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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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Title: informative but concise, without abbreviations and not including the names of new genera or species
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(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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Footnotes should be avoided unless they are short and essential.

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4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters. If Letraset is used authors are requested to use Helvetica-style lettering, if possible.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al.* 1927) . . .'

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For books give title in italics, edition, volume number, place of publication, publisher.
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **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 ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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MORPHOLOGY, SYSTEMATICS, AND VARIABILITY OF THE SOUTHERN AFRICAN SOFT CORAL *ALCYONIUM VARIABILE* (J. STUART THOMSON, 1921) (OCTOCORALLIA, ALCYONIIDAE)

By

GARY C. WILLIAMS

Cape Town Kaapstad

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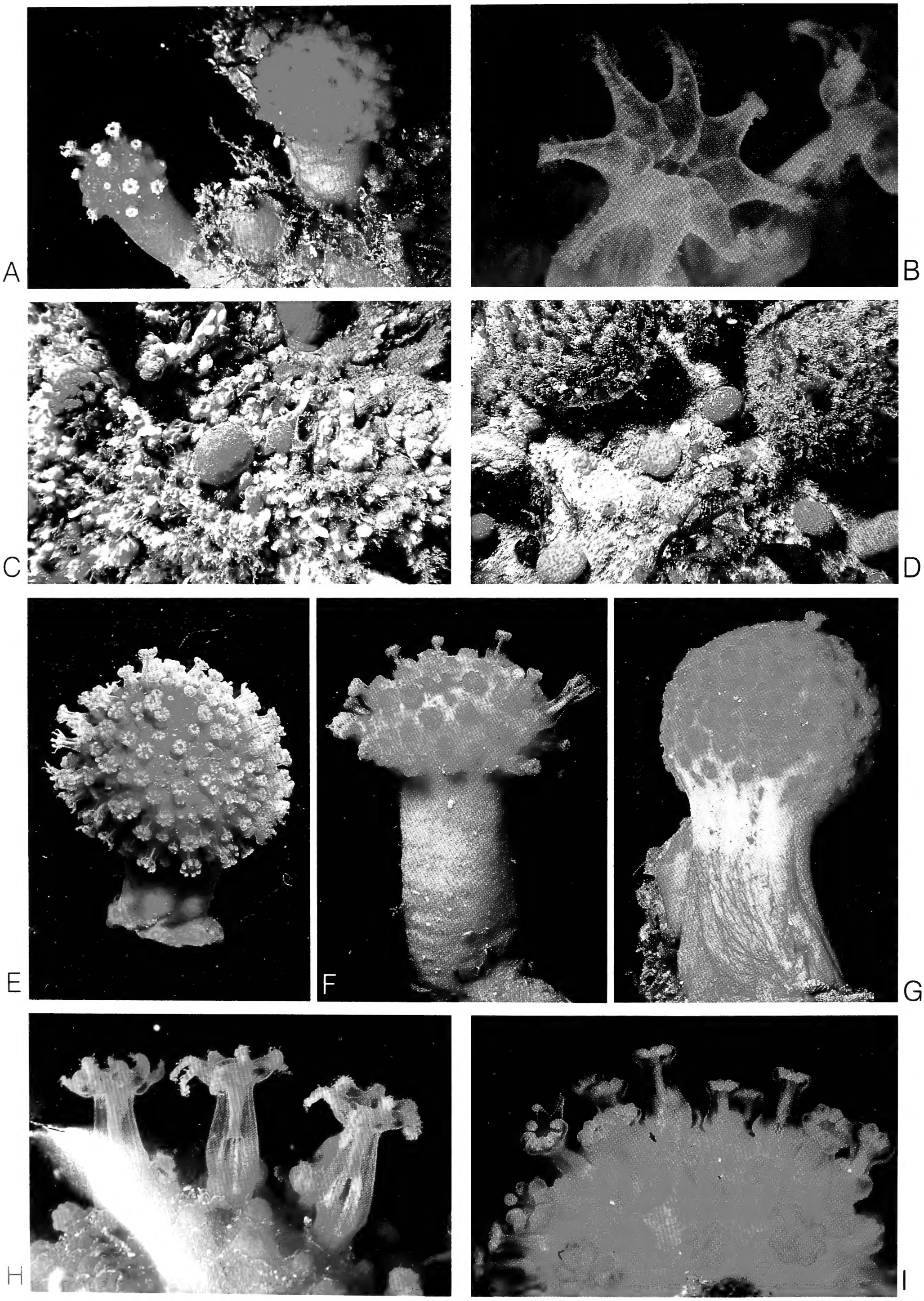

Fig. 1. Living colonies of *Alcyonium variabile*. A. Red and yellow morphs. B. Peristome from colony of yellow morph. C. Underwater photograph showing two colonies of the red morph. D. Underwater photograph showing red and yellow morphs in close proximity. E. Red morph. F. Yellow morph. G. Red, yellow, and pink variety from the eastern Cape Province. H. Three polyps from capitulum of red morph. I. Detail of capitulum of yellow morph.

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By

Gary C. Williams

Marine Biology Department, South African Museum, Cape Town

(With 15 figures and 1 table)

[*MS accepted 7 October 1985*]

ABSTRACT

The fungiform alcyoniid soft coral, *Alcyonium variabile*, is shown to be widely distributed in the colder waters of southern Africa at depths of 13–468 m. New phenotypes from a shallow-water population found off the Atlantic side of the Cape of Good Hope Peninsula add further evidence of extreme intraspecific colour variation. Aspects of morphological variation, anatomy, colour polymorphism, sclerite structure, and geographic distribution are described. The systematic status of the species and its relations to other species of *Alcyonium* as well as other alcyoniid genera are discussed. *Alcyonium fungiforme* Tixier-Durivault, 1954, *A. luteum* Tixier-Durivault, 1954, and *Metalcyonium variabile* Thomson, 1921, are considered synonyms of *A. variabile*.

CONTENTS

INTRODUCTION

Alcyonium variabile (J. Stuart Thomson, 1921) is a highly variable, often beautifully coloured soft coral from southern Africa. The history of the literature pertaining to this species, as well as to the genera *Alcyonium*, *Metalcyonium*, *Bellonella*, *Cactogorgia*, and *Nidalia*, has been plagued with considerable confusion. This is partially due to an often high degree of intraspecific variation,

Ann. S. Afr. Mus. **96** (6), 1986: 241–270, 15 figs, 1 table.

the dubious nature of the original descriptions of some genera such as *Metalcyonium*, the lack of attention by some previous investigators to correct identification of material or accurate comparison with other known species, and the lack of clear and consistent morphological distinctions between nominal genera.

Previously published accounts have been purely taxonomic in nature; virtually nothing has been recorded on other aspects of the biology of this species. Previous workers relied on preserved material that was either dredged or trawled from deep water. Observation of subtidal octocorals in their natural habitats was technically unfeasible. Study of living colonies *in situ* was made possible by the advent of SCUBA, but still very little is known about the ecology, natural history, and other aspects of the biology of most octocoral species.

Alcyonium variabile has previously been known only from depths exceeding 47 m. A survey of the shallow sublittoral regions of the western side of the Cape Peninsula by use of SCUBA has revealed a presumably large but previously unrecorded polymorphic population. This paper presents an examination of various aspects of the biology of this species from southern Africa, together with an assessment of its great variability. An examination of the systematics of the species and a discussion of the status of related genera is also presented.

Alcyonium variabile has been confused in the past with other species of *Alcyonium* such as *A. paessleri* May, 1899, from Patagonia and Antarctica. These species are here considered separate and a comparison of the two is presented.

This paper attempts to unify the many known colour varieties of *Alcyonium variabile* (many of which were previously assigned specific status) into a single highly variable species based on consistencies in sclerite distribution and form as well as other comparative morphological aspects.

The material is deposited in the South African Museum, Cape Town (SAM).

MATERIAL EXAMINED

SAM–H3165 and H3166: 10 specimens, 23 m depth, Hottentots Huisie, western side of Cape Peninsula (33°59′S 18°21′E); 15 June 1983; coll. W. R. Liltved, SCUBA.

SAM–H3167: 12 specimens; 13–16 m depth, Hottentots Huisie, western side of Cape Peninsula (33°59′S 18°21′E); 18 August 1983; coll. G. C. Williams, SCUBA.

SAM–H3602: 1 specimen; 90 m depth, off East London (33°12′S 28°01′E); 17 July 1984; coll. G. C. Williams (R.V. *Meiring Naude*, XX 51), dredge.

SAM–H3271: 1 specimen; 26 m depth, off Llandudno, western side of Cape Peninsula (34°01′S 18°20′E); 4 February 1984; coll. G. C. Williams, SCUBA.

SAM–H1042: 2 specimens; 148–159 m depth, 16 km SW of Cape Point (34°27′S 10°23′E); 28 October 1903; SS *Pieter Faure* survey, PF 18171, large trawl.

SAM–H895: 5 specimens; 82 m depth; 10 km E of Cape Morgan (32°44′S 28°30′E); 13 August 1901; SS *Pieter Faure* survey, PF 13388A, dredge.

SAM–H1040: 8 specimens; 141 m depth; 17 km E of Cape Morgan (32°44′S 28°30′E); 26 July 1901; SS *Pieter Faure* survey, PF 13174, dredge.

SAM–H924: 5 specimens; 86 m depth; 36 km SE of Tugela River mouth, Natal (29°20′S 31°30′E); 29 January 1901; SS *Pieter Faure* survey, PF 11537, large dredge.

SAM–H3245: 2 specimens; 168 m depth; 30 km S of Cape Hangklip (34°39′S 18°42′E); 10 February 1948; coll. University of Cape Town Ecological Survey Collection, Station AFR 882J, dredge.

SAM–H883: 7 specimens; 95 m depth; 18 km S of Knysna Heads (34°10′S 23°15′E); 2 July 1902; SS *Pieter Faure* survey, PF 15291, shrimp trawl.

DESCRIPTION

Class ANTHOZOA Ehrenberg, 1834

Subclass OCTOCORALLIA Haeckel, 1866

Order ALCYONACEA Lamouroux, 1816 (emended by Verrill, 1866; Bayer, 1981)

Family **Alcyoniidae** Lamouroux, 1812

Genus *Alcyonium* Linnaeus, 1758

Alcyonium variabile (Thomson, 1921) comb. nov.

Figs 1–15

Alcyonium antarcticum (*non* Wright & Studer, 1899) Hickson, 1900: 73.
Alcyonium (*Metalcyonium*) *patagonicum* (*non* May, 1899) Kükenthal, 1906: 47 (*partim*).
Metalcyonium patagonicum (*non* May, 1899) Thomson, 1910: 562.
Metalcyonium variabile Thomson, 1921: 152; 1924: 47, 69.
Metalcyonium variabile var. *molle* Thomson, 1921: 162; 1924: 47, 69.
Metalcyonium variabile var. *durum* Thomson, 1921: 165; 1924: 47, 69.
Alcyonium paessleri (*non* May, 1899) Molander, 1929*a*: 50; 1929*b*: 4 (*partim*).
Alcyonium fungiforme Tixier-Durivault, 1954: 385.
Alcyonium luteum Tixier-Durivault, 1954: 388.

Morphology and sclerites

The colonies examined range in total length from 8 to 70 mm. They are mushroom-shaped; composed of a spherical capitulum and a conspicuous stalk (Fig. 1). Both parts are separated by a clear delimitation (Fig. 2A).

The globular capitulum is wider than the stalk. The surface layer is filled with closely-set sclerites. They vary from stout coarsely tuberculate rods less than 0,22 mm long to capstans less than 0,08 mm long (Figs 3A, 4A–D). Some rods may be clubbed. Capstans may predominate in some colonies. Some capstans may be modified and sharply pointed tubercles. The sclerites from the interior of the capitulum are usually arranged parallel to the gastric cavities. They are

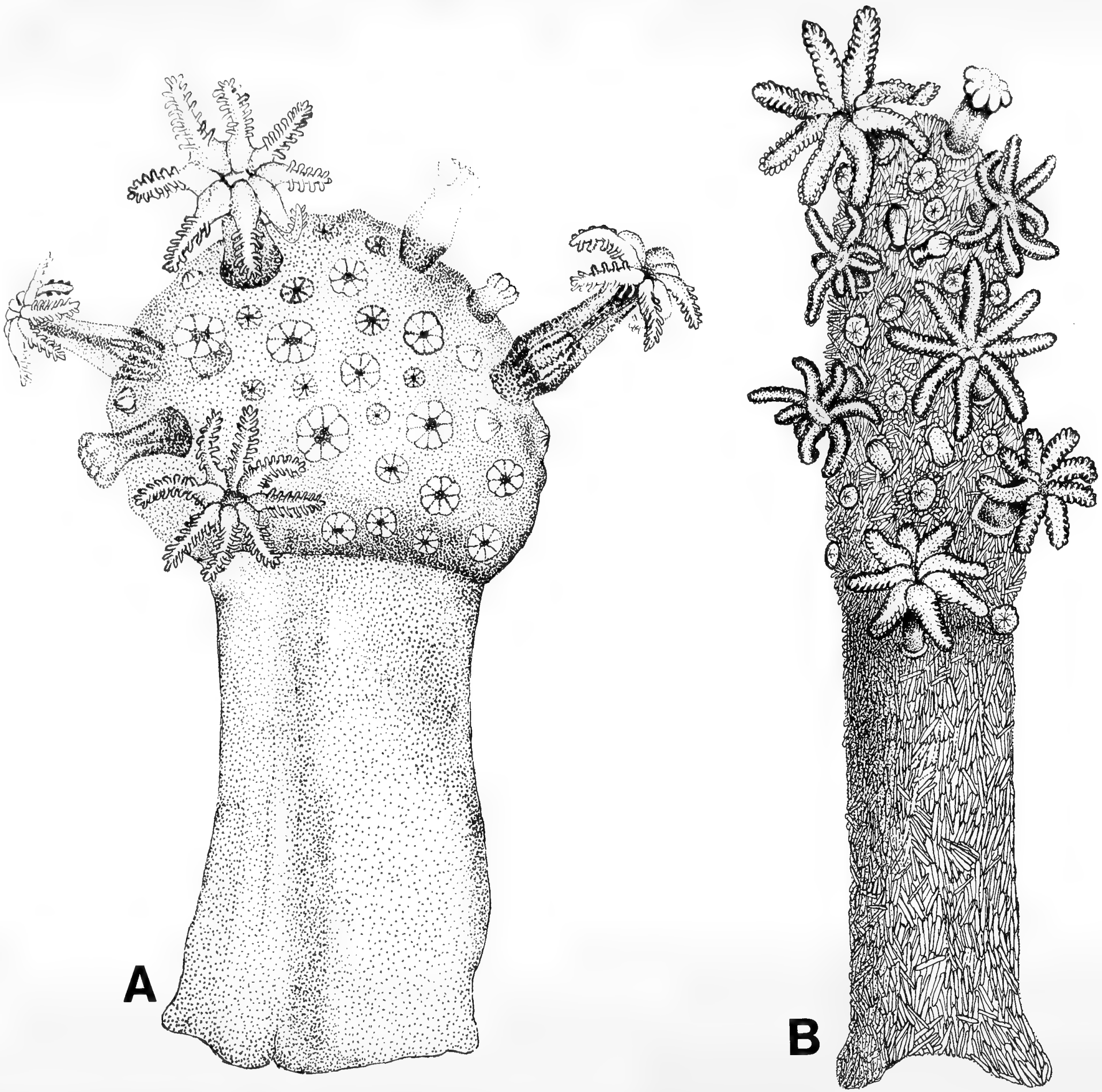

Fig. 2. A. *Alcyonium variabile* showing typically fungiform–capitate colony shape (40 mm total length). B. Digitiform colony shape characteristic of many alcyoniid species; *Metalcyonium unilobatum* (Thomson, 1921) is shown as an

