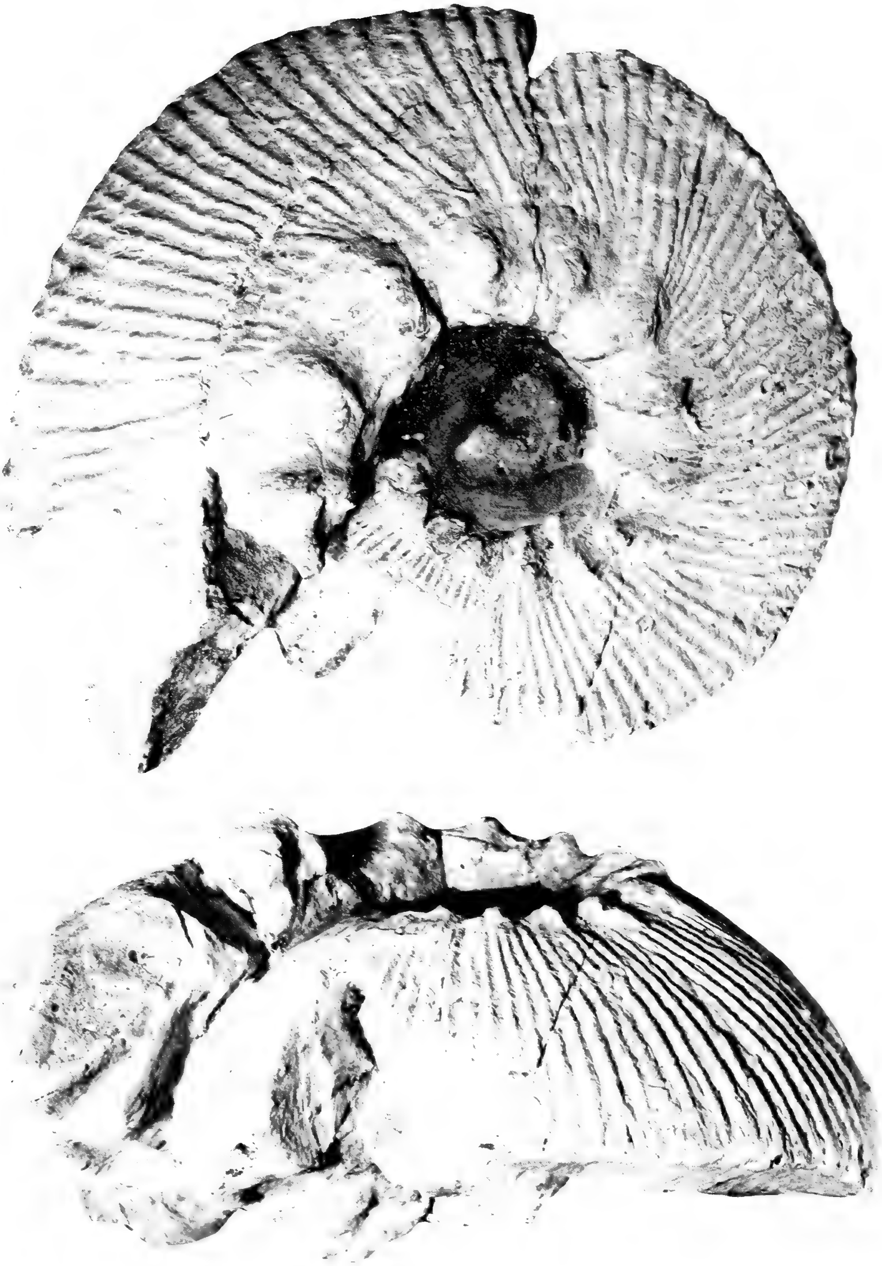

Fig. 126. *Olcostephanus* (*Olcostephanus*) cf. *baini baini* (Sharpe) (♀). Front and lateral views of SAM-PCU1591. Note the swollen umbilical bullae. × 0,44.

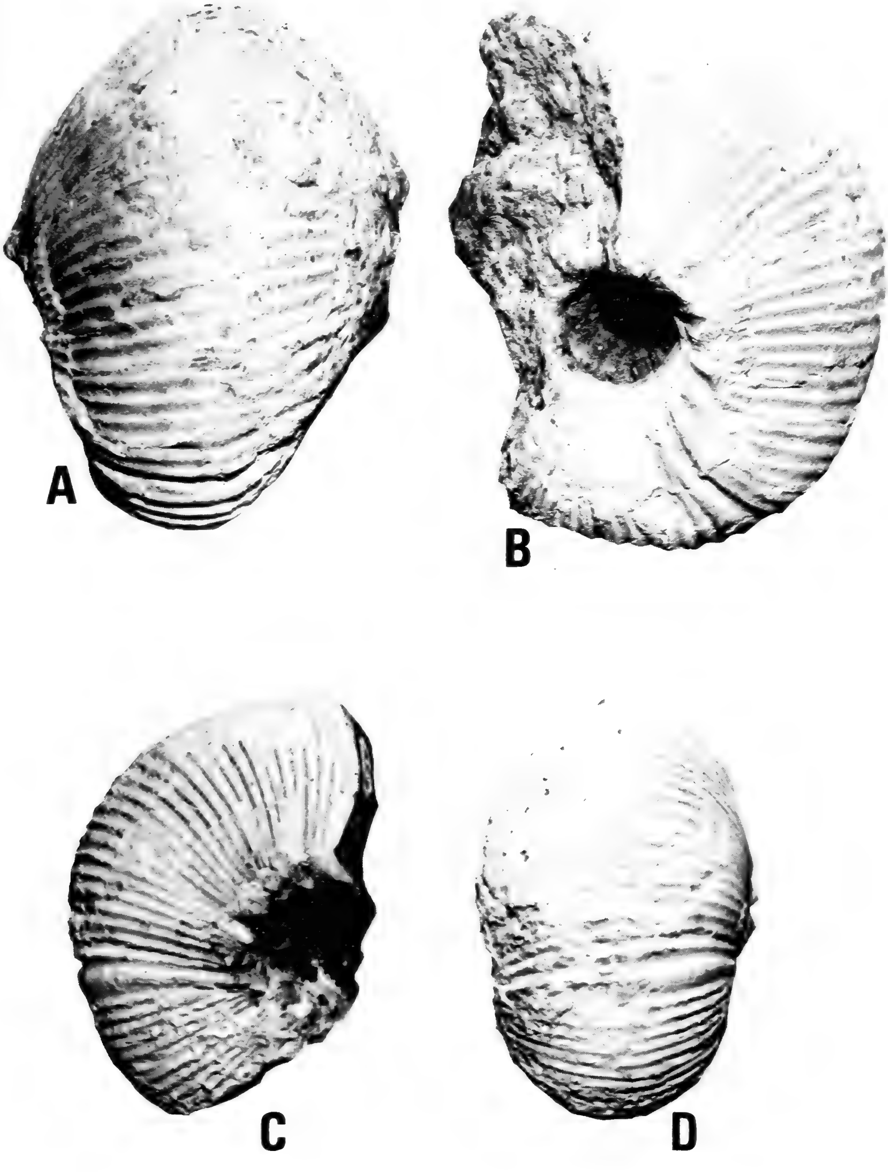

Fig. 127. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀), × 0,44. A–B. Ventral and lateral views of SAM–PCU1609. C–D. Lateral and ventral views of SAM–PCU1570.

Fig. 128. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Lateral and ventral views of a somewhat crushed specimen, PEM–1468/80. × 0,44.

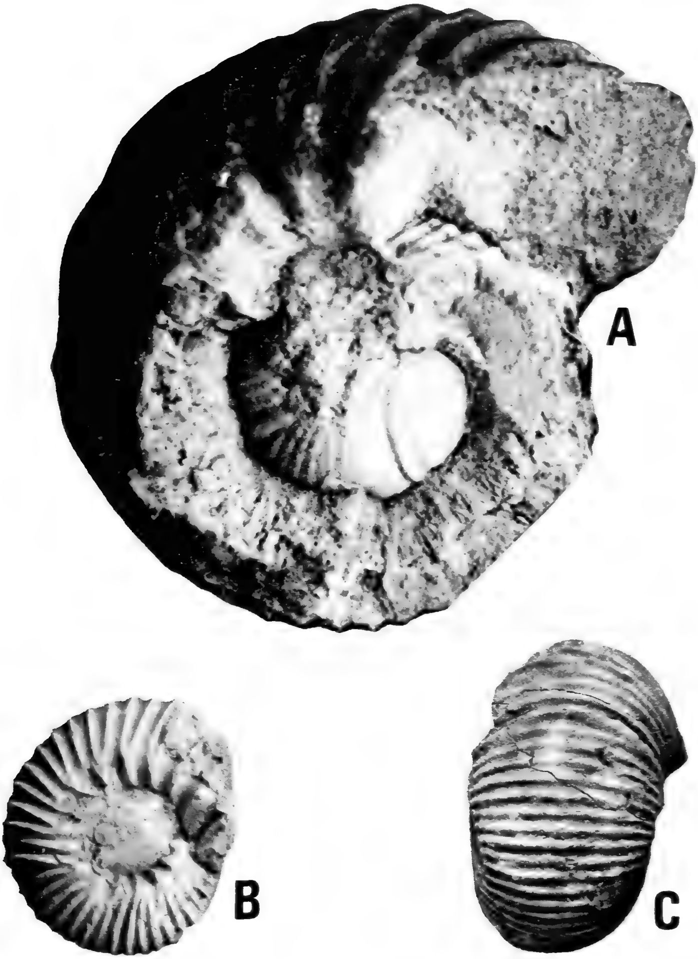

Fig. 129. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A. A nucleus which possibly belongs here, in the South African Museum. Note the prominent parabolae at a stage when ribs are still absent, × 2,5. B. Lateral view of a microconch, BM–52052, × 1. C. Ventral view of an immature macroconch, SAM–PCU1533, × 1.

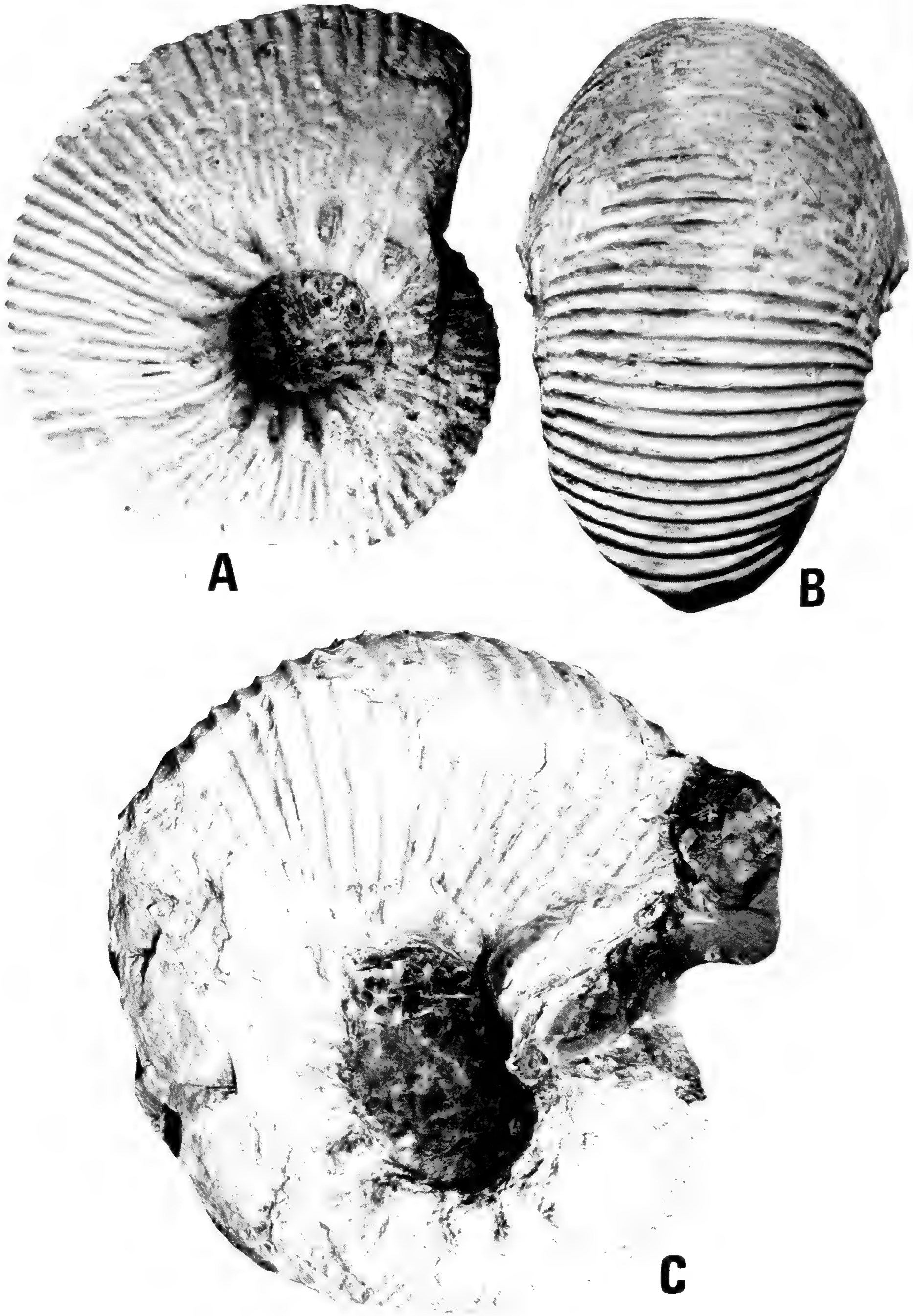

Fig. 130. A–B. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe) (♀). Lateral and ventral views of AAS–369b, somewhat resembling *O. actinotus* (Baumberger), but with parabolae. × 0,75. C. *Olcostephanus* (*Olcostephanus*) sp. (♀). Lateral view of a crushed macroconch, SAM–PCU1551. Note peristome and coarse ribbing on adoral portion of the body chamber. × 0,44

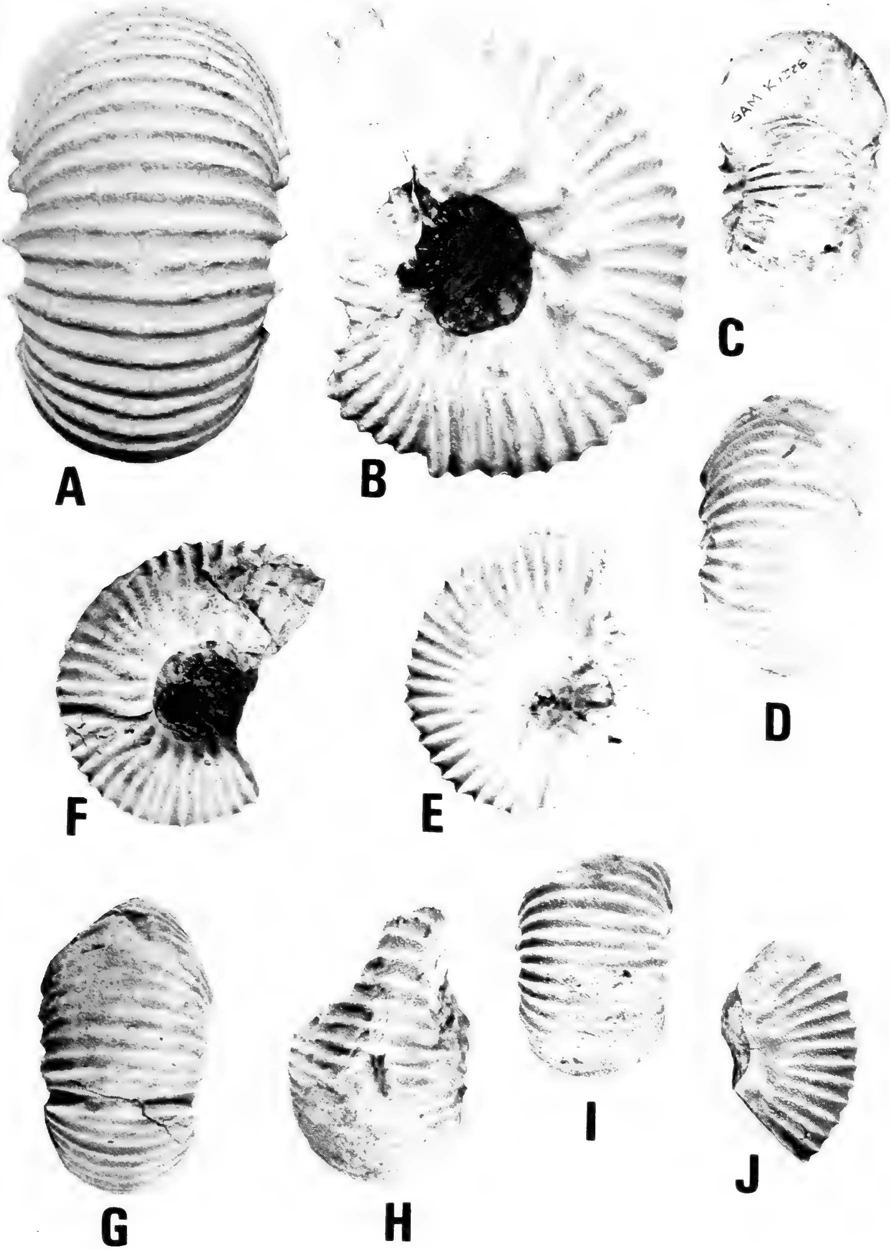

Fig. 131. A–B. *Olcostephanus* (*Olcostephanus*) cf. *rogersi* (Kitchin) (♂). Ventral and lateral views of SAM–PCU1527. Note inflexion in the apertural constriction which is lacking in the parabola, × 0,75. C–J. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♂). C–E. Front, ventral and lateral views of SAM–PCU1528. F–H. Lateral and two ventral views of PEM–1463/40a; note peculiar chevron-shaped crushing of peristomal region suggestive of a bite-mark. × 0,75. I–J. Ventral and lateral views of SAM–525, × 1.

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1544	105	50	81	1,62	20	? (♀)
SAM–PCU1538	120	50	85	1,70	42	? (♀)
,,	87	40	57	1,42	30	?
SAM–PCU1594	150	70	115	1,64	40	28 (19) (♀)
,,	130	52	80	1,54	43	27 (21)
AM–2978	50	15	27	1,80	23	12 (24) (♂)
,,	40	16	22	1,38	17	7 (18)
PEM–1463/40a	39	17	22	1,29	21	11 (28) (♂)
,,	28	9	16	1,78	?	?
LJE–989f	27	7	14	2,00	11	6 (22) (♂)
,,	17	5	10	2,00	8	3 (18)
AAS–369a	43	15	21	1,40	20	10 (23) (♂)
,,	30	9	16	1,78	?	?
PEM–1462/76	48	15	24	1,60	21	12 (25) (♂)
,,	30	11	20	1,82	13	7 (23)
SAM–PCU1528	50	17	24	1,41	22	12 (24) (♂)
,,	38	12	18	1,50	15	7 (18)
PEM–1468/76	65	22	33	1,50	25	13 (20) (♂)
,,	51	17	22	1,29	18	9 (18)

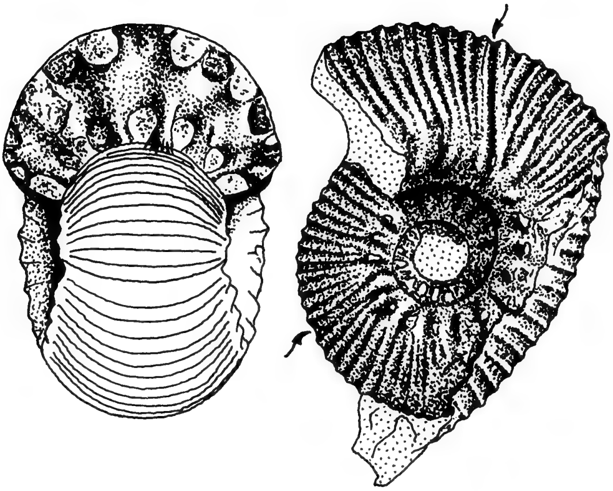

Fig. 132. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Olcostephanus schenki* (Oppel) from the Salt Range of Pakistan (after Uhlig 1903). × 1.

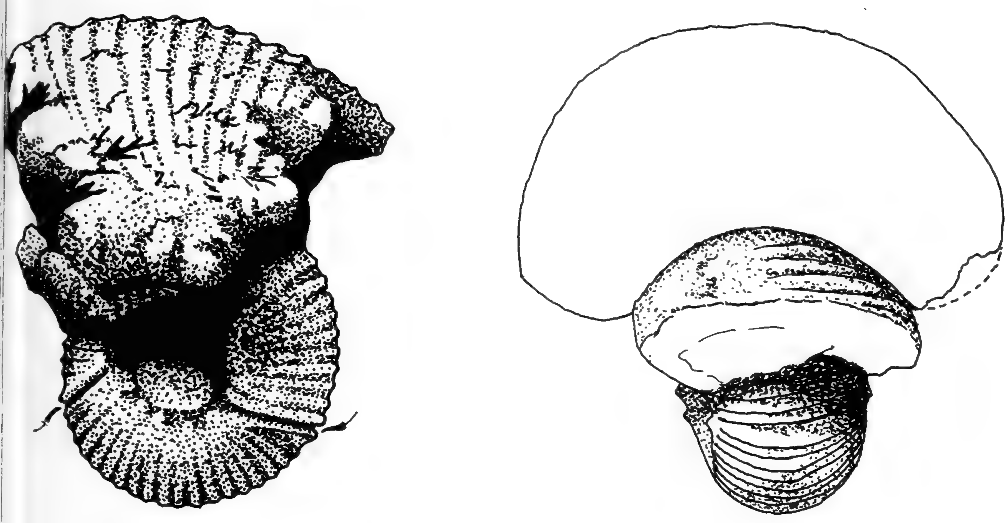

Fig. 133. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Rogersites douvillei* Besairie (*fide* Collignon 1962) and also *Rogersites baini* var. *ambikyi* Besairie, from the Upper Valanginian of Ambiky, Madagascar (after Collignon 1962). × 1.

Discussion

As has been pointed out by many previous workers, *O. baini* (♂) forma typica bears a close resemblance to *O. schenki* (Oppel) (Fig. 132). It becomes apparent from the present study that the differences are merely those due to a comparison of the inner whorls of a macroconch with a microconch form. Consequently, *O. schenki* (Oppel) is regarded as a junior subjective synonym of *O. baini baini*. Riccardi *et al.* (1971) considered *O. schenki* to represent the inner whorls of the *O. atherstoni* macroconch. However, as warned by Makowski (1962*a*: 21), they failed to recognize the homoeomorphy between macroconch forms. Hence the *O. atherstoni* fauna recorded by Riccardi *et al.* (1971) from west-central Argentina includes both *O. atherstoni* and *O. b. baini*, as evidenced by the presence of young macroconchs both with and without parabolae. This same phenomenon recurs in the Uitenhage fauna, the homoeomorphy being recognized by the differing rates of inflation of the two forms (Fig. 118).

Olcostephanus douvillei (Besairie) (Fig. 133) was erected for strongly inflated forms with commonly three prorsiradiate secondaries per bulla, and parabolae on the inner whorls. This species is undoubtedly conspecific with the *O. b. baini* macroconch, representing merely an immature growth stage. *Olcostephanus baini* var. *ambikyi* Besairie has the same holotype as *O. douvillei* and is thus a junior objective synonym.

In 1930, Besairie figured an example of *O. schenki* (Oppel) which he considered '. . . tout a fait semblable aux figures d'Uhlig'. The large size and numerous secondaries, together with the presence of parabolae, suggest this

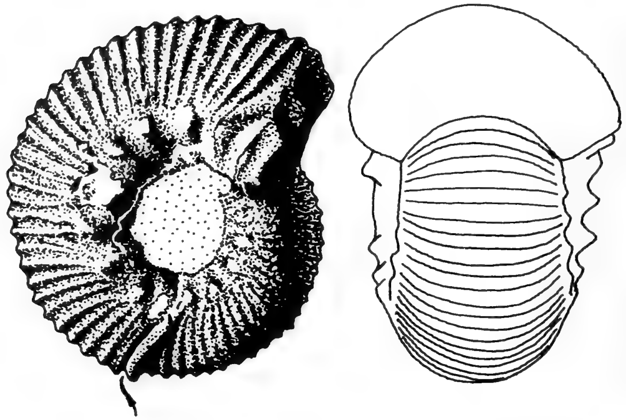

Fig. 134. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The specimen figured by Spath (1939) as *R. schenki* (Oppel), and considered to represent the holotype by Collignon (1962) (after Spath 1939). This is an immature macroconch. × 1.

specimen represents the inner whorls of an *O. baini* macroconch. This example does not, however, show the rapid inflation which characterizes the Uitenhage forms at a similar growth stage. Collignon (1962: 36), in refiguring Besairie's specimen, made the interesting assertion that Uhlig had, in error, figured the wrong specimen as Oppel's holotype, and that the specimen of *O. schenki* figured by Spath (1939, pl. 18 (fig. 9a–b)) (Fig. 134) was, in fact, the holotype. There appears no justification, however, in this assertion since, according to Oppel (1863: 287), the holotype came from 'Schangra, west of Puling in Gnari-Khorsum (Tibet)', whereas Spath's specimen came from '. . . near loc. 682', i.e. the northern side of Maranwal Nala, Makerwal Colliery. To suggest that Spath's specimen is the actual holotype would suggest that both Uhlig (1903) and Spath (1939) had made the same mistake (A. C. Riccardi pointed out this fact to the author).

Olcostephanus sphaeroidalis (Spath) is a macroconch form erected for those species differing from *O. atherstoni* (♀) in their greater inflation and more depressed whorl section. These are the characters which distinguish the *O. baini* macroconch from that of *O. atherstoni*. It is of interest to note, therefore, that a re-examination of Spath's holotype shows the inner whorls to bear parabolae. Since the outer whorls of the macroconchs of *O. baini* (Sharpe) and *O. sphaeroidalis* (Spath) cannot be distinguished, the latter is treated as a variety of the former.

Olcostephanus (*Subastieria*) *nicklesi* Wiedmann & Dieni (Fig. 48) closely resembles the microconch of *O. baini baini*, from which it differs largely in having a sloping umbilical wall at all growth stages. This causes the umbilical bullae to be situated at about mid-flank, resulting in a pentagonal whorl section. This subtle difference is readily apparent, but whether it is of subgeneric rank

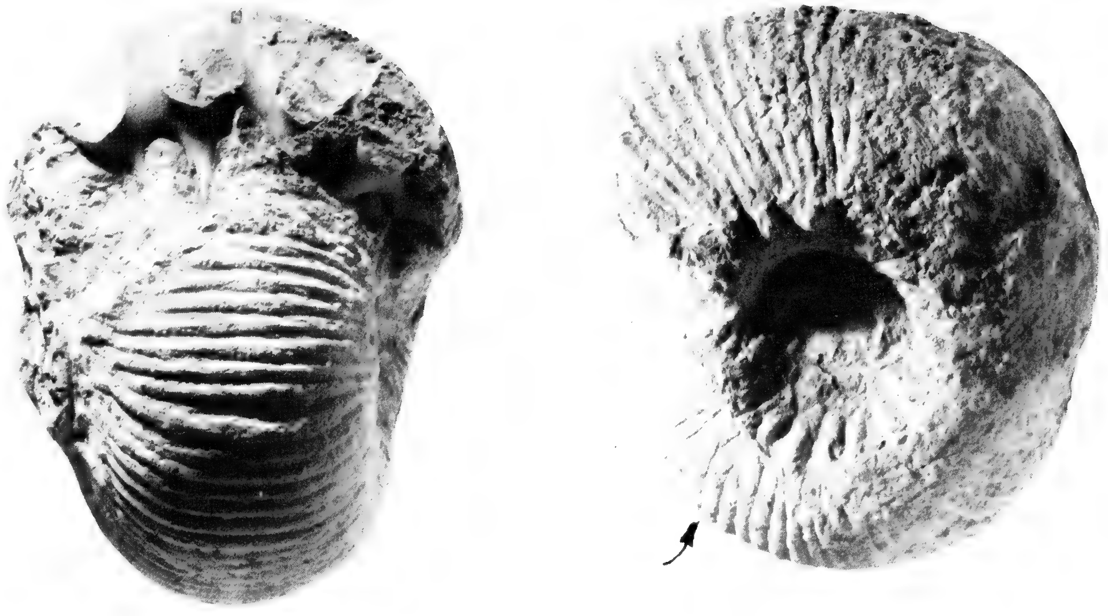

Fig. 135. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). The holotype of *Rogersites tsimihetensis* Besairie from the Upper Valanginian of Ambiky, Madagascar. Parabola arrowed. × 1.

would seem to depend on the recognition of sexual dimorphism in this subgenus, if it exists, and the morphology of the corresponding macroconch. It is of interest to note that Wiedmann & Dieni (1968) included forms both with and without parabolae in their species.

In 1923 Böse recorded a specimen of '*Astieria* aff. *baini*' from the Taraises Formation of northern Mexico. Cantu Chapa (1966) subsequently made this specimen the type of his new genus *Taraisites*, renaming it *T. bosei* (Fig. 9). This genus was erected within the new subfamily Taraisitinae for those forms of *Olcostephanus* in which 2–3 secondaries arise from each umbilical bulla. Riccardi *et al.* (1971) have already shown this genus to be a synonym of *Olcostephanus* s.s., also supported by the fact that the *Ammonites baini* of Sharpe, assigned to *Taraisites* by Cantu Chapa (1966), represents nothing more than the microconch of a much larger, more densely ribbed macroconch. The preservation of '*Taraisites bosei*' leaves much to be desired, but as it appears to lack parabolae, and in view of the abundance of *O. atherstoni* in these beds, it is probably best referred to that species.

The holotype of '*Rogersites*' *tsimihetensis* Besairie (Fig. 135) is poorly preserved but shows no features whereby it can be distinguished from the *O. baini* macroconch. It is, therefore, a junior subjective synonym of Sharpe's (1856) species.

Fig. 136. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). The holotype of *Rogersites sanlazarensis* Imlay from the Taraises Formation of northern Mexico (after Imlay 1937). × 1.

'*Rogersites*' *sanlazarensis* Imlay (Fig. 136) was created for large, fairly inflated forms with a deep and narrow umbilicus, and steep umbilical walls. About 18 rursiradiate primaries terminate in small umbilical bullae from which arise bundles of 3–4 prorsiradiate secondaries, with 1–2 intercalated ribs between bundles. The inner whorls bear prominent parabolae. It is clear from the above description and figure that '*R.*' *sanlazarensis* should be considered a junior subjective synonym of the *O. baini* macroconch, perhaps of the variety *sphaeroidalis* (Spath).

'*Astieria*' *taurica* Karakasch (Fig. 137) resembles the *O. baini* microconch, but has more numerous constrictions and seems to lack umbilical bullae to most secondary ribs. This species is very close to *Jeanthieuloyites quinquestriatus* (Besairie), from which it seems to differ in that the secondary ribs do not bifurcate before crossing the venter. It is, however, perhaps best referred to this genus.

Fig. 137. *Olcostephanus* (?*Subastieria*) *tauricus* (Karakasch). The syntypes, of which the larger is herein selected as lectotype, from Crimea (after Karakasch 1907). × 1.

Fig. 138. *Olcostephanus* (?*Subastieria*) *pavlowi* (Karakasch). The holotype, by monotypy, from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

'*Astieria*' *pavlowi* Karakasch (Fig. 138) is based upon a tiny individual with a strongly depressed whorl section, narrow umbilicus, rursiradiate secondaries and prominent parabolae. It was compared with *O.* (*Subastieria*) *sulcosus* Pavlow (*in* Pavlow & Lamplugh 1892) and differs from *O. baini* in the rursiradiate direction of its secondary ribbing.

Olcostephanus hispanicus (Mallada 1882) was considered to lie at the 'triple-junction' of the subgenera *Parastieria*, *Subastieria* and *Olcostephanus* by Wiedmann & Dieni (1968), although they placed the holotype within the subgenus *Subastieria*. The writer has not seen Mallada's (1882) original figure or description but, as figured by Nicklès (1890), this species is remarkably similar

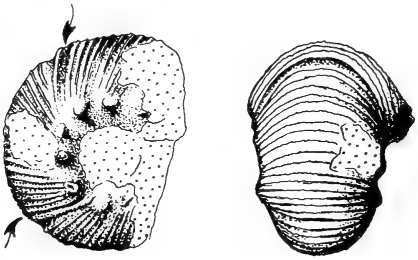

Fig. 139. *Olcostephanus* (*Olcostephanus*) *dacquei* (Krenkel). The holotype, by monotopy, from the Mikadi region of Tanzania (after Krenkel 1910). × 1.

to the inner whorls of the *O. baini* macroconch. Topotype material is necessary to determine the specific and subgeneric status of the Spanish species.