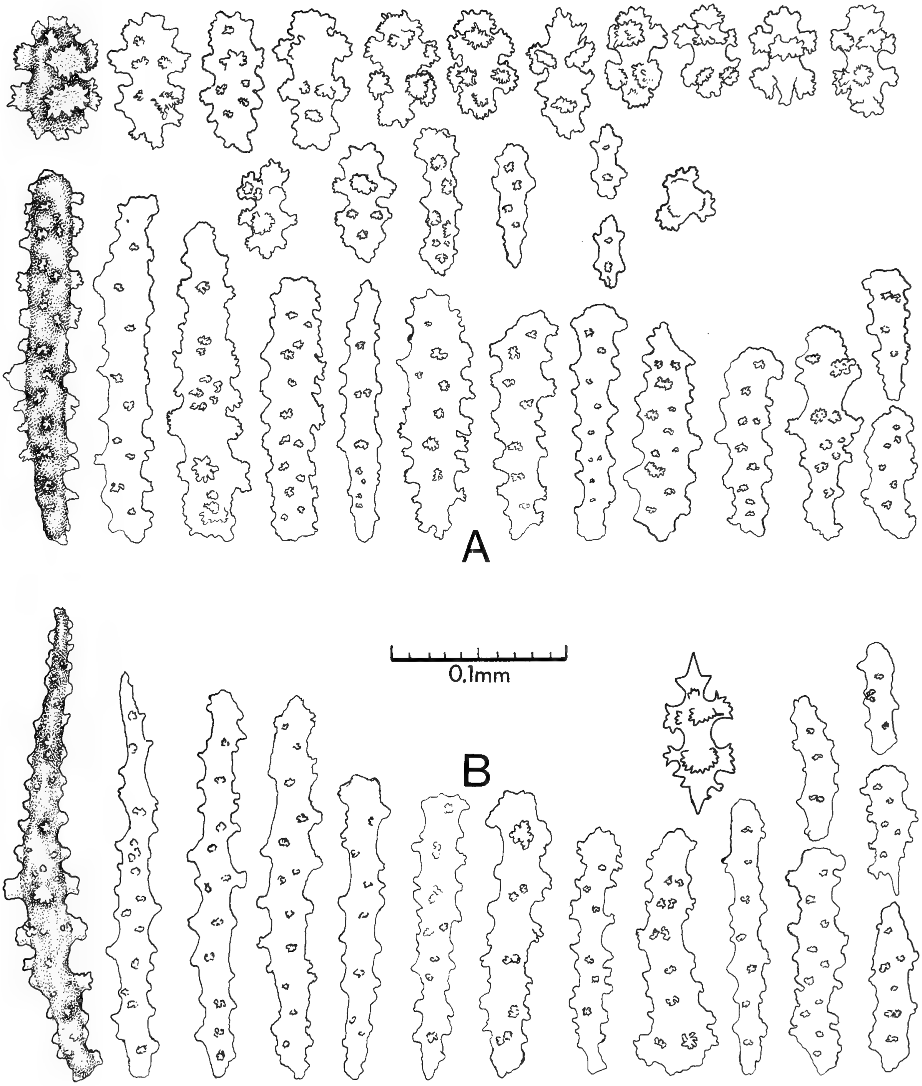

Fig. 3. *Alcyonium variabile*. A. Capitulum sclerites from surface coenenchyme. B. Capitulum sclerites from inner coenenchyme.

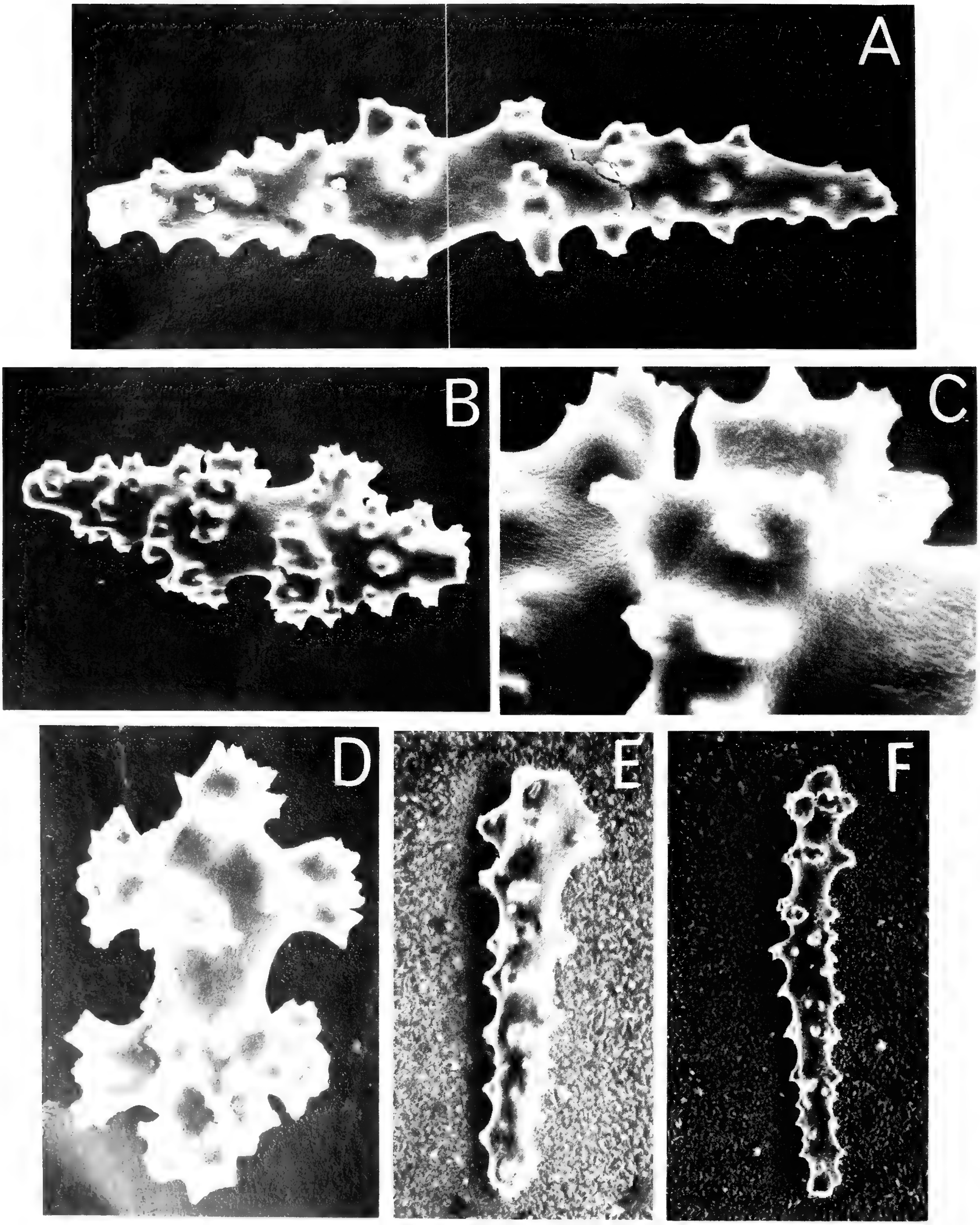

Fig. 4. *Alcyonium variabile*. Scanning electron micrographs of capitulum sclerites. A–D. Sclerites of outer coenenchyme. A. Spindle, 0,17 mm. B. Club, 0,12 mm. C. Detail of middle portion of club in B, 0,03 mm. D. Capstan, 0,07 mm. E–F. Slightly clubbed rods of the inner coenenchyme. E. 0,15 mm. F. 0,25 mm.

predominantly rods, sometimes slightly clavate, often with coarse to ornate tubercles, and vary from approximately 0,07 to 0,27 mm in length (Figs 3B, 4E–F). Modified, sharply pointed capstans may also occur.

The polyps are restricted to the entire surface of the capitulum. When fully expanded they may reach a length of 12 mm. In expanded condition the polyp shows two differentiated regions: the basal or proximal region and the distal anthocodia (Fig. 5A). The proximal portions possess varying concentrations of capstans or double cones, from 0,04 to 0,12 mm in length. These sclerites are relatively consistent in form and size (Figs 6C, 7C–F). Partially retracted polyps can form rounded calyx-like protuberances on the surface of the capitulum; however, these are not permanent calyces since they are not rigid and are capable of total retraction into the capitulum (Fig. 1G). The anthocodia consists of three parts: the neck zone or introvert, the anthocodial wall with crown and points, and the tentacles (Fig. 5A). Sclerites of the crown, points, and tentacles are rods and spindles of varying length and coarseness (Fig. 6A). The neck zone is usually unarmed and translucent—the pharynx and the mesenterial filaments are plainly visible through it. In one red colony from the western Cape Peninsula, the polyps possess sparsely scattered capstans in the neck zone. The crown consists of 6–12 tiers of very slender sclerites. These are finely tuberculated needles up to 0,6 mm in length (Fig. 8A, E). Superposing the crown are eight points, each consisting of numerous spindles of which the undermost are arranged *en chevron*; more distally they are longitudinally placed (Fig. 5A). The point sclerites are mostly very similar to those of the crown, but distally some may be shorter and more coarsely tuberculated (Fig. 8B–D). The tentacles are narrow and reach a length of 2,5 mm. On each side they bear one row of approximately 12 pinnules (Fig. 5B). The backs of the tentacles are armed proximally with the uppermost point sclerites, and distally with short spindles or coarse rods usually less than 0,13 mm in length (Figs 6A, 8F–G). These sclerites are not arranged in any distinctive alignment or pattern (Fig. 5A). Rod-like sclerites may also occur in between the bases of most pinnules (Fig. 5B). Similar short spindles or rods may occur along the grooves of the peristome in a radial pattern of eight lines extending from the mouth to the areas between the bases of the tentacles (Fig. 5C). The wall of the pharynx is strongly impregnated with many short spindles or rod-like sclerites. These are coarsely tuberculated and usually less than 0,14 mm in length (Figs 6B, 7A–B).

The stalk is barren, being completely devoid of anthocodiae. The height of the stalk is variable (Fig. 12). The base may produce finger-like or flattened projections forming a holdfast. The surface layer of the stalk contains densely set sclerites that are almost exclusively capstans varying in length from 0,05 to 0,10 mm (Figs 9A, 10A–C). In the interior of the stalk there are mainly large stout spindles or clubbed forms that are ornately tuberculated. They vary from 0,10 to 0,28 mm in length and up to 0,06 mm in width. Modified, pointed capstans may occur rarely (Figs 9B, 10D–G).

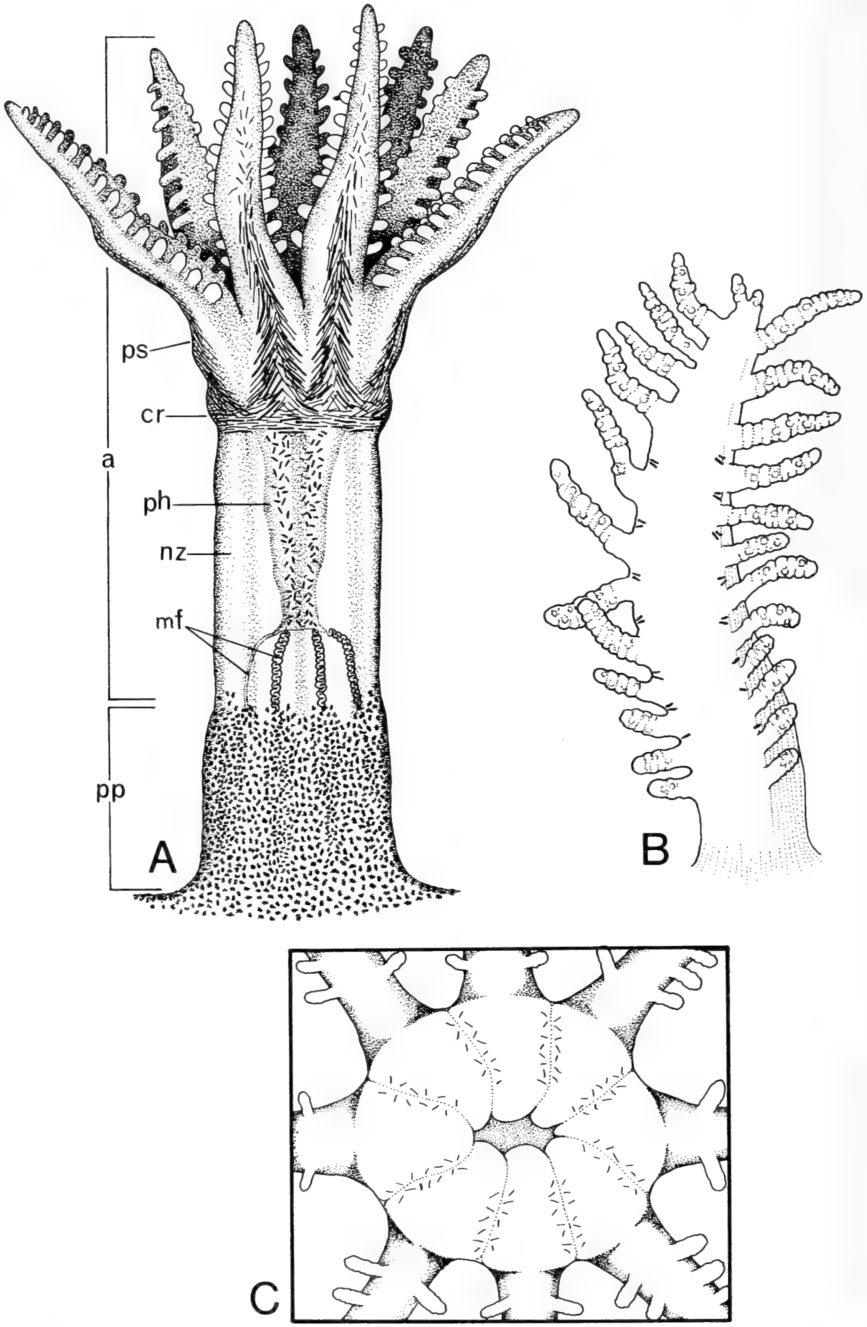

Fig. 5. Polyp armature of *Alcyonium variabile*. A. Expanded polyp showing capstans forming calyx-like proximal region, short spindles of the pharynx, and long spindles of the anthocodia; total length of polyp 9 mm. B. Single tentacle showing rod-like sclerites at the base of the pinnules; total length of tentacle 2,5 mm. C. Peristome showing alignment of rod-like sclerites; diameter of disc 2 mm.
a–anthocodia, cr–crown, mf–mesenterial filament, nz–neck zone, ph–pharynx, pp–proximal region of polyp, ps–points.

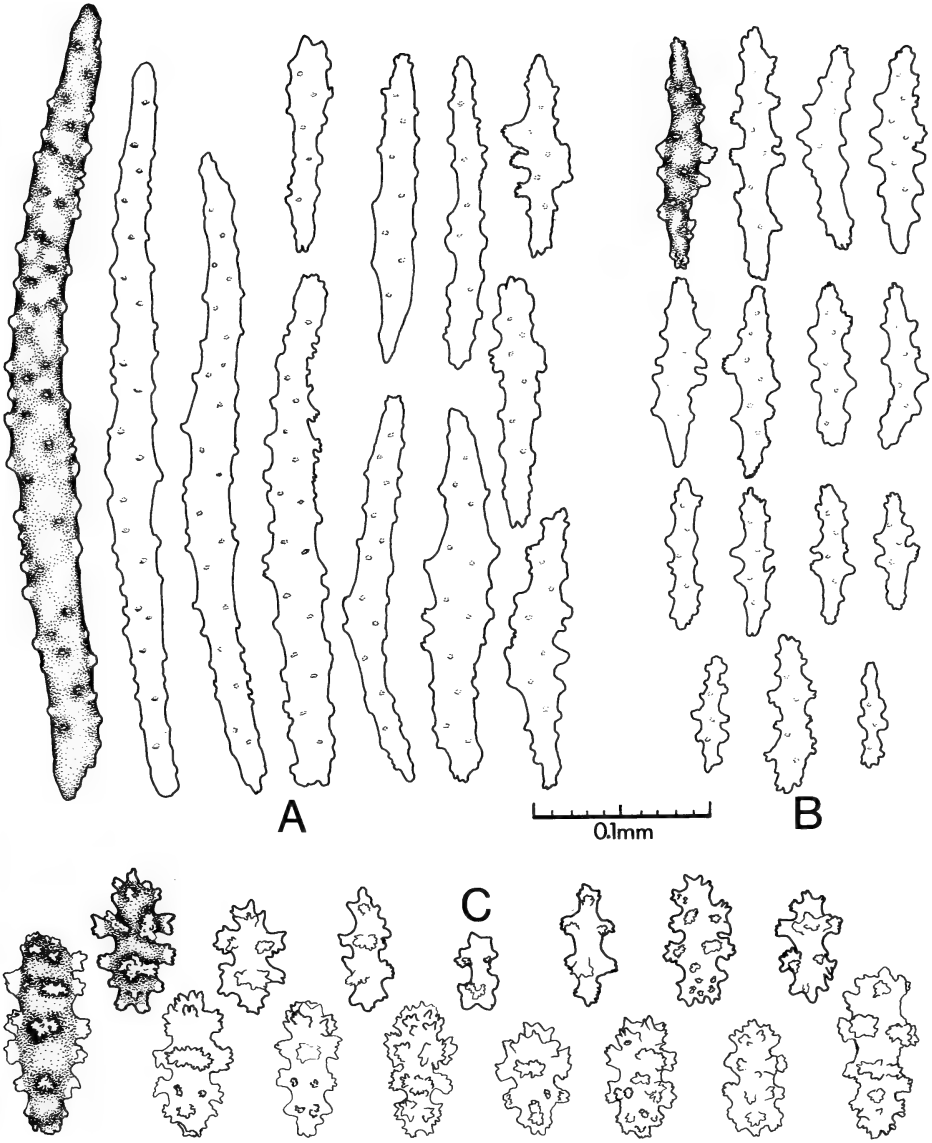

Fig. 6. *Alcyonium variabile*. A. Polyp sclerites from crown, points, and tentacles of anthocodia. B. Polyp sclerites from wall of pharynx. C. Polyp sclerites from wall of proximal region of polyp.

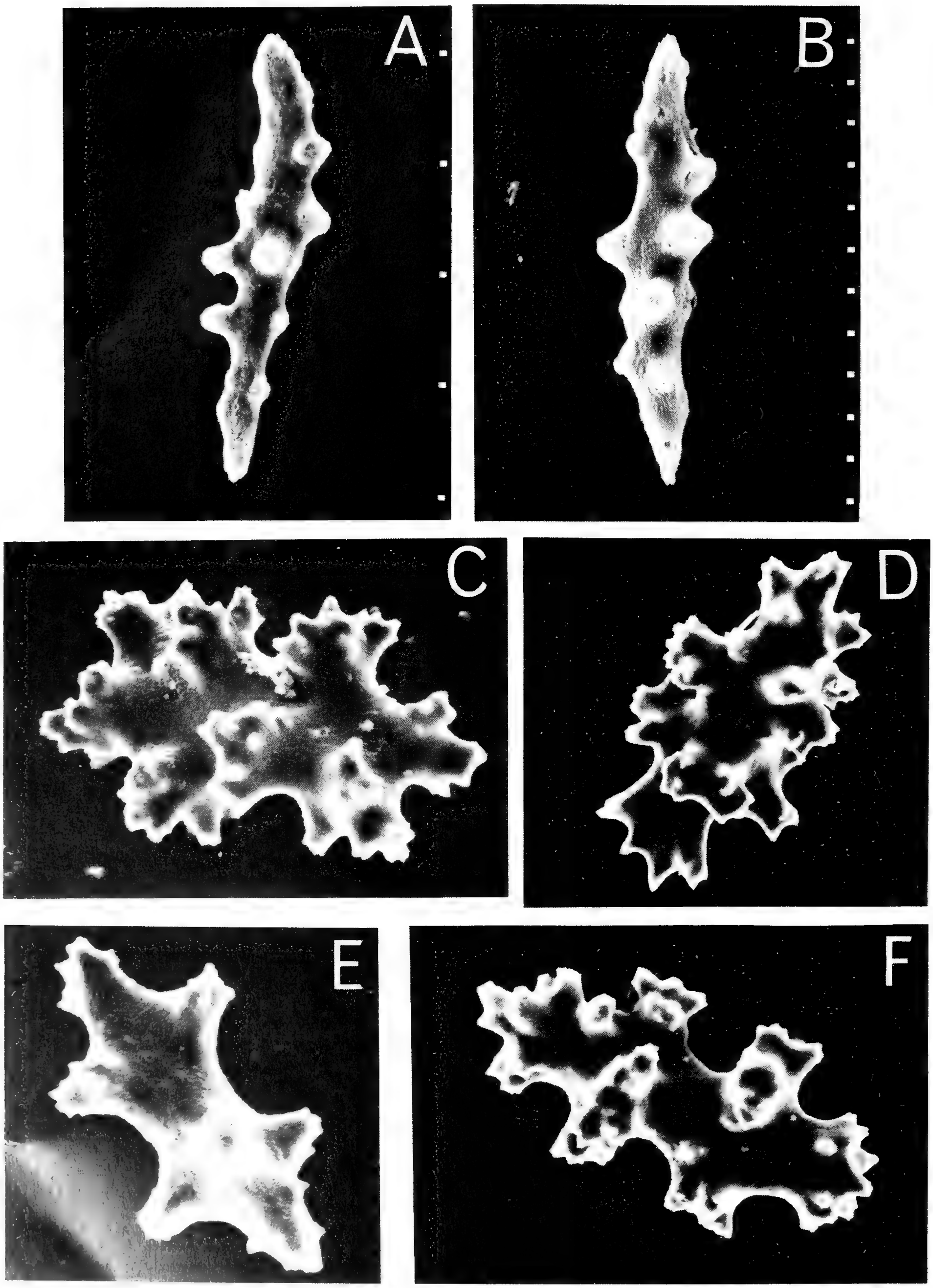

Fig. 7. *Alcyonium variabile*. Scanning electron micrographs of sclerites from pharynx and calyx-like base of polyp. A–B. Spindles of pharyngeal wall. C–F. Capstans from wall of proximal region of polyp. A. Scale between squares 30 μm (0,12 mm total length). B. Scale between squares 10 μm (0,11 mm total length). C–E. 0,07 mm. F. 0,09 mm.

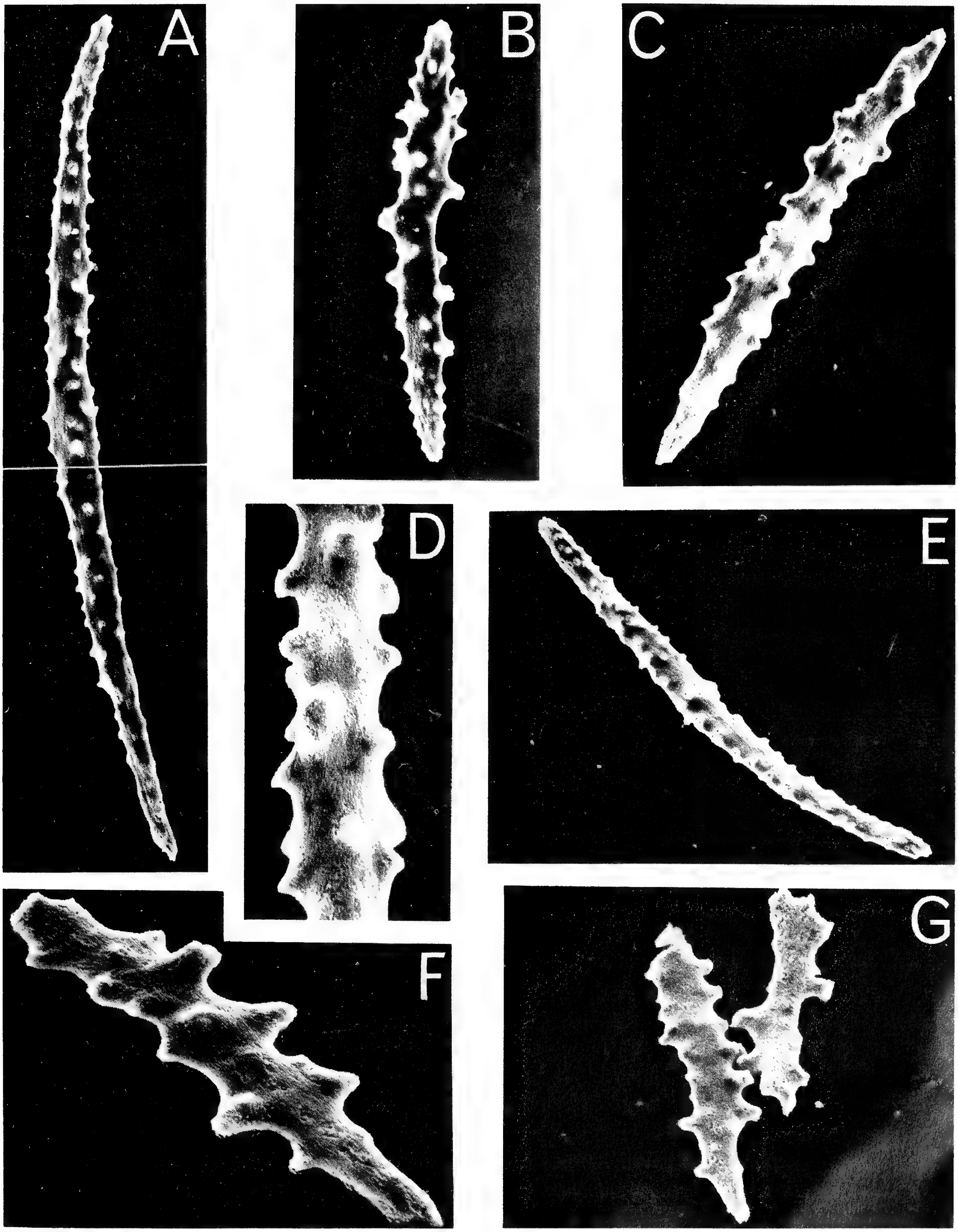

Fig. 8. *Alcyonium variabile*. Scanning electron micrographs of anthocodial sclerites. A. Needle from crown, 0,60 mm. B–C. Spindles from points. B. 0,21 mm. C. 0,23 mm. D. Detail of central portion of spindle in C; length of photograph 0,09 mm. E. Needle from crown, 0,37 mm. F–G. Rod-like sclerites from distal portion of tentacles. F. 0,12 mm. G. 0,12 and 0,09 mm.