Olcostephanus dacquei (Krenkel) (Fig. 139) is based upon a juvenile with a rather narrow umbilicus and a depressed, coronate whorl section. Prominent primary ribs terminate in 7 well-developed, somewhat rounded umbilical tubercles from which arise 4–5 prorsiradiate secondaries, frequently with an intercalated rib between bundles. There are about 37 ribs per half whorl, as well as two prominent parabolae. This species differs from *O. baini* in possessing fewer umbilical tubercles from which arise finer, more numerous secondary ribs.

The holotype of *O. sublaevis* Spath (Fig. 140) is entirely septate and seems to be based upon the inner whorls of a macroconch. Based upon Fatmi's (1977) interpretation of this species, there are about 20 rursiradiate primaries (certainly more in Spath's holotype) which terminate in bullae on the umbilical shoulder and give rise to 4–6 slightly flexuous, prorsiradiate ribs. There is little to distinguish this species from the *O. baini* macroconch, of which it seems

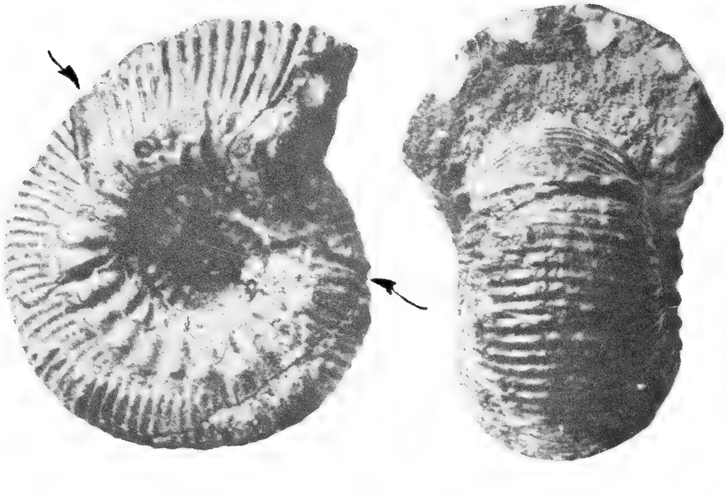

Fig. 140. *Olcostephanus* (*Olcostephanus*) *sublaevis* Spath (♀). The holotype from the Spiti Shales of Pakistan (after Spath 1939). × 1.

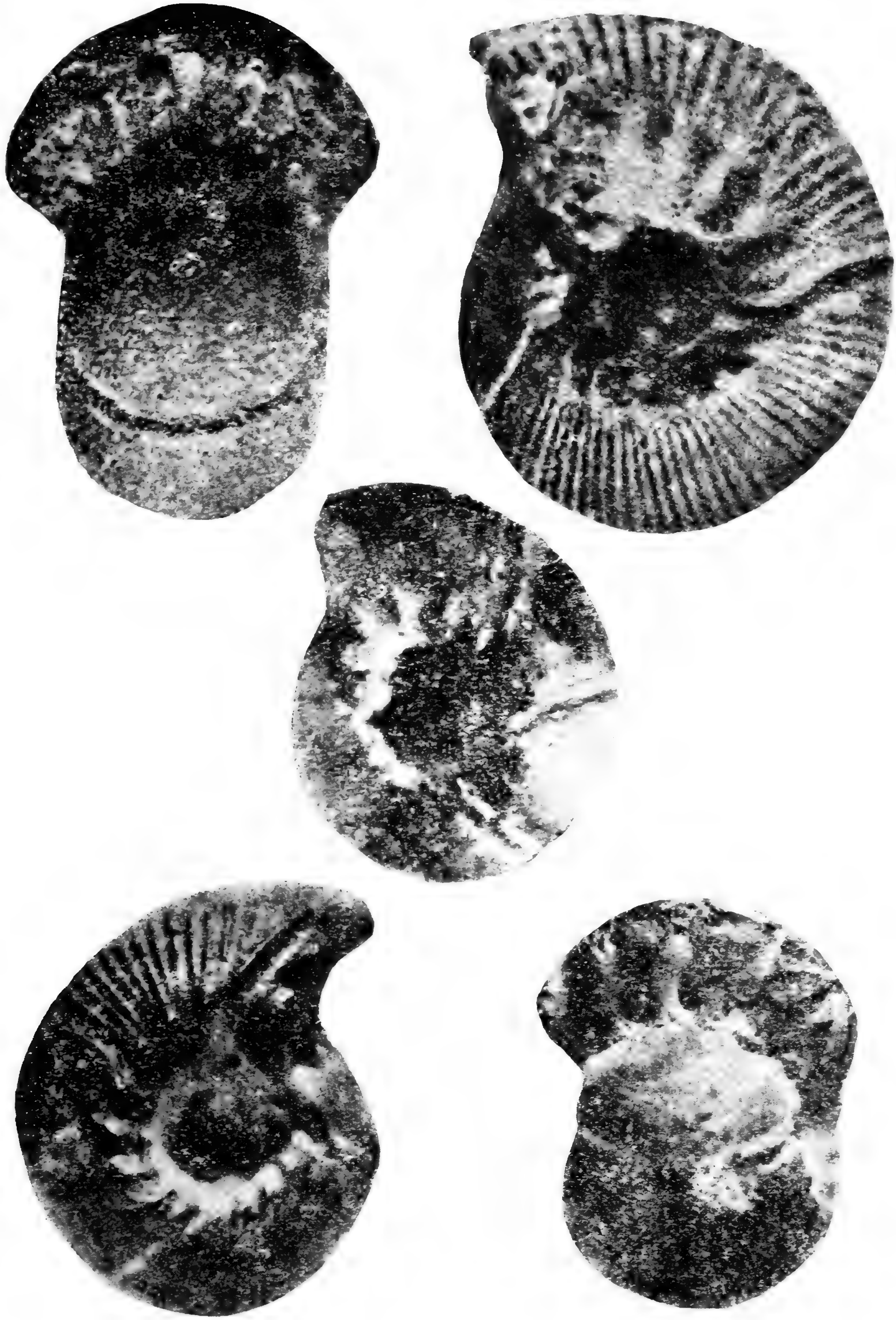

Fig. 141. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov). The syntypes from the Upper Valanginian–Lower Hauterivian of Tchakantsi, Bulgaria, of which the upper specimen is herein selected as lectotype (after Tzankov 1943). × 5.

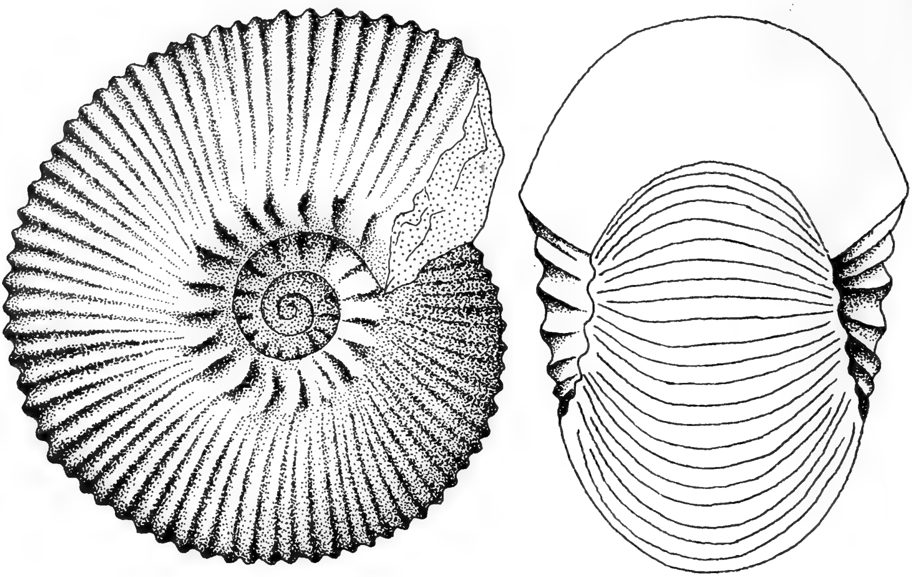

Fig. 142. *Olcostephanus* (*Olcostephanus*) *inordinatus* (Tzankov) (♀) (after Pictet 1860). × 1.

merely to represent an early growth stage. *Olcostephanus sublaevis* is tentatively included in the synonymy of *O. baini*.

Olcostephanus inordinatus (Tzankov) (Fig. 141) was based upon nuclei, some of which are still partially smooth and hence comparison is difficult. At this growth stage the whorl section is coronate, strongly depressed, and the umbilicus is fairly narrow, with sloping umbilical walls. There seem to be between 15 and 17 umbilical bullae on the outer whorl of the largest individual, which is herein selected as lectotype, from which arise 3–4 prorsiradiate secondary ribs. There are prominent parabolae. Since Tzankov (1943) included the specimen figured by Pictet (*in* Pictet & Campiche 1860, pl. 17 (fig. 4), pl. 18 (fig. 3)) (Fig. 142) into this species, this suggests that *O. inordinatus* loses its parabolae in maturity. There is, thus, little to distinguish Tzankov's (1943) species from the *O. baini* macroconch, of which it may prove to be a synonym.

As already pointed out, *O. crassicostatus* (Spath) (Fig. 80) was originally compared with *O. baini* but is herein interpreted as a gerontic *O. rogersi* (Kitchin) microconch.

Occurrence

As interpreted here, this species appears to be known from Tibet, Pakistan, ?Spain, Madagascar, Argentina, northern Mexico, ?Oregon, and South Africa, while the occurrence of strongly inflated forms with constricted inner whorls in the Swiss Jura and Bulgaria suggests its presence in these areas as well.

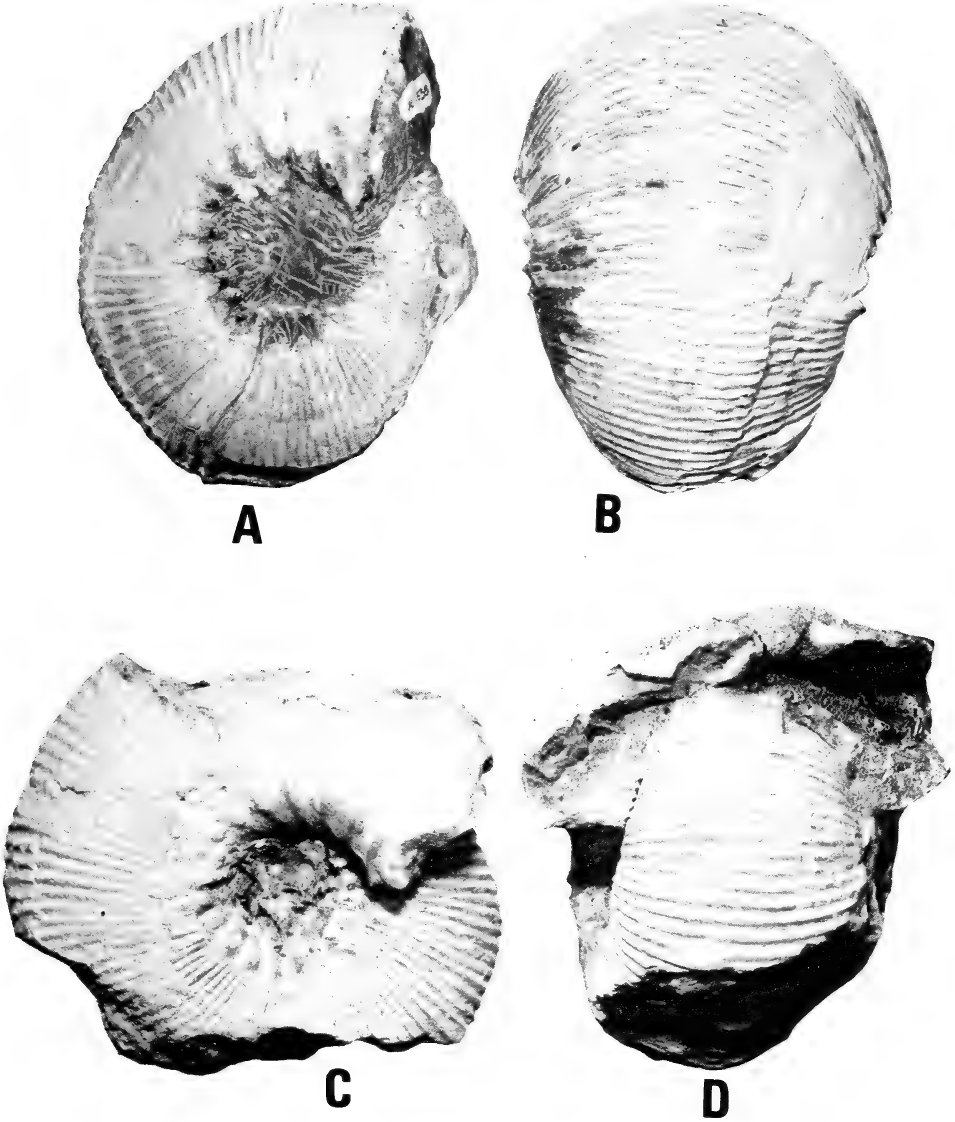

Fig. 143. A–B. *Olcostephanus* (*Olcostephanus*) *baini* (Sharpe) (♀). Lateral and ventral views of SAM–PCU1538, × 0,50. C–D. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀) Lateral and front views of SAM–PCU1604, × 0,66.

Olcostephanus (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath, 1930)

Figs 144E–G, 145–150A–B, F, 153

Microconch (♂)

? *Astieria leptoplana* Baumberger, 1908: 9, pl. 26 (fig. 4 only).
? *Olcostephanus glaucus* Spath, 1939: 17, pl. 6 (figs 7–8 only).
Holcostephanus ankaranensis Collignon, 1962: 40, pl. 191 (fig. 870).
Olcostephanus (*Rogersites*) *madagascariensis* var. *isakhelensis* Fatmi, 1977: 272, pl. 5 (fig. 3).

Macroconch (♀)

Rogersites sphaeroidalis Spath, 1930: 144, pl. 13 (fig. 5), pl. 15 (fig. 1).
? *Olcostephanus sublaevis* Spath, 1939: 21, pl. 3 (figs 1–3), pl. 19 (fig. 2); Fatmi, 1977: 269, pl. 4 (fig. 2).
? *Rogersites sanlazarensis* Imlay, 1937: 560, pl. 72 (figs 1–3), pl. 74 (fig. 1).
Olcostephanus (*Olcostephanus*) *sakalavensis* Fatmi (*non* Besairie), 1977: 267, pl. 2 (fig. 3 only), pl. 3 (fig. 2), pl. 4 (fig. 3).

Material

8 microconchs (SAM–PCU1534, SAM–PCU1592, SAM–PCU1593, SAM–PCU1523, SAM–1525, PEM–1468/76, BM–C41733, BM–C41731), and 1 macroconch (SAM–9241).

Holotype

By monotypy, the original of *Rogersites sphaeroidalis* figured by Spath (1930: 144, pl. 13 (fig. 5), pl. 15 (fig. 1)) from the Sundays River and now in the South African Museum, SAM–9241.

Diagnosis

Microconch moderately small, about 70–80 mm diameter, rather compressed but with a depressed whorl section. Rursiradiate primaries terminate in 18–22 umbilical bullae from which arise bundles of 3–4, rarely only 2, prorsiradiate secondaries. Parabolae prominent. Macroconch large, outer whorls indistinguishable from those of *O. b. baini* Inner whorls more finely ribbed, with commonly 4 secondaries per bulla, and 1–2 intercalated ribs between bundles. Parabolae present on inner whorls.

Description

Microconch (♂): moderately small cadicones, about 70–80 mm diameter, with somewhat compressed shells. The whorl section is depressed, with an evenly arched venter. The whorls are involute up to the umbilical bullae, covering about 80 per cent of the preceding whorl, except on the adoral portion of the body chamber when the umbilical seam egresses slightly.

Primary ribs begin at, or close to, the umbilical seam and curve backwards (rursiradiate) to 18–22 prominent bullae, on the umbilical shoulder of the final whorl. Secondary ribbing commonly arises in prorsiradiate bundles of 3–4, rarely only 2, often with an intercalated rib between bundles. The secondary ribbing recurves on the flanks so as to cross the venter transversely. There may be a slight adorally concave inflexion where the ribbing crosses the siphonal line. Along the venter of the adoral portion of the body chamber there are

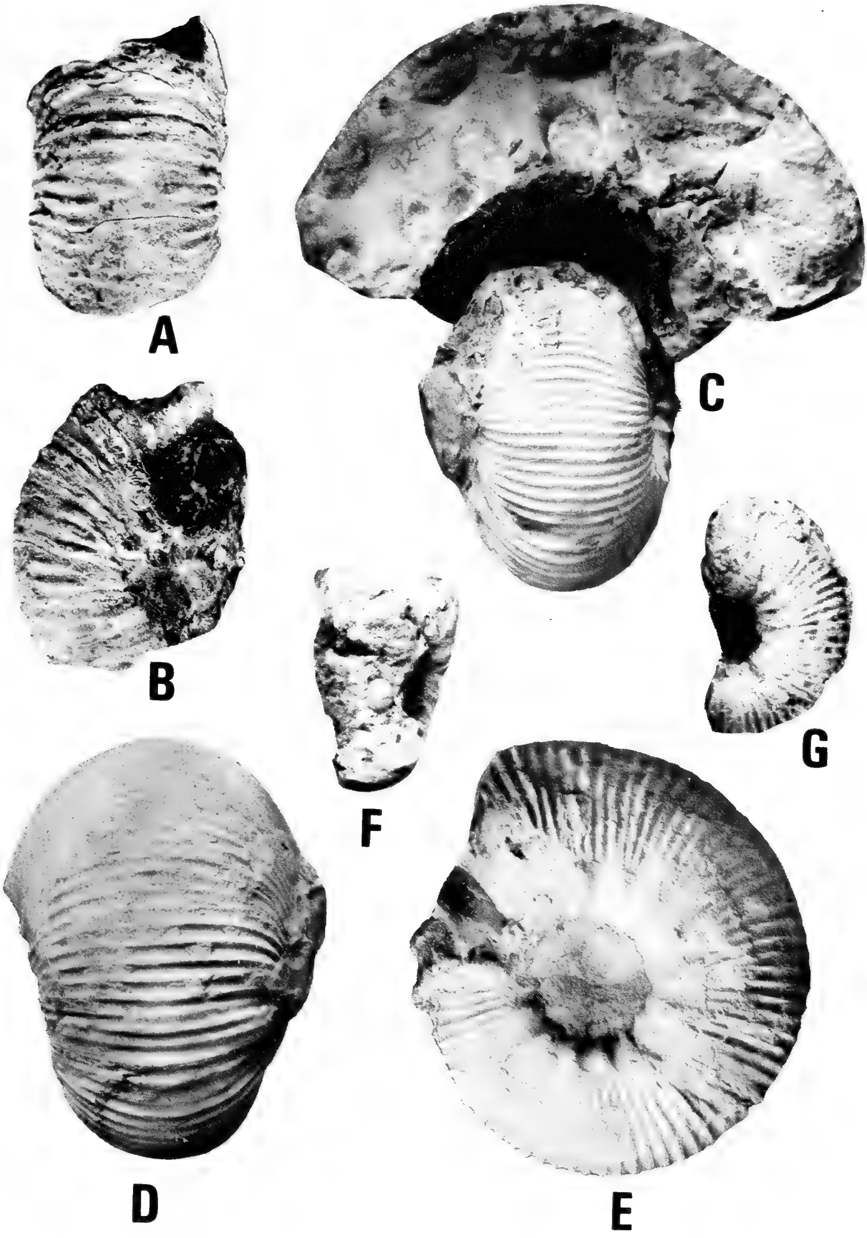

Fig. 144. A–B, F–G. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). A–B. Ventral and lateral views of SAM–581, a microconch, × 0,75. F–G. Front and lateral views of an immature specimen, SAM–PCU1579, × 0,66. Note fine ribbing and prominent parabola on smooth nucleus. C–E. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♀). Front, ventral and lateral views of the holotype of *Rogersites sphaeroidalis* Spath. SAM–9241. × 0,62.

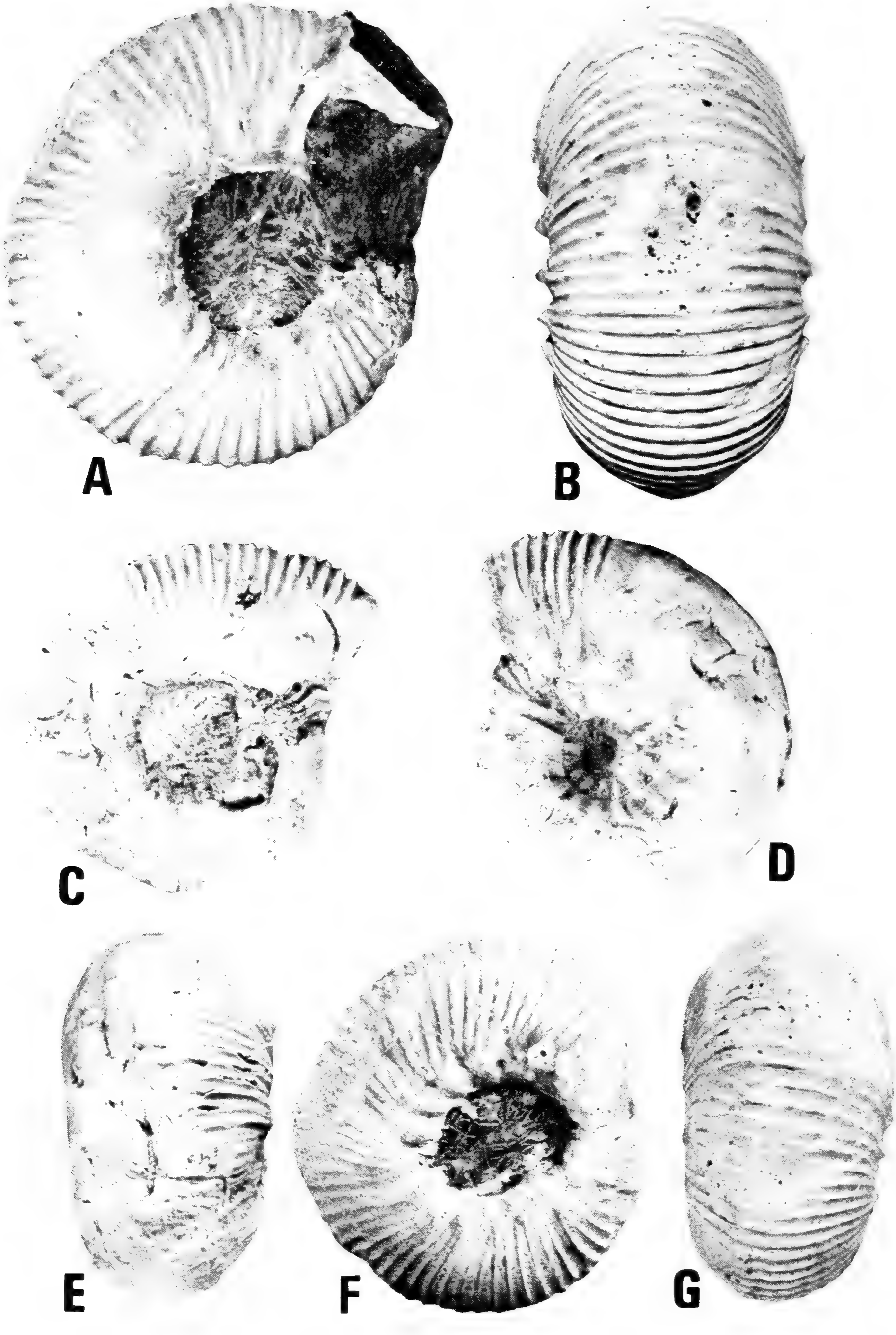

Fig. 145. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–B. Lateral and ventral views of SAM–PCU1592, × 0,75. C–E. Right lateral, left lateral and ventral views of SAM–PCU1534, × 0,75. F–G. Lateral and ventral views of SAM–PCU1575, × 0,66.

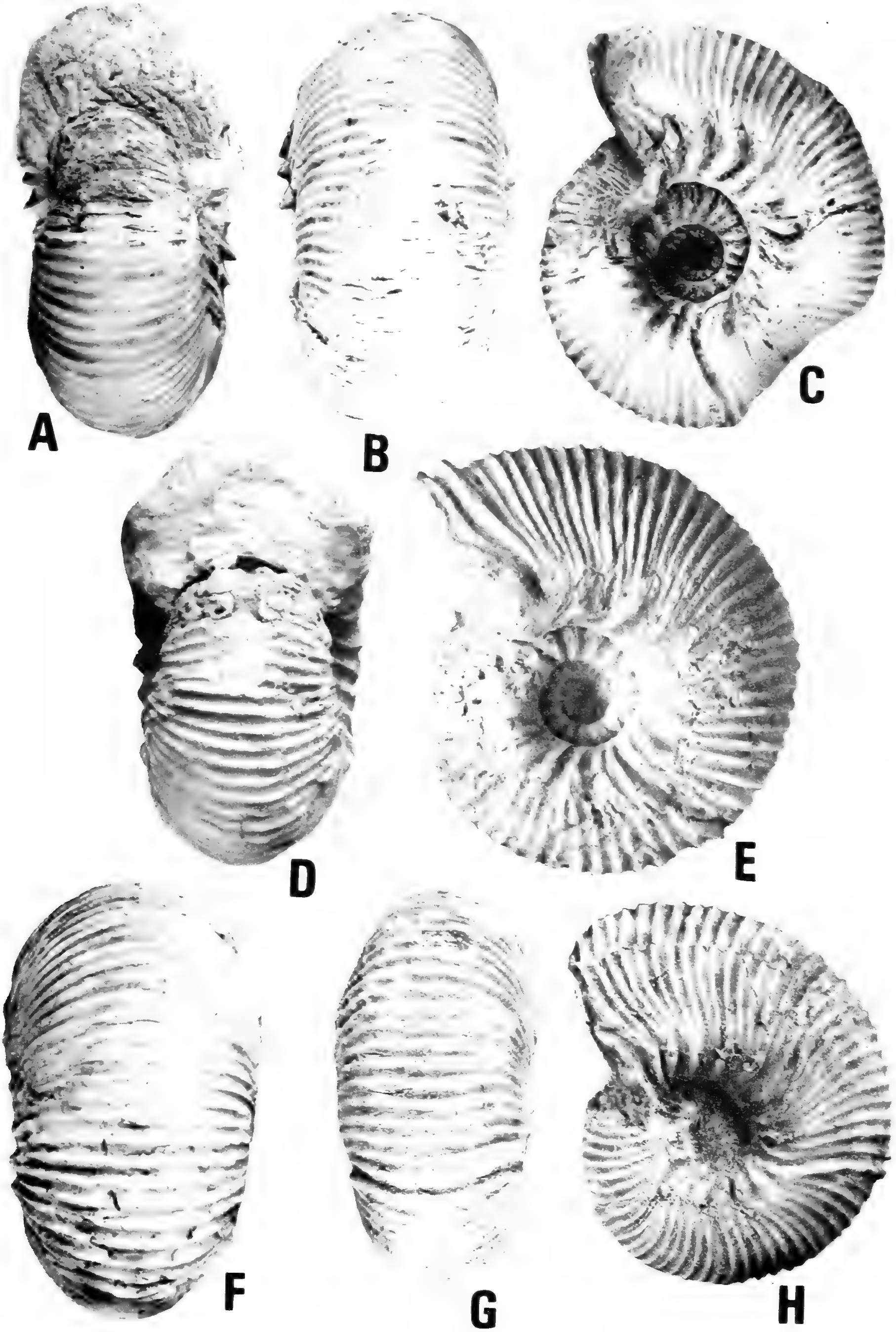

Fig. 146. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–C. Front, ventral and lateral views of SAM–PCU1523, × 0,66. D–F. Front, lateral and ventral views of PEM–1468/76, a specimen transitional to *O. b. baini*, × 0,86. G–H. Ventral and lateral views of SAM–PCU1525, × 0,75.

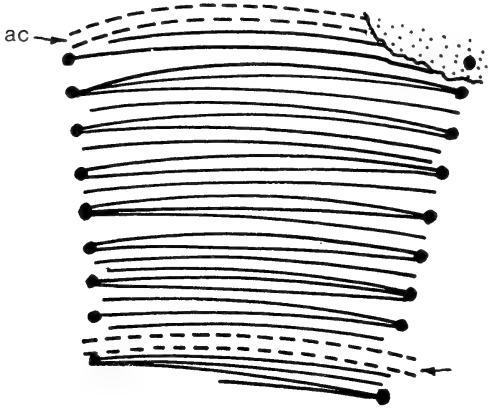

Fig. 147. Schematic representation of the rib pattern of *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂) on PEM–1462/76a (ac = apertural constriction).

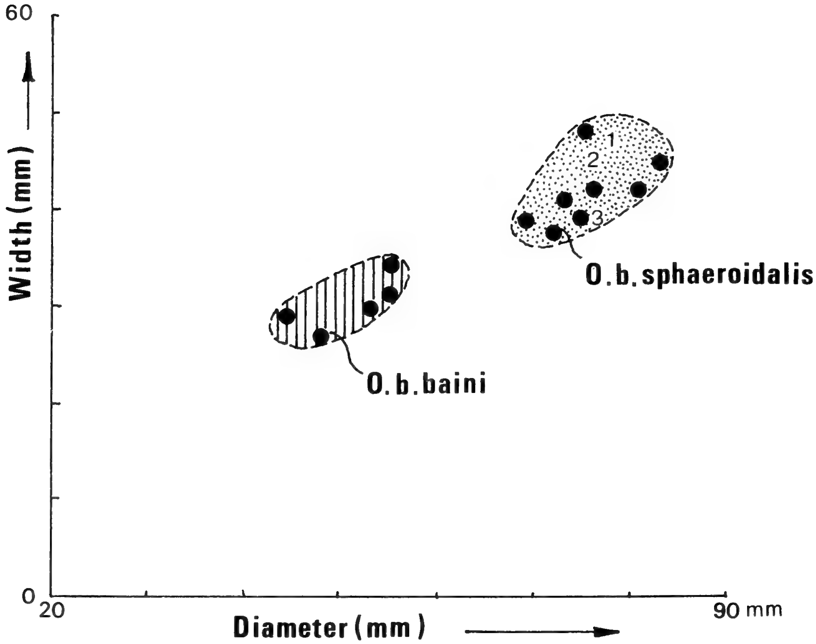

Fig. 148. Diameter/width plot showing the relationship between microconchs of *O. b. bain,* and *O. baini* var. *sphaeroidalis.*

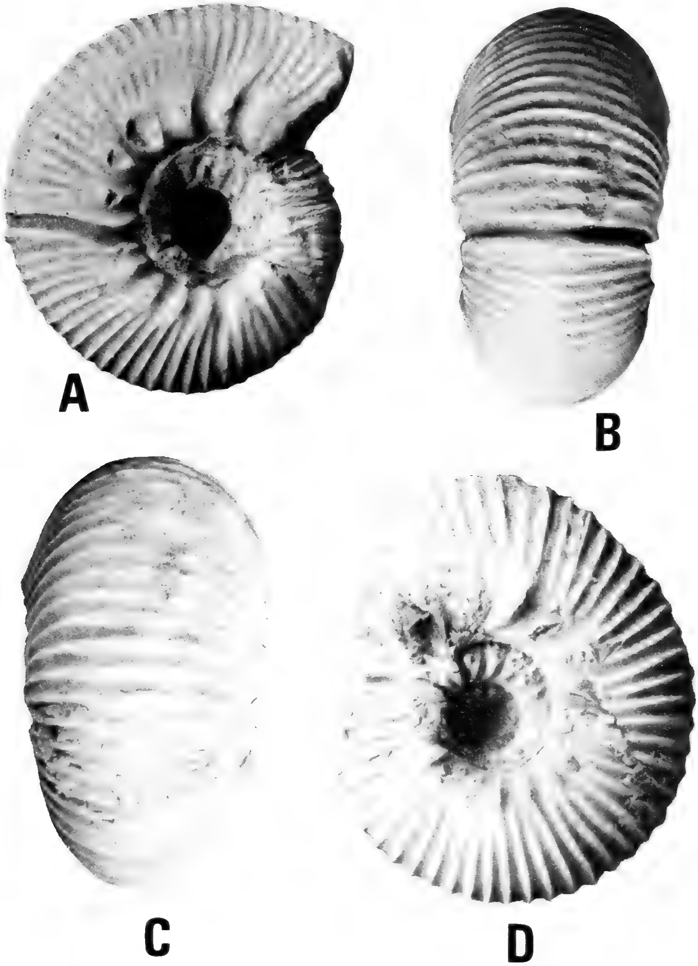

Fig. 149. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). A–B. Lateral and ventral views of BM–C47133. C–D. Ventral and lateral views of BM–C47131. × 0,75.