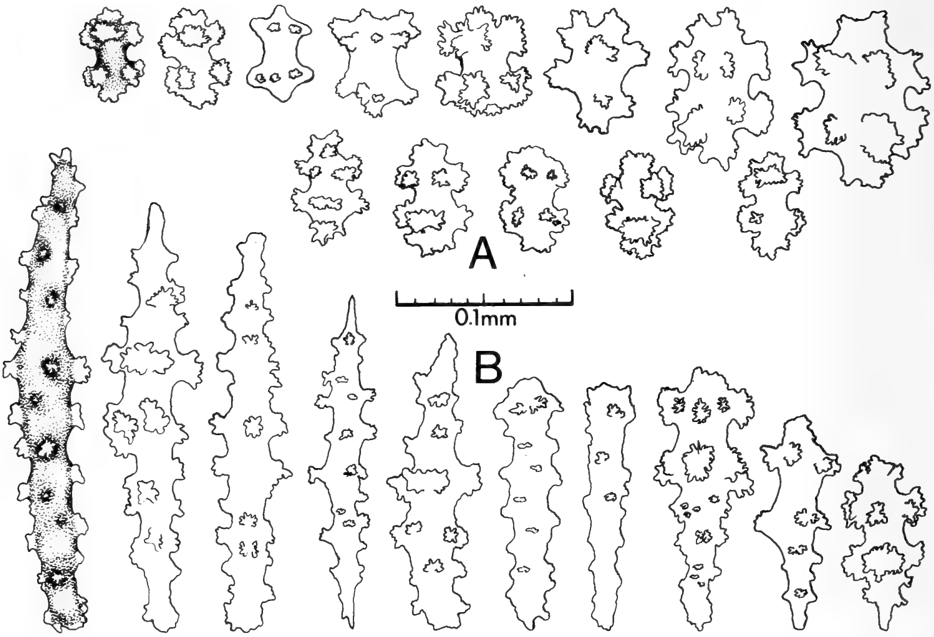

Fig. 9. *Alcyonium variabile*. A. Stalk sclerites from surface coenenchyme. B. Stalk sclerites from interior coenenchyme.

Anatomy

A 35 mm-long red-purple colony collected from the sublittoral of the Cape Peninsula (SAM–H3166) was sectioned longitudinally. The epidermis is a thin transparent layer, which separates readily from the underlying mesogloea. The coenenchyme consists partially of an outer area approximately 0,16 mm thick. This region is very densely imbedded with primarily red capstans, giving a rough textured appearance to the colony. Below the outer layer is the inner coenenchyme, which fills the interior of the colony between the tube-like polyps. The colour of this region is pink due to the combined effect of white mesogloea and gastrodermis and light-red sclerites. Numerous spindles and clubbed forms are contained in the region just below the outer coenenchyme. These sclerites become less dense toward the interior of the capitulum and stalk regions. The interior coenenchyme adjacent to the gastric cavities is profusely set with clear to light-reddish spindles approximately 0,22 mm in length. Many of the gastric cavities contain spherical ova varying in diameter between 0,06 and 0,12 mm. The gastrodermal solenial network is readily visible in the inner coenenchyme below the outer layer of the capitulum. The long thin gastric cavities extend to the base of the stalk. Anthocodiae are in varying states of contraction and retraction. The eight-ridged protuberances of the calyces of some polyps are readily visible (Fig. 11).

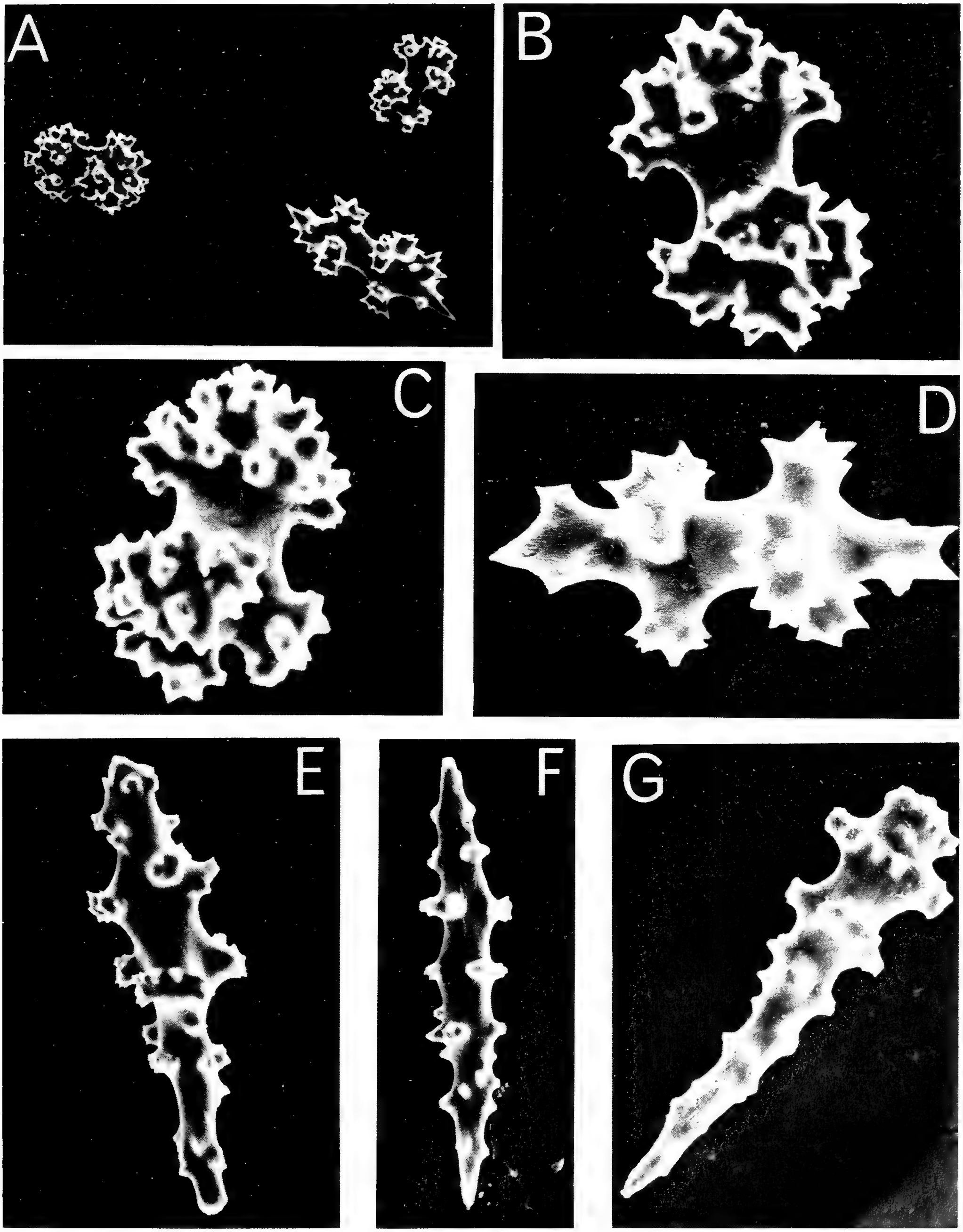

Fig. 10. *Alcyonium variabile*. Scanning electron micrographs of stalk sclerites. A–C. Capstans from outer coenenchyme. A. 0,06–0,13 mm. B. 0,07 mm. C. 0,08 mm. D–G. Sclerites from inner coenenchyme. D. Modified capstan, 0,10 mm. E. Clubbed spindle, 0,20 mm. F. Spindle, 0,20 mm. G. Club, 0,17 mm.

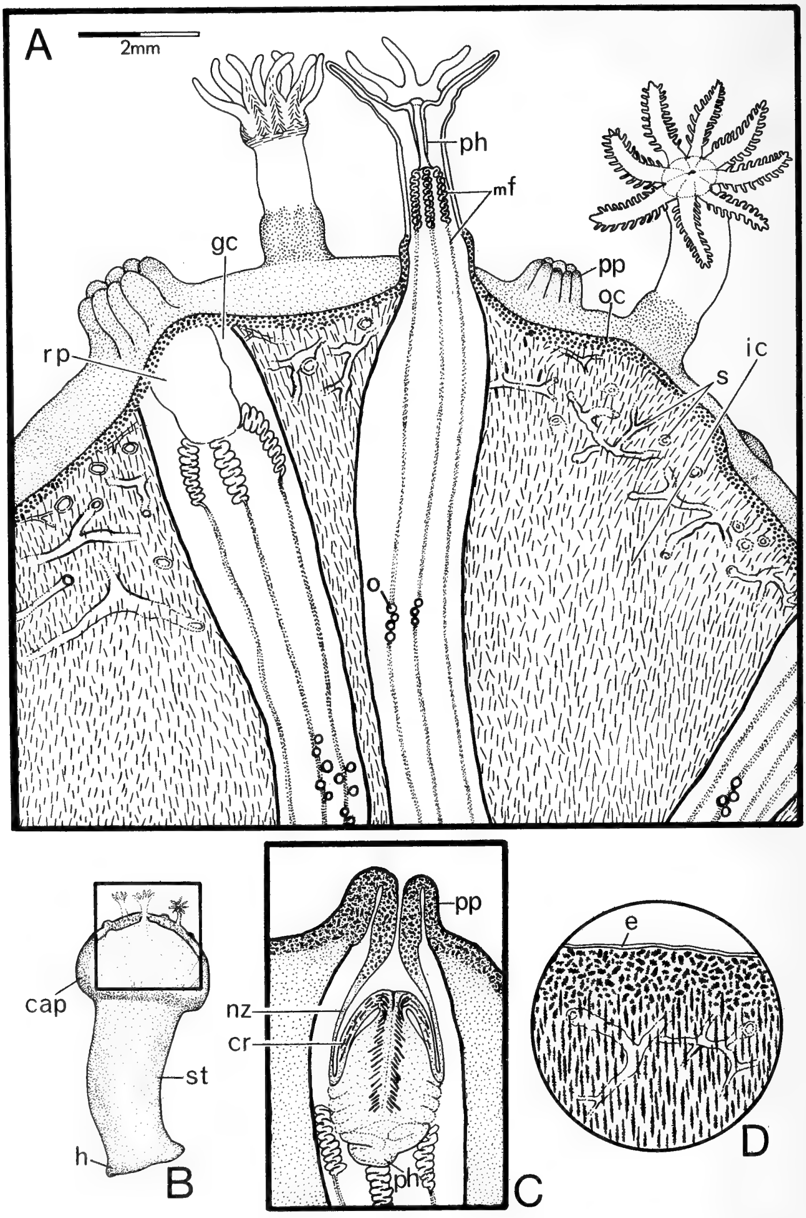

Fig. 11. Anatomy of *Alcyonium variabile*. A. Longitudinal section through capitulum of 35 mm-long colony from the Cape Peninsula. B. Area of section (shown enlarged from A) from the entire colony. C. Longitudinal section of a retracted polyp; sclerites of interior coenenchyme omitted; width of diagram 4 mm. D. Detail of section through coenenchyme of capitulum showing thin outer layer of capstans and interior of spindles; diameter of diagram 1 mm.
cap–capitulum, cr–crown, e–epidermis, gc–gastric cavity, h–holdfast, ic–interior coenenchyme, mf–mesenterial filament, nz–neck zone, o–ova, oc–outer coenenchyme, ph–pharynx, pp–proximal region of polyp, rp–retracted polyp, s–solenial tubes, st–stalk.

Variability and coloration

The high degree of variability found in many sedentary organisms, such as octocorals, due to isolation of populations, lack of mobility and ephemeral larval stages, has been noted by several authors (Thomson 1921: 166; Hickson 1907*a*: 25–36).

Alcyonium variabile is remarkable in that the colonies often resemble young mushrooms of the genus *Amanita* in shape, appearance, and even colour in some instances. The most extraordinary aspect of the nature of this species is its extreme intraspecific variability, particularly in regard to external coloration. Stalk development is also variable. Sclerite form and distribution are the most consistent and least variable characteristics between geographically isolated populations or individual colonies, and serve to unify the various widespread populations into one highly variable species. These southern African populations exemplify a wide range of variability in regard to coloration (Table 1).

Most southern African material is known to have a well-developed barren stalk, the length of which may exceed twice the diameter of the capitulum. In some colonies from the southern Transkei and East London regions the stalk is reduced in size: the spherical capitulum arises from a very short stalk with a spreading base (Fig. 12). The development of the stalk is considered a variable feature in other species as well. In the original description of *Metalcyonium capitatum*, Pfeffer (1889: 50) states that the colony has the appearance of a young mushroom, being short-stemmed with a bulbous head, or the stalk is entirely missing and the entire colony is of a head-like shape.

It appears that both continuous and polymorphic colour variation are exhibited in populations of *Alcyonium variabile*. The recently discovered localized populations of *A. variabile* from the western side of the Cape Peninsula are remarkable in that they exhibit distinctive polymorphism. The individual colonies of the populations are morphologically very consistent but are sharply differentiated and discontinuous in colour due to the striking permanent coloration of calcium carbonate sclerites that are embedded in the outer coenenchyme.

The populations are obviously dimorphic as two clearly delineated colour morphs can be recognized (Fig. 1):

Yellow morph. The colonies are a golden-yellow to yellowish-orange. In some colonies the stalk may have a slightly rose tint due to some sclerites of the outer coenenchyme being red. The armature of the anthocodial crowns and tentacles is usually composed of deep orange-yellow sclerites.

Red morph. The colonies are red to mauve to vivid reddish-purple. The armature of the anthocodiae within a given colony may be composed of either all red or all yellow sclerites. The pharyngeal sclerites may also be yellowish or light red; these combined give the anthocodiae as a whole a pinkish-white or yellowish appearance.

TABLE 1

Colour variability in *Alcyonium variabile*.

Locality	Calyx	Capitulum	Stalk
W side of Cape Peninsula, Cape Agulhas region	mauve to red	mauve to red	mauve-red to pinkish
NW side of Cape Peninsula	orange-yellow	golden-yellow to orange-yellow	orange to pinkish-orange
SW of Cape Point	white	white	white
SW of Cape Point	rose	white	brownish-white
S of Cape Hangklip, Knysna	yellow	yellow	white to yellowish-white
East London	brownish-white	brownish-white	brownish-white
East London	mauve-pink	mauve-pink	brownish-white
East London	pinkish-tan	pinkish-tan	pinkish-tan
East London	orange	red	yellowish
East London	yellow	white	tan
East London	yellow	yellow	pink
East London	white to yellow	white to yellow	yellowish
East London	red	yellow	pinkish-white to reddish
East London	greyish-white	greyish-white	greyish-white
East London	red	pink	pink
East London	yellow	orange	pinkish-white
East London	pale pink	pale pink	pinkish-white
East London	red	yellow	white
East London	yellow	red	reddish
Cape Morgan	orange-red	yellow	yellow to white
Cape Morgan	salmon-pink	salmon-pink	salmon-pink
Cape Morgan	bright yellow	light orange	pinkish-white
Cape Morgan	yellow	salmon-orange	salmon-orange
Cape Morgan	red	yellow	yellow
Sandy Point	yellow	yellowish-white	pinkish-white
Sandy Point	yellow	orange to red	yellowish-white to rose
Sandy Point	red to red-violet	white to yellowish	white to yellowish
Sandy Point	red	white to reddish	white to pink
Port Grosvenor	red	white to reddish	white to pink
Durban, Cape Morgan, East London	yellow	yellow	yellow
Tugela River, Cape Morgan	red	white	white
Tugela River, Durban, Port Shepstone, Cape Morgan	yellow	orange to red	white to pink

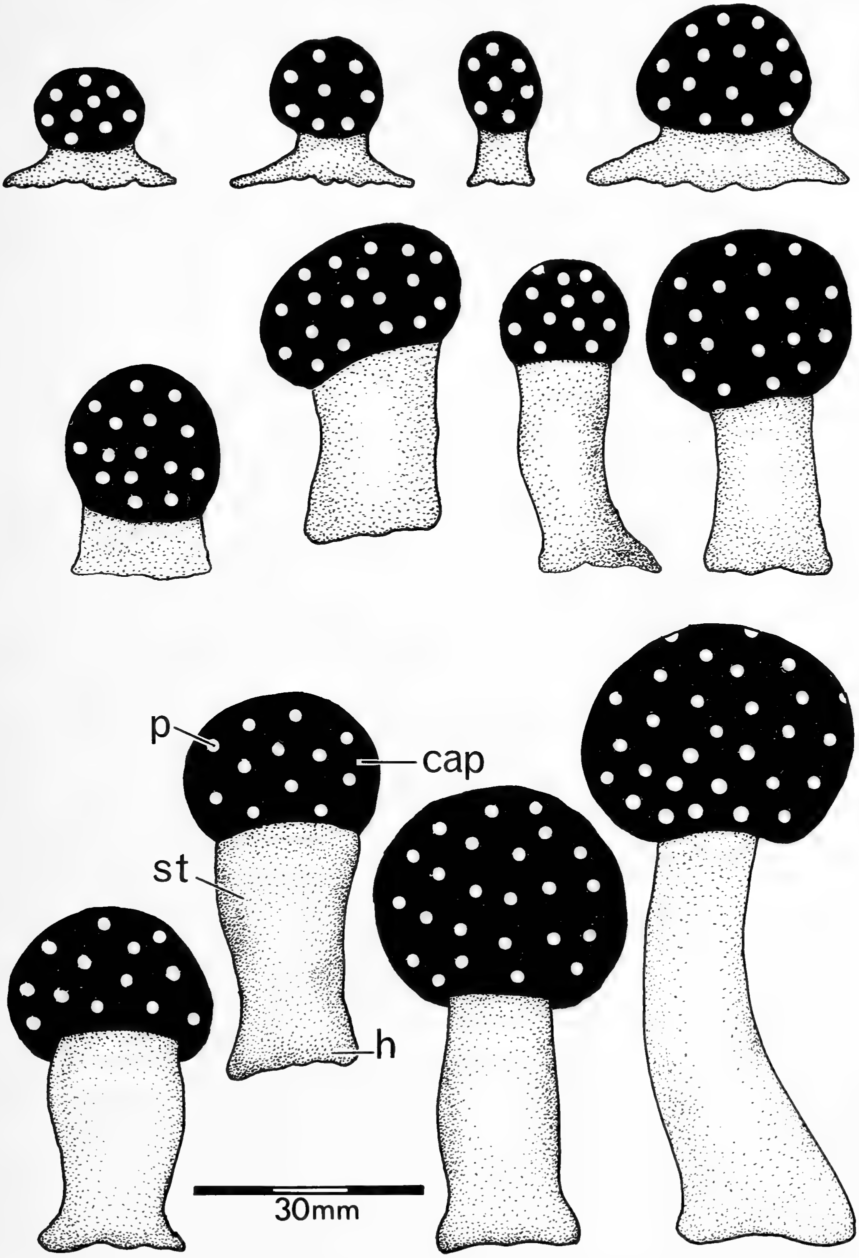

Fig. 12. Variability of colony shape and stalk development in *Alcyonium variabile*. Polyp-bearing portion (capitulum) is differentiated from stalk or base.
cap–capitulum, h–holdfast, p–polyp, st–stalk.

In both morphs, within a given colony, the calyces and outer coenenchyme of the capitulum and stalk are uniformly coloured. Thus, a colony is entirely red or yellow. The sclerites in both morphs exhibit tints of red or yellow: sclerites of other colours have not been observed.

The individual colonies of the yellow or red morphs can occur sympatrically and may grow as little as 10 mm apart at depths of 13–30 m. Individual colonies have been observed to be as much as 55 mm in total length. At Hottentots Huisie, these two morphs are apparently equally represented. At Llandudno and Kommetjie (34°09′S 18°18′E), however, the red morph is frequently encountered while the yellow morph has not been observed. The yellow morph seems to be confined to the Atlantic side of the Cape Peninsula, while the red morph is also common off the Cape Agulhas region between 24 and 54 m in depth.

A white form, known only from deeper water (150–163 m) off Cape Point, has not been found in association with either of the other two morphs. It is known only from five large colonies (52–71 mm in total length) described by Thomson (1921: 165), collected in 1903 by trawl. Thomson relegated this form to the complex he named *Metalcyonium variabile* var. *molle*. The colonies are a uniform bright white as sclerites from all parts of the colony are white.

All observed colonies of the dimorphic populations, as well as the white form, have in common a well-developed and conspicuous stalk. The stalk is at least as long as the height of the capitulum and is commonly up to twice its height. One colony of the white form has a stalk length three times the height of the capitulum. This is the maximum known development of the stalk for the species.

The numerous colonies that have been collected from Cape Point to Natal exhibit a more continuous variation. The many populations sampled by the SS *Pieter Faure* surveys from 1898 to 1906 and the R.V. *Meiring Naude* dredge surveys from 1981 to 1985 exhibit the following differences from the dimorphic populations and the white form of the western Cape Peninsula: (a) none of the specimens exceed 40 mm in total length; (b) stalk length is variable, from less than half the height of the capitulum to approximately twice the height; (c) colonies are known only from deeper water (47–480 m); (d) colonies are rarely monochromatic, usually bicoloured or tricoloured. The stalk, capitulum, and proximal portions of polyps often exhibit different colours. A wide range of colour combinations exists (Table 1). The stalk varies from whitish to pale rose to yellowish, while the surface of the capitulum can be white or greyish-white, yellow, orange, or red. The calyces of an individual colony are either all red or all yellow. Some very striking and beautiful combinations are thus evident.

The colour of all colonies observed is due to the permanent coloration of the sclerites, for the colonies contain little if any alcohol-soluble pigment. Colour has been observed to be well preserved in material maintained in ethanol for over eighty years. Colour patterns are extremely varied and often very striking.

The colour of the individual sclerites ranges from rich orange-yellow, light lemon-yellow, deep red to maroon or mauve, to white or almost translucent.

Some spindles are observed to be reddish towards one end and transparent towards the opposite end.

Capitulum or stalk sclerites of the outer coenenchyme are often quite vividly coloured, while those of the interior coenenchyme are only slightly tinted with red or yellow, or are often colourless and transparent.

The high degree of variability in the collected material led Thomson (1921) to propose the name *Metalcyonium variabile* for this species and to name two varieties: (1) *M. variabile* var. *molle* for colonies with stalk surface of a 'leathery consistency' and sclerites primarily of capstans; and (2) *M. variabile* var. *durum* with stalk surface of a 'much harder and somewhat stony consistency' and sclerites of capstans, spindles, rods, and clubs. Thomson also recognized a range of intermediate cases that were not readily identifiable with either subspecies. Because of the intermediate nature exemplified by some colonies and since the populations exhibit continuous and extreme variability, the recognition of formal taxonomic variations or subspecies must be disregarded.

Distribution and habitat

Alcyonium variabile is known only from the following South African localities: off East London (Hickson 1900, as *A. antarcticum*); many stations from Cape Point to central Natal (Thomson 1910, as *Metalcyonium patagonicum*; 1921, 1924, as *M. variabile*); Cape Infanta (Molander 1929*a*, 1929*b*, as *A. paessleri*); Cape Peninsula region (Tixier-Durivault 1954, as *A. fungiforme* and *A. luteum*); western side of Cape of Good Hope Peninsula, southern Natal and Transkei coast to eastern Cape Province (present study) (Fig. 13).

Alcyonium variabile is a sublittoral benthic organism of shallow to mid-water and is known from a depth range of 13–468 m. It is recorded by Hickson (1900) and Thomson (1910, 1921) at depths of 47–468 m. Dimorphic populations of red and yellow morphs have recently been observed from the western Cape Peninsula between depths of 13 and 20 m. Thomson (1921: 165) records an entirely white morph from 146 to 159 m.

Colonies are usually found attached to hard substrata such as shells and rocks or relatively soft substrata such as encrusting sponges. They are commonly observed growing on vertical rock walls amongst sponges, gorgonians, bryozoans, tunicates, and other soft corals.

Colonies have been observed with polyps fully expanded or in varying states of retraction during daylight hours.

DISCUSSION

HISTORICAL SURVEY

Pfeffer (1889: 49) established the genus *Metalcyonium* to include two new species of supposedly clavate and capitate, monomorphic alcyoniids from South Georgia Island in the southern Atlantic: *M. clavatum* and *M. capitatum*. Unfortunately, as Utinomi (1964: 7) pointed out, Pfeffer did not designate either

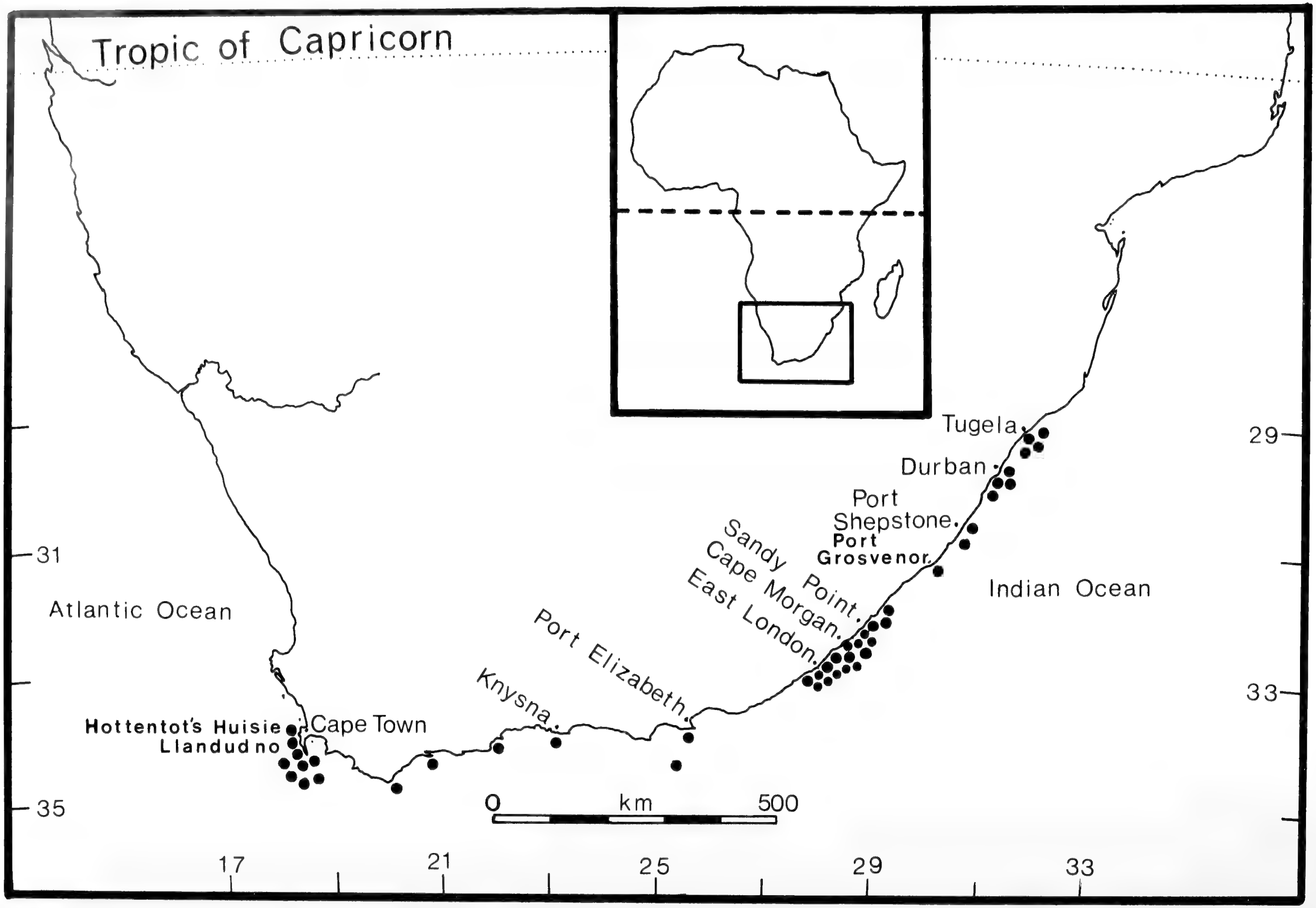

Fig. 13. Map of southern Africa showing the known distribution of *Alcyonium variabile*.

of these divergent forms as the type-species of the genus, and gave a vague diagnosis.

May (1899: 6, 8) described two new species from Patagonia: *Alcyonium paessleri* for a globular form and *Metalcyonium patagonicum* for a clavate species. He also amended Pfeffer's original definition of the genus. Tixier-Durivault (1970: 148) altered the name of *M. patagonicum* to *Bellonella patagonica* for northern Patagonian material.

According to Thomson (1910: 564), Hickson (1900: 73) apparently misidentified two specimens of capitate forms from the East London region of South Africa as *Alcyonium antarcticum* Wright & Studer, 1889. Kükenthal (1906: 47) considered Hickson's material to possibly be young colonies of *M. patagonicum*. Burchardt (1903: 673) described a fungiform-capitate species from the Malay Archipelago, *M. molle*. Thomson (1921: 162) later identified material from Natal as conspecific with this species.