12–14 secondaries within a 40 mm distance, with 19–22 secondaries per 5 bullae. There are prominent parabolae on the outer whorl, while the peristome is ornamented with lateral lappets.

Macroconch (♀): as already pointed out, the outer whorls of the macroconch of this variety appear to be indistinguishable from those of *O. baini baini*. Consequently, it is only the inner whorls of this macroconch form that can be recognized. In SAM–9241 (the holotype of *O. sphaeroidalis* (Spath)), which represents an immature macroconch, the whorls are moderately inflated to a diameter of 55 mm, whereafter they increase very rapidly in width to become extremely inflated and strongly depressed. On the outer whorl, at 68 mm diameter, about 16 rursiradiate primaries terminate in bullae from which bundles of commonly 4, rarely 3 or 5, rather fine, prorsiradiate secondaries arise and recurve slightly so as to cross the venter transversely. There are 26 secondaries per 5 bullae at this growth stage, with 16 ribs in a 40 mm distance along the venter. Beyond this growth stage it seems unlikely that this variety can be distinguished from *O. baini baini* (♀).

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1593	79	33	43	1,30	40	29 (37) (♂)
SAM–PCU1592	85	36	48	1,33	41	? (♂)
SAM–PCU1596	79	37	51	1,38	35	26 (33) (♂)
SAM–PCU1595	73	33	41	1,24	?	? (♂)
SAM–PCU1523	83	35	42	1,20	40	26 (31) (♂)
,,	64	30	35	1,17	29	18 (28)
SAM–PCU1534	73	32	42	1,31	37	27 (37) (♂)
SAM–PCU1525	70	30	35	1,17	?	? (♂)
PEM–1468/76	68	30	38	1,27	29	18 (26) (♂)
,,	43	20	28	1,40	22	11 (26)
BM–C47133	68	27	34	1,26	34	22 (32) (♂)
,,	53	20	30	1,50	23	15 (28) (♂)
BM–C47131	68	27	35	1,30	32	19 (28) (♂)
SAM–9241	*c.*130	65	110	1,69	?	? (♀)
,,	68	30	47	1,57	28	?
,,	55	24	32	1,33	?	?

Discussion

The microconch of this variety differs from the *O. baini baini* microconch in its larger size (about 70–80 mm diameter as against 50–60 mm), more compressed form, greater number of umbilical bullae (18–22 as against 14–18), and more secondaries per bulla (3–4 as against 2–3). While these differences in the microconchs were at first thought to be of specific value, the fact that the macroconchs can be distinguished only during their early ontogenetic stages suggests that the differences are of no more than varietal importance.

A single example, from the Sundays River Formation, PEM–1468/76 (Fig. 146D–F), appears to be transitional between *O. baini baini* (♂) and *O. baini* var. *sphaeroidalis* (♂). In this specimen the whorl section is coronate at the peristome and thus resembles *O. baini baini* in this respect, while there are eighteen bullae on the final whorl, corresponding to the upper limit of *O. baini baini* but below the average of about twenty for the *O. baini* var. *sphaeroidalis* microconch. Moreover, the ribbing is finer and closer than in typical examples of *O. baini baini*, while its dimensions are within the range of *O. baini* var. *sphaeroidalis*.

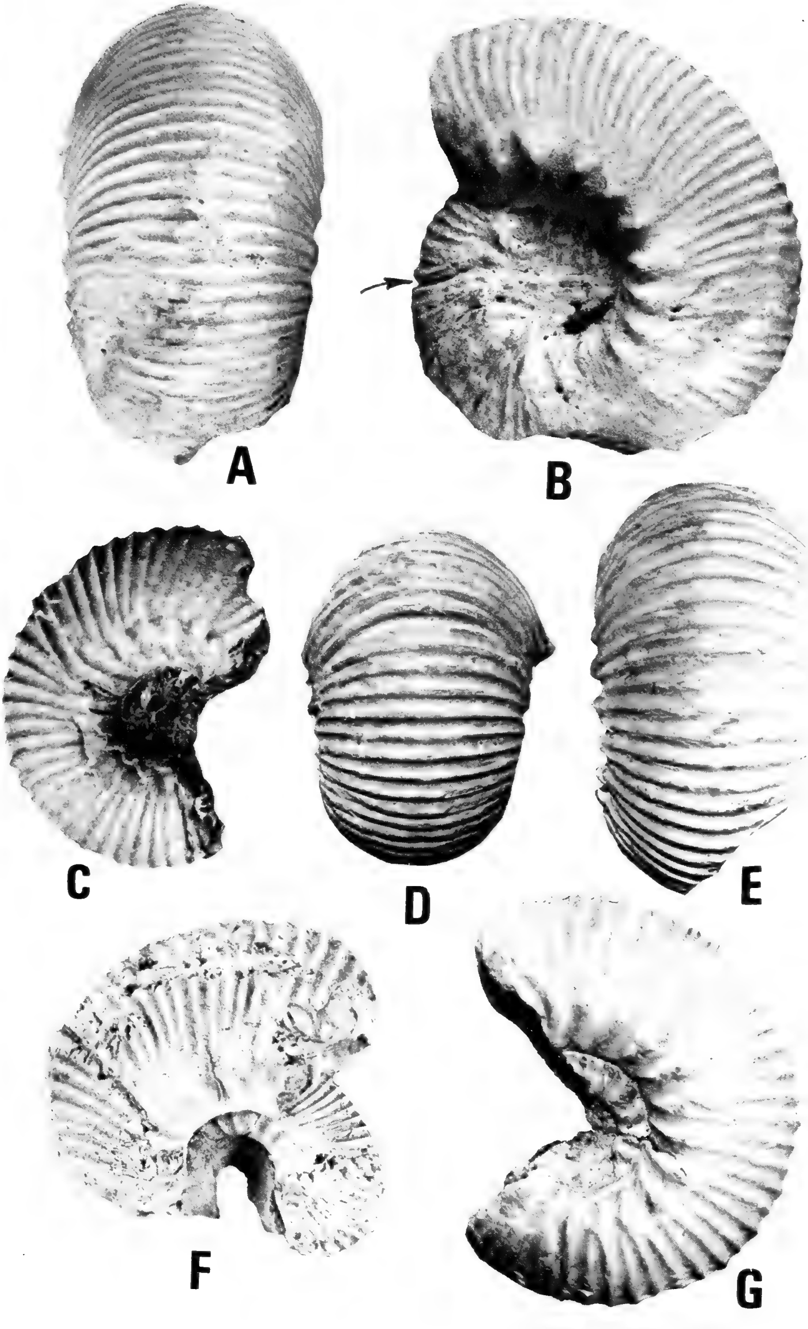

Fig. 150. A–B. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂). Ventral and lateral views of SAM–PCU1592, × 0,75. C–D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe). Lateral and ventral views of AAS–370, an immature macroconch, × 0,75. E, G. *Olcostephanus* (*Olcostephanus*) cf. *rogersi* (Kitchin) (♂). Ventral and lateral views of PEM–1468/42, × 0,75. F. *Olcostephanus* (*Olcostephanus*) cf. *baini* (Sharpe). Lateral view of SAM–PCU1591, an immature macroconch, possibly referable to the variety *sphaeroidalis* (Spath), × 0,66.

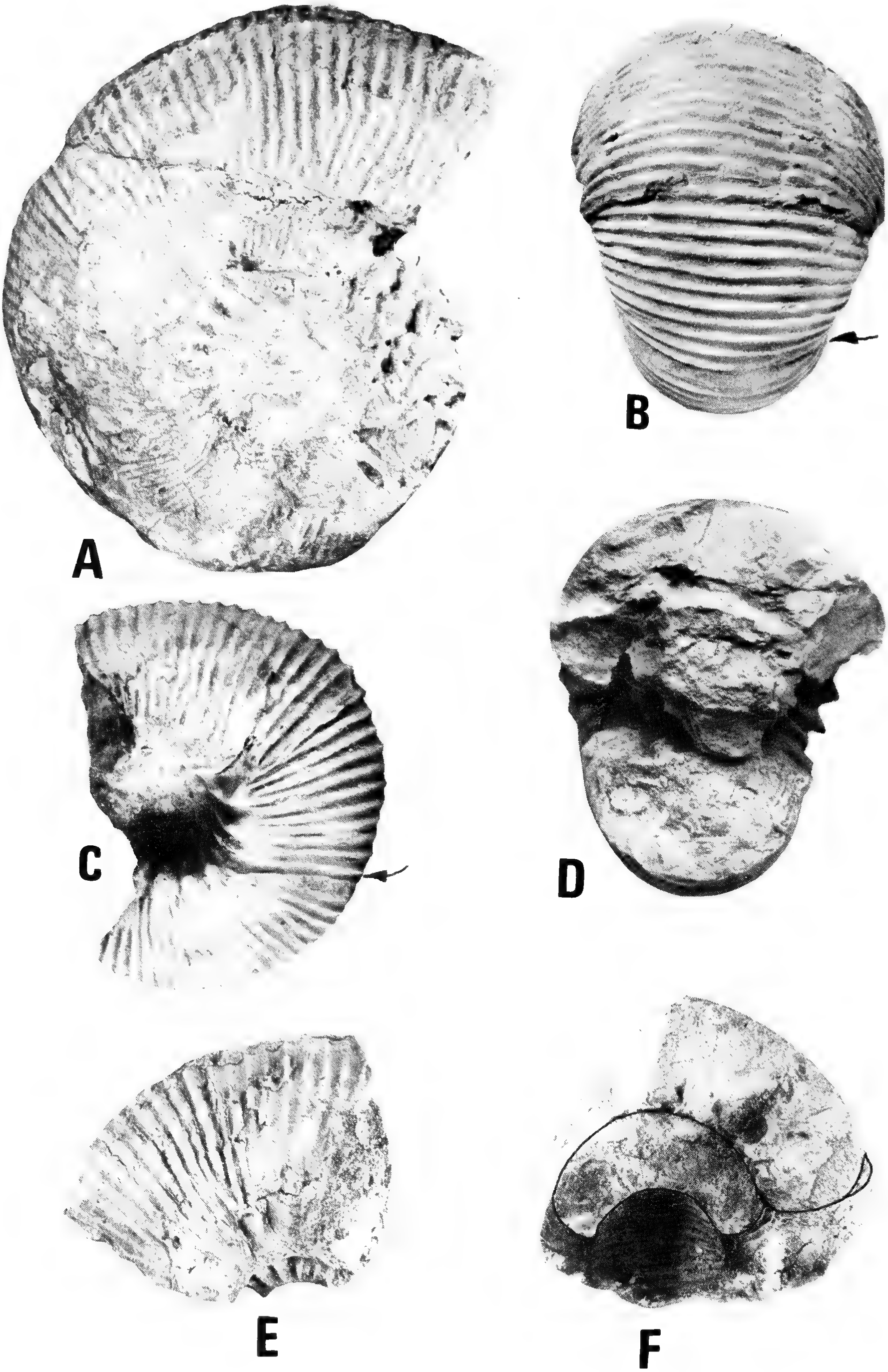

Fig. 151. A. *Olcostephanus* (*Olcostephanus*) *atherstoni* (Sharpe) (♀). Lateral view of the crushed inner whorls of SAM–320, × 0,66. B–D. *Olcostephanus* (*Olcostephanus*) *baini baini* (Sharpe) (♀). Ventral, lateral and front views of a specimen in the Albany Museum. Note the increase in inflation immediately after a parabola, × 0,75. E–F. *Olcostephanus* (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀). Lateral and front views of AAS–425. Note the extreme inflation and fine ribbing, × 0,55.

Fig. 152. *Olcostephanus* (*Olcostephanus*) *glaucus* Spath (♀). The holotype from the Spiti Shales of Pakistan. (after Spath 1939). × 1.

As can be seen from Fatmi's (1977) figure and description, *Olcostephanus* (*Rogersites*) *madagascariensis* var. *isakhelensis* Fatmi is a junior subjective synonym of the microconch of this taxon.

Olcostephanus glaucus Spath (1939) (Fig. 152) differs from the present species in being less inflated, more finely and densely ribbed and, in the holotype, lacking constrictions. The constricted paratype (Spath 1939, pl. 6 (fig. 7)) is very close, however, to the microconch of the present variant, and may prove to be identical.

Collignon (1962: 44) considered *O. ankaranensis* (Fig. 153) to be characterized by '. . . ses tours subcylindriques dont l'épaisseur reste à peu près constante, la réduction des flancs qui sont limités a la partie garnie de tubercules ombilicaux, et par un ombilic profond et trés large'. So far as the writer is able to judge, there are no features whereby this species can satisfactorily be separated from the microconch of the present form, of which *O. ankaranensis* (Collignon) thus becomes a probable junior subjective synonym.

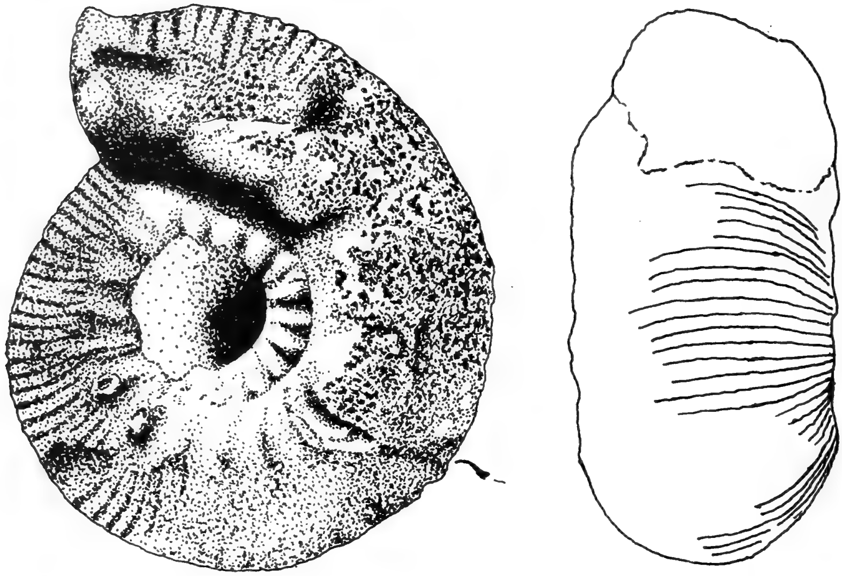

Fig. 153. *Olcostephanus* (*Olcostephanus*) *baini* var. *sphaeroidalis* Spath (♂). The holotype of *Holcostephanus ankaranensis* Collignon from the Upper Valanginian of Ambiky, Madagascar (after Collignon 1962). × 1.

The constricted example of *Astieria leptoplana* figured by Baumberger (1908, pl. 26 (fig. 4)) shows no features satisfactorily to distinguish it from the present material with which it is here included.

Occurrence

This variety is known from the Swiss Jura, Pakistan, Madagascar, South Africa, and possibly Mexico.

Olcostephanus (*Olcostephanus*) *ventricosus* (von Koenen, 1902)

Figs 154–156

Olcostephanus multiplicatus Neumayr & Uhlig (*non* Roemer), 1881: 150, pl. 33 (fig. 2).
Astieria ventricosa von Koenen, 1902: 144. Kitchin, 1908: 189.
? *Astieria convoluta* von Koenen, 1902: 146, pl. 39 (fig. 4a–b).
Astieria rigida Baumberger, 1908: 7, pl. 28 (fig. 1), fig. 121.
Holcostephanus (*Astieria*) *ventricosus* (von Koenen) Wegner, 1909: 87.

Material

Two specimens, LJE–989a, SAM–PCU1607.

Holotype

The original of *Olcostephanus multiplicatus* Römer (Fig. 155) figured by Neumayr & Uhlig (1881: 150, pl. 33 (fig. 2)) from Höheneggelsen, northern Germany.

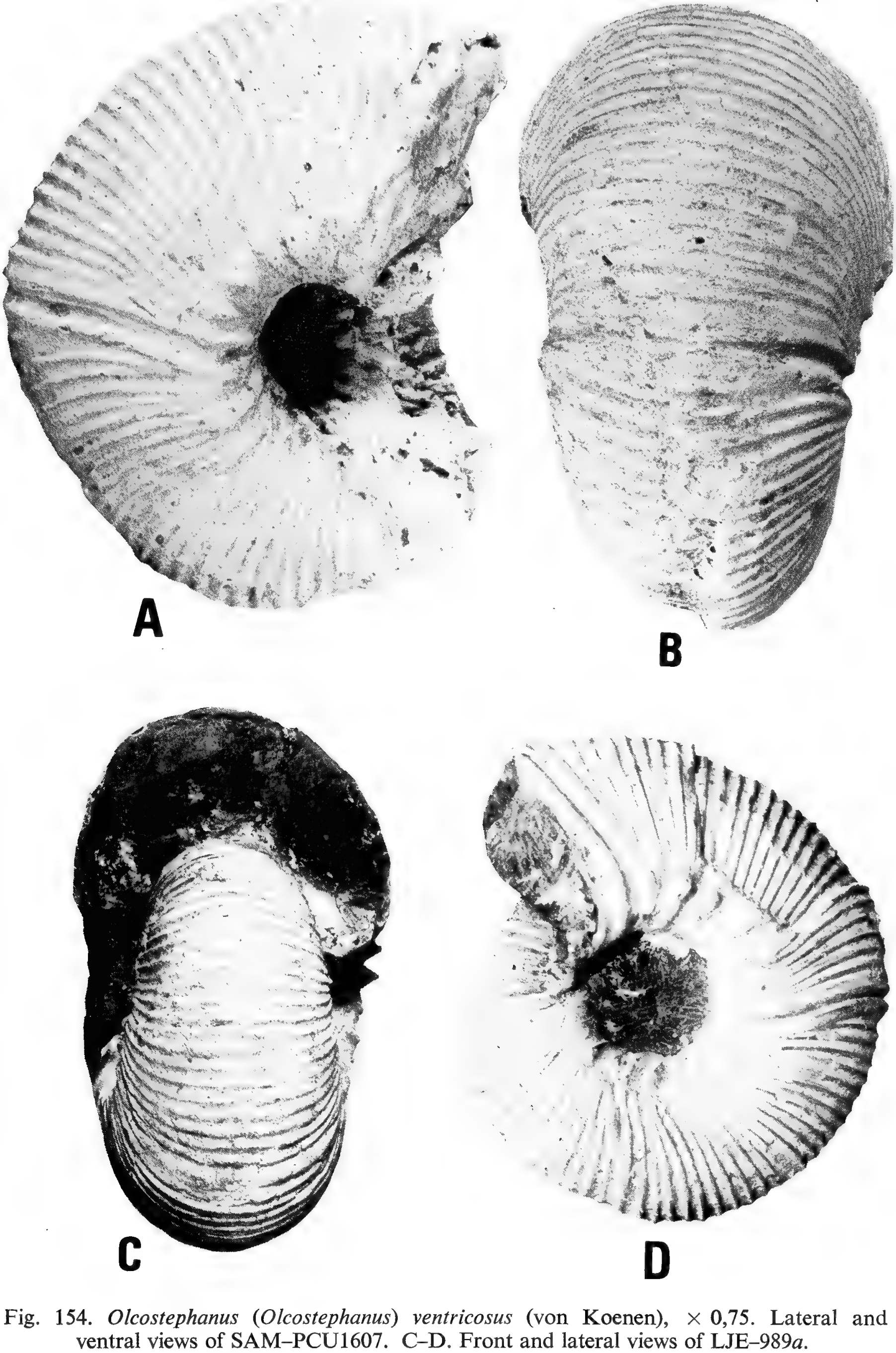

Fig. 154. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen), × 0,75. Lateral and ventral views of SAM–PCU1607. C–D. Front and lateral views of LJE–989*a*.

Diagnosis

Medium-sized, somewhat inflated, with a semicircular whorl section. About 18–22 rursiradiate primaries terminating in sharp bullae, from which arise 2–4, commonly 3, prorsiradiate, slightly flexuous, secondaries. Prominent deep parabolae present. Possibly the inner whorls of a macroconch.

Description

Two specimens from the Sundays River beds, one rather crushed, are referable to this species. LJE–989a has the recrystallized test preserved, and closely resembles the type figured by Neumayr & Uhlig.

This example is somewhat inflated and moderately large. It is involute up to the umbilical bullae and has a steep umbilical wall. The whorl section is depressed, with an almost perfectly semicircular whorl section. Distinctly rursiradiate primaries terminate in 20 sharp bullae on the umbilical shoulder of the outer whorl. These in turn give rise to 2–4, commonly 3, prorsiradiate secondaries which recurve slightly on the upper part of the flanks so as to cross the venter transversely. There are 25 secondaries per 7 bullae on the adapical portion of the outer whorl (about 65 mm diameter) and 24 per 6 bullae on the adoral portion. There are invariably 1–2 intercalated ribs between bundles, with 11 secondaries within a 30 mm distance along the venter of the outer whorl. The outer whorl is ornamented with 2 prominent parabolae.

SAM–PCU1607 is very similar, but rather crushed at the adapical portion of the outer whorl. This specimen would appear to have part of a peristome preserved, but there are no signs of lateral lappets.

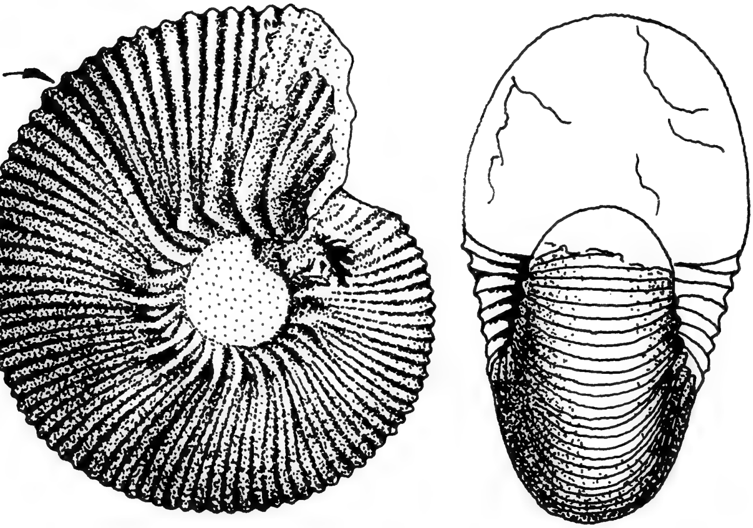

Fig. 155. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen). The holotype of *Astieria ventricosa* von Koenen, from north-west Germany (after Neumayr & Uhlig 1881). × 1.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
LJE–989a	80	27	44	1,63	26	14 (18)
,,	60	23	33	1,43	25	12 (20)
,,	45	17	23	1,35	17	8 (18)
SAM–PCU1607	109	53	64	1,21	34	21 (19)

Discussion

This is a rather problematical form since it is uncertain whether it represents the inner whorls of a macroconch, or if it is a large microconch species. Its large size would seem to favour the former, whilst its lack of inflation suggests the latter.

This species is clearly very closely related to *O. baini* from which it seems to differ only in remaining relatively compressed to large diameters.

According to Von Koenen (1902), *Astieria convoluta* is a moderately inflated form with a deep, narrow umbilicus. Rursiradiate primaries terminate on the umbilical shoulder in bullae, of which there are about 8 per half whorl. There are generally 3 prorsiradiate secondaries per bulla, with an intercalated rib between bundles, and a prominent parabola on the outer whorl. There is little to separate this species from *O. ventricosus*, of which it may prove to be a junior subjective synonym.

Astieria dalpiazi Rodighiero (1919) was compared with *O. ventricosus* but has never been figured. It was said to have short, weak, thin primary ribs which terminate in tubercles on the umbilical shoulder from which arise 2–3 secondary ribs. The secondaries bifurcate at various levels on the flanks so that 4–6 ribs cross the venter for each tubercle. Parabolae are present. According to Rodighiero (1919), '*A.*' *dalpiazi* differs from *O. ventricosus* in being more inflated, with a narrower, deeper umbilicus. However, Von Koenen's (1902) species does not have bifurcating secondaries and is probably specifically distinct.

Olcostephanus rigidus (Baumberger) (Fig. 156) does not appear to be specifically distinct from this form, and supports its treatment as the inner whorls of a macroconch. Baumberger's species was erected for moderately inflated forms with 23–24 rursiradiate primaries on the outer whorl, each terminating in umbilical bullae from which arise bundles of 3–4 prorsiradiate secondaries commonly with 2 intercalated ribs between bundles. There is a prominent parabola on the outer whorl. The whorl section is semicircular. Thus, there is no significant feature by which this species can be distinguished from *O. ventricosus* and they should be considered conspecific.

Since the outer whorls of this probable macroconch form are unknown, as is the microconch dimorph, its true status is not known, and must await study of topotype material.

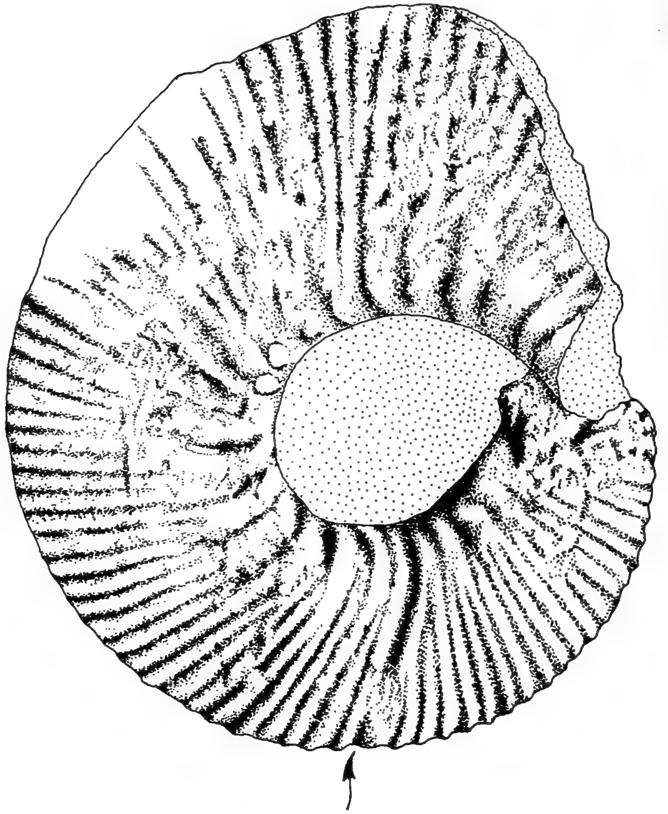

Fig. 156. *Olcostephanus* (*Olcostephanus*) *ventricosus* (von Koenen). The lectotype, designated herein, of *Astieria rigida* Baumberger, from the Swiss Jura (after Baumberger 1908). × 1.

Occurrence

This species is known from the Swiss Jura, northern Germany, South Africa, the south of France, and possibly Tanzania.

Olcostephanus (*Olcostephanus*) *uitenhagensis* (♀) (Kitchin, 1908)
Figs 157, 158C–D, 159, 160C–D

Holcostephanus uitenhagensis Kitchin, 1908: 206, pl. 11.
Holcostephanus (*Astieria*) *uitenhagensis* Kitchin, Wegner, 1909: 89. Kilian, 1910: 214.
Holcostephanus uitenhagensis Kitchin, Hatch & Corstorphine, 1909: 295, fig. 73 (right-hand specimen only).
Rogersites uitenhagensis (Kitchin) Spath, 1930: 150. Besairie, 1936: 141.
Olcostephanus uitenhagensis (Kitchin) Spath, 1939: 19. Riccardi *et al.*, 1971: 90. Reyment & Tait, 1972: 60.

Material

Three specimens, all macroconchs (SAM–5069, SAM–PCU1524, SAM–PCU1605).

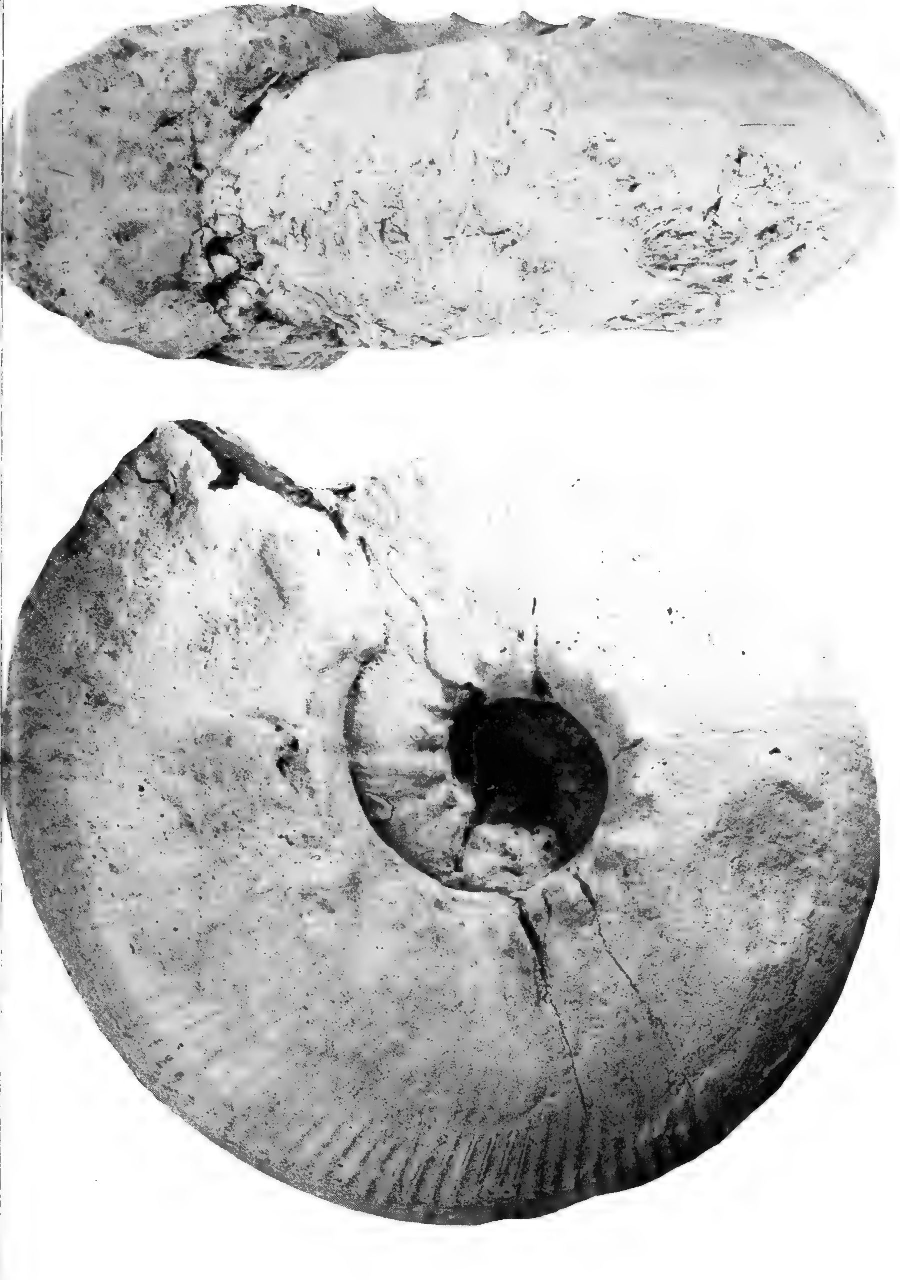

Fig. 157. *Olcostephanus (Olcostephanus) uitenhagensis* (Kitchin) (♀). Lateral and front views of the holotype, SAM-5069, a poorly preserved internal mould. × 0,55.