Kükenthal (1906: 42) revised the genus *Alcyonium* Linnaeus, 1758, and relegated *Metalcyonium* to subgeneric status. However, this was not widely accepted by workers after that time. Kükenthal considered *Alcyonium* to be composed of three subgenera of monomorphic soft corals, differentiated by colonial growth habit: *Alcyonium* for all forms with a massive upright stalk and more or less lobate capitulum; *Metalcyonium* for unbranched, cylindrical or conical forms; and *Erythropodium* for membranous, broadly spreading forms. This redefinition ignored capitate forms and left their position doubtful.

Broch (1912: 21) changed the subgeneric name *Alcyonium* to *Eualcyonium*, and Kükenthal (1916: 174) proposed the name *Parerythropodium* for membranous forms since *Erythropodium* Kölliker, 1865, was previously applied to an unrelated but presumably superficially similar genus of the scleraxonian family Anthothelidae (Briareidae of Kükenthal 1916: 172). Kükenthal (1906: 48) also described *Metalcyonium novarae*, a cylindrical species from the Cape of Good Hope (False Bay), and Thomson (1921: 167, 172) described two other cylindrical forms: *M. lanceatum* and *Sinularia unilobata*, both from the eastern Cape Province and Natal.

Thomson (1910, 1921) added to an already chaotic situation by describing the common and variable South African species under two different names: first (following Kükenthal 1906: 47) *M. patagonicum* (1910: 562) and then later as two varieties of a new species, *M. variabile* var. *molle* (1921: 162) and *M. variabile* var. *durum* (1921: 165). Molander (1929*a*: 50; 1929*b*: 4) considered Thomson's South African material to be identical with the Patagonian and Antarctic species, *Alcyonium paessleri* May, 1899. Verseveldt (1967: 10) disagreed with Molander's contention and considered *A. paessleri* and *M. variabile* as separate species.

Hickson (1907*b*: 3) identified material from Franklin Island in Antarctica as *A. paessleri*. However, Lüttschwager (1922: 534) considered Hickson's determination as a misidentification and gave Hickson's species (plus apparently similar material from the Philippines) the new name *Alcyonium equisetiforme*. Lüttschwager (1922: 522) and Roxas (1933: 356) provided keys to the 19 worldwide species of *Alcyonium* (subgenus *Eualcyonium*) known at that time, and defined *A. paessleri* as a globular species without a distinctive stalk.

Yamada (1950: 114, 115) described two new species of globular, capitate soft corals from northern Japan, *A. pacificum* and *A. muricatum*, providing only very brief descriptions and not designating type material. Uchida (1969: 397) gave a more detailed description of *A. pacificum*.

Tixier-Durivault (1954: 385, 388) added two new species of capitate monomorphic alcyoniids, described as *Alcyonium fungiforme* and *A. luteum*, both from the region of the Cape of Good Hope.

Utinomi (1958: 111; 1964: 7) attempted to arrange some sense of order out of a chaotic situation by suggesting that in order to validate the status of the genus *Metalcyonium*, it should be restricted to markedly capitate forms and that problematic cylindrical forms such as *M. clavatum* should be assigned to other genera. This position is now held to be incorrect (Verseveldt pers. comm.; present study).

SYSTEMATIC STATUS

The most familiar members of the genus *Alcyonium* Linnaeus, 1758, are more or less lobate; the polyp-bearing portions of the colonies are divided into varying degrees of digitate or lobate processes that arise from a common stalk or base (Bayer 1981: 916).

However, several other additional species, which are in no way lobate and show remarkably different growth forms, can be allocated to the genus. For example, several species that have previously been assigned to the genus *Parerythropodium* Kükenthal, 1906, do not have a defined stalk but consist usually of a thin and pliable form that assumes the shape of the substratum that it covers, or may be globular to irregular in shape. Groot & Weinberg (1982) have recently shown that these membranous and encrusting species can be accommodated in *Alcyonium* since the type-species, *P. coralloides*, is consistent with characters of the genus. A number of other species are strongly fungiform in shape with a single spherical, hemispherical, or flattened disc-shaped capitulum arising from an unbranched stalk. Several of these have been placed in the genus *Metalcyonium* by various authors following the original description of *Metalcyonium capitatum* Pfeffer, 1889 (e.g. *Metalcyonium variabile* Thomson, 1921; *M. molle* Burchardt, 1903).

Species, or individual colonies within a species, are known that grade between several of these disparate morphological growth forms and thus serve to amalgamate the various species within the single genus. It appears then, that the genus *Alcyonium* is a large variable complex of broad morphological scope, and that attempts to subdivide the genus on the basis of colony shape must be considered unjustified or tenuous at best.

Utinomi (1964) maintained that in order to validate the genus *Metalcyonium*, *M. capitatum* should be designated as the type-species of the genus and that *Metalcyonium* should be reserved for strongly capitate, mushroom-shaped forms with globular or spherical capitulums. This differentiation of genera based solely on colony shape or growth form is in this case difficult to vindicate, since 'subcapitate' forms are also known that tend to be intermediate between digitiform and capitate forms. Colonies of *Metalcyonium patagonicum* May, 1899, for example, are slightly clavate, having a distally swollen or somewhat club-shaped form that seems to be intermediate between cylindrical and capitate. Individual colonies of *Alcyonium variabile* may have thickened stalks that approach the width of the capitulum, thus making the colony appear more clavate than capitate. *Alcyonium fauri* J. S. Thomson, 1910, and *A. paessleri* May, 1899, may form globular heads upon a membranous or spreading base. I therefore see no justification for generic separation of capitate forms and feel that such forms can be accommodated within the genus *Alcyonium*. *Alcyonium variabile* (Thomson, 1921) should therefore be considered as a new combination of *Metalcyonium variabile* Thomson, 1921. I therefore consider the following worldwide species that possess capitate and unbranched growth forms but lack permanent calyces, to be members of the genus *Alcyonium*:

Alcyonium capitatum (Pfeffer, 1889) (South Georgia Island)
    (= *Metalcyonium capitatum* Pffeffer, 1889)
Alcyonium laeve Tixier-Durivault, 1955 (Gabon)
Alcyonium molle (Burchardt, 1903) (Amboina)
    (= *Metalcyonium molle* Burchardt, 1903)
Alcyonium muricatum Yamada, 1950 (Japan)
Alcyonium pacificum Yamada, 1950 (Japan)
Alcyonium planiceps Williams, 1986 (South Africa)
Alcyonium variabile (Thomson, 1921) (South Africa)
    (= *Metalcyonium variabile* Thomson, 1921)
Alcyonium verseveldti (Benayahu, 1982) (Red Sea)
    (= *Metalcyonium verseveldti* Benayahu, 1982)
Alcyonium violaceum Tixier-Durivault, 1955 (West Africa)

However, the status of unbranched, truly digitiform to cylindrical forms with monomorphic polyps is not completely resolved as yet. These include such species as *Metalcyonium novarae* Kükenthal, 1906, *M. lanceatum* Thomson, 1921, *M. unilobatum* (Thomson, 1921) (Fig. 2B), the many species assigned to the genus *Bellonella* after the description of (but not including) *B. granulata* Gray, 1862, and the genera *Nidalia* Gray, 1834, and *Cactogorgia* Simpson, 1907. Pfeffer (1889: 49) originally described *Metalcyonium clavatum* as a clavate species. It is actually not clavate, but rather digitiform or cylindrical in shape (Molander 1929*a*, pl. 4 (fig. 9); Verseveldt pers. comm.).

According to Verseveldt (pers. comm.) most of the species previously assigned to the genera *Bellonella*, *Cactogorgia*, and *Metalcyonium* can probably be accommodated in *Nidalia* by priority—a genus characterized by digitiform or capitate colony shape and the possession of permanent calyces into which the anthocodia are retractile. Most other digitiform or capitate species that do not possess permanent calyces can probably be assigned to the morphologically diverse genus *Alcyonium*. Both Verseveldt (Zwolle, The Netherlands) and Bayer (Smithsonian Institution) are currently studying this matter in detail.

SYNONYMY

Alcyonium fungiforme Tixier-Durivault, 1954, was described from a single colony collected off Cape Point, South Africa (34°33′S 18°20′E). The colony, as described by Tixier-Durivault, has a brownish-white stalk and a white capitulum spotted with rose-red calyces. The obviously fungiform and capitate colony shape is distinctive. The capstans and thorny spindles figured in the original description of *A. fungiforme* and considered by Tixier-Durivault (1954) to be so disparate from those of material of *A. variabile* examined by Hickson (1900) and Thomson (1910, 1921), can undoubtedly be viewed within the context of intraspecific variation. The spindles illustrated by Tixier-Durivault (1954, fig. 3) from the capitulum and polyps are very similar to those that have been isolated and observed from several recently acquired colonies and from Thomson's SS *Pieter Faure* survey material. The stalk sclerites of *A. fungiforme* are a bit more pronounced (Fig. 14B). However, this minor discrepancy does not justify the status of a separate species, since the characteristic sclerite pattern and form are consistent with *A. variabile*. The description of *A. fungiforme* is thus considered to fall well within the realm of *A. variabile*; *A. fungiforme* should therefore be considered a junior synonym of *A. variabile*.

Tixier-Durivault (1954: 388) described another new species of capitate alcyoniid, *Alcyonium luteum*, from the Cape of Good Hope region (34°39′S 14°42′E). An examination of type material has shown that this species should also be considered conspecific with *A. variabile*. The holotype of *A. luteum* is very similar to material that Thomson (1921: 164) considered characteristic of *Metalcyonium variabile* var. *molle* (SAM–H883) from Knysna Heads (34°10′S 23°15′E). These colonies all have lemon-yellow capitulums with yellowish-white to yellow stalks. The form and distribution of the sclerites are typical of *A. variabile*—long spindles forming a transverse band around the base of the crown of the anthocodia with double rows of spindles arrayed *en chevron* along the axis of each tentacle; short capstans in the calyx-like base of the polyp forming eight ridges; capstans and clubbed forms in the outer coenenchyme with thick spindles dominating in the inner coenenchyme. The illustration of the complete colony of *A. luteum* provided by Tixier-Durivault (1954, fig. 4A) does not show the obviously capitate, spherical shape of the capitulum. Examination of the holotype of *A. luteum* (SAM–H3245), has shown it to be markedly capitate in nature (Fig. 14A). The morphological features of these colonies also fall well within the realm of intraspecific variation of *A. variabile*. As is the case with *A. fungiforme*, I see no justification for considering these species as separate from the variable *A. variabile* complex. If *A. fungiforme* and *A. luteum* are considered separate species because of their slight variance from other *A. variabile* material, then perhaps a dozen or more other species could also be separated. If one

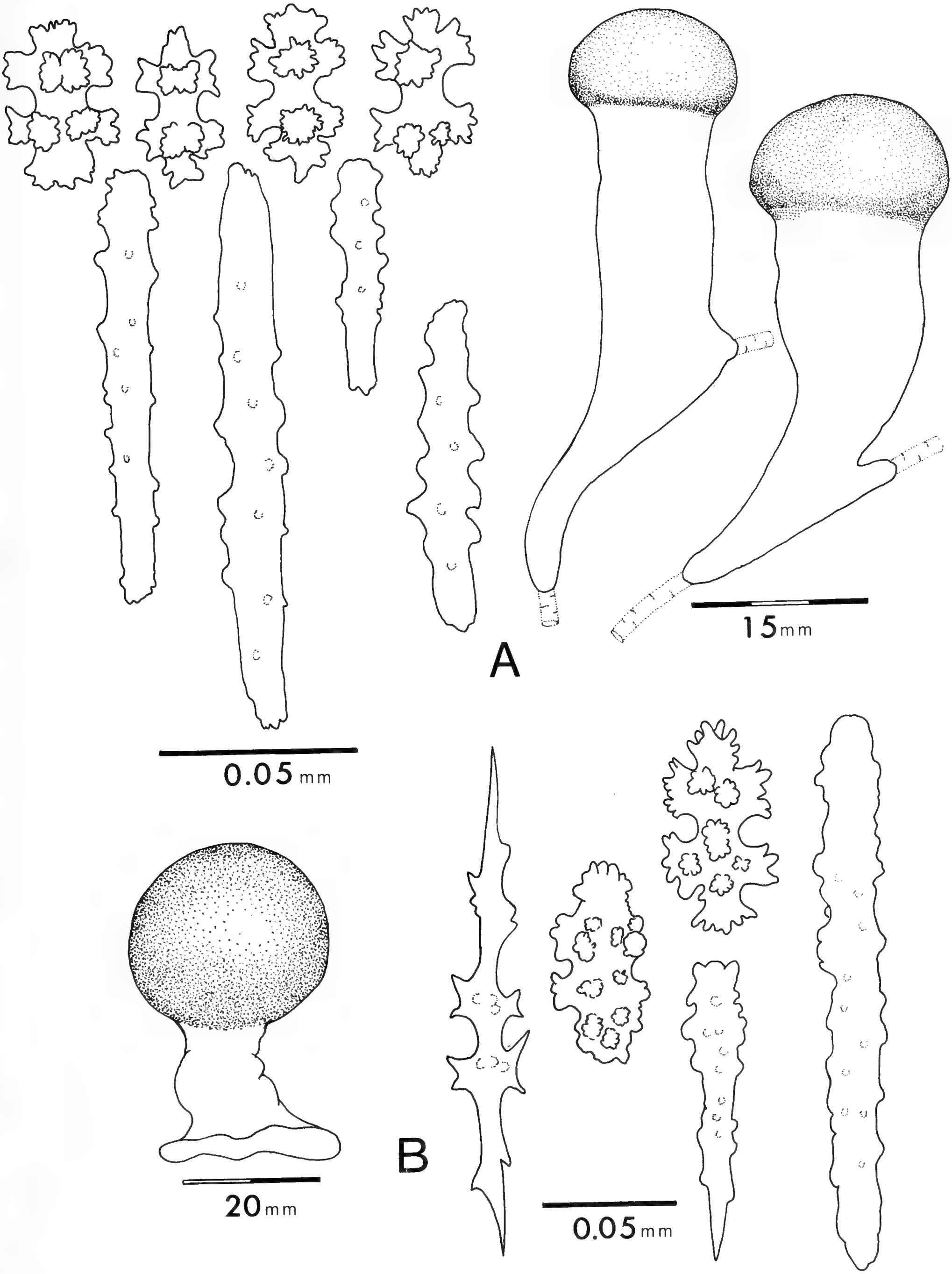

Fig. 14. Comparative morphology of material synonymous with *Alcyonium variabile*. A. Coenenchyme sclerites and two entire colonies of *A. luteum* Tixier-Durivault, 1954 (from type material). B. Entire colony and sclerites of *A. fungiforme* Tixier-Durivault, 1954 (adapted from Tixier-Durivault 1954). Stippling represents polyp-bearing capitulum; polyps not shown.

recognizes the fact of intraspecific variation and the extreme range of variability possible in sedentary marine organisms such as soft corals, then the coherence of a single variable complex encompassed by *A. variabile* is evident.