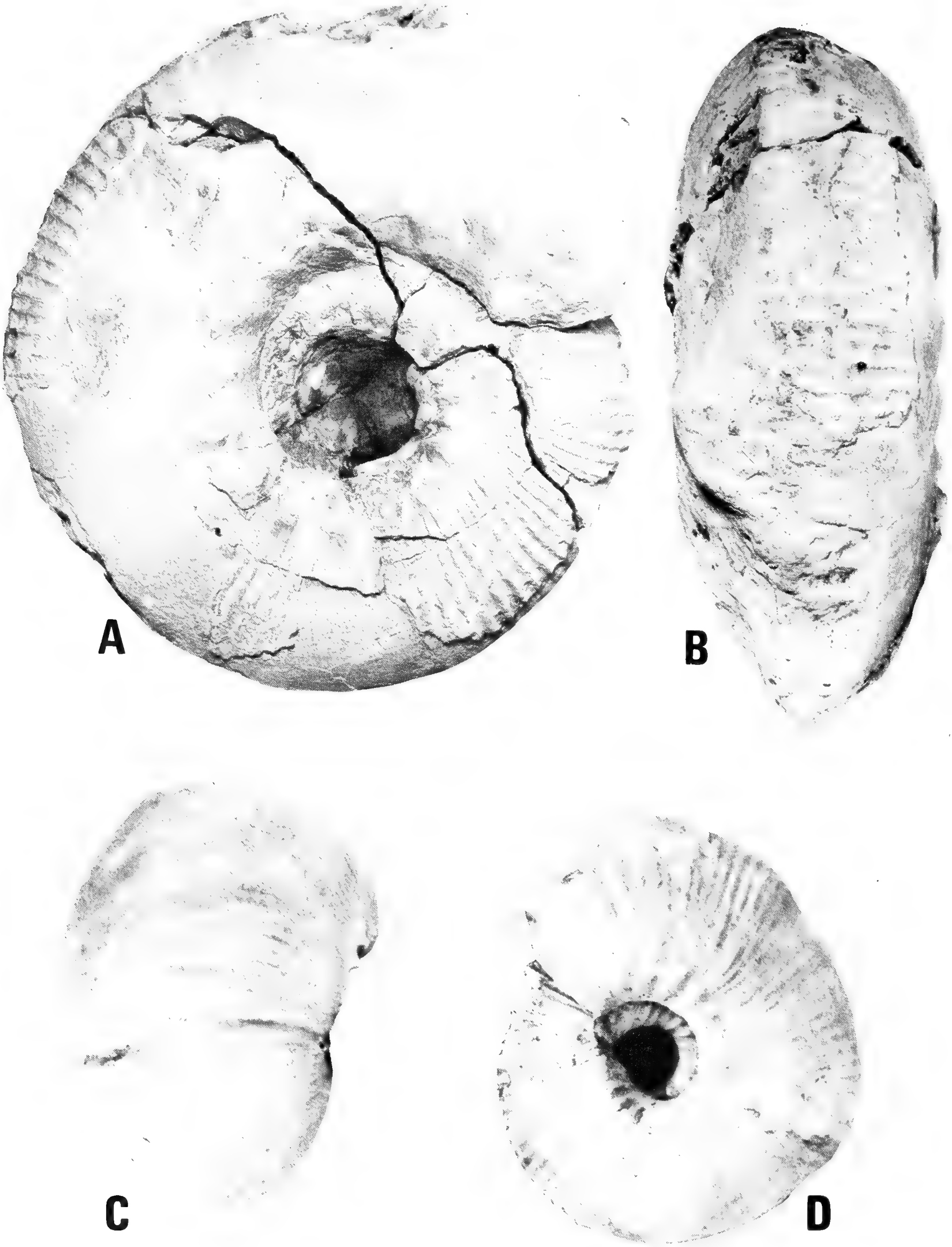

Fig. 158. A–B. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Lateral and ventral views of SAM–PCU1605, retaining patches of recrystallized test. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) sp. (♀). Ventral and lateral views of SAM–PCU1531. Note fine, flexuous ribbing and parabola. × 0,55.

Holotype

By monotypy, the original of *Holcostephanus uitenhagensis* Kitchin (1908: 206, pl. 11) (Fig. 157) from '. . . between milestones 24½–24¾ on the Graaff-Reinet railway, about three miles from Uitenhage'. The holotype, SAM–5069 is in the South African Museum.

Diagnosis

Large (about 200 mm diameter), compressed macroconchs which become markedly evolute on the final whorl. Flanks prominent, steep and slightly convex. On the penultimate whorl rursiradiate primaries terminate in 19 bullae on the umbilical shoulder. On the final whorl the primaries become very weak, disappearing entirely on the internal mould, and the tubercles become swollen and rounded, as well as fewer (15) in number. Flexuous prorsiradiate secondaries arise in bundles of 3–5, with 1–2 intercalated ribs between bundles. Parabolae lacking, on outer whorls at least. Peristome simple.

Description

Only macroconchs of this species have been described, and until the ontogenetic variation is known it is highly unlikely that the microconch dimorphs will be recognized.

The shell is a large, compressed cadicone, involute up to the umbilical bullae except on the last two-thirds of the body chamber when the umbilical seam egresses rapidly and the final whorl becomes about 30 per cent evolute at the peristome. The umbilicus is fairly narrow and rather deep, with vertical umbilical walls on the inner whorls and an acute umbilical shoulder. On the body chamber, with the egression of the umbilical seam, the slope of the umbilical wall decreases markedly and the shoulder becomes rounded.

Also with the egression of the umbilical seam, the prominent rursiradiate primaries weaken considerably and are almost entirely effaced on the adoral portion of the final whorl. At the same time, the distinctly bullate umbilical tubercles of the penultimate whorl become swollen and rounded. There are 15 umbilical tubercles on the body chamber, whereas the penultimate whorl is ornamented with 19 bullae.

Specimen SAM–PCU1524 is a well-preserved example of this species which, unlike the holotype which represents an internal mould, has the recrystallized test preserved. Unfortunately it has been slightly crushed laterally.

On this example, the secondary ribbing is rather fine and slightly prorsiradiate, becoming distinctly coarser and more inclined near the peristome. On the penultimate whorl the secondaries are slightly flexuous, arising radially from the umbilical bullae only to curve forward low down on the flanks and then gently recurve so as to cross the venter transversely. On the penultimate whorl there are 16 secondaries per 3 bullae, while on the adoral portion of the body chamber there are 25, with 13 ribs within a 60 mm distance along the

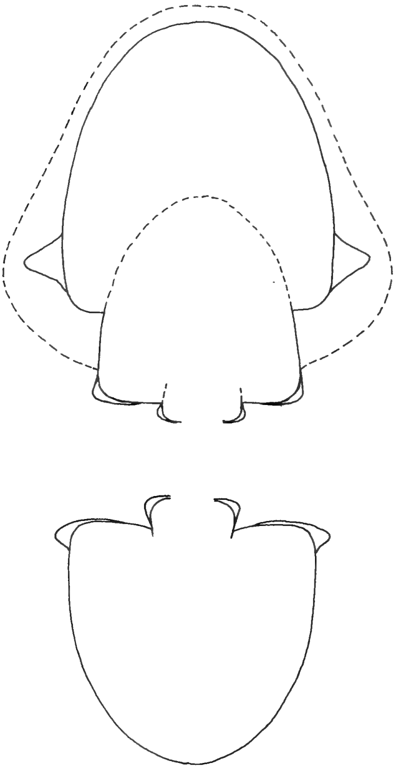

Fig. 159. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Whorl section of SAM–PCU1524. Dotted line represents shape of the final peristome. × 0,5.

venter. Parabolae are lacking on the outer whorls, although the peristome is strongly constricted, cutting obliquely across 4 ribs to the posterior, and with a prominently flared adapical margin.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–5069	225	88	*c.*93	1,11	87	67 (30)
,,	*c.*155	69	82	1,19	49	37 (24)
SAM–PCU1524	188	71	*c.*71	1,00	74	51 (27)
,,	155	67	*c.*64	0,96	52	35 (22)

Discussion

Olcostephanus uitenhagensis is a macroconch characterized by the marked egression of the umbilical seam on the final whorl, its compressed form, and the change in the nature of the tuberculation on the body chamber.

Olcostephanus of the *astierianus* plexus do not show the marked egression

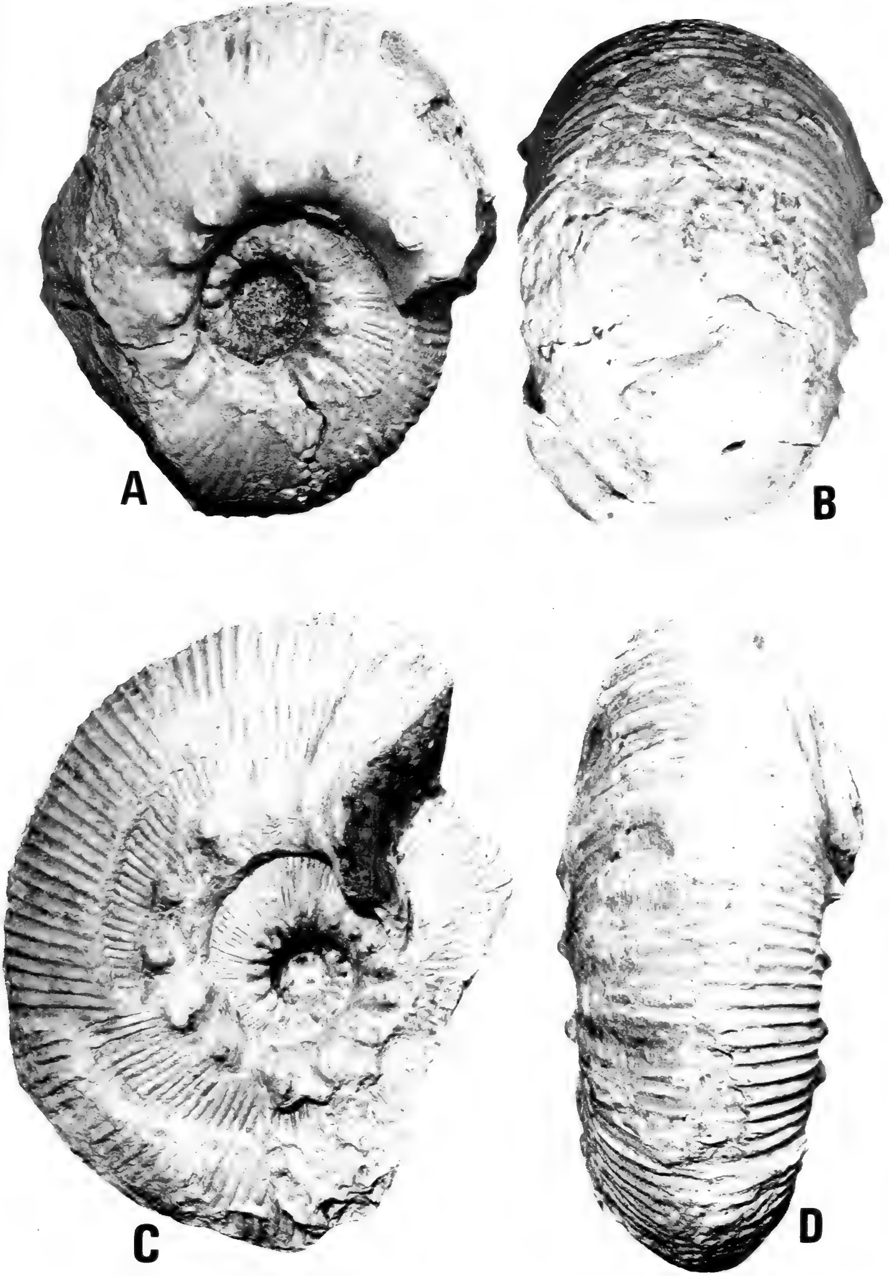

Fig. 160. A–B. *Olcostephanus* (*Olcostephanus*) *riccardii* sp. nov. (♀). Lateral **and ventral** views of the holotype, SAM–PCU1577. Note inflated form, lack of parabolae and rounded umbilical tubercles on the body chamber. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀). Lateral and ventral views of SAM–PCU1524. Note compressed form, egression of the umbilical seam, rounded tubercles on the body chamber and constricted peristome. × 0,44.

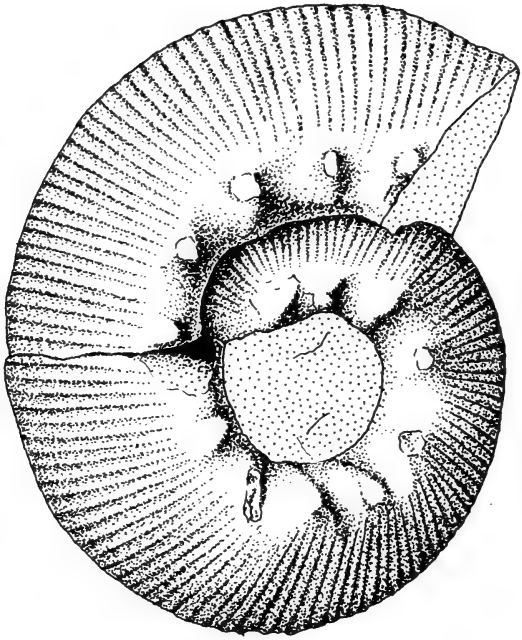

Fig. 161. *Olcostephanus* (*Olcostephanus*) *singularis* (Baumberger). The lectotype, designated herein, from the Swiss Jura (after Baumberger 1908). × 1.

of the umbilical seam displayed by *O. uitenhagensis* in maturity, as well as commonly retaining bullate umbilical tubercles to the peristome.

Olcostephanus singularis (Baumberger) (Fig. 161) is the closest species to *O. uitenhagensis*. It has a moderately inflated shell with a strongly depressed whorl section and shows marked egression of the umbilical seam on the outer (?final) whorl. About 12, rounded, swollen, umbilical tubercles on the outer whorl give rise to bundles of 5–6 slightly prorsiradiate secondaries, between which are 2–3 intercalated ribs. Parabolae are lacking. This species differs from *O. uitenhagensis* in that the umbilical tubercles are swollen and rounded even on the inner whorls as witnessed by *O. klaatschi* (Wegner) which is merely based upon a juvenile of Baumberger's (1908) species.

Olcostephanus rabei (Besairie) (Fig. 69A–B), as noted by Besairie (1936), is indeed very close to the inner whorls of *O. uitenhagensis*. However, without knowledge of the final whorls, the true affinities of *O. rabei* are obscure as it also closely resembles *O. sakalavensis*.

Occurrence

This species has been known with certainty only from South Africa, although Reyment & Tait (1972) have recently reported its occurrence in Argentina.

Olcostephanus* (*Olcostephanus*) *riccardii sp. nov.

Figs 162–163

Material

Two specimens, SAM–PCU1577 and BM–C47130, of which the former is designated as the holotype, and the latter is a paratype.

Holotype

SAM–PCU1577 from the Algoa Brick & Tile quarries at Coega.

Diagnosis

A strongly inflated, globose species of *Olcostephanus* with a very depressed whorl section and a deep, narrow umbilicus. Inner whorls with about nineteen umbilical bullae becoming swollen and rounded on the body chamber. Parabolae lacking.

Fig. 162. *Olcostephanus* (*Olcostephanus*) *riccardii* sp. nov. (♀). Lateral view of the paratype, BM–C47130. × 0,44.

Etymology

For Dr A. C. Riccardi of the Museo de Ciencias Naturales, La Plata, Buenos Aires, in appreciation of his help in providing literature and constructive criticism of the original manuscript.

Description

The holotype is a strongly inflated, globose cadicone with a narrow umbilicus and steep umbilical walls. The whorls, involute up to the umbilical bullae on the inner whorls, become rather evolute on the adoral portion of the outer whorl. Distinct primaries begin at the umbilical seam and pass backwards (rursiradiate) to 19 bullae on the sharp umbilical shoulder. On the outer whorl the bullae become swollen and distinctly rounded and the primaries are effaced (on the internal mould). There are about 15 tubercles on the final whorl.

On the penultimate whorl secondary ribbing arises in slightly prorsiradiate bundles of 3–4 ribs, commonly with an intercalated rib between bundles, so that there are 17 ribs per 4 bullae. The secondaries recurve slightly so as to cross the venter transversely. On the adoral portion of the body chamber there are 28 secondaries per 4 bullae, with 8 ribs in a 40 mm distance along the venter, whereas on the adapical portion of the outer whorl there are 10 secondaries within a similar distance.

The peristome is not preserved, but the inflated shell leaves little doubt that this form represents a macroconch.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1577	150	62	94	1,52	60	45 (30)
,,	110	50	83	1,66	39	26 (24)
BM–C47130	182	77	?	?	80	52 (29)

Discussion

The ornament of this species is almost identical to that of the holotype of *O. uitenhagensis*, the only difference being that whereas Kitchin's type, together with further topotype material, has a noticeably compressed form, this taxon is distinctly inflated and globose. To admit extremely inflated and strongly compressed individuals into the same dimorph would so drastically alter the taxonomy of the group that present evidence does not justify such a move, and hence a new species is created for the present material.

The inner whorls of this species may be distinguished from *O. atherstoni* (♀) by their much greater inflation, and more depressed whorl section.

Mature *O. baini* macroconchs attain a much larger size than this species, while the tubercles remain bullate to the peristome. Moreover, *O. riccardii* does not show the decrease in inflation near the peristome which characterizes *O. baini* macroconchs. Immature examples of *O. baini* (♀) differ in having parabolae.

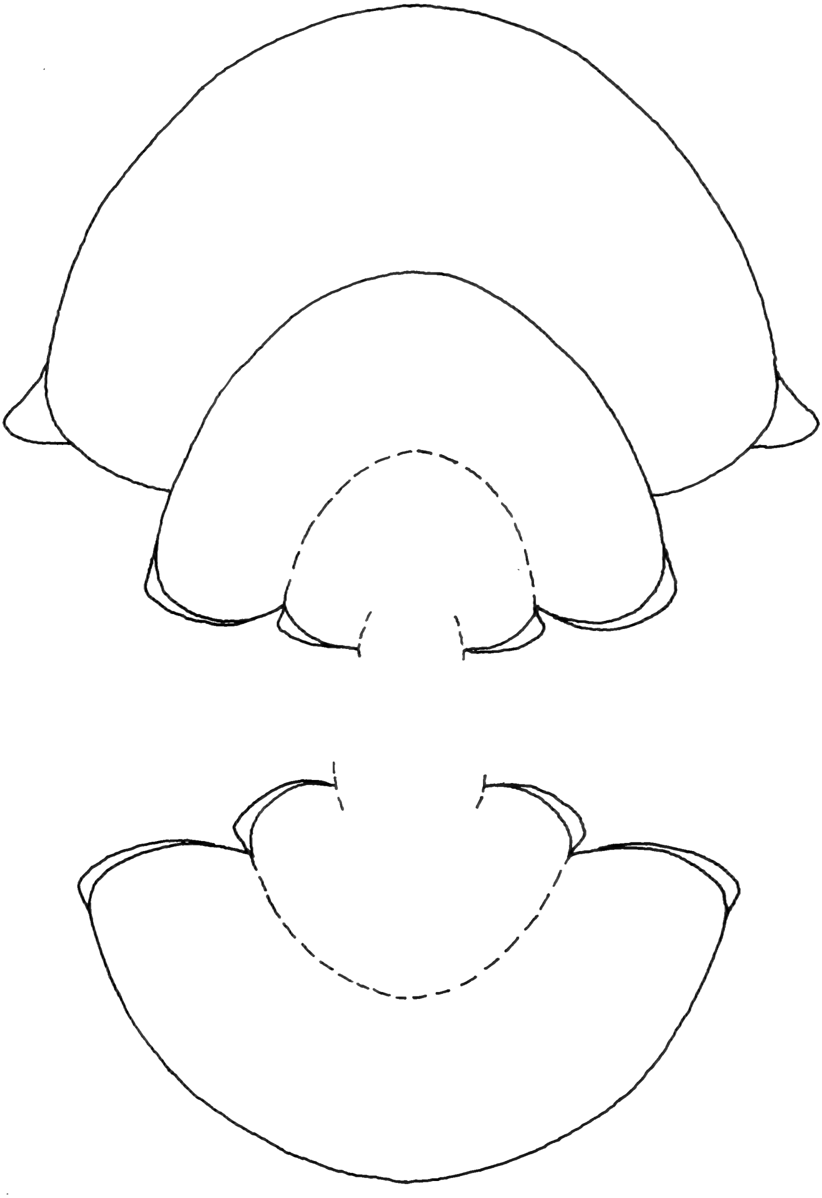

Fig. 163. *Olcostephanus* (*Olcostephanus*) *riccardii* sp. nov. (♀). Whorl section of the holotype, SAM–PCU1577. × 1.

Olcostephanus perinflatus (Matheron) is close to the inner whorls of *O. riccardii* but has radial secondaries, and retains bullate tubercles on to the body chamber.

Occurrence

This species is known only from the Sundays River Formation.

Olcostephanus (*Olcostephanus*) sp.

Fig. 158C–D

Material

A single specimen, SAM–PCU1531, representing an immature macroconch.

Description

A moderately large, strongly inflated cadicone, involute up to the umbilical bullae at all stages on the outer whorl which includes the body chamber. The umbilicus is very narrow and crater-like, with steep convex walls and subangular shoulders. Rursiradiate primaries begin at, or close to, the umbilical seam and terminate in 19 small bullae on the umbilical shoulder of the outer whorl. Each bulla gives rise to bundles of 3–4 fine secondaries, often with an intercalated rib between bundles. On the adapical portion of the outer whorl, however, the nature of the secondary ribbing changes significantly. The secondaries become noticeably finer and distinctly flexuous. From the bullae the secondaries are directed radially for a short distance, before curving forwards to become slightly prorsiradiate and finally recurving so as to cross the venter transversely. There are 17 ribs per 4 bullae on the adoral portion of the outer whorl, with 10 secondaries within a 30 mm distance along the venter. Two indistinct parabolae, due to the fact that the outer whorl is preserved as an internal mould, are present on the body chamber. The whorl section is strongly depressed with a broad, rounded venter.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–K1531	93	41	67	1,63	33	19 (20)

Discussion

This example differs from *O. baini* macroconchs at a similar diameter by its finer, more flexuous secondary ribbing.

Olcostephanus (*Olcostephanus*) *astieriformis* (Böse, 1923) (♀)

Figs 164–169

Astieria astieriformis Böse, 1923: 72, pl. 1 (figs 1–4). Riedel, 1938: 13.
Olcostephanus astieriformis (Böse) Imlay, 1938: 553.

Fig. 164. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral view of a slightly crushed specimen, BM–C47129. × 0,44.

Fig. 165. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral view of BM–C47132. × 0,44.

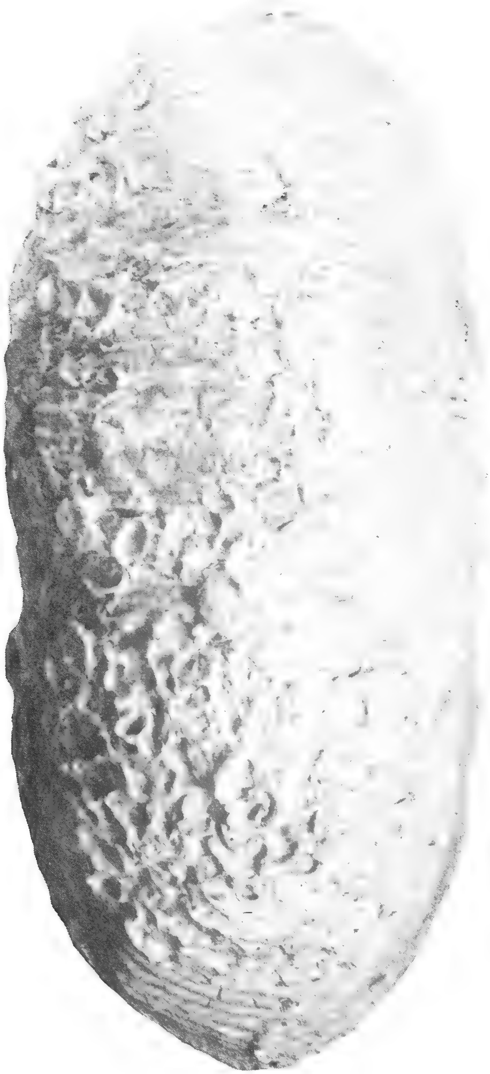

Fig. 166. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Ventral view of BM–C47132. × 0,44.

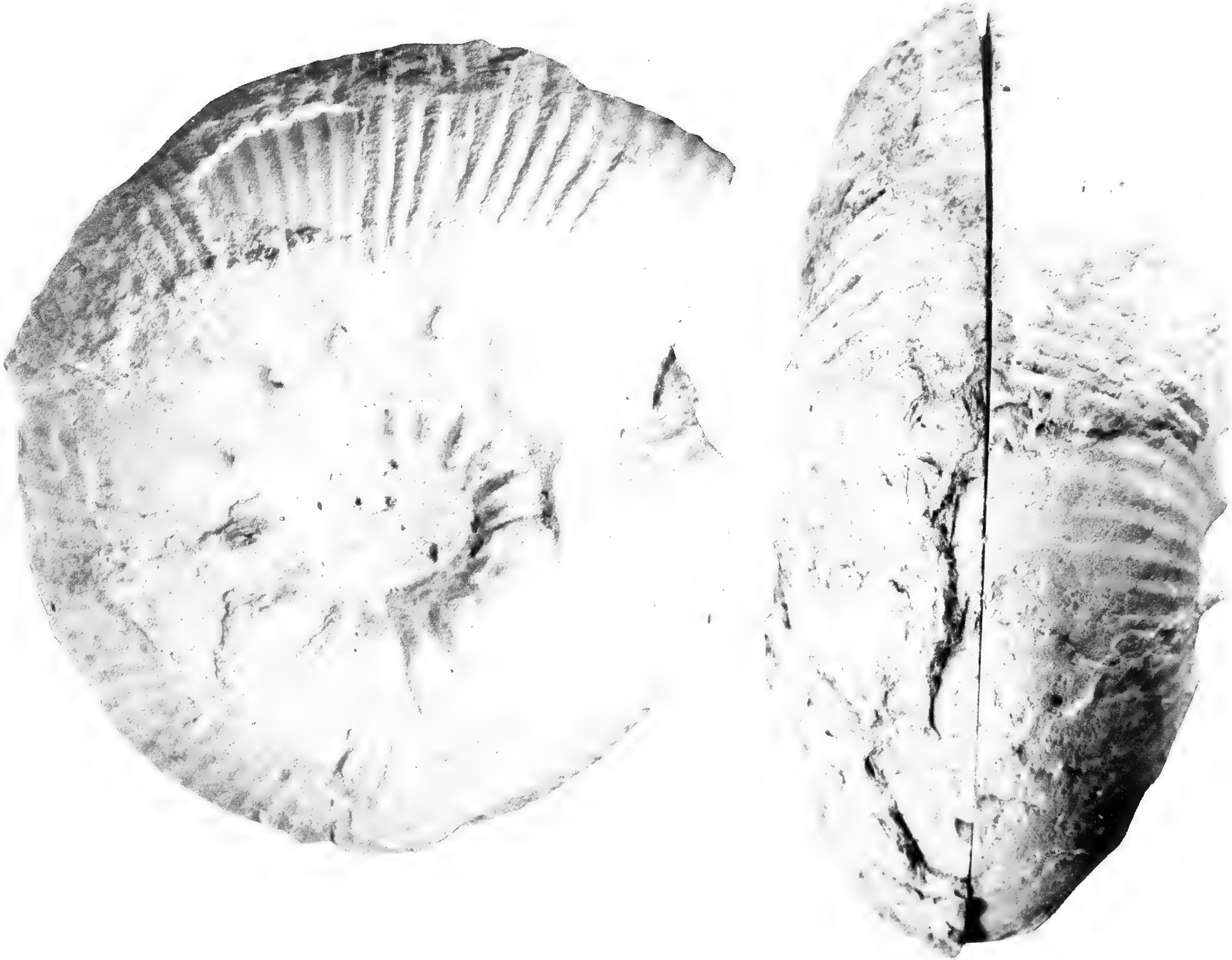

Fig. 167. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). Lateral and ventral views of a specimen in the South African Museum. × 0,58.

Material

Nine crushed and fragmentary specimens, all macroconchs (BM–C47132, BM–C47129, BM–C47125, SAM–PCU1555, SAM–PCU1541, SAM–PCU1554 SAM–PCU1558, SAM–PCU1553, SAM–PCU1557).

Holotype

By monotypy, the original of *Astieria astieriformis* Böse (Fig. 168), from Durango-Zacatecas, northern Mexico.

Description

A rather variable collection of compressed macroconchs belong here, as well as showing affinities to numerous other nominal species (Figs 169–170).

They are all compressed and show little or no egression of the umbilical seam of the body chamber. The primary ribs are rursiradiate, terminating in 16–25 bullae on the umbilical shoulder from which arise commonly 3–4 prorsiradiate secondaries, usually with intercalatories between bundles. The secondaries very occasionally bifurcate. Parabolae are lacking on the outer whorls, at least, while the inner whorls are currently unknown.

The best preserved example from the Sundays River Formation assignable to this species is BM–C47132. It is an extremely large macroconch (diameter 275 mm) which shows only slight egression of the umbilical seam of the final whorl. The shell is rather compressed, with a narrow deep umbilicus and vertical umbilical walls. The latter are ornamented with 18 rursiradiate primaries terminating in prominent bullae from which bundles of 4–6, fewer at earlier growth stages, flexuous secondaries arise. There is invariably 1–2 intercalatories between bundles. On the adoral portion of the body chamber there are 37 secondaries per 5 bullae, whereas on the adapical portion there are only 23. Parabolae appear to be lacking.