Molander (1929*b*: 5) maintained that Thomson's *Metalcyonium variabile* complex can be accommodated by *Alcyonium paessleri*. Molander based his consideration on the presence of capstans ('Doppelspindeln') in the calyx and outer coenenchyme as characteristic of the species and present in all material from the three geographically disjunct regions (Patagonia, Antarctica, and southern Africa). Verseveldt (1967: 10) disagreed with Molander's contention, acknowledging the disparate colonial growth forms of the two species in addition to divergent characteristics of the polyps. I agree with Verseveldt's assessment that the Patagonian–Antarctic and southern African forms are indeed two separate species.

Metalcyonium patagonicum May, 1899, and *M. variabile* have been confused by Kükenthal (1906: 47) and Thomson (1910: 562). Kükenthal listed Hickson's (1900) identification of *Alcyonium antarcticum* as a possible synonym of *A. patagonicum*, and Thomson originally identified South African *A. variabile* material as *M. patagonicum*. *Metalcyonium patagonicum* differs from the variable *A. variabile* complex in its clavate growth form and the strongly clubbed nature of the capitulum sclerites. Tixier-Durivault (1970) placed this species in the genus *Bellonella*. *Alcyonium patagonicum* seems to be the correct binomial designation for this form but a formal assignment must await a thorough systematic revision of the cylindrical to clavate alcyoniids.

COMPARISON WITH *ALCYONIUM PAESSLERI* MAY, 1899

Alcyonium Paessleri May, 1899: 6.
Alcyonium paessleri May, 1899. Molander, 1929*a*: 50; 1929*b*: 4 (*partim*). Verseveldt, 1967: 7.

Alcyonium paessleri May, 1899, has subsequently been described by Molander (1929*a*, 1929*b*) and Verseveldt (1967). May's type-locality was the Smyth Channel in south-western Patagonia. Molander (1929*a*) described material from off Seymour Island in the Antarctic Peninsula, and Verseveldt described four colonies from the Straits of Magellan and eastern Patagonia (Fig. 15). The various specimens are apparently consistent in the lack of a stalk: the polyp-bearing capitulums are globular swellings that arise directly from the attached membranous base with no clear differentiation between capitulum and base. They may often have short knob-like branches. The colonies are recorded as uniformly whitish to greyish-brown in colour and up to 50 mm in height. Colonies of *Alcyonium variabile* usually have well-developed stalks, are unbranched and upright with well-differentiated capitulum. The colonies are often vividly multi-coloured.

Although the colony shapes and growth forms of *A. paessleri* and *A. variabile* are strongly divergent, sclerite form and distribution are remarkably similar. Both species have essentially the same sclerite patterns: anthocodia with a crown and points of long, narrow spindles or needles; capstans, double cones,

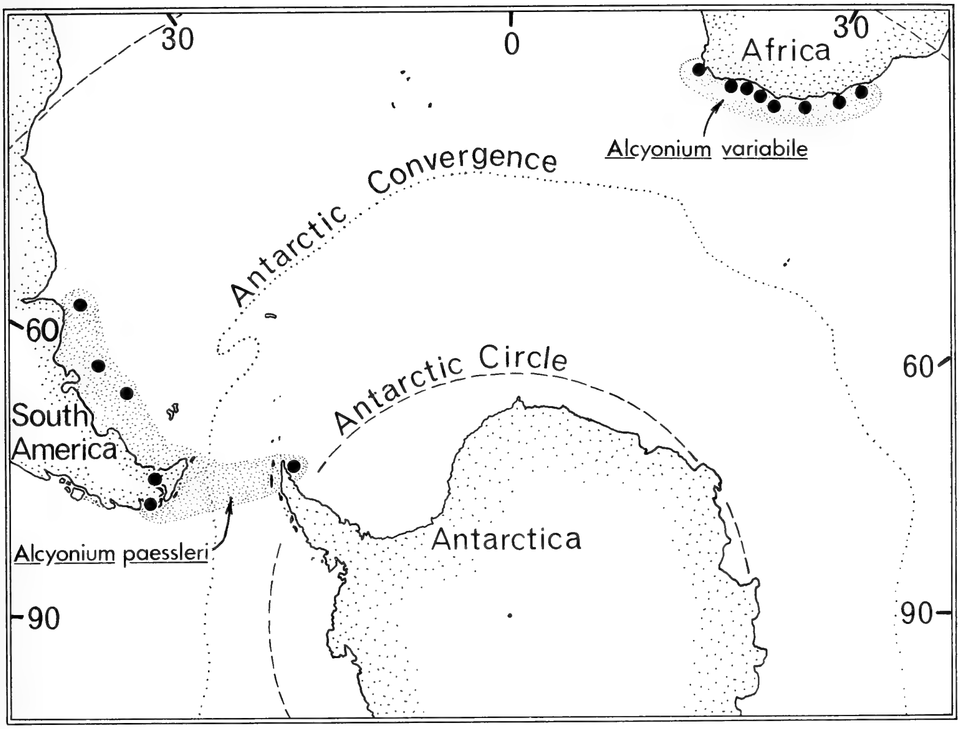

Fig. 15. Map showing known world-wide distributions of *Alcyonium paessleri* and *A. variabile*.

or clubbed forms in the polyp bases and outer coenenchyme; and thorny spindles in the interior coenenchyme. Sclerite form also shows considerable similarity. The capstans, double cones, needles, clubs, and thorny spindles are similar in structure and ornamentation in both species.

In *A. variabile*, the capstan-impregnated polyp bases may completely withdraw into the capitulum, resulting in eight lines radiating from the centre. Verseveldt (1967: 8) reported that in colonies of *A. paessleri* with retracted polyps, well-defined rounded anthosteles project from the capitular surface, these not being retractile. The aperture presents a small round hole with no radiating pattern of lines.

ZOOGEOGRAPHY

As shown above, there is remarkable similarity of sclerite form and distribution between *A. paessleri* and *A. variabile*. This fact led Molander (1929*a*, 1929*b*) to consider them synonymous. It can be postulated that this occurrence is either purely coincidental, or that the two species share a common ancestry.

Powell (1951: 64, fig. A) postulated a possible benthic bridge system for the distribution of certain prosobranch mollusc genera in the Atlantic Subantarctic region. A continuous bridge between Patagonian South America and the Antarctic Peninsula is seen as the Scotia Ridge. Similarly, a plausible but discontinuous zoogeographical link between the Scotia Arc region and southern Africa is shown by the African–Antarctic Ridge and Agulhas Plateau systems. These are regions of less than 4 000 m in depth that separate various abyssal basins of the Atlantic and Southern oceans. This hypothetical model takes into account periodic declines in sea-level (of at least 140 m) (Dingle & Rogers 1972: 155) during Pleistocene glacial episodes.

According to Powell's hypothesis, stenothermic species are shown to live in relatively shallow water in cold-water polar or subpolar regions, and are linked by deep-water distribution through temperate and tropical latitudes. The west side of the Cape Peninsula is swept by the Antarctic-influenced Benguela Current, which contains colder upwelled water. The eastern and southern coasts of southern Africa are affected by the warmer water of the Agulhas Current, which comes from tropical latitudes. *Alcyonium variabile* and *A. paessleri* are presumably stenothermic species, which seem only to be tolerant of relatively cold water. *Alcyonium paessleri* is known from 150–642 m depths; *Alcyonium variabile* is also known only from sublittoral areas; it has not been recorded intertidally. This alcyonacean is recorded in relatively shallow water (less than 40 m) only from the west side of the Cape Peninsula. It is known from all other localities in deeper water (up to 468 m). The species is not presently known from the east side of the Cape Peninsula in False Bay or in shallow-water coastal regions to the east, which are influenced by the warmer Agulhas Current. The present incomplete state of knowledge is a consequence of the limited extent of shallow-water collecting that has taken place by means of SCUBA and the nature of collecting techniques in the past, i.e. deeper-water trawling and dredging.

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Yamada, M. 1950. Descriptions of two *Alcyonium* from northern Japan. *Annotnes zool. jap.* **23**: 114–116.

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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:
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
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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

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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
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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.

GARY C. WILLIAMS

MORPHOLOGY, SYSTEMATICS, AND VARIABILITY OF THE SOUTHERN AFRICAN SOFT CORAL *ALCYONIUM VARIABILE* (J. STUART THOMSON, 1921) (OCTOCORALLIA, ALCYONIIDAE)

’ART 7 DECEMBER 1986

ISSN 0303–2515

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OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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Number of illustrations (figures, enumerated maps and tables, in this order)
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(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions 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.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

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(continued inside back cover)

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APTIAN AMMONITES FROM THE ARGENTINIAN AUSTRAL BASIN. THE SUBFAMILY HELICANCYLINAE HYATT, 1894

By

MARÍA BEATRIZ AGUIRRE URRETA

Cape Town Kaapstad

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APTIAN AMMONITES FROM THE ARGENTINIAN AUSTRAL BASIN. THE SUBFAMILY HELICANCYLINAE HYATT, 1894

By

María Beatriz Aguirre Urreta

Department of Invertebrate Palaeontology,
*South African Museum, Cape Town**

(With 19 figures)

[*MS accepted 1 October 1984*]

ABSTRACT

Representatives of the subfamily Helicancylinae are locally common in deposits of Aptian age in the northern central Austral Basin, Patagonia. A stratigraphical synthesis of the Lower Cretaceous deposits in the area studied is outlined. Schematic sequences of the measured sections at the principal localities, which also exhibit the various levels containing ammonites, are shown. The section on systematic palaeontology comprises a discussion of the subfamily Helicancylinae, and generic and specific descriptions of all taxa represented in the Austral Basin. In addition to the study of the Patagonian material, bibliographical research reveals the necessity of redefining the genera *Helicancylus* and *Hamiticeras* in order to clarify the systematics of the subfamily. The following species are identified: *Helicancylus patagonicus, Helicancylus bonarellii, Toxoceratoides nagerai, Toxoceratoides* cf. *biplex, Toxoceratoides? haughtoni, Toxoceratoides?* sp., and *Tonohamites aequicingulatus*. The fauna shows some affinities with that of Zululand and western Europe.

CONTENTS

INTRODUCTION

The subfamily Helicancylinae comprises a group of small ancyloceratids that have a nearly worldwide distribution. In the Austral or Magellanes Basin, Patagonia, Argentina, they are locally common in rocks of Aptian age. Although small heteromorphs, now referred to this subfamily, were described from this

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* Present address: Facultad de Ciencias Exactas y Naturales. Universidad de Buenos Aires.

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basin by various authors, those works dealt with general faunal descriptions; taxonomic and stratigraphic problems concerning this group were still unresolved. A description of the representatives of the subfamily Helicancylinae is necessary in order to advance our knowledge of the Aptian palaeontology and biostratigraphy of the Austral Basin.

Generic comparisons allow a nearly cosmopolitan correlation. At specific level, most of the taxa seem to be geographically restricted; some species,

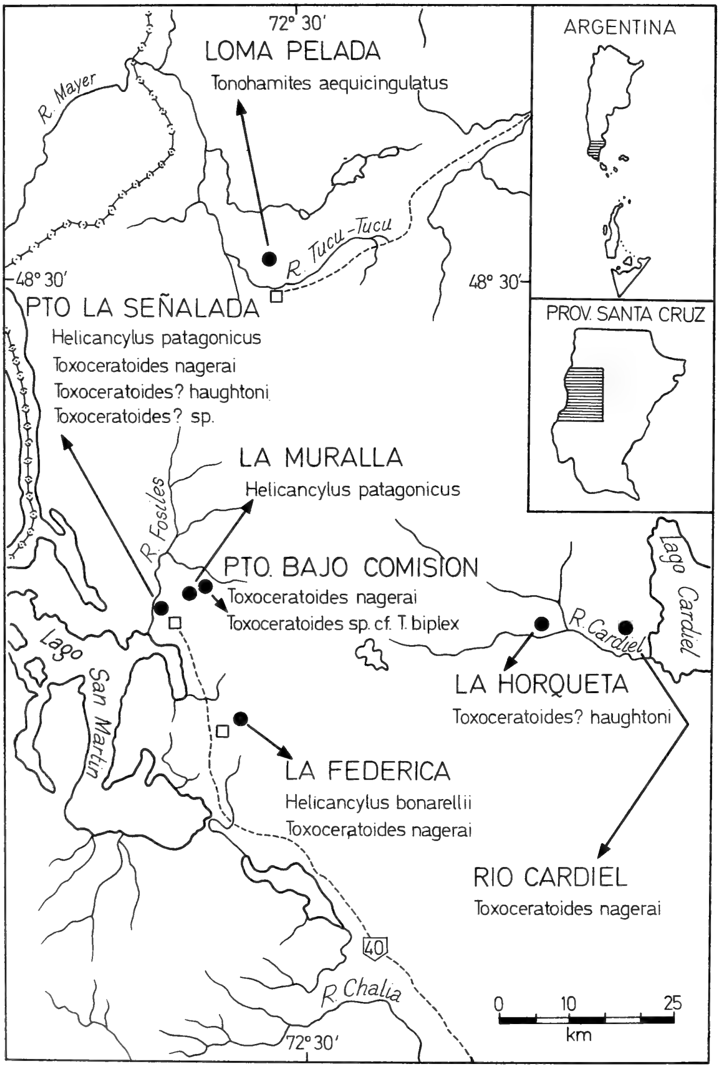

Fig. 1. Index map of the western region of the Province of Santa Cruz, showing location of the collecting sites.

however, show affinities with species described from Zululand and western Europe.

The localities studied are situated in the north-western province of Santa Cruz, in the northern central part of the Austral Basin (Fig. 1).

LOCATION OF SPECIMENS

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

CPBA	Cátedra de Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.
MLP	División Paleozoología de Invertebrados, Museo de Ciencias Naturales de La Plata.
CORD-Pz	Cátedra de Paleontología, Universidad Nacional de Córdoba.
DNGM	División Paleontología, Servicio Geológico Nacional, Argentina.