A second example, SAM–PCU1555, is a moderately large (190 mm diameter), compressed cadicone which shows virtually no egression of the umbilical seam on the final whorl. Primary ribs begin at the umbilical seam and pass backwards (rursiradiate) to 17 bullae on the umbilical shoulder, from which 3–5 slightly flexuous, prorsiradiate secondaries arise. There is commonly an intercalated rib between bundles. On the adoral portion of the final whorl there are 18 secondaries per 3 bullae, with a rib spacing of 6 mm. The whorl section is about as wide as high.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C47132	275	120	125	1,04	94	74 (27)
,,	220	100	?	?	70	54 (25)
SAM–PCU1555	190	87	?	?	70	50 (26)

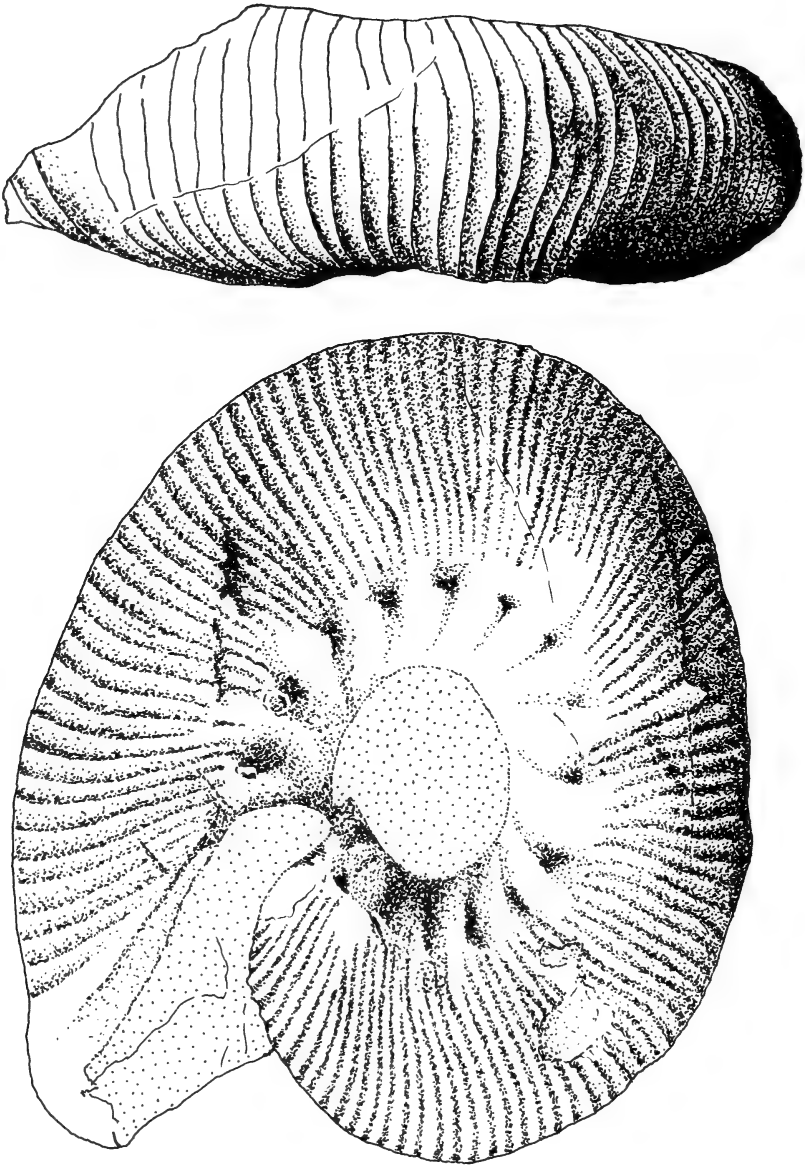

Fig. 168. *Olcostephanus* (*Olcostephanus*) *astieriformis* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

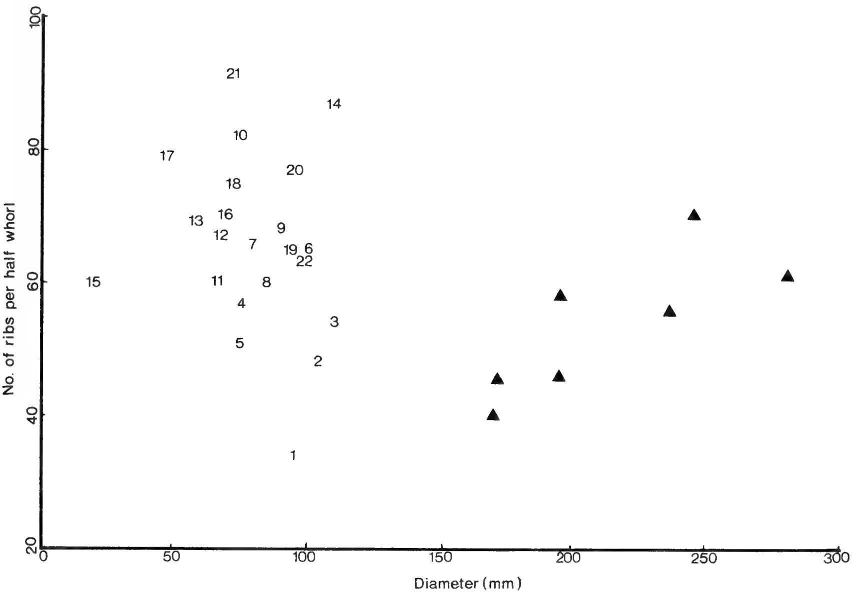

Fig. 169. Plot of rib density against diameter for 'species' of the *O. astierianus* plexus. Triangles represent individuals from the Sundays River Formation. 1 = *O. raricostatus* (Böse) (after Böse 1923, pl. 4 (fig. 1)), 2 = *O. quadriradiatus* Imlay (after Imlay 1938, pl. 5 (fig. 2)), 3 = *O. astieriformis* (Böse) (after Böse 1923, pl. 1 (fig. 2)), 4 = *O. scissus* (Baumberger) (after Baumberger 1907, fig. 107), 5 = *O. discoideus* Imlay (after Imlay 1938, pl. 2 (fig. 5)), 6 = *O. symonensis* (Böse) (after Böse 1923, pl. 2 (fig. 7)), 7 = *O. catulloi* (Rodighiero) (after Rodighiero 1919, pl. 9 (fig. 9)), 8 = *O. rabei* (Besairie) (after Besairie 1936, pl. 12 (fig. 8)), 9 = *O. astierianus* (d'Orbigny) (after Baumberger 1910, pl. 32 (fig. 1)), 10 = *O. sayni* (Kilian) (after Baumberger 1910, pl. 32 (figs 2–3)), 11 = *O. astierianus* (d'Orbigny) (*in* Baumberger 1910, pl. 29 (fig. 3)), 12 = *O. sayni* (SAM–9270), 13 = *O. scissus* (Baumberger) (*in* Baumberger 1907, pl. 23 (fig. 2)), 15 = *O. elongatus* (Tzankov) (after Tzankov 1943, pl. 6 (figs 3–4)), 16 = *O. scissus* (Baumberger) (*in* Matheron 1878, pl. B–20 (fig. 8)), 17 = *O. catulloi* (Rodighiero) (*in* Tzankov 1943, pl. 4 (figs 1–2)), 18 = *O. boesei* (Riedel) (after Riedel 1938, pl. 3 (fig. 1)), 19 = *O. astierianus* (d'Orbigny) (*in* Riedel 1938, pl. 3 (fig. 3)) 20 = *O. schafarziki* (Somogyi) (after Somogyi 1916, pl. 13 (fig. 3)), 21 = *O. filosus* (Baumberger) (*in* Bayle 1878, pl. 55 (fig. 2)), 22 = *O. astierianus* (d'Orbigny) (*in* Somogyi 1916, pl. 13 (fig. 2)).

Discussion

Amongst the collections from the Sundays River Formation are a rather large number of compressed macroconchs, unfortunately generally rather crushed and fragmentary. These forms differ from *O. uitenhagensis* in lacking the marked egression of the umbilical seam of the body chamber, and in that the tubercles remain bullate to the peristome.

These specimens are undoubtedly close to the type of the genus, *O. astierianus* (d'Orbigny) (Fig. 171). The latter species is rather compressed, with a moderately wide, deep, umbilicus and sloping umbilical walls ornamented with 16 radial primaries on the outer whorl. These terminate in prominent, somewhat

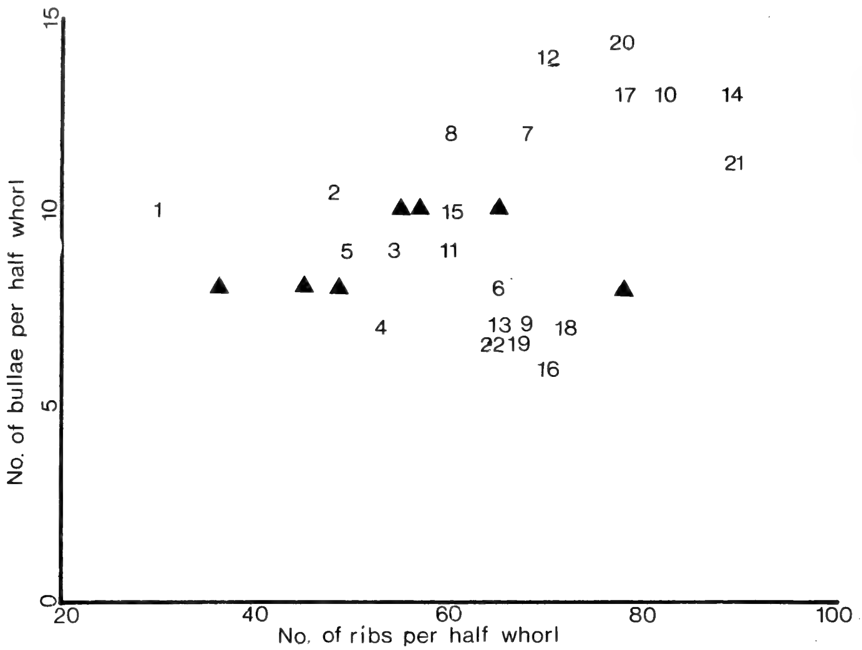

Fig. 170. Plot of rib density against umbilical bullae for 'species' of the *O. astierianus* plexus. Numbers and symbols as for Figure 85.

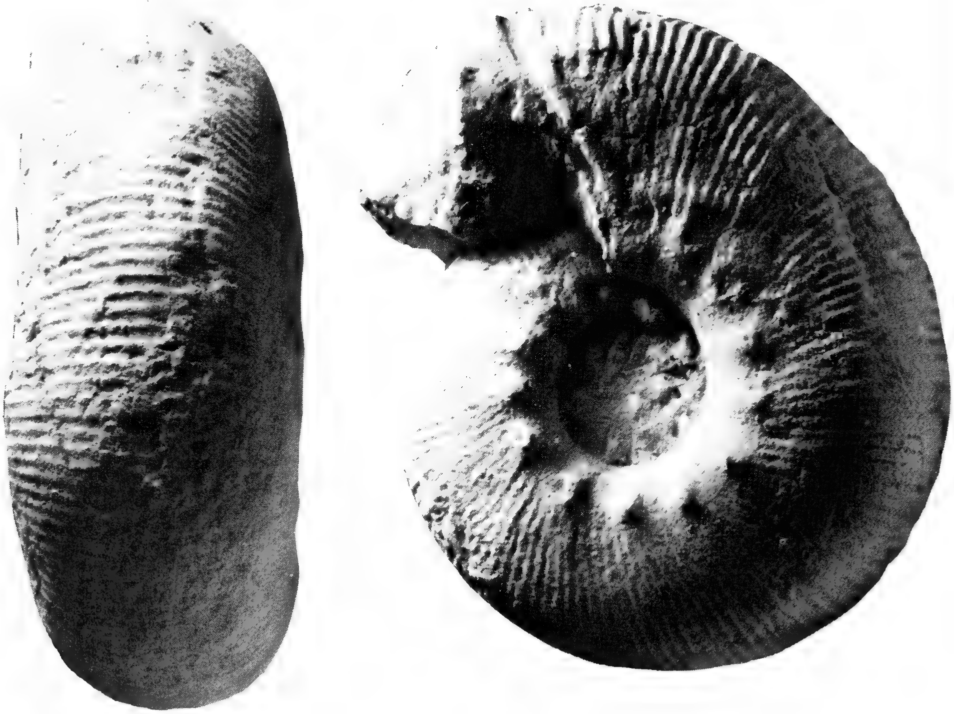

Fig. 171. *Olcostephanus astierianus* (d'Orbigny) (♀). Ventral and lateral views of the lectotype from the Lower Hauterivian of Castellane, France. × 1.

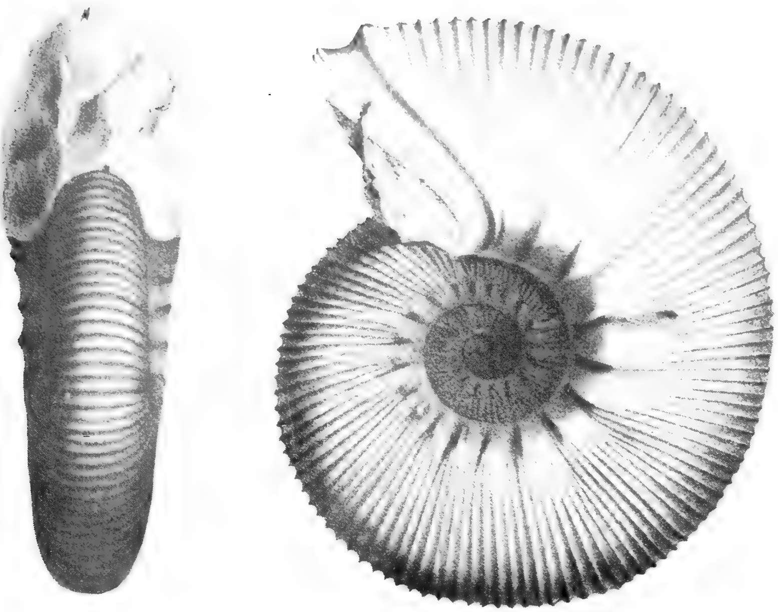

Fig. 172. *Olcostephanus (Olcostephanus) astierianus* (d'Orbigny) (♀). A copy of D'Orbigny's (1842*a*) protograph. × 1.

rounded umbilical tubercles on the outer whorl that give rise to bundles of 5–6, fine, prorsiradiate secondary ribs, commonly with 2–4 intercalatories between bundles. Contrary to D'Orbigny's (1840) (Fig. 172) protograph, the umbilical seam does not egress on the outer whorl, but remains just above the umbilical tubercles. This species seems to be based upon a macroconch, with a (?) simple peristome preserved at only 89 mm. According to Baumberger (1907: 28), the inner whorls bear parabolae, in which case they are to be expected on the outer whorls of the microconch. *Olcostephanus astierianus* differs from the present species in having fewer, rounded tubercles on the outer whorl and, perhaps, in possessing parabolae on the early whorls. Its small adult size, like much of the west European material, is probably environmentally controlled and is not herein considered of specific importance.

Olcostephanus astierianus globulosus (Kilian) (*in* Roch 1930: 313) was erected for the example of '*Astieria sayni*' figured by Baumberger (1908: 1, pl. 25 (fig. 3a–b)). Since, however, the specimen in question is listed as '*Astieria guebhardi*', presumably it is this individual to which Kilian referred. In the writer's opinion, it is too inflated and with too many bullate umbilical tubercles to be conspecific with *O. astierianus*. Indeed, the original identification, that is as *O. guebhardi*, is more likely to be correct.

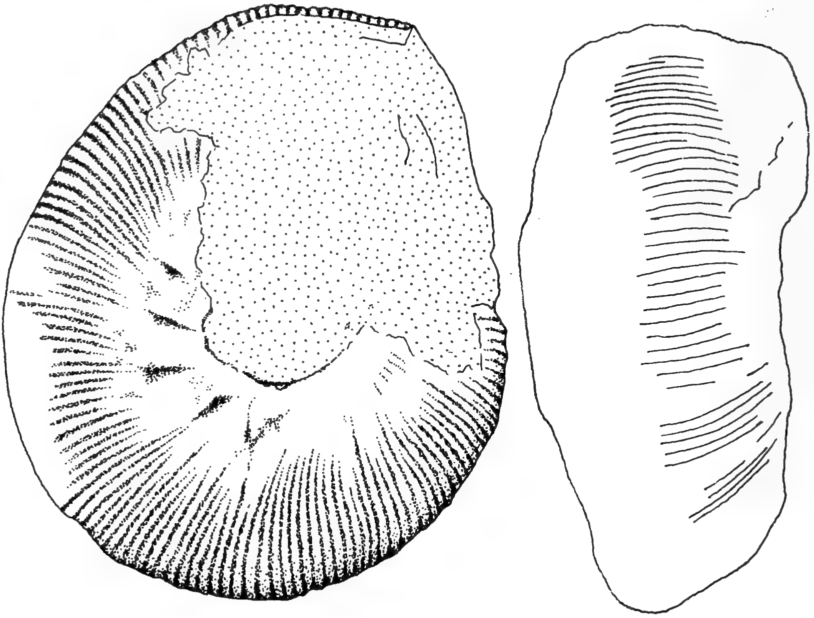

Fig. 173. *Olcostephanus* (*Olcostephanus*) *boesei* (Riedel). The holotype from the Upper Valanginian of Caqueza, Colombia (after Riedel 1938). × 1.

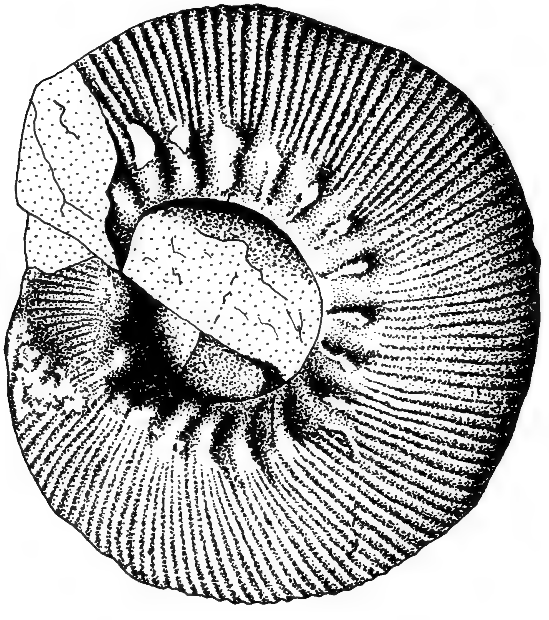

Fig. 174. *Olcostephanus* (*Olcostephanus*) *catulloi* (Rodighiero). The holotype from Venice (after Rodighiero 1919). × 1.

Olcostephanus boesei (Riedel) (Fig. 173) is a somewhat compressed species with a moderately wide umbilicus and steep umbilical walls. The latter are ornamented with 7–8 relatively pronounced primary ribs per half whorl, each terminating in a bulla on the umbilical shoulder and giving rise to 4–5 fine, prorsiradiate secondaries. There is commonly 3–4 intercalated ribs between bundles. Parabolae seem to be lacking. This is a finely ribbed species of the *astierianus* plexus which was compared with *O. sayni* (Kilian), from which it was distinguished by its fewer umbilical bullae. It is, therefore, doubtfully separable from *O. scissus* (Baumberger).

Olcostephanus catulloi (Rodighiero) (Fig. 174) is a moderately involute species with a fairly narrow umbilicus. About 25 primary ribs on the outer whorl terminate in prominent bullae on the umbilical shoulder, from which arise 3–5 prorsiradiate secondaries with 1–3 intercalated ribs between bundles. There are 16 secondaries per 3 bullae, with about 125 ribs across the venter of the outer whorl. This species differs from *O. astieriformis* in being more finely and densely ribbed, with more numerous umbilical bullae. It is, therefore, close to *O. sayni.*

Olcostephanus destefanii (Rodighiero, 1919) is a finely ribbed species, allied to *O. sayni*, which is yet to be figured. Between 14 and 15 primary ribs terminate in tubercles on the umbilical shoulder and give rise to bundles of fine, slightly flexuous secondaries, with intercalated ribs between bundles. It differs from *O. astieriformis* in its finer, denser, flexuous secondary ribbing, in which respect it approaches *O. sayni gerecseiensis* Somogyi.

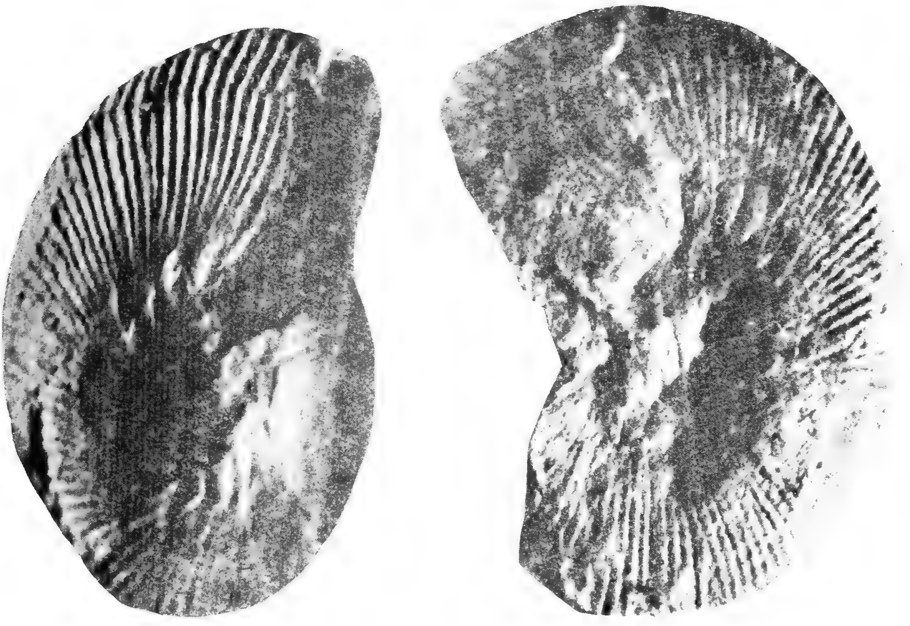

Fig. 175. *Olcostephanus* (*Olcostephanus*) *elongatus* (Tzankov). The holotype from the Upper Valanginian of Placovo, Bulgaria (after Tzankov 1943). × 4.

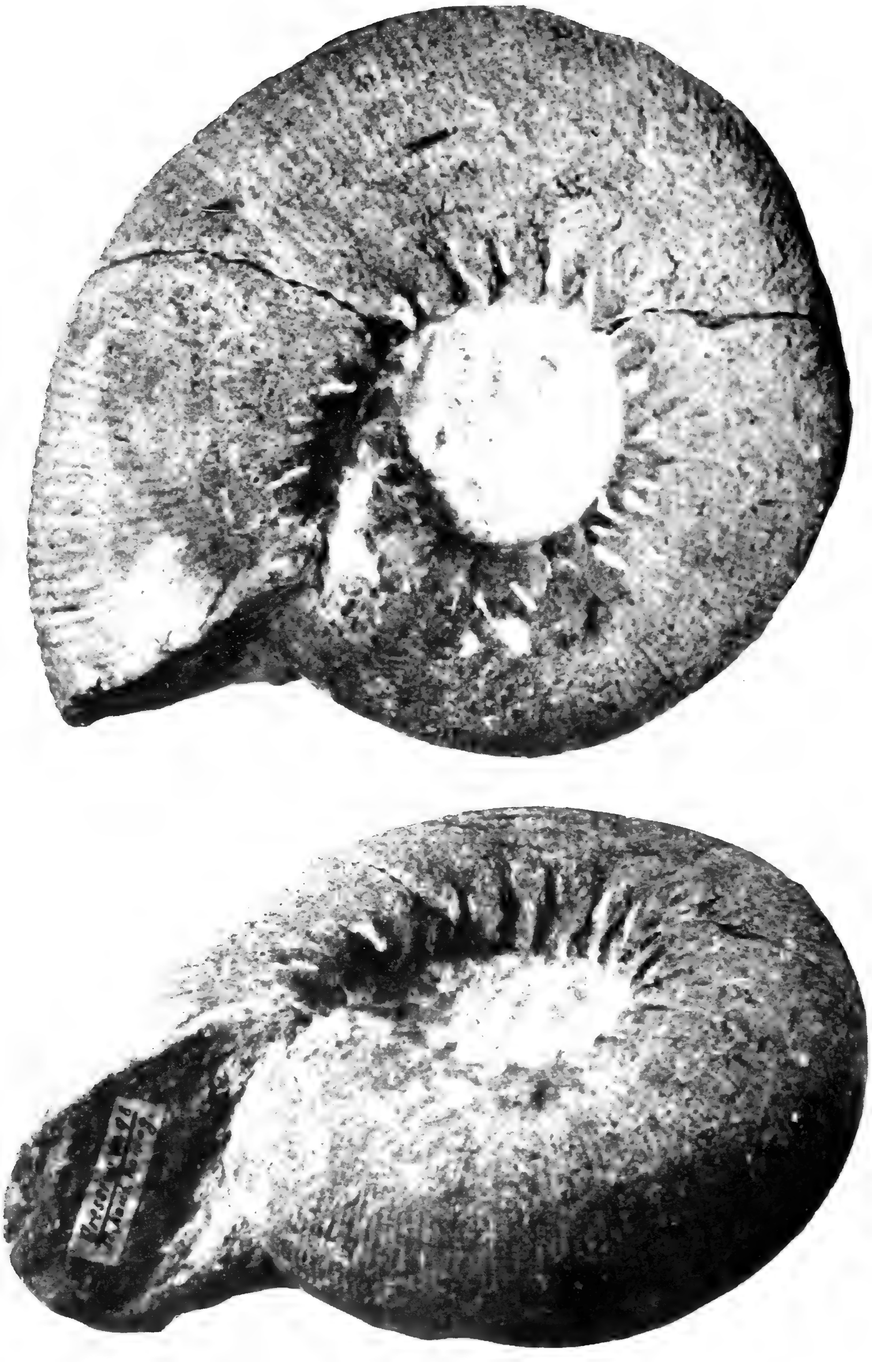

Fig. 176. *Olcostephanus* (*Olcostephanus*) *filosus* (Baumberger) (♀). The lectotype, designated herein, from the Swiss Jura (after Baumberger 1907). × 1.

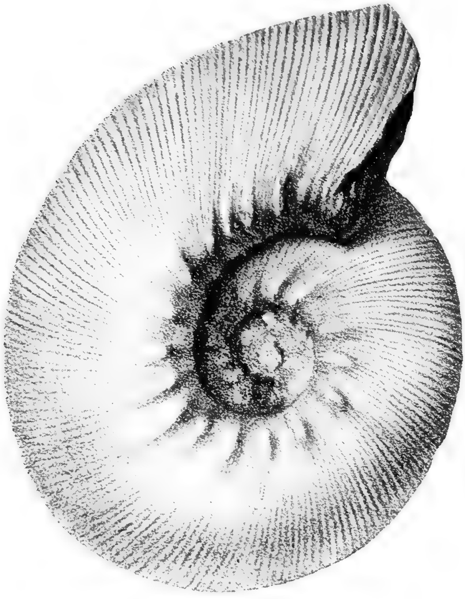

Fig. 177. *Olcostephanus* (*Olcostephanus*) *filosus* (Baumberger) (after Bayle 1878), × 1.

Olcostephanus elongatus (Tzankov) (Fig. 175) is based upon a strongly compressed, crushed juvenile only 20 mm in diameter. There are about 20 primaries on the outer whorl which terminate in bullae on the umbilical shoulder, from which arise 4–5 prorsiradiate secondaries, some of which occasionally bifurcate. Parabolae are lacking and the outer whorl shows a rapid increase in height (? due to crushing). This species is close to *O. astieriformis* but seems to be more densely ribbed and is thus doubtfully separable from *O. symonensis* (Böse).

Olcostephanus filosus (Baumberger) (Fig. 176) is a rather compressed macroconch species with a moderately wide umbilicus and steep umbilical walls. About 26 slightly rursiradiate primary ribs terminate in bullae on the umbilical shoulder and give rise to bundles of 9–10, very fine, prorsiradiate secondaries between which are fine intercalatories. Parabolae apparently lacking. This species is readily distinguishable from *O. astieriformis* by its much denser, finer ribbing. Although *O. filosus* has somewhat more primary ribs than *O. sayni*, individuals such as that figured by Bayle (1878) (Fig. 177 herein) suggest that this character is somewhat variable and population studies are likely to show that *O. filosus* is a junior subjective synonym of *O. sayni*. Unfortunately the concept of *O. filosus* has become somewhat confused by the inclusion of the specimen figured by Matheron (1878) as *Ammonites mittreanus* [*sic*] d'Orbigny into Baumberger's (1907) species. Matheron's (1878) example (Fig. 178) is

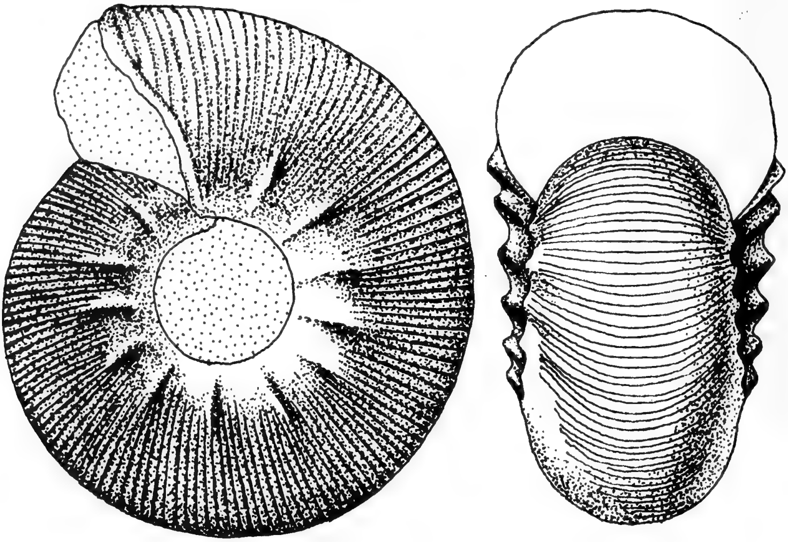

Fig. 178. *Olcostephanus* (*Olcostephanus*) *scissus* (Baumberger). Matheron's oft-quoted figure of *O. mittreanus* d'Orbigny, based on a specimen from the south of France, and assigned by most authors to *O. filosus* (Baumberger) (after Matheron 1878). × 1.

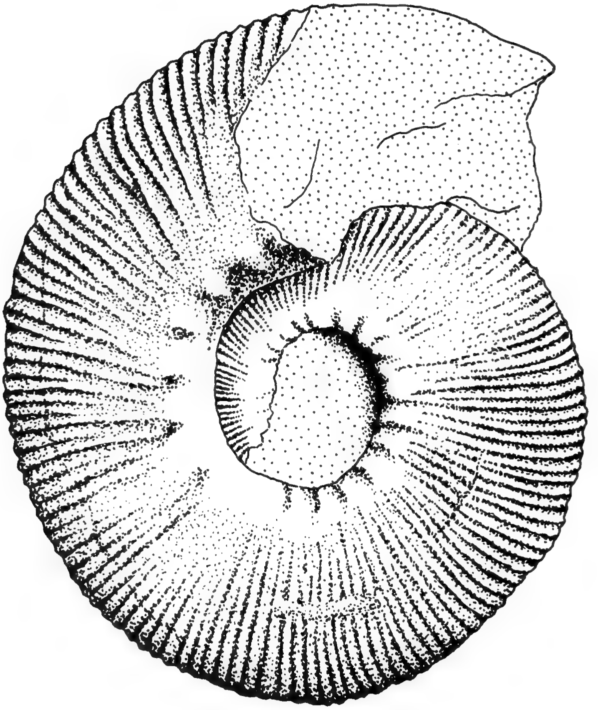

Fig. 179. *Olcostephanus* (*Olcostephanus*) *paronae* (Rodighiero). The holotype, by monotypy, from Venice (after Rodighiero 1919). × 1.

easily distinguished, from both *O. sayni* and *O. filosus*, in the presence of only 14 umbilical bullae on the outer whorl. This individual should, therefore, be assigned to *O. scissus* (Baumberger).

Olcostephanus paronae (Rodighiero) (Fig. 179) is another species which is closely allied to *O. sayni*. It shows marked egression of the umbilical seam on the outer (?final) whorl so that about 40 per cent of the preceding whorl is visible in the umbilicus. The umbilical wall is steep on the inner whorls. The final whorl is ornamented with about 20 umbilical tubercles from which arise bundles of 3–4 prorsiradiate secondary ribs which frequently bifurcate. On the adoral half of the outer whorl (?the body chamber), nearly every long rib bifurcates and has an adjacent intercalated rib high up on the flank. The finer, denser secondaries, and their frequent bifurcation, distinguish this species from *O. astieriformis*.

Olcostephanus potosinus Castillo & Aguilera (Fig. 180) was based upon two individuals, without type designation. Consequently, the original of the specimen here figured is selected as lectotype. This specimen is a strongly compressed, crushed, individual which shows frequent umbilical bullae from which arise 3–6 prorsiradiate secondaries so that there are about 120–130 secondary ribs across the venter of the lectotype. This species is close to *O. astieriformis* but seems to be more finely ribbed and, as such, probably has priority over *O. symonensis* (Böse) from the same region.

Olcostephanus quadriradiatus Imlay (Fig. 181) has an ovate, compressed whorl section with a moderately narrow umbilicus and vertical umbilical walls. Primary ribs terminate in 23 prominent umbilical bullae on the outer whorl from which arise bundles of 3–5 slightly prorsiradiate, almost radial secondaries with 1–2 intercalated ribs between bundles. This is a macroconch species in which parabolae are apparently lacking. This species differs from *O. astieriformis* only in the almost radial direction of its secondary ribs. Population studies may show that this character is not of specific importance.

Olcostephanus raricostatus (Böse) (Fig. 182) is a compressed species with a narrow umbilicus and arched venter. Rursiradiate primaries terminate in 18–23 bullae on the umbilical shoulder, from which arise 3–4 slightly flexuous, prorsiradiate secondary ribs which frequently bifurcate. Parabolae are apparently lacking. The distant ribbing of this species is distinctive and it seems likely that *O. huizachensis* (Cantu Chapa) is based upon either the microconch or the inner whorls of the macroconch of *O. raricostatus*.

Olcostephanus sayni (Kilian) (Fig. 183) is a compressed species with a moderately narrow umbilicus and a subtrigonal whorl section. The umbilical seam of the lectotype egresses markedly on the outer whorl, suggesting this is also the final whorl. The steep umbilical walls are ornamented with about 22 radial primaries which terminate in bullae on the umbilical shoulder and give rise to bundles of 4–5, fine, prorsiradiate secondaries which frequently bifurcate. There are 1–2 intercalated ribs between bundles. On the adoral portion of the outer whorl of the lectotype there are 23 ribs across the venter per 4 umbilical

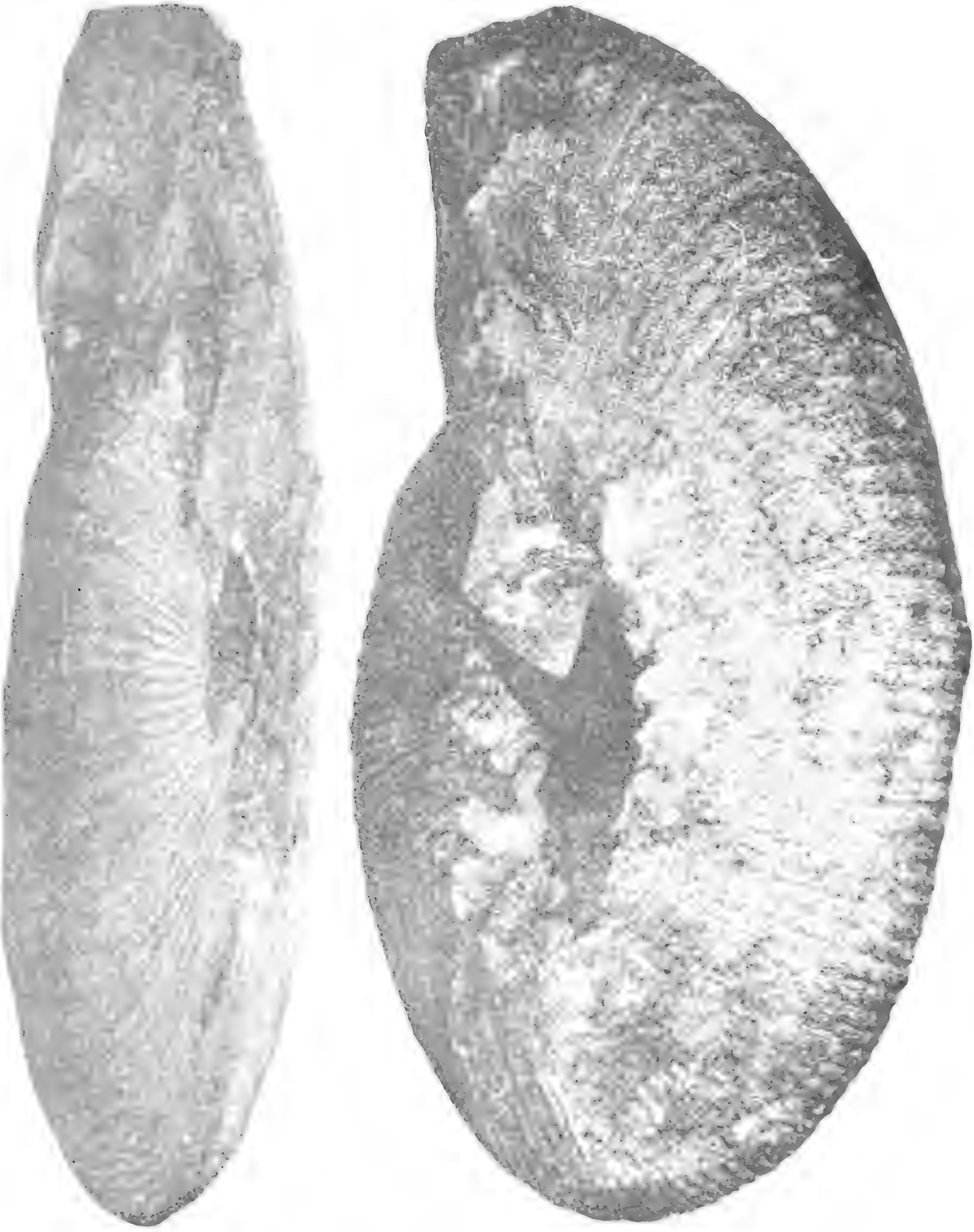

Fig. 180. *Olcostephanus* (*Olcostephanus*) *potosinus* Castillo & Aguilera (♀). The lectotyde, designated herein, from northern Mexico (after Castillo & Aquilera 1895). × 1.

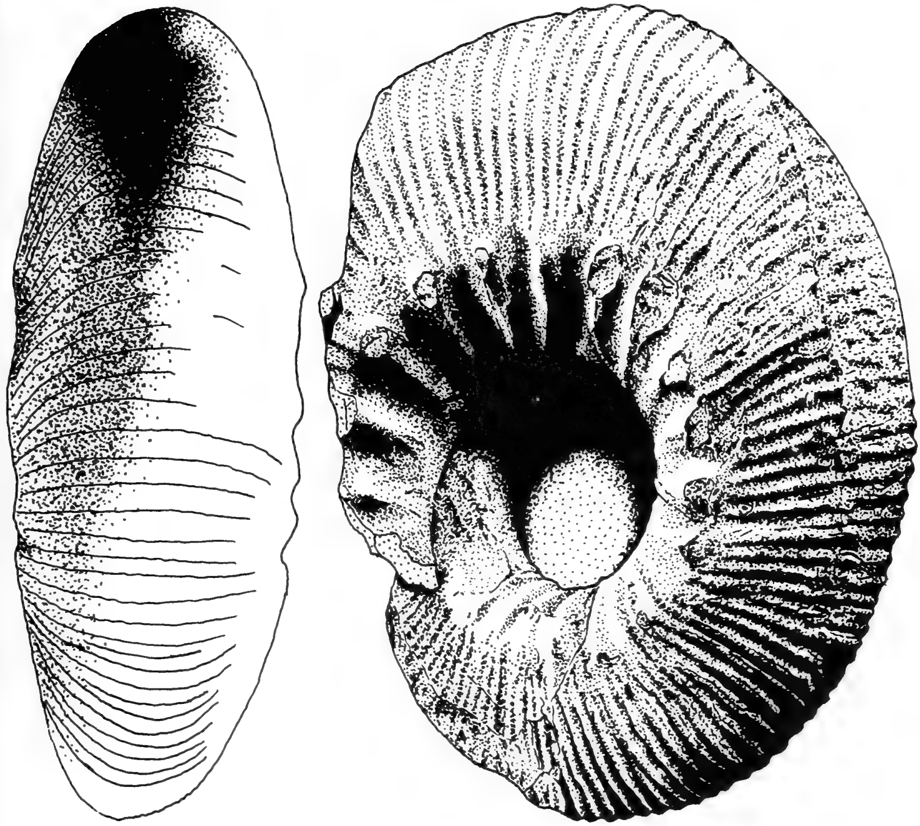

Fig. 181. *Olcostephanus* (*Olcostephanus*) *quadriradiatus* Imlay (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

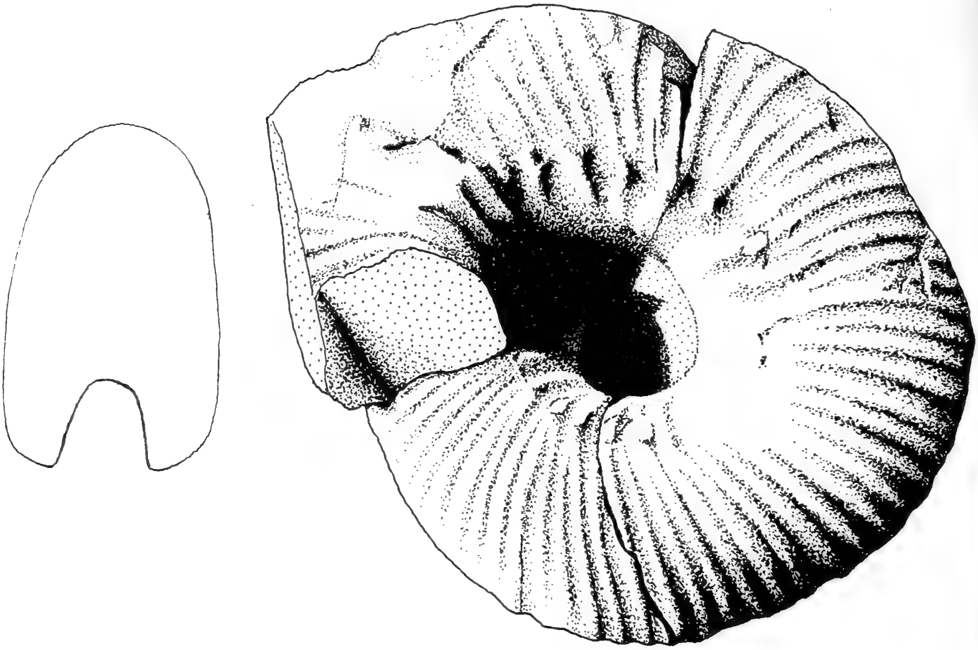

Fig. 182. *Olcostephanus* (*Olcostephanus*) *raricostatus* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

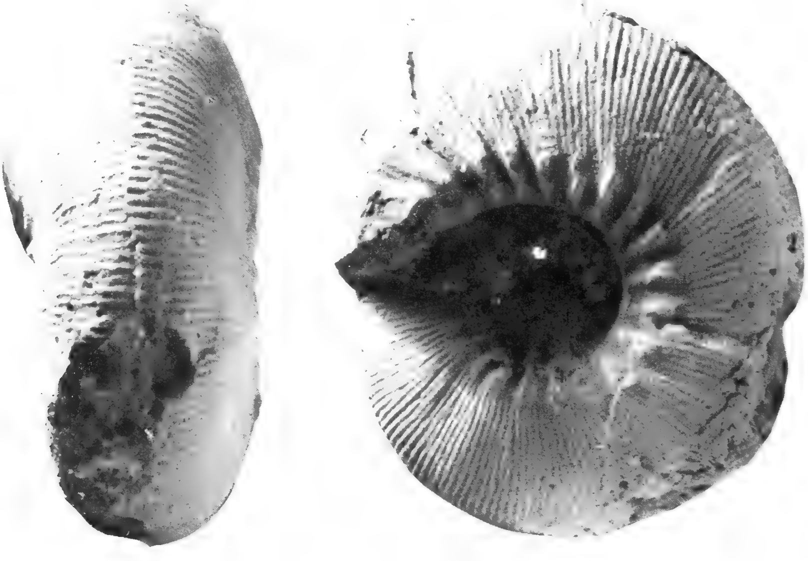

Fig. 183. *Olcostephanus* (*Olcostephanus*) *sayni* (Kilian). The lectotype from the Lower Hauterivian of Castellane, France × 1.

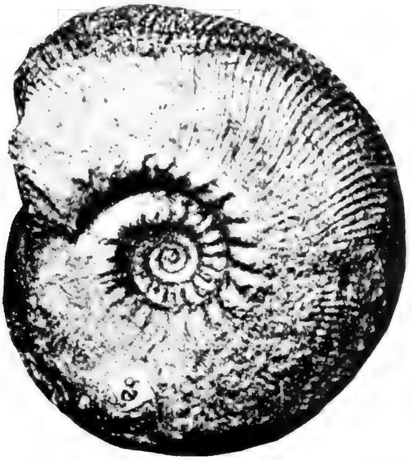

Fig. 184. *Olcostephanus (Olcostephanus) sayni gerecseiensis* (Somogyi). The holotype (after Somogyi 1916). × 1.

bullae. Parabolae are lacking. This species may be distinguished from the present material by its more numerous umbilical bullae and finer, denser secondary ribs. Somogyi (1916) distinguished *O. sayni gerecseiensis* (Fig. 184) on the basis of its flexuous secondary ribbing.

Olcostephanus scissus (Baumberger) (Fig. 185) is a species which has long been confused with *O. filosus* and *O. sayni*, from which it is readily distinguishable by its fewer umbilical bullae. It is a compressed form with a narrow umbilicus and sloping umbilical walls ornamented with 14 radial primaries. These terminate in bullae giving rise to generally 4, fine, prorsiradiate secondaries which frequently bifurcate high up on the flank. There are frequent intercalated ribs between bundles and parabolae are apparently lacking. This species is very close to *O. astierianus* from which it seems to differ only in possessing bullate umbilical tubercles and in the frequent bifurcation of the secondary ribs in *O. scissus*. *O. astieriformis* has more numerous bullae and does not show bifurcation of the secondary ribs.

Olcostephanus subfilosus Spath (Fig. 186) is based upon a nucleus which bears parabolae and displays about 16 umbilical bullae from which arise numerous fine, prorsiradiate secondaries, with intercalated ribs between bundles. A topotype example (Fig. 187) in the Oxford University Museum, OUM–K1207, shows a rather narrow, deep, crater-like umbilicus with steep, convex walls and an evenly rounded umbilical shoulder. Primary ribs begin at, or close to, the umbilical seam and curve backwards (rursiradiate) to about 20 bullae on the umbilical shoulder of the outer whorl. Each bulla gives rise to 4–6 prorsiradiate secondaries with 1–2 intercalated ribs between bundles. There are about 125 ribs on the outer whorl. The flanks are convex, converging towards the narrowly arched venter and giving the whorl section a subtrigonal outline.

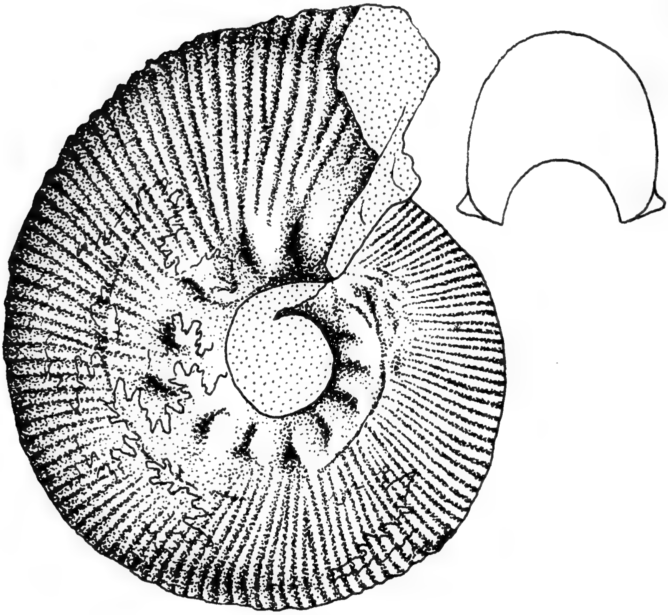

Fig. 185. *Olcostephanus* (*Olcostephanus*) *scissus* (*Baumberger*). The holotype, by lectotype designation herein, from the Swiss Jura (after Baumberger 1907). × 1.

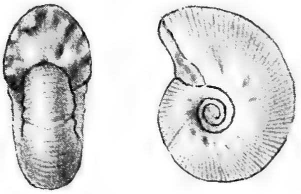

Fig. 186. *Olcostephanus* (*Olcostephanus*) *subfilosus* Spath. The holotype from Speeton, Yorkshire (after Pavlow & Lamplugh 1892). × 0,5.

There are two distinct, oblique parabolae on the outer whorl. This species seems to be based upon a juvenile of *O. sayni*, although the presence of parabolae have still to be proven on the inner whorls of the latter species.

Olcostephanus symonensis (Böse) (Fig. 188) was distinguished from *O. astieriformis* by its finer, more numerous secondaries with 60 in a space where *O. astieriformis* shows only 45. It is, therefore, close to *O. potosinus*, as well as resembling *O. sayni* in the frequent bifurcation of secondary ribs. With revision, it seems likely that Böse's (1923) species will fall into synonymy.

There is in the Natural History Museum in Paris a cast of the original of Paquier's (1900) *Holcostephanus variegatus* (Fig. 189). It shows the original to

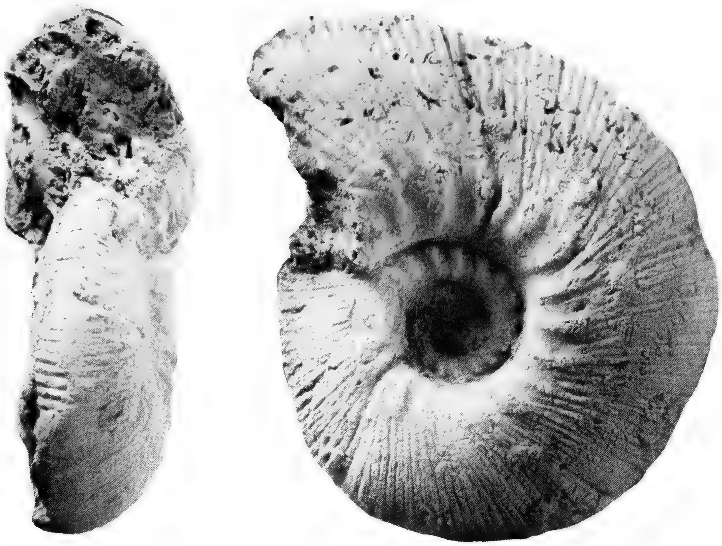

Fig. 187. *Olcostephanus* (*Olcostephanus*) *subfilosus* Spath. A topotype example in the Oxford University Museum. Note the subtrigonal whorl section, numerous bullae and parabolae. This species may be based on the inner whorls of *O. sayni* (Kilian). × 2.

be poorly preserved and abraded, so much so that it is difficult to discern many of the umbilical bullae and ribs on the outer whorl and these could not be counted. What can be seen of the ribbing shows rather fine secondaries, about as wide as the interspaces, which frequently bifurcate on the flanks. There is a prominent parabola near the adoral end of the outer whorl, which displays a subtrigonal whorl section. This species is close to *O. sayni* but with distinctly coarser ribbing. It can be distinguished from *O. scissus* and *O. astieriformis* by the presence of parabolae.

Occurrence

This species is currently known only from northern Mexico and South Africa.

Olcostephanus (*Olcostephanus*) *coahuilensis* Imlay, 1938 (♀)

Figs 190A–B, 191

Olcostephanus coahuilensis Imlay, 1938: 553, pl. 1 (figs 1–3).

Material

A single macroconch, SAM–PCU1550, retaining recrystallized test.

Holotype

The original of *Olcostephanus coahuilensis* Imlay (Fig. 191) from the Taraises Formation of northern Mexico.

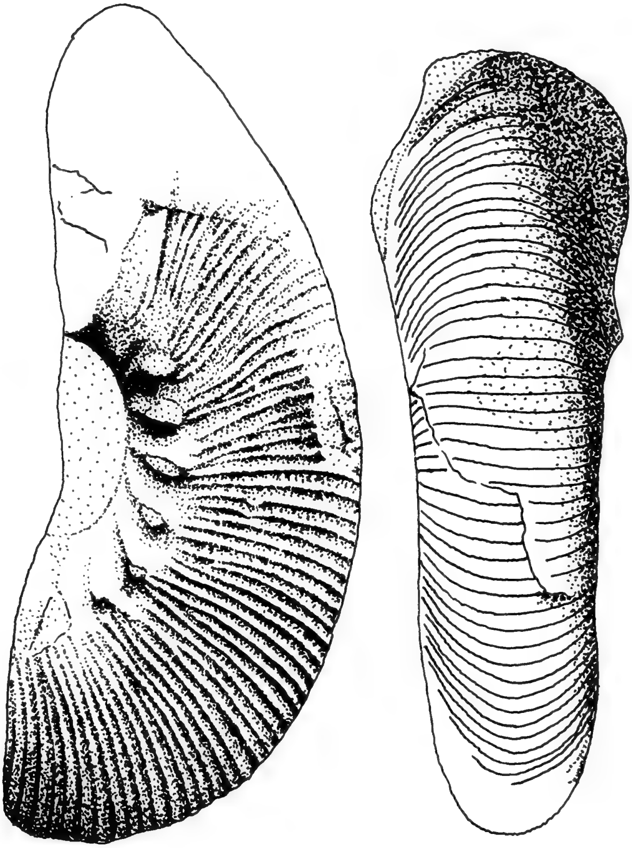

Fig. 188. *Olcostephanus* (*Olcostephanus*) *symonensis* (Böse) (♀). The lectotype, designated herein, from the Taraises Formation of northern Mexico (after Böse 1923). × 1.

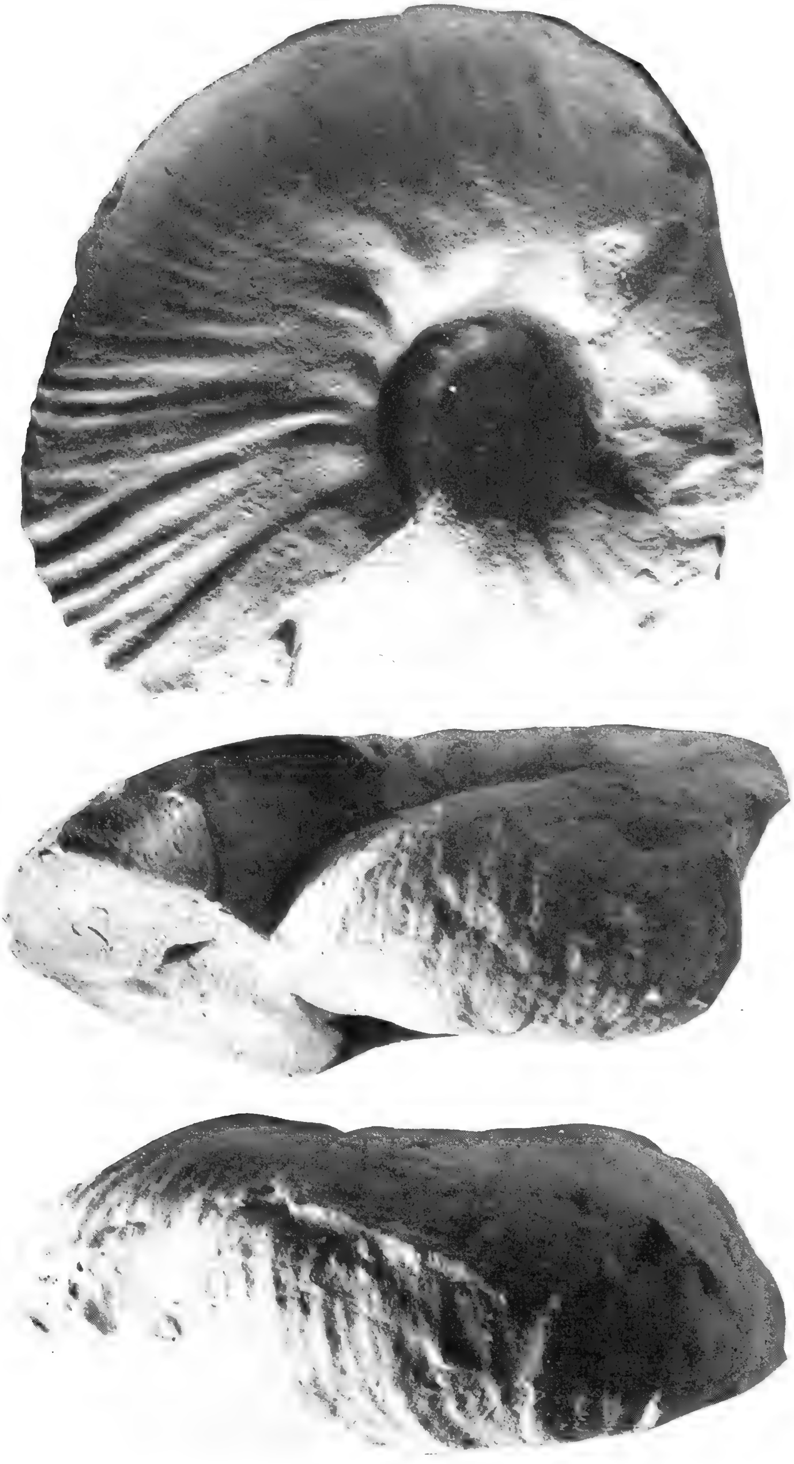

Fig. 189. *Olcostephanus* (*Olcostephanus*) *variegatus* (Paquier). A cast of the holotype in the Natural History Museum, Paris. × 1.

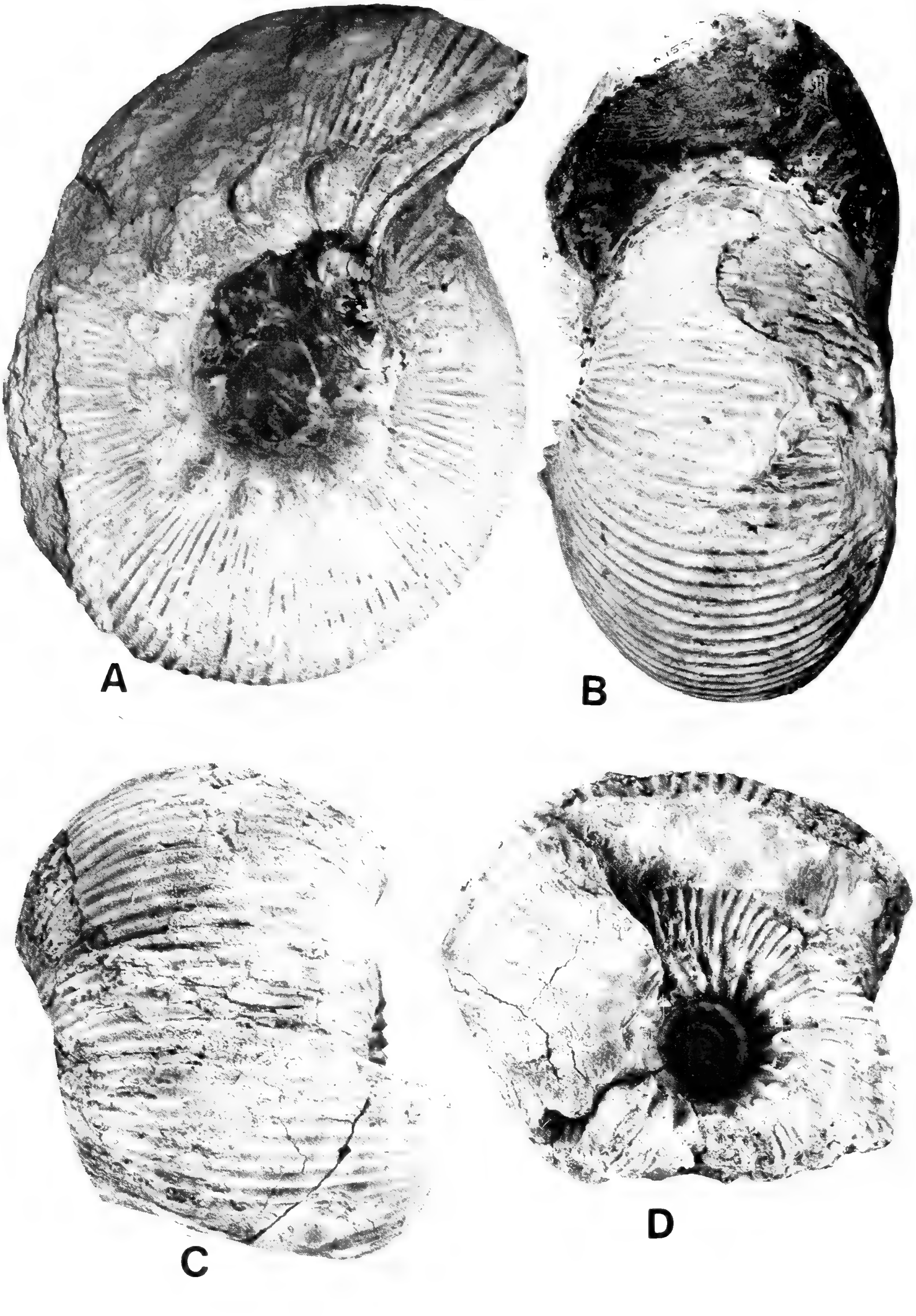

Fig. 190. A–B. *Olcostephanus* (*Olcostephanus*) *coahuilensis* Imlay (♀). Lateral and front views of SAM–PCU1550, showing moderate inflation and fine, radial secondaries. × 0,44. C–D. *Olcostephanus* (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀). Ventral and lateral views of AM–4292b. Note small umbilicus, extreme inflation, fine secondaries occasionally bifurcating, and apparent absence of parabolae. × 0,75.

Description

The shell is a large, inflated cadicone, involute up to the umbilical bullae, except on the final whorl when the umbilical seam egresses somewhat. The umbilicus is narrow with moderately steep, convex umbilical walls, the latter ornamented with 17 rursiradiate primaries which terminate in bullae on the umbilical shoulder. From these arise 4–5 radial secondaries, commonly with 1–2 intercalatories between bundles. There are 32 secondaries per 5 bullae on the outer whorl, with 11 ribs in a 50 mm distance along the venter, and about 50 ribs per half whorl. Maximum inflation is attained about half a whorl behind the peristome.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
SAM–PCU1550	195	75	90	1,20	87	52 (27)

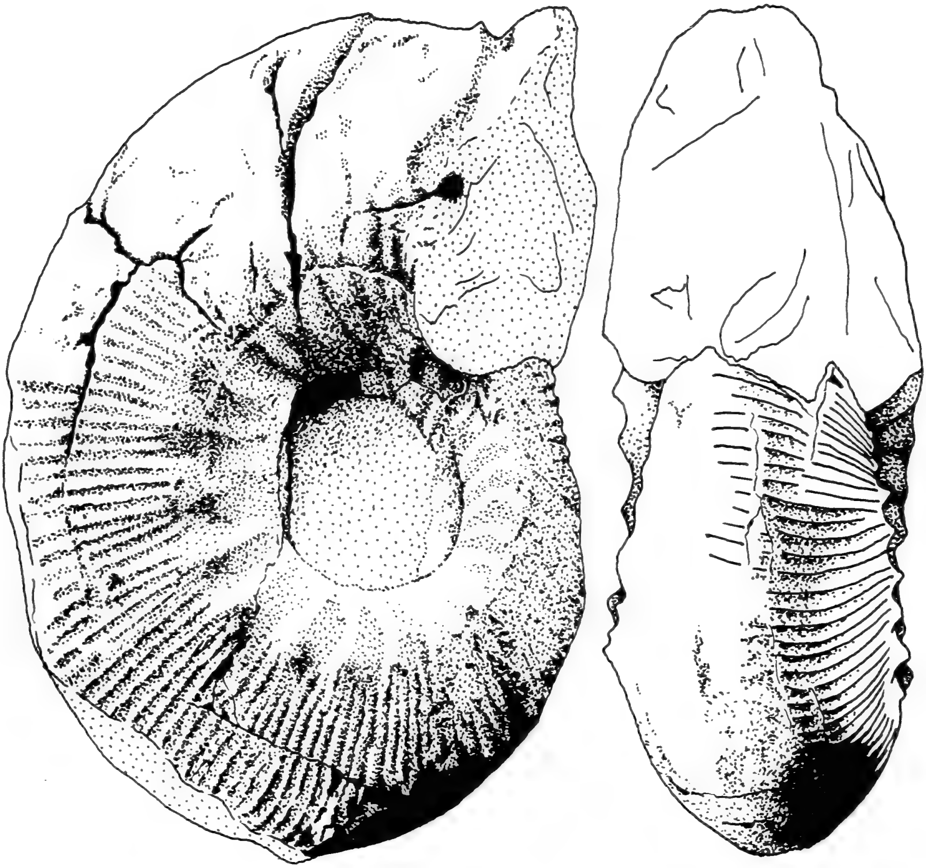

Fig. 191. *Olcostephanus* (*Olcostephanus*) *coahuilensis* (Imlay) (♀). The holotype from the Taraises Formation of northern Mexico (after Imlay 1938). × 1.

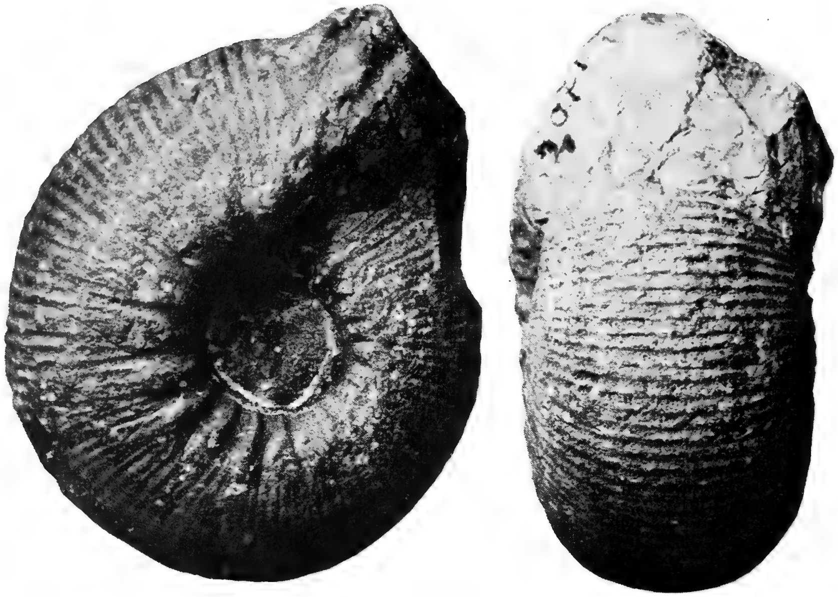

Fig. 192. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian). The holotype from Escragnolles, France (after Kilian 1902). × 1.

Discussion

The Uitenhage example differs from Imlay's type only in having slightly fewer umbilical bullae per whorl, a difference which is not considered of specific importance.

Olcostephanus guebhardi (Kilian) (Fig. 192), of which *O. sharpei* (Karakasch) (Fig. 193) is a synonym, closely resembles the South African material, but is much smaller and does not show the inflation seen in the present shell The differences may well be those between dimorphs, but until the European material is revised, the writer prefers to use Imlay's name. *Olcostephanus actinotus* (Baumberger) also resembles the present species, but has a very different, subtrigonal whorl section.

Occurrence

Olcostephanus coahuilensis is currently known only from Mexico and South Africa.

Olcostephanus (*Olcostephanus*) cf. *perinflatus* (Matheron, 1878) (♀)

Figs 151E–F, 190C–D, 194–195

Compare

Ammonites perinflatus Matheron, 1878: pl. 20B (fig. 8a–b).
Ammonites stephanophorus Matheron, 1878: pl. 20B (fig. 9).

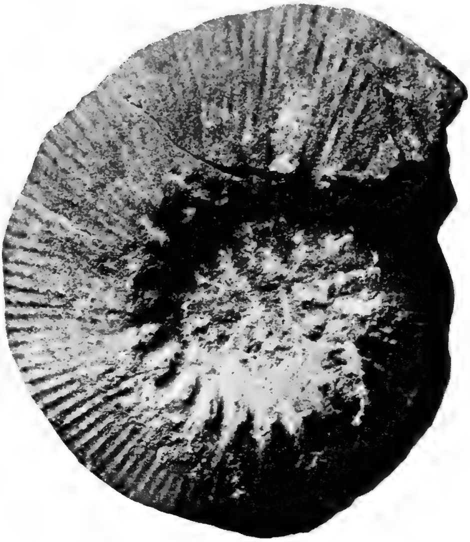

Fig. 193. *Olcostephanus* (*Olcostephanus*) *guebhardi* (Kilian). The holotype of *Astieria sharpei* Karakasch from the Upper Valanginian of the Crimea (after Karakasch 1907). × 1.

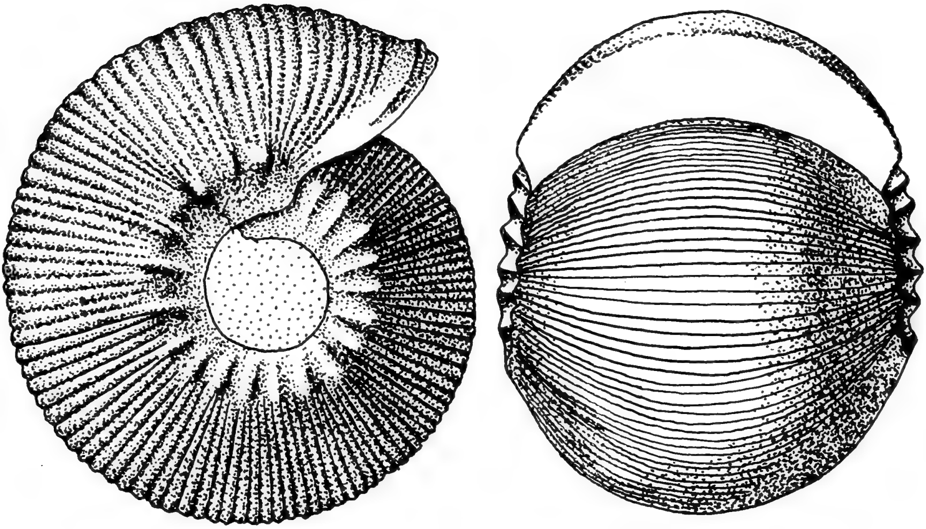

Fig. 194. *Olcostephanus* (*Olcostephanus*) *perinflatus* (Matheron) (♀). The holotype, by monotypy, from the south of France (after Matheron 1878). × 1.

Olcostephanus perinflatus (Matheron) Spath, 1939: 23. Fatmi, 1977: 270.
Olcostephanus cf. *perinflatus* (Matheron) Spath, 1939: 25, pl. 6 (fig. 6).

Material

Two specimens, AM–4292b, and PEM–1468/89, the latter a mere fragment, both preserved as internal moulds.

Holotype

The original of Matheron's (1878) plate 20B (fig. 8a–b) (Fig. 194 herein) from the south of France.

Description

The shell of AM–4292b is an extremely inflated, globose, cadicone, with a very narrow, deep, crater-like umbilicus. The umbilical walls are steep, convex, and slightly overhanging, and ornamented with about 22 rursiradiate primaries terminating in small bullae on the umbilical shoulder. The latter give rise to 3–4 rather fine, slightly prorsiradiate secondaries, which on the outer whorl are slightly flexuous, and between which are generally a single intercalated rib. Very occasionally a secondary rib is seen to bifurcate on the flanks, so that there are about 50–60 secondaries per half whorl on the outer whorl. Parabolae are absent on the outer whorl, but it is unknown whether they occur on the inner whorls.

Discussion

As suggested by Kilian (1892), the writer believes *Ammonites stephanophorus* Matheron (Fig. 195) merely to represent the juvenile growth stages of *Olcostephanus perinflatus*. The Uitenhage specimens are only tentatively referred to Matheron's species because of uncertainty as to what *O. perinflatus* really looks like, since it has never been photographically refigured or redescribed and there is reason to believe that Matheron's (1878) illustration may be somewhat idealized.

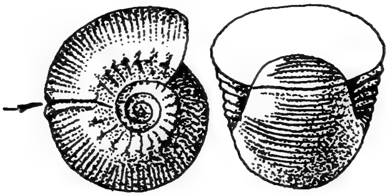

Fig. 195. *Olcostephanus* (*Olcostephanus*) *perinflatus* (Matheron) (♀). The holotype of *Olcostephanus stephanophorus* (Matheron) from the south of France, a juvenile (after Matheron 1878). × 1.

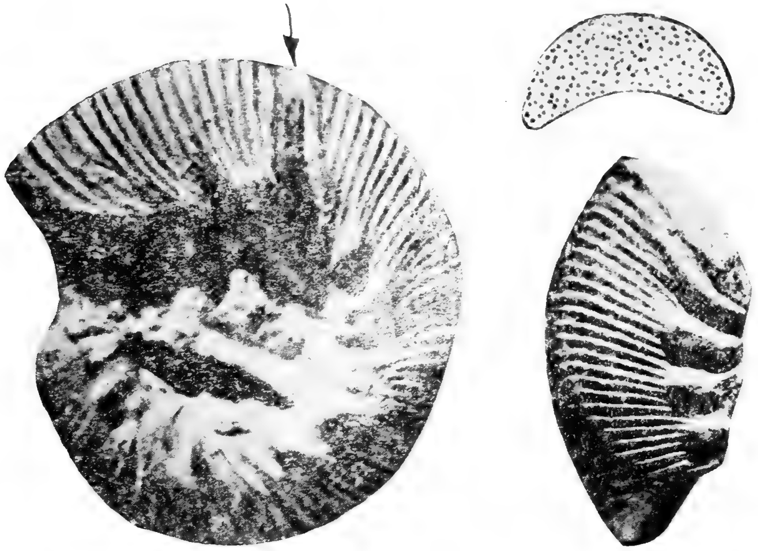

Fig. 196. *Olcostephanus* (*Olcostephanus*) *balkanicus* (Tzankov). The syntypes from the Lower Hauterivian of Bulgaria (after Tzankov 1943). × 3.

Olcostephanus globosus Spath, of which *O. pachycyclus* Spath represents an early growth stage (Fatmi 1977), is a macroconch species which is undoubtedly close to *O. perinflatus*. Indeed, it would seem to differ from Matheron's (1878) illustration only in its larger adult size, a character which is possibly environmentally related and hence doubtfully of specific importance. However, the Pakistan material is retained as distinct until Matheron's (1878) species is restudied on the basis of type and topotype material.

Olcostephanus balkanicus (Tzankov) (Fig. 196) is based upon a strongly inflated nucleus which seems to differ from the inner whorls of *O. perinflatus*, that is from *O. stephanophorus*, in having a much wider umbilicus, somewhat fewer (15–17) umbilical bullae and distinctly prorsiradiate secondaries. However, it shows prominent parabolae.

Occurrence

Olcostephanus perinflatus is at present known with certainty only from the south of France, but it may also be present in South Africa and Pakistan.

Family **Berriasellidae** Spath, 1922

Subfamily Neocomitinae Spath, 1924

Genus *Neohoploceras* Spath, 1939

Type species *Ammonites submartini* Mallada, 1882;
by original designation of Spath, 1939

Neohoploceras subanceps (Tate, 1867)

Fig. 197

Ammonites subanceps Tate, 1867: 150, pl. 7 (fig. 3a–b).
Reineckia subanceps (Tate) Newton, 1896: 150.
? *Leopoldia depereti* Sayn, 1907: 59, pl. 4 (figs 6–7).
Solgeria subanceps (Tate) Spath, 1930: 151, pl. 13 (fig. 4a–c). Du Toit, 1954: 384.
Neohoploceras subanceps (Tate) Klinger & Kennedy, 1979: 18.

Material

The holotype, BM–C32197, from the Sundays River is the only undoubted specimen known.

Holotype

By monotypy, the original of *Ammonites subanceps* figured by Tate (1867: 150, pl. 7 (fig. 3a–b)), from the Sundays River, and now in the British Museum, BM–C32197.

Fig. 197. *Neohoploceras subanceps* (Tate). The holotype, BMNH–C32197, from the Sundays River Formation. × 2. Photo: W. J. Kennedy.

Diagnosis

Small, somewhat inflated, with 12–14 ribs beginning at the umbilical seam of the outer whorl, each rib with a weak umbilical bulla and terminating in a swollen tubercle at about mid-flank, from which prorsiradiate ribs bifurcate or trifurcate. There are occasional single and intercalated ribs. All ribs terminate in small ventrolateral tubercles and are interrupted across the venter by a smooth zone. Constrictions are present.

Description

The following description is based on a plastercast of the type sent to the writer by M. K. Howarth: the specimen is small, but appears to have recrystallized test preserved. The shell is somewhat compressed, with a whorl section about as wide as high. The umbilicus is rather shallow and moderately evolute, the outer whorl covering slightly more than half of the preceding whorl. Maximum width is at mid-flank. The umbilical wall is gently sloping, with a well-rounded umbilical shoulder.

On the outer whorl, about 12–14 ribs begin at the umbilical seam and pass almost radially outwards to the umbilical shoulder where they develop small but distinct umbilical bullae. From here the ribbing is slightly prorsiradiate, and commonly swells at about mid-flank into a lateral tubercle, from which ribs frequently bifurcate or trifurcate. Occasionally only a single rib arises from the mid-lateral tubercle, in which case the latter is usually weakly developed, while there is also the odd intercalated rib. Ribbing is very weakly developed across the venter on the adoral portion of the outer whorl, and gives the impression that the smooth zone may have disappeared with age. There appear to be two constrictions on the outer whorl.

Measurements

No.	D	H	Wi	W/H	Uo	Ui
BM–C32197	16	8	7,5	0,94	7	5 (31)

Discussion

The small size of the holotype, which represents a juvenile growth stage, does not allow for proper comparison with other species, especially since juveniles are rarely figured or described. One of the few exceptions is the work of G. Sayn (1907). Amongst the examples figured by Sayn, *N. depereti* and *N. provinciale* (Sayn) both bear a close resemblance to *Ammonites subanceps*.

Neohoploceras depereti (Sayn) is moderately inflated and bears prominent constrictions. The ribbing is of two types, simple ribs lacking tubercles and stronger ribs which bifurcate or trifurcate from a prominent lateral tubercle and also have umbilical tubercles. All ribs bear weak ventrolateral clavi. The venter is grooved and smooth. The only difference between *N. depereti* and *N. subanceps* appears to be in the possession of more prominent tubercles by the former. However, since the larger of Sayn's syntypes is 33 mm in diameter, as against only 20 mm for *N. subanceps*, the differences are probably only ontogenetic.

Neohoploceras provinciale (Sayn) is similar to *N. subanceps* but is even larger than *N. depereti* and consequently comparison is still more difficult. It is, however, more closely ribbed than *N. depereti*, although its validity will be resolved only with a revision of the French material.

It is not possible to compare satisfactorily the South African species with the rich Madagascan faunas due to the size differences. Such a comparison will have to await ontogenetic studies on the Madagascan material.

Occurrence

Neohoploceras subanceps is present in the Sundays River Formation and perhaps the zone of *Saynoceras verrucosum* in south-east France.

Genus *Distoloceras* Hyatt, 1900

Type species *Ammonites hystrix* Phillips, 1829;
by original designation of Hyatt, 1900

Distoloceras spinosissimum (Hausmann, 1837)

Figs 198–200

Ammonites spinosissimum Hausmann, 1837: 1458.
Crioceras spinosissimum (Hausmann) Holub & Neumayr, 1882: 273, pl. 1 (fig. 1a–c). Kitchin, 1908: 225.
? *Distoloceras* cf. *spinosissimum* (Hausmann) Spath, 1924: 75.
Distoloceras spinosissimum (Hausmann) Spath, 1930: 152, pl. 13 (fig. 1). Besairie, 1932: 44, pl. 16 (fig. 13). Du Toit, 1954: 384. Collignon, 1962: 51, fig. 887.
Distoloceras hirtzi Collignon, 1962: 32, pl. 185 (figs 846–849).

Material

The holotype, in the Greifswalde Universitäts-Museum, and two examples in the British Museum (BM–C32194, C10819) are the only specimens so far recorded from the Sundays River Formation.

Holotype

By monotypy, the original of *Crioceras spinosissimum* (Hausmann) figured by Holub & Neumayr (1882: 273, pl. 1 (fig. 1a–c)) from the Sundays River.

Diagnosis

Only uncoiled fragments of this species are known from the Uitenhage Group. At this stage the whorl section is polygonal, slightly compressed, with flat flanks. Ornament comprises strong radial ribs ornamented with umbilical, lateral and ventrolateral tubercles, between which are intercalated varying numbers of weaker, more flexuous ribs which may or may not have lateral and ventrolateral tubercles. The umbilical and ventrolateral tubercles frequently form spines. Ribbing joining the ventrolateral spines across the venter is convex adorally.

Description

This is a large species of *Distoloceras* of which only uncoiled fragments are currently known from the Sundays River Formation.

In the holotype, judging from Holub & Neumayr's figure, the adapical

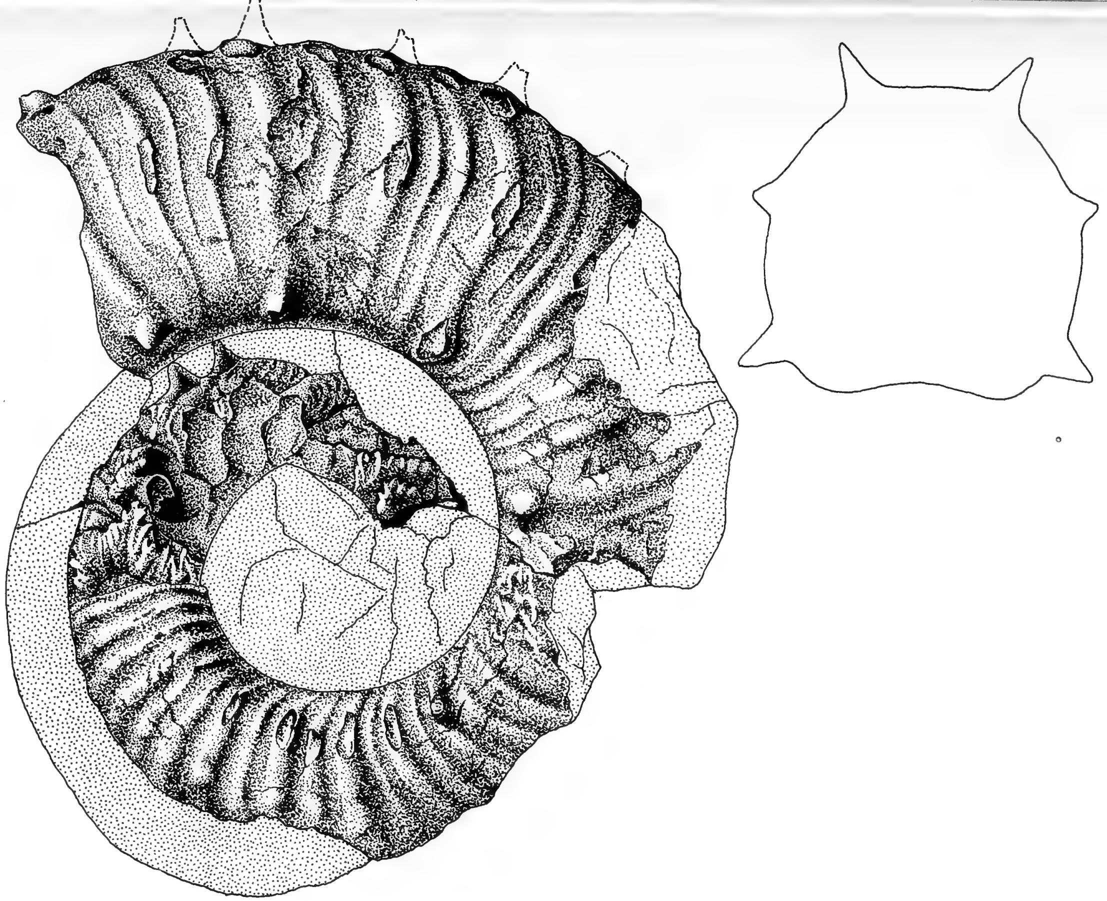

Fig. 198. *Distoloceras spinosissimum* (Hausmann). The holotype from the Sundays River Formation (after Holub & Neumayr 1882). × 0,75.

portion of the outer whorl, which has already lost contact with the previous whorl, shows simple straight, uniformly developed radial ribbing, with umbilical and lower ventrolateral swellings (corresponding to the lateral tubercles on the adoral portion), although Spath (1930: 152) thought this was possibly due to corrosion.

Beyond a diameter of about 100 mm intercalated ribs start appearing, always lacking umbilical tubercles, but occasionally with swelling corresponding to the lateral tubercles. These intercalatories commonly arise at the umbilical shoulder, although some may be intercalated half-way up the flank, and vary considerably in strength.

With the appearance of intercalated ribs, the ventrolateral and umbilical tubercles frequently form long spines. These ventrolateral spines may also be developed on intercalated ribs.

Ribbing weakens somewhat across the tabulate venter and is convex adorally. The suture line is complex.

A cast of the specimen figured by Spath (1930: pl. 13 (fig. 1)) (BM–C32194), provided by M. K. Howarth, shows the following features:

Whorl compressed, polygonal in costal section, elliptical intercostally. Dorsum with a weak median furrow, from which at least some of the ribs arise and pass backwards (rursiradiate) to the dorsal (umbilical) shoulder. On the adapical portion of this uncoiled fragment, the flank ribs are very slightly prorsiradiate. Some are more prominent than others and show faint umbilical bullae, midlateral, and ventrolateral tubercles. Between these prominent ribs are intercalated finer ribs which arise above the level of the dorsal shoulder and show weak midlateral bullae and ventrolateral swellings. All ribs bend sharply forwards at the level of the midlateral tubercles. On the adoral portion of this specimen the main ribs all possess well-developed umbilical, midlateral, and ventrolateral spines, and are separated by 3–4 much finer, slightly flexuous ribs with small midlateral bullae and ventrolateral swellings. The ribbing is poorly developed across the venter.

Discussion

In describing a fragment of a tightly coiled form from the Upper Valanginian of Ambiky, Madagascar, Collignon (1962) considered this species to be characterized by '. . . section subcarrée, ornamentation de côtes à tubercles ou les externes acquierent la preponderance'.

Comparison of *D. spinosissimum* with coiled species of *Distoloceras* is most unsatisfactory and consequently the validity of this species will have to await the further collection of topotype material. It should be noted, however, that both Besairie (1932) and Collignon (1962) consider fragments of this species, which occurs plentifully in Madagascar, to be easily recognizable and typical.

Distoloceras hystrix (Phillips) would seem to be very similar, but with a more compressed whorl section (although it seems highly likely that the whorl

Fig. 199. *Distoloceras spinosissimum* (Hausmann). Ventral and lateral views of BMNH–C32194, figured by Spath (1930). × 0,66. Photo: W. J. Kennedy.

Fig. 200. *Distoloceras spinosissimum* (Hausmann). Ventral and lateral views of BMNH–X108A, showing well-developed main ribs and thus very close to *D. hirtzi* Collignon. × 0,66. Photo: W. J. Kennedy.

section would change with uncoiling), while prior to the appearance of intercalated ribs in *D. hystrix*, the ribbing is seen to arise in pairs from umbilical tubercles, whereas in *D. spinosissimum* they are simple.

Distoloceras laticostatum Imlay is known only from tightly coiled, pyritic specimens. It is more compressed, with closer, more strongly developed ribs which may bifurcate at either the umbilical shoulder, or at mid-flank. Bifurcation of ribbing has not been recorded from *D. spinosissimum*. *Distoloceras* *capulinense* Imlay is very compressed, with closer, more regular ribs, some of which branch at the lateral tubercles.

Distoloceras hirtzi Collignon, from the Lower Valanginian of Madagascar, is very similar to *D. spinosissimum*, but was said to differ in having a more elliptical whorl section, prorsiradiate and not radial ribs, and in having more strongly developed midlateral tubercles. These are the features shown by Spath's topotype example, BM–C32194, and any differences are probably due to the better preservation of the Madagascan material. Consequently, *D. hirtzi* is considered a junior subjective synonym of *D. spinosissimum*.

Occurrence

Distoloceras spinosissimum is known from the Upper Valanginian of South Africa, Madagascar, and possibly England.

Distoloceras cf. *irregulare* Imlay, 1938

Figs 201–202

Compare
Distoloceras irregulare Imlay, 1938: 577, pl. 14 (figs 3, 5, 8–11).

Material

A single specimen, SAM–PCU1613, from an unknown locality.

Holotype

The original of Imlay's (1938) plate 14, figures 8–11, from the Taraises Formation of northern Mexico.

Description

In this fragment of an uncoiled example, the whorl section is subtrigonal, the flanks converging to the narrow, arched venter, the greatest width being at the dorsolateral shoulder. The dorsum, which was not in contact with the previous whorl, shows a furrowed median ridge from which initially radial, but soon becoming strongly rursiradiate, growth lines arise. Also on the dorsum, and arising from this median ridge, are very weakly developed rursiradiate ribs which strengthen towards the dorsal shoulders where they form distinct bullae. On the flanks the ribbing is rather variable, generally being prorsiradiate, although one rib is radial, and bending forwards near the venter. Between main ribs are 2–4 intercalated ribs which are prominent only across the venter. The tuberculation on the ribbing is rather variable and asymmetrical. There may be umbilical, lateral, ventrolateral and siphonal tubercles. A spine on one flank may be completely absent on the opposite side, or represented only by a weakly developed node. Siphonal tubercles are not developed on all ribs and may occasionally be eccentrically placed. The strength of the ribbing is also highly variable, fading and swelling at random. Ribs occasionally bifurcate from a lateral node.

Fig. 201. *Distoloceras* cf. *irregulare* Imlay. Front, ventral and lateral views of an uncoiled fragment, SAM–PCU1613. × 0,66.

Discussion

The solitary fragment from the Sundays River Formation is very close to *D. irregulare* Imlay, the latter differing only in having an elliptical whorl section and almost radial ribbing. It would seem that the development of siphonal spines is an ontogenetic feature as evidenced in the holotype of *D. irregulare*.

This specimen differs from *D. spinosissimum* (Hausmann) in having a subtrigonal and not polygonal whorl section, in possessing siphonal tubercles, and in the lack of regularity in the tuberculation.

Occurrence

Distoloceras irregulare Imlay is recorded from the middle part of the Upper Member of the Taraises Formation in Mexico, considered by Imlay (1938) to be of Lower Hauterivian age, and may also be present in the Sundays River Formation.

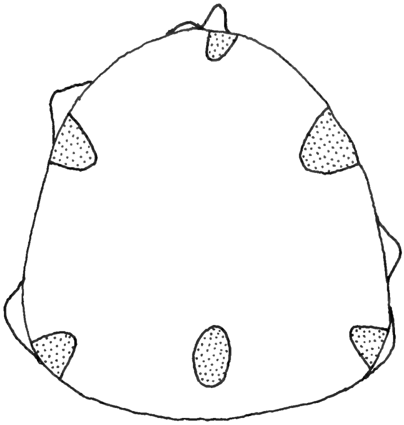

Fig. 202. *Distoloceras* cf. *irregulare* Imlay. Whorl section of SAM–PCU1613. × 0,66.

Superfamily HOPLITACEAE Douvillé, 1890

Family **Desmoceratidae** Zittel, 1895

Subfamily Eodesmoceratinae Wright, 1955

Genus *Eodesmoceras* Spath, 1924

Type species *Ammonites celestini* Pictet & Campiche, 1858;
by original designation of Spath, 1924

Discussion

Two subgenera are recognized within this genus (Wright *in* Arkell *et al.* 1957), viz. *E.* (*Eodesmoceras*) and *E.* (*Miodesmoceras*). *Miodesmoceras* is a Barremian form, distinguished from *Eodesmoceras* in being more compressed and in lacking constrictions, whilst the latter is considered of Valanginian–Lower Hauterivian age. *Eodesmoceras haughtoni* Spath from the Uitenhage Group lacks constrictions, and is much more compressed than the type of *E.* (*Eodesmoceras*) *celestini* (Pictet & Campiche). Consequently, the differences between these two subgenera blurr and they appear to be of little taxonomic use.

Eodesmoceras haughtoni Spath, 1930

Fig. 203

Eodesmoceras haughtoni Spath, 1930: 141, pl. 13 (fig. 2a–e). Du Toit 1954: 384.

Material

The holotype, SAM–227, is the only specimen known.

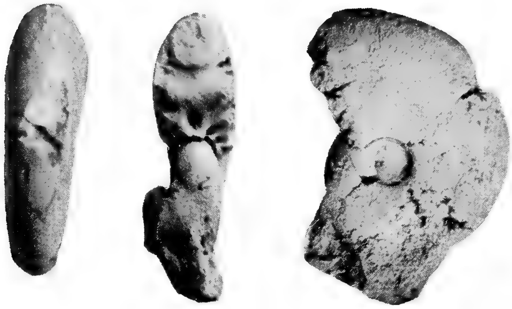

Fig. 203. *Eodesmoceras haughtoni* Spath. Ventral, front and lateral views of the holotype, SAM–227, preserved as an internal mould. × 2.

Holotype

By monotypy, the original of the specimen figured by Spath (1930, pl. 13 (fig. 2a–e)) from '. . . Shore of pan, Zoutpan, Uitenhage', and now in the South African Museum.

Diagnosis

A compressed, immature *Eodesmoceras* in which the only ornament is very faint sigmoidal growth striae. Constrictions are lacking.

Description

The holotype is small, preserved as an internal mould, and rather involute, the outer whorl covering about two-thirds of the preceding whorl. The shell is strongly compressed with broad, flat flanks converging slightly to the narrow evenly rounded venter. At 14 mm diameter the specimen is still entirely septate. Constrictions are lacking, whilst Spath presumably observed the growth striae on the inner whorls where the shell material was preserved. The specimen has since been glued together and this feature could not be verified.

Measurements

No.	D	H	Wi	W/H	Ui
SAM–227	14	8	5	0,63	3 (21)

Discussion

Despite the fact that Spath (1930: 142) considered this species '. . . probably represents merely the inner whorls of a larger form like *Eodesmoceras celestini* (Pictet & Campiche)', he still described it as a new species.

The very small size of *E. haughtoni* makes comparison difficult. It is more compressed than the type of *E. celestini*, but this is possibly ontogenetic variation since the latter is 28 mm in diameter. According to Wright's (*in* Arkell *et al.*

1957) diagnosis of *E.* (*Eodesmoceras*), presumably based on the type species *E. celestini*, constrictions are present although they are not visible in the illustration of the lectotype. Lack of comparative material does not allow for a definite statement on the validity of Spath's species.

Occurrence

This species is known only from the Sundays River Formation.

Subclass DIBRANCHIATA Owen, 1832
Order DECAPODA Leach, 1818
Suborder BELEMNOIDEA Naef, 1912
Family **Belemnitidae** D'Orbigny, 1845
Subfamily Belemnopsinae Naef, 1922
Genus *Belemnopsis* Bayle, 1878

Type species *Belemnites sulcatus* Miller;
by subsequent designation of Douvillé, 1879

Belemnopsis africana (Tate, 1867)

Fig. 204

Belemnites africanus Tate, 1867: 151, pl. 7 (fig. 2). Kitchin, 1908: 225.
Belemnopsis africana (Tate) Spath, 1930: 155. Besairie, 1930; pl. 11 (fig. 12). Spath, 1939, pl. 24 (fig. 15). Stevens, 1965: 164.
Non Belemnopsis africana (Tate) Besairie, 1930, pl. 23 (figs 6–7, 20–21).

Material

A single unnumbered specimen in the South African Museum.

Fig. 204. *Belemnopsis africana* (Tate). Lateral and ventral views of an apical fragment in the South African Museum. × 1.

Holotype

By monotypy, the original of the specimen figured by Tate (1967, pl. 7 (fig. 2)), from the Sundays River, now in the British Museum.

Diagnosis

Guard non-hastate, expanding slowly adorally. Ventral groove deep and broad, prominent throughout growth. Cross-section depressed.

Description

The following description, based on the holotype, is taken from Stevens (1965: 164): '. . . the guard is non-hastate, its diameter gradually increasing forwards. The ventral groove, broad and deep, is very prominent throughout the growth stages of the guard. Cross-sections throughout the length of the guard are depressed (maximum transverse diameter, 19 mm: maximum sagittal diameter, 18 mm).'

Discussion

The genus *Belemnopsis* is characteristic of the Kimmeridgian–Tithonian of the Indo-Pacific, with a relict fauna surviving in South Africa and Madagascar until the late Valanginian. Spath (1930: 156) remarked that an alveolar fragment of *B. africana* could not be distinguished from *B. gerardi* Oppel (= *B. uhligi* Stevens).

The examples referred by Besairie (1936) to this species are considered by Stevens (1965) as probably distinct. They differ from Tate's species in being more elongate and slender, with an elongate sharply pointed apical region, while the ventral groove is not as deep.

The rarity of this species in the Uitenhage Group led Stevens (1965: 164) to '. . . suggest derivation from Upper Jurassic strata, since removed by erosion. However, the holotype is quite well preserved and not corroded so is probably not derived from older strata.'

Belemnopsis gladiator Willey (1973: 33, fig. 2) from the Berriasian of Antarctica is very close to Tate's species. According to Willey, *B. africana* differs in being somewhat shorter, comparatively more robust, with a deeper, flat-bottomed ventral groove with concave sides and sharp margins. The differences are, however, slight and since *B. africana* is still known only from a handful of fragmentary specimens, probably would not stand up were a population of individuals known. This is supported by the fact that Willey (1973) assigned an apical fragment of *Belemnopsis* from the Sundays River Formation, in the British Museum, BM–C6217, to *B. gladiator*. *Belemnopsis africana* may prove, therefore, to be longer ranging than is generally suspected.

Occurrence

Belemnopsis africana is known from the Lower and Upper Valanginian of Madagascar, the Upper Valanginian of South Africa, and possibly the Berriasian of Antarctica.

Order NAUTILOIDEA Agassiz, 1847

Suborder Nautilina Agassiz, 1847

Family **Nautilidae** de Blainville, 1825

Genus *Eutrephoceras* Hyatt, 1894

Type species *Nautilus dekayi* Morton, 1834;
by subsequent designation of Hyatt, 1894.

Eutrephoceras uitenhagense Spath, 1930

Fig. 205

Nautilus sp. Sharpe, 1856: 201. Kitchin, 1908: 225.
Eutrephoceras uitenhagense Spath, 1930: 139.
Nautilus (*Eutrephoceras*) ?*uitenhagense* Spath, Besairie, 1936: 145.

Material

The holotype is still the only specimen recorded from the Sundays River Formation.

Holotype

The specimen recorded by Sharpe (1856: 201) from the Sundays River now in the British Museum (BM–11034, Geol. Soc. Coll.).

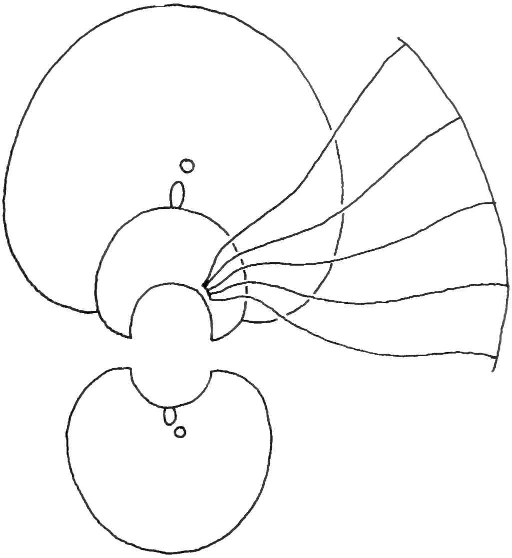

Fig. 205. *Eutrephoceras uitenhagense* Spath. Whorl section and suture (after Spath 1930). × 0,66.

Diagnosis

'Coiling occlusal, with umbilicus nearly closed. Whorl section rounded, slightly compressed at first, later flaring, with greatest thickness at inner third and no edge to high umbilical wall. Suture line with slight umbilical saddle and shallow lateral lobe, straight across venter. Annular lobe strongly developed. Test entirely smooth, thick' (Spath 1930: 139).

Measurements

No.	D	H	W	W/H	U
BM–11034	135	55	74	1,35	7 (5)

Discussion

The excentric position of the ventral siphuncle in this species was thought not to be significant by Spath (1930). He compared this species with '*Nautilus*' *boissieri* Pictet, from which *E. uitenhagense* was distinguished by its greater inflation.

Occurrence

This species is known only from the Sundays River Formation and perhaps Madagascar.

SUMMARY

The cephalopod fauna from the Sundays River Formation is revised and shown to comprise the following species:

AMMONOIDEA

Partschiceras rogersi (Kitchin)
Bochianites glaber Kitchin
Bochianites africanus (Tate)
O. (*Olcostephanus*) *atherstoni* (Sharpe) (♂ and ♀)
O. (*Olcostephanus*) *densicostatus* (Wegner) sp. juv.
O. (*Olcostephanus*) *rogersi* (Kitchin) (♂ and ♀)
O. (*Olcostephanus*) *victoris* Spath (♀)
O. (*Olcostephanus*) *fascigerus* Spath (♀)
O. (*Olcostephanus*) aff. *durangensis* (Cantu Chapa) (♂)
O. (*Olcostephanus*) *baini baini* (Sharpe) (♂ and ♀)
O. (*Olcostephanus*) *baini* var. *sphaeroidalis* (Spath) (♂ and ♀)
O. (*Olcostephanus*) *ventricosus* (Von Koenen) (?♀)
O. (*Olcostephanus*) *uitenhagensis* (Kitchin) (♀)
O. (*Olcostephanus*) *riccardii* sp. nov. (♀)

O. (*Olcostephanus*) *astieriformis* (Böse) (♀)
O. (*Olcostephanus*) *coahuilensis* Imlay (♀)
O. (*Olcostephanus*) cf. *perinflatus* (Matheron) (♀)
Neohoploceras subanceps (Tate)
Distoloceras spinosissimum (Hausmann)
Distoloceras cf. *irregulare* Imlay
Eodesmoceras haughtoni Spath

COLEOIDEA

Belemnopsis africana (Tate)
Belemnopsis gladiator Willey

NAUTILOIDEA

Eutrephoceras uitenhagense Spath

The fauna is dominated by species of *Olcostephanus*, within which sexual dimorphism is recognized for the first time from these beds. The fact that three morphologic types—microconch, macroconch, and inner whorls of the macroconch—may be distinguished within a single species (dimorphic pair), together with occasional gerontic individuals, has led to a proliferation of nominal species. This, together with complete disregard for intraspecific variation, has led to taxonomic chaos.

A literature review of sexual dimorphism in ammonites reveals that the inner whorls of many macroconchs (♀) are indistinguishable from their microconch (♂) counterparts. This, together with the occurrence of rare aberrant mutants (Cope 1967: 53), supports the contention that some sexually dimorphic ammonites display consecutive hermaphroditism or protandrism.

Many microconch species of *Olcostephanus* exhibit parabolae, as do the immature growth stages of the corresponding macroconch. Not only are parabolae virtually identical, morphologically, to the peristome but they also have an identical mode of formation. Consequently, parabolae in *Olcostephanus* are interpreted as relict peristomes. Accepting this suggestion, it is of interest to note that the whorls of many extant gastropods are ornamented with varices, representing the position of relict apertures developed during pauses in growth. They would appear, therefore, to be homologous to the parabolae occurring in *Olcostephanus*. The fact that in extant Gastropoda varices are known to be of specific importance supports the contention that they were of equal significance in *Olcostephanus*.

A significant feature associated with sexual dimorphism in *Olcostephanus* is the striking degree of convergence in the outer whorls of macroconch forms. Since *O. atherstoni* (Sharpe) was one of the earliest such macroconchs to be described, this name consistently crops up in the older literature when, in fact, the inner whorls show a different species to be involved. It is probably also this homoeomorphy which has led to the neglect of parabolae as a specific criterion.

The importance of a knowledge of the early ontogenetic stages of macroconchs for their specific determination cannot be over-emphasized, as well as being imperative for the recognition of the microconch dimorph. A slight, but apparently consistent, difference between microconch forms and the inner whorls of their macroconch appears to be a somewhat higher rib density in the latter.

The subfamily Olcostephaninae is reviewed and considered to include the following genera and subgenera: *Saynoceras* (*Saynoceras*), *S.* (*Ceratotuberculus*), *Olcostephanus* (*Olcostephanus*), *O.* (*Subastieria*), *O.* (*Parastieria*), *O.* (*Jeannoticeras*), *O.* (*Mexicanoceras*), *Jeanthieuloyites*, *Valanginites*, *Capeloites*, and *Dobrodgeiceras*. The genera *Holcostephanus*, *Astieria*, *Rogersites*, *Taraisites* and *Satoites* are considered junior synonyms of *Olcostephanus* s.s., whilst *Maderia* and *Lemurostephanus* comprise a heterogeneous assemblage of *O.* (*Olcostephanus*) and perhaps *O.* (*Subastieria*) nuclei, and are thus superfluous. In order to incorporate the new subgenera, the diagnosis of *Olcostephanus* as given by Wright (*in* Arkell *et al.* 1957) is emended. The new genus *Jeanthieuloyites* is proposed for *Rogersites quinquestriatus* Besairie.

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REFERENCES

Anderson, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap geol. Soc. Am.* **16**: 1–244.

Arkell, W. J., Kummel, B. & Wright, C. W. 1957. Mesozoic Ammonoidea. Systematic description. *In:* Moore, R. C., *ed. Treatise on invertebrate paleontology.* Part 1. Mollusca 4. Cephalopoda. Ammonoidea: L129–L437. Boulder: Geological Society of America; Lawrence: University of Kansas Press.

Atherstone, W. G. 1857. Geology of Uitenhage. *The Eastern Province Monthly Magazine* **1**(11): 580–595.

Bacci, G. 1947. L'inversione del sesso ed il ciclo stagionale della gonade in *Patella coerulea* L. *Pubbl. Staz. zool. Napoli* **21**: 183–217.

Bain, A. G. 1856. On the geology of South Africa. *Trans. geol. Soc. Lond.* (2)**7**: 175–192.

Barbier, R. & Thieuloy, J. P. 1963. Étage Valanginien. *In*: Colloque sur le Crétacé inférieur. *Mem. Bur. Rech. Geol. Min.* **34**: 79–84.

Barnes, R. D. 1968. *Invertebrate zoology.* 2nd ed. Philadelphia: Saunders.

Baumberger, E. 1903–1910. Die ammonitiden der unteren Kreide im westschweizerichen Jura. *Mem. soc. Paléont. Suisse* **30**(1903): 1–60; **32**(1905): 1–80; **33**(1906): 1–30; **34**(1907): 1–47; **35**(1909): 1–40; **36**(1910): 1–57.

Bayle, E. 1878. Fossiles principaux des terrains. *Explic. Carte géol. Fr.* **4**(1) (Atlas).

Besairie, H. 1930. Les rapports du Crétacé malgache avec le Crétacé de l'Afrique australe. *Bull. Soc. géol. Fr.* (4)**25**: 613–643.

Besairie, H. 1932. Fossiles caractéristiques du nord et du nord-ouest de Madagascar. *Annls géol. Serv. Mines Madagascar* **2**: 37–53.

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 cretácicas de Zacatecas, Durango y Guerrero. *Bol. Inst. Geol. Méx.* **42**: 1–219.

Burckhardt, C. 1906. La fauna jurassique de Mazapil, avec un appendice sur les fossiles du crétacique inférieur. *Bol. Inst. Geol. Méx.* **23**: 1–216.

Busnardo, R. & Cotillon, P. 1964. Stratigraphie du Crétacé inférieur dans la région des gorges du Verdon (Basses-Alpes et Var). *C.r. hebd. Séanc. Acad. Sci., Paris* **8**: 321.

Callomon, J. H. 1957. Field meeting in the Oxford Clay and Kellaways Beds at Kidlington, Oxfordshire, and the zones of the Callovian stage. *Phil. Trans. R. Soc.* (B) **239**: 215–264.

Callomon, J. H. 1963. Sexual dimorphism in Jurassic ammonites. *Trans. Leicester lit. phil. Soc.* **57**: 21–56.

Cantu Chapa, A. 1966. Se propone una nueva Subdivisión de la Familia Olcostephanidae (Ammonoidea) del Cretácico Inferior (Taraisitinae subfam. nov. y Taraisites gen. nov.). *Ingeniería Petrolera* (6)**12**: 15–17.

Castillo, A. D. & Aguilera, J. G. 1895. Fauna fosil del le Sierra de Catorce en San Luis Potosi. *Bolm Com. Geol. Méx.* **1**: 1–55.

Cobban, W. A. 1969. The late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (DeKay) in the Western Interior of the United States. *Prof. Pap. U.S. geol. Surv.* **619**: 1–27.

Coe, W. R. 1936. Sexual phases in *Crepidula. J. exp. Zool.* **72**: 455–477.

Coe, W. R. 1938*a*. Conditions influencing change of sex in mollusks of the genus *Crepidula. J. exp. Zool.* **77**: 401–424.

Coe, W. R. 1938*b*. Influence of the association on the gastropods having protandric consecutive sexuality. *Biol. Bull. mar. biol. Lab, Wood's Hole* **75**: 274–285.

Coe, W. R. 1944. Sexual differentiation in mollusks. II. Gastropods, amphineurans, schaphopods, and cephalopods. *Q. Rev. Biol.* **19**: 85–97.

Coe, W. R. 1948. Nutrition and sexuality in protandric gastropods of the genus *Crepidula. Biol. Bull. mar. biol. Lab., Wood's Hole* **94**: 158–160.

Coe, W. R. 1953. Influences of association, isolation and nutrition on the sexuality of snails of the genus *Crepidula. J. exp. Zool.* **122**: 5–19.

Collignon, M. 1962. *Atlas des fossiles caracteristiques de Madagascar* (*Ammonites*). VIII. Berriasien, Valanginien, Hauterivien, Barremien. Tananarive: Service géologique.

COPE, J. W. C. 1967. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay of Dorset. *Bull. Br. Mus. nat. Hist.* (Geol.) **15**: 1–79.

DAMES, W. 1873. Ueber *Ptychomya*. *Z. dt. geol. Ges.* **25**: 379.

DEBELMAS, J. & THIEULOY, J. P. 1963. Étage Hauterivien. *In*: Colloque sur le Crétacé Inférieur. *Mem. Bur. Rech. geol. Min.* **34**: 85–96.

DOUVILLÉ, H. 1880. Note sur l'*Ammonite pseudoanceps* et sur la forme de son ouverture. *Bull. Soc. géol. Fr.* (3)**8**: 239–246.

DU TOIT, A. L. 1954. *The geology of South Africa*. Edinburgh: Oliver & Boyd.

FATMI, A. N. 1977. Neocomian ammonites from northern areas of Pakistan. *Bull. Br. Mus. nat. Hist.* (Geol.) **28**: 255–296.

FRETTER, V. & GRAHAM, A. 1964. Reproduction *In*: WILBUR, K. M. & YONGE, C. M., *eds*., *Physiology of Mollusca*. New York: Academic Press.

FUTTERER, K. 1897. Beiträge zur Kenntniss des Jura in Ost-Afrika. *Z. dt. geol. Ges.* **49**: 568.

GERTH, E. 1925. La fauna Neocomiana de la Cordillera Argentina an la parte meridional de la Provincia de Mendoza. *Actas Acad. nac. Cienc. Cordoba* **9**: 57–132.

GIOVINE, A. 1950. Algunos cefalópodos del Hauterivense de Neuquén. *Revta Assoc. geol. argent.* **5**: 35–76.

GOLDFUSS, G. A. 1826–1840. *Petrefacta Germaniae*. Düsseldorf.

GOULD, H. N. 1919. Studies on sex in the hermaphrodite mollusc *Crepidula plana*. III. Transference of the male-producing stimulus through sea water. *J. exp. Zool.* **29**: 113–120.

GOULD, H. N. 1947. Conditions affecting the development of the male phase in *Crepidula plana*. *Biol. Bull. mar. biol. Lab., Wood's Hole* **93**: 194.

GOULD, H. N. 1952. Studies on the sex in the hermaphrodite mollusc *Crepidula plana*. IV. Internal and external factors influencing growth and sex development. *J. exp. Zool.* **119**: 93–160.

GRIESBACH, C. L. 1880. Geological notes. *Rec. geol. Surv. India* **13**(2): 83.

GÜRICH, G., 1887. Ueberblick über den geologischen Bau des Africanischen Kontinents. *Petermanns Mitt.* **33**: 257.

HAAS, O. 1960. Lower Cretaceous ammonites from Colombia, South America. *Am. Mus. Novit.* **2005**: 1–62.

HATCH, F. H. & CORSTORPHINE, G. S. 1909. *The geology of South Africa*. 2nd ed. New York: Macmillan.

HAUG, E. 1893. Étude sur les ammonites des étage moyens du système Jurassique. *Bull. Soc. géol. Fr.* (3)**20**.

HAUGHTON, S. H. 1963. *The stratigraphic history of Africa south of the Sahara*. Edinburgh: Oliver & Boyd.

HAUSMANN, J. F. L. 1837. Beiträge zur Kunde der geognostischen Constitution von Süd-Afrika. *Gotting. gelehrte Anz.* **1837**: 1449.

HENDERSON, I. F. & HENDERSON, W. D. 1967. *A dictionary of biological terms*. Edinburgh: Oliver & Boyd.

HOLUB, E. & NEUMAYR, M. 1882. Ueber einige fossilien aus der Uitenhage—Formation in Süd-Afrika. *Denkschr Akad. Wiss., Wien*, Math.-nat. Kl. **44**: 12.

HOUŠA, V. 1965. Sexual dimorphism and the system of Jurassic and Cretaceous Ammonoidea (Preliminary note). *Casopsis Musea Narodniho* (Prague) **134**(1): 33–35.

IMLAY, R. W. 1937. Lower Neocomian fossils from the Miquihauna region, Mexico. *J. Paleont.* **11**: 552–574.

IMLAY, R. W. 1938. Ammonites of the Taraises Formation of northern Mexico. *Bull. geol. Soc. Am.* **49**: 539–602.

IMLAY, R. W. 1940. Neocomian faunas of northern Mexico. *Bull. geol. Soc. Am.* **51**: 117–190.

IMLAY, R. W. 1960. Ammonites of early Cretaceous age (Valanginian and Hauterivian) from the Pacific Coast States. *Prof. Pap. U.S. geol. Surv.* **334–F**: 167–228.

IMLAY, R. W. & JONES, D. L. 1970. Ammonites from the *Buchia* zones in north-western California and south-western Oregon. *Prof. Pap. U.S. geol. Surv.* **647–B**: 1–59.

JEKELIUS, E. 1913. Die Mesozoischen Faunen der Berge von Brasso. *Mitt. Jb.k. ung. geol. Anst.* **23**(2): 114–135.

JONES, T. R. 1884. On the geology of South Africa. *Nature, Lond.* **30**: 553.

KARAKASCH, N. 1902. Note sur le crétacé inférieur de Biassala. *Trav. Lab. Géol. Univ. Grenoble* **6**: 93–107.

KARAKASCH, N. 1907. Le crétacé inférieur de la Crimée et sa faune. *Soc. Imp. nat. St Petersbourg* **32**: 1–482 (in Russian).

KARSTEN, H. 1856. Ueber die geognostischen Verhältnisse des westlichen Columbien, der heutigen Republiken Neu-Granada und Equador. *Amtl. Ber. Versamm. dt. Naturf. Aertze* **32**.

KENNEDY, W. J. & COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Spec. Pap. Palaeontology* **17**: 1–94.

KILIAN, W. 1892. Sur quelques cephalopodes nouveaux ou peu connus de la période secondaire. *Trav. Lab. Géol. Univ. Grenoble* **1**: 211–227.

KILIAN, W. 1895. Sur le Néocomien des environs de Moustiers. *Bull. Soc. géol. Fr.* (3) **23**: 762–765.

KILIAN, W. 1902. Sur quelques fossiles remarquables de l'Hauterivien de la région d'Escragnolles. *Bull. Soc. géol. Fr.* (4)**2**: 864–867.

KILIAN, W. 1910. Unterkreide (Palaeocretacicum). *In*: FRECH, F., *ed. Lethaea Geognostica.* II. Mesozoicum, 3, Kreide: 169–287.

KILIAN, W. & LEENHARDT, F. 1895. Sur le Néocomien des environ de Moustiers Ste Marie (Basses-Alpes). *Bull. Soc. géol. Fr.* (3) **23**: 970–981.

KITCHIN, F. L. 1908. The invertebrate fauna and palaeontological relationships of the Uitenhage Series. *Ann. S. Afr. Mus.* **7**: 21–225.

KLINGER, H. C. & KENNEDY, W. J. 1979. Cretaceous faunas from southern Africa. Lower Cretaceous ammonites, including a new bochianitid genus, from Umgazana, Transkei. *Ann. S. Afr. Mus.* **78**: 11–19.

KRAUSS, F. 1843. Ueber die geologischen Verhältnisse der östlichen Küste des Kaplandes. *Amtl. Ber. Gesell. dt. Naturf. Aertze* **1843**: 126.

KRAUSS, F. 1850. Ueber einige petrefacten aus der untern Kreide des Kaplandes. *Nova Acta Acad. Caesar. Leop. Carol.* **22**: 439.

KRENKEL, E. 1910. Die Untere Kreide von Deutsch-Ostafrika. *Beitr. Paläont. Ost.-Ung.* **23**: 201–250.

KOENEN, A. von. 1902. Die Ammonitiden des norddeutschen Neocom. *Abh. K. preuss geol. Landesanst* (n.f.) **24**: 1–451.

LEANZA, A. 1944. Las ápofisis yugales de *Holcostephanus. Notas Mus. La Plata* (Paléont.) IX **62**: 13–22.

LEANZA, A. F. 1957. Acerca de la existencia de *Simbirskites* en el Neocomiano Argentino. *Revta Assoc. geol. argent.* **12**: 5–17.

LEHMANN, U. 1966. Dimorphismus bei Ammoniten der Ahrensburger Lias-Geschiebe. *Paläont. Z.* **40**: 26–55.

LEHMANN, U. 1969. Dimorphismus und Apophysen-Ausbildung bei *Grammoceras doertense* (Denkmann) (Ammonoidea; Oberes Toarcium). *Paläont. Z.* **43**: 169–176.

LEMOINE, P. 1906. Études géologiques dans le nord de Madagascar. *Annls Hébert* **3**: 1–520.

LYCETT, J. 1872–1883. A monograph of the British fossil Trigoniae. *Palaeontogr. Soc.* (*Monogr.*): 1–245.

MAKOWSKI, H. 1962*a*. Problem of sexual dimorphism in ammonites. *Paleont. Polon.* **12**: 1–92.

MAKOWSKI, H. 1962*b*. Récherches sur les dimorphism sexuel chez les Ammonoïdés. *In:* Ksiega Pamiatkowa ku czci Profesora Jana Samsonowicza. *Polska Akad. nauk. Kom. Geol.:* 31–55.

MALLADA, L. 1882. Reconocimiento geologico de la provincia de Navarra. *Boln Comn Mapa geol. Esp.* **9**: 1–64.

MATHERON, P. 1878. *Récherches paléontologiques dans le midi de la France.* Marseille.

MOLENGRAAF, G. A. F. 1890. Schets van de Bodemgesteldheid van de Zuid Africaansche Republiek. *Tijdschr. K. ned. aardrijksk. Genoot.*

MOLENGRAAF, G. A. F. 1900. Die Reihenfolge und Correlation der geologischen Formationen in Südafrika. *Neues Jb. Miner. Geol. Paläont.* **1**: 113.

MOULLADE, M. & THIEULOY, J. P. 1967. Les zones d'ammonites du Valanginien supérieur et de l'Hauterivien vocontiens. *C. R. somm. Seanc. Soc. géol. Fr.* **6**: 228–229.

MOULLE, A. 1885. Mémoire sur la géologie génerále et sur les mines de diamants de l'afrique du Sud. *Annls Mines Carbur., Paris* **7**: 193.

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

Neumayr, M. & Uhlig, V. 1881. Ueber Ammonitiden aus den Hilsbildungen Norddeutschlands. *Palaeontographica* **27**: 129–303.

Newton, R. B. 1896. On the occurrence of *Alectryonia ungulata* in S.E. Africa, with a notice of previous researches on the Cretaceous conchology of southern Africa. *J. Conch., Lond.* **8**: 136.

Newton, R. B. 1924. A contribution to the palaeontology of Portuguese East Africa. *Trans. geol. Soc. S. Afr.* **26**: 141–159.

Nicklès, R. 1890. Contributions a la paléontologie du sud-est de l'Espagne. Terrain crétacé. I. Néocomien. *Mém. Soc. géol. Fr.* (1) **2**: 1–30.

Nikolov, T. 1962. *Dobrogeites*, a new genus of Valanginian ammonites. *C.r. Acad. bulg. Sci.* **15**: 69–71.

Oppel, A. 1863. Ueber ostindische fossilreste aus den sekundaren Ablagerungen von Spiti und Gnari Khorseum in Tibet. *Paläont. Mitt.* **1863**: 267–304.

Orbigny, A. d'. 1840–1842*a*. *Paléontologie française. Terrains crétacés.* I. Cephalopodes. Paris: Masson.

Orbigny, A. d'. 1842*b*. *Coquilles et echinodermes fossiles de Colombie, recueillis de 1821 à 1833 par M. Boussingault.* Paris: Masson.

Orton, J. H. 1920. Sea temperature, breeding and distribution in marine animals. *J. mar. biol. Assoc. U.K.* **12**: 339–366.

Orton, J. H., Southward, A. J. & Dodd, J. M. 1956. Studies on the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *J. mar. biol. Assoc. U.K.* **35**: 149–176.

Palframann, D. F. B. 1966. Variation and ontogeny of some Oxfordian ammonites: *Taramelliceras richei* (de Loriol) and *Creniceras renggeri* (Oppel) from Woodham, Buckinghamshire. *Palaeontology* **9**: 290–311.

Palframann, D. F. B. 1967. Variation and ontogeny of some Oxford Clay ammonites: *Distichoceras bicostatum* (Stahl) and *Horioceras bauieri* (d'Orbigny), from England. *Palaeontology* **10**: 60–90.

Paquier, V. 1900. Récherches géologiques dans le Diois et les Baronnies orientales. *Trav. Lab. Géol. Univ. Grenoble* **5**: 1–549.

Passarge, S. 1904. *Die Kalahari.* Berlin.

Pavlow, A. & Lamplugh, G. W. 1892. Argiles de Speeton et leur equivalent. *Bull. Soc. Imp. Nat. Moscow*, n.s., **5**: 455–599.

Pellegrini, O. 1948. Richerche statistiche sulla sessualita di *Patella coerulea* L. *Boll. Zool.* **15**: 115–121.

Pickford, G. 1947. Comments. *Science, N.Y.* (n.s.) **105**: 522.

Pictet, F. J. & Campiche, G. 1858–1860. *Materiaux pour la páleontologie Suisse. Description des fossiles du terrain crétacé des environs de Ste Croix.* II (2). Geneva: Bâle & Lyon.

Portlock, ?. 1852. Note on fossils collected by R. Rubidge at Sundays River, exhibited by Lieut-Col. Portlock at the Ipswich meeting of the British Association, 1851. *Rep. Br. Assoc. Advmt Sci.* **1852**: 68.

Rawson, P. L. 1971. Lower Cretaceous ammonites from north-eastern England: the Hauterivian genus *Simbirskites*. *Bull. Br. Mus. nat. Hist.* (Geol.) **20**: 27–86.

Reyment, R. A. 1971. Vermuteter dimorphismus bei der Ammonitengattung *Benueites*. *Bull. geol. Instn Univ. Uppsala* (n.s.) **3**: 1–18.

Reyment, R. A. & Tait, E. A. 1972. Biostratigraphical dating of the early history of the South Atlantic Ocean. *Phil. Trans. R. Soc.* (B) **264**: 55–95.

Riccardi, A. C. & Westermann, G. E. G. 1970. The Valanginian *Dobrodgeiceras* Nikolov (Ammonitina) from Peru. *J. Paleont.* **44**: 888–892.

Riccardi, A. C., Westermann, G. E. G. & Levy, R. 1971. The Lower Cretaceous Ammonitina *Olcostephanus*, *Leopoldia*, and *Favrella* from west-central Argentina. *Palaeontographica* 136(A): 83–121.

Riedel, L. 1938. Ammonitas del cretácico inferior de la Cordillera Oriental. *In: Estudios geológicos y paleontológicos sobre la Cordillera Oriental de Colombia* **2**: 7–80.

Roch, E. 1930. Études géologiques dans la region meridionale du Maroc Occidental. *Notes Mém. Serv. Mines Carte géol. Maroc* **9**: 7–541.

Rodighiero, A. 1919. Il sistema Cretaceo del Veneto Occidentale compreso fra l'Adige e il Piave con speciale riguardo al Neocomiano dei Sette Comuni. *Palaeontogr. ital.* **25**: 39–125.

SATO, T. 1958. Presence du Berriasien dans la stratigraphie du plateau de Kitakami (Japon septentrional). *Bull. Soc. géol. Fr.* (6)**8**: 585–599.

SAYN, G. 1889. Note sur quelques ammonites nouvelles ou peu connues du Neocomien inférieur. *Bull. Soc. géol. Fr.* (3)**17**: 679–688.

SAYN, G. 1907. Les ammonites pyriteuses des marnes valanginiennes du S.E. de la France. *Mém. Soc. géol. Fr.* (Paléont.) (23) **15**: 29–68.

SCHENK, A. 1888. Die geologische Entwickelung Südafrikas. *Petermanns Mitt.* **34**: 225.

SHARPE, D. 1856. Description of fossils from the secondary rocks of Sundays River and Zwartkops River, South Africa, collected by Dr. Atherstone and A. G. Bain Esq. *Trans. geol. Soc. Lond.* **7**: 193–203.

SOMOGYI, K. 1916. Das Neokom des Gerecse Gebirges. *Mitt. Jb. K. ung. geol. Anst.* **22**: 325.

SPATH, L. F. 1923*a*. On the ammonite horizons of the Gault and contiguous deposits. *Summ. Prog. Geol. Surv.* **1922**: 139–149.

SPATH, L. F. 1923*b*. A monograph of the Ammonoidea of the Gault. *Palaeontogr. Soc.* (*Monogr.*): 1–72.

SPATH, L. F. 1924. On the ammonites of the Speeton Clay and the subdivision of the Neocomian. *Geol. Mag.* **61**: 73–89.

SPATH, L. F. 1930. On the Cephalopoda of the Uitenhage Beds. *Ann. S. Afr. Mus.* **28**: 131–157.

SPATH, L. F. 1939. The Cephalopoda of the Neocomian Belemnite Beds of the Salt Range. *Mem. geol. Surv. India Palaeont. indica*, n.s., (25) **1**: 1–154.

STEVENS, G. R. 1965. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific region. *Palaeont. Bull., Wellington* **36**: 1–283.

STOLICZKA, F. 1870–1871. Cretaceous faunas from southern India. III. The Pelecypoda, with a review of all known genera of this class, fossil and recent. *Mem. geol. Surv. India Palaeont. indica* (6)**3**: 1–537.

TATE, R. 1867. On some secondary fossils from South Africa. *Q. Jl geol. Soc. Lond.* **23**: 139–174.

THIEULOY, J. P. 1964. Un cephalopode remarquable de l'Hauterivien basal de la Drôme: *Himantoceras* nov. gen. *Bull. Soc. géol. Fr.* (7)**6**: 205–214.

THIEULOY, J. P. 1969. Sur la presence de genre *Capeloites* Lissón (Ammonoidea) dans le Néocomien des Basses-Alpes et la signification des especes migratrices transatlantiques. *C. R. somm. Séanc. Soc. géol. Fr.* **7**: 256–257.

THIEULOY, J. P. 1972. Biostratigraphie des lentilles à peregrinelles (Brachiopodes) de l'Hauterivien de Rottier (Drôme, France). *Geobios* **5**(1): 1–53.

THIEULOY, J. P. 1977*a*. Les ammonites boréales des formation néocomiennes du sud-est français (province subméditerranéenne). *Geobios* (10)**3**: 395–461.

THIEULOY, J. P. 1977*b*. La zone à *callidiscus* du Valanginien supérieur vocontien (sud-est de la France). Lithostratigraphie, ammonitofaune, limite Valanginien–Hauterivien, correlations. *Geologie Alpine* **53**: 83–143.

THIEULOY, J. P. & GAZAY, M. 1967. Le genre *Dobrodgeiceras* Nikolov en Haute Provence. *Trav. Lab. Géol. Univ. Lyon*, n.s., **14**: 69–78.

TZANKOV, V. 1943. Contribution à l'étude du genre *Holcostephanus* Neumayr 1875. *Rev. Soc. géol. Bulgare* **14**: 167–206.

UHLIG, V. 1903. Himalayan fossils. The fauna of the Spiti Shales. *Mem. geol. Surv. India Palaeont. indica* (15)**4**: 1–511.

WEAVER, C. E. 1931. Palaeontology of the Jurassic and Cretaceous of west central Argentina. *Mem. Univ. Wash.* (1) **1–15**: 1–469.

WEGNER, R. N. 1909. Uebersicht der bischer bekannten *Astieria*-Formen der ammonitengattung *Holcostephanus* nebst beschreibung zweier neuer Arten. *N. Jb. Miner. Geol. Paläont.* **1**: 77–92.

WESTERMANN, G. E. G. 1954. Monographie der Otoitidae (Ammonoidea). *Beih. geol. Jb.* **15**: 1–364.

WESTERMANN, G. E. G. 1964. Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die taxionomie der Otoitidae. *Palaeontographica* **124**(A): 33–73.

WESTERMANN, G. E. G. *ed.* 1969. Sexual dimorphism in fossil Metazoa and taxonomic implications. *Internat. Union Geol. Sci.* (A)**1**: 1–251.

WESTERMANN, G. E. G. 1971. Form, structure and function of shell and siphuncle in coiled Mesozoic ammonoids. *Life Sci. Contr., R. Ont. Mus.* **78**: 1–39.

WHITEAVES, J. F. 1893. Description of two new species of ammonites from the Cretaceous rocks of the Queen Charlotte Islands. *Can. Rec. Sci.* **1893**: 441–446.

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

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

WILLEY, L. E. 1973. Belemnites from south-eastern Alexander Island: II. The occurrence of the family Belemnopseidae in the Upper Jurassic and Lower Cretaceous. *Bull. Br. Antarct. Surv.* **36**: 33–59.

WINDHAUSEN, A. 1931. *Geologia Argentina.* Segunde parte. Buenos Aires.

WINTER, H. DE LA R. 1973. Geology of the Algoa basin, South Africa. *In:* BLANT, G. (ed.), *Sedimentary basins of the African coasts:* 17–48. Paris: Assoc. Afr. Geol. Surv.

WYLEY, A. 1859. Notes of a journey in two directions across the Colony made in the years 1857–8, with a view to determine the character and order of the various geological formations. Appendix to Parliamentary Report G54. Cape Town.

ZACHAROV, Y. D. 1969. Problems of sexual dimorphism in fossil cephalopods, an important subject in modern systematics (in Russian). *In:* GRAMM, M. N. & KRASSILOV, V. S., *Problems of phylogeny and systematics*: 108–127. Acad. Sci. U.S.S.R., Far East Geol. Inst; All-Union Palaeont. Soc., Vladivostok branch.

ZWIERZYCKI, J. 1914. Die Cephalopodenfauna der Tendaguruschichten in Deutsch-Ostafrika. *Arch. Biontol.* (3)**4**: 7–96.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

M. R. COOPER

REVISION OF THE LATE VALANGINIAN CEPHALOPODA FROM THE SUNDAYS RIVER FORMATION OF SOUTH AFRICA, WITH SPECIAL REFERENCE TO THE GENUS *OLCOSTEPHANUS*