Casts of some of the figured specimens are deposited at the Department of Invertebrate Palaeontology of the South African Museum.

Most of the specimens were collected by the author. If not, the name of the collector is given in the systematic descriptions.

DIMENSIONS

No standard set of abbreviations is in common use for heteromorph ammonoids. The abbreviations used here are as follows:

L = total length
H_M = maximum whorl height
H_O = whorl height opposite to aperture
H_m = minimum whorl height
Wh/Wb = relation between whorl height and whorl breadth.

Dimensions of specimens are given in millimetres.

STRATIGRAPHIC SYNTHESIS

All ammonites studied are (with one exception) from the upper part of the Río Mayer Formation. This unit was defined by Hatcher (1897) as 'a series of black, very hard, but much fractured slates, with ammonites fairly abundant, but not sufficiently well-preserved to admit of identification' on the upper reaches of the Mayer River. The Río Mayer Formation outcrops over an extensive belt parallel to the present main cordillera. The exposures in the area studied, extending to the north and south of the type locality, have a complex distribution, controlled by a complicated series of faults and folds (Ramos 1981). Complete exposures of the Río Mayer Formation are rare and it is difficult to correlate partial sections. The selected sections, although not always complete, show at least definite relations with the under- or overlying formations.

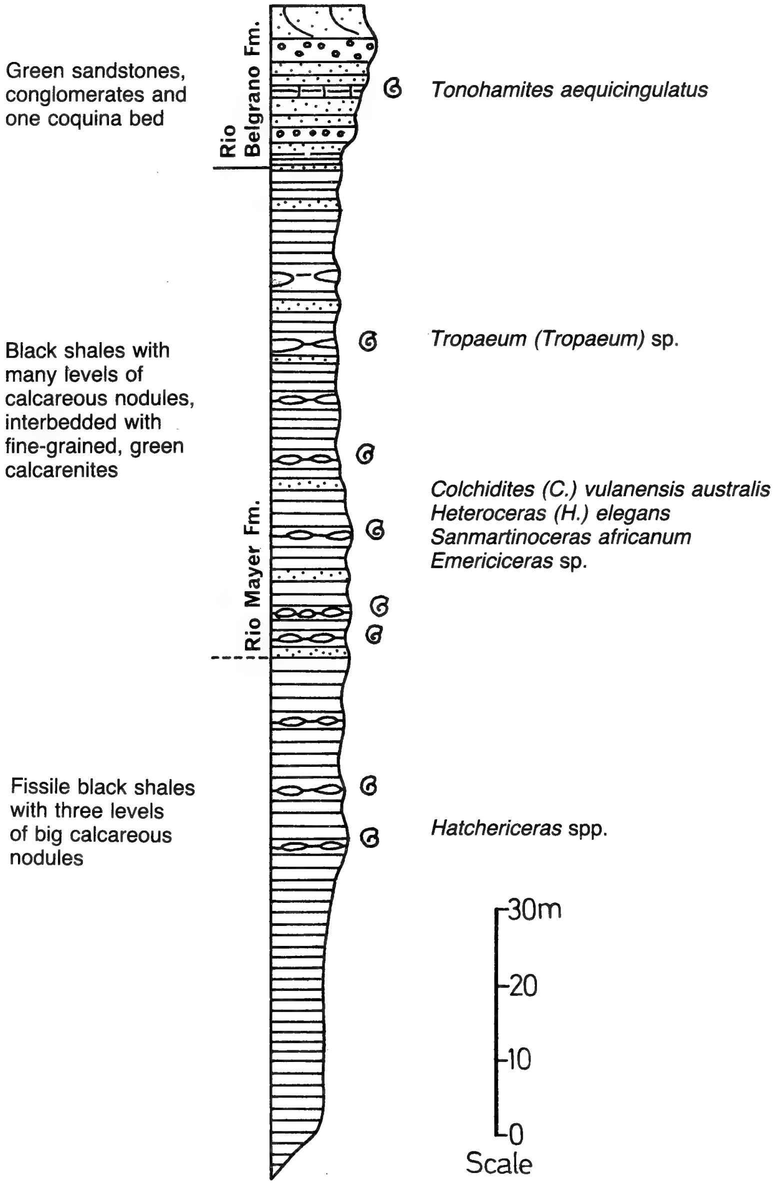

Fig. 2. Stratigraphical section at Loma Pelada, Tucu-Tucu.

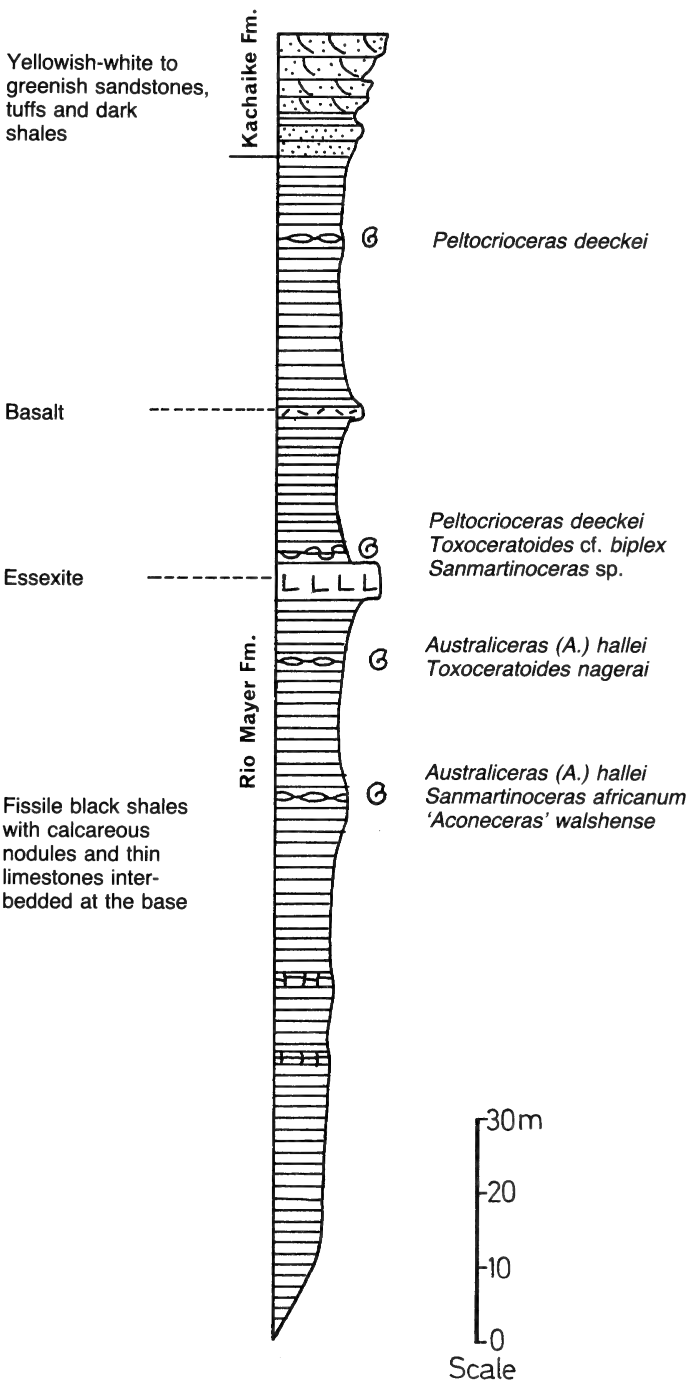

Fig. 3. Stratigraphical section at Puesto Bajo Comisión, Lake San Martín.

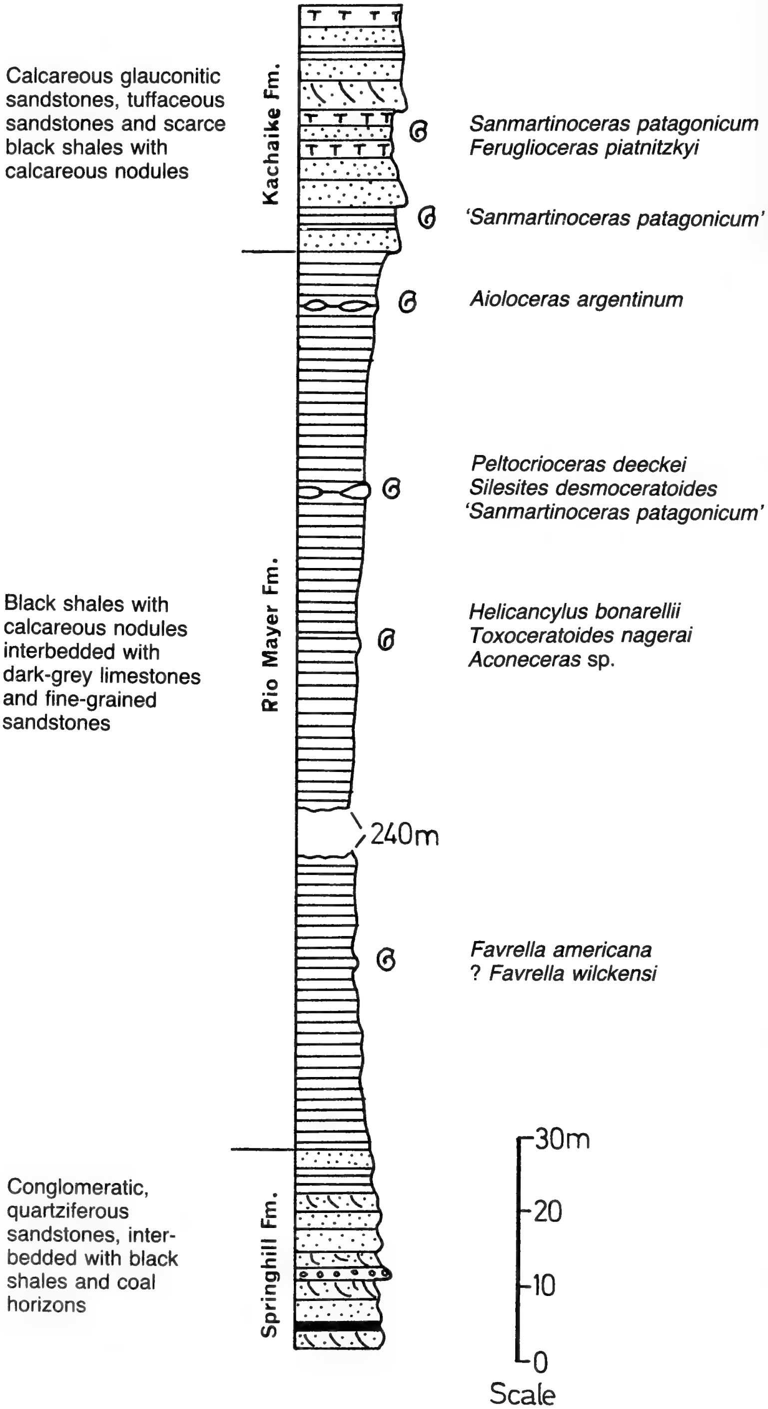

Fig. 4. Stratigraphical section at La Federica, Lake San Martín.

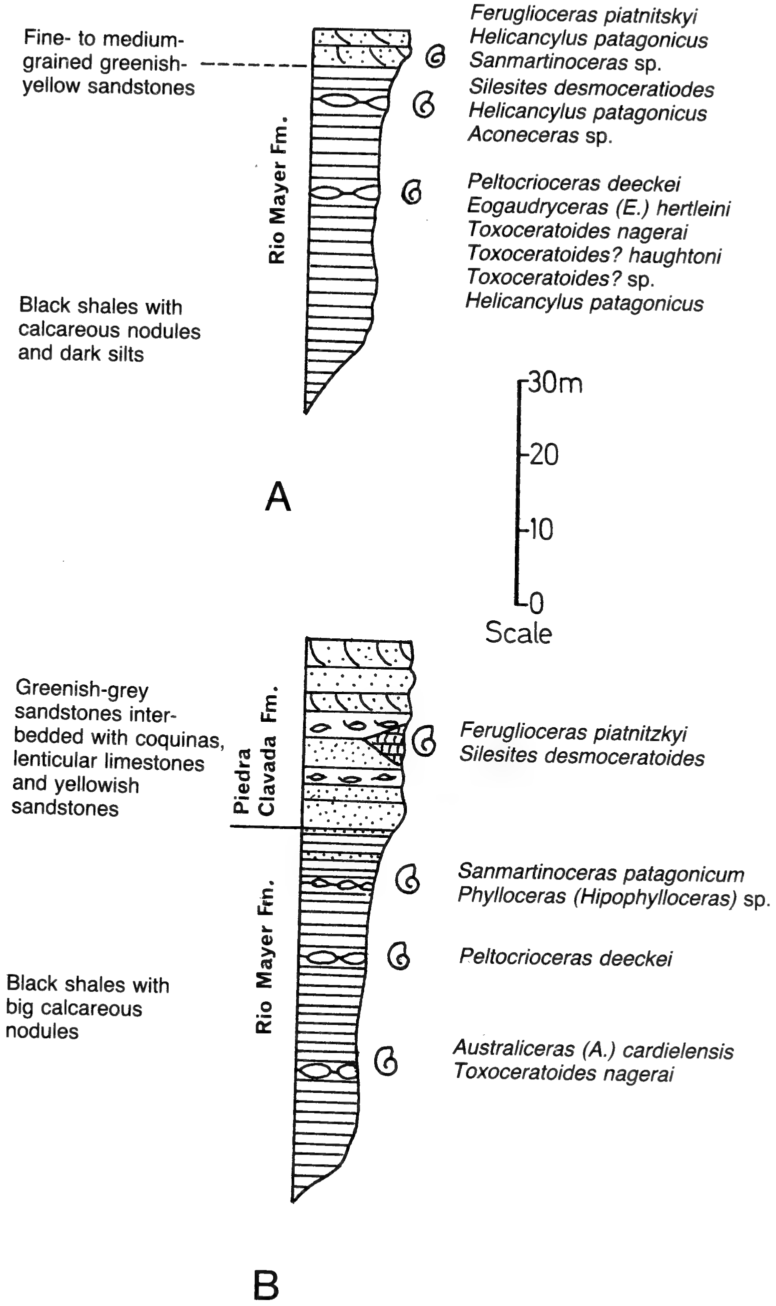

Fig. 5. Stratigraphical sections. A. Puesto La Señalada, Lake San Martín. B. La Horqueta, Lake Cardiel.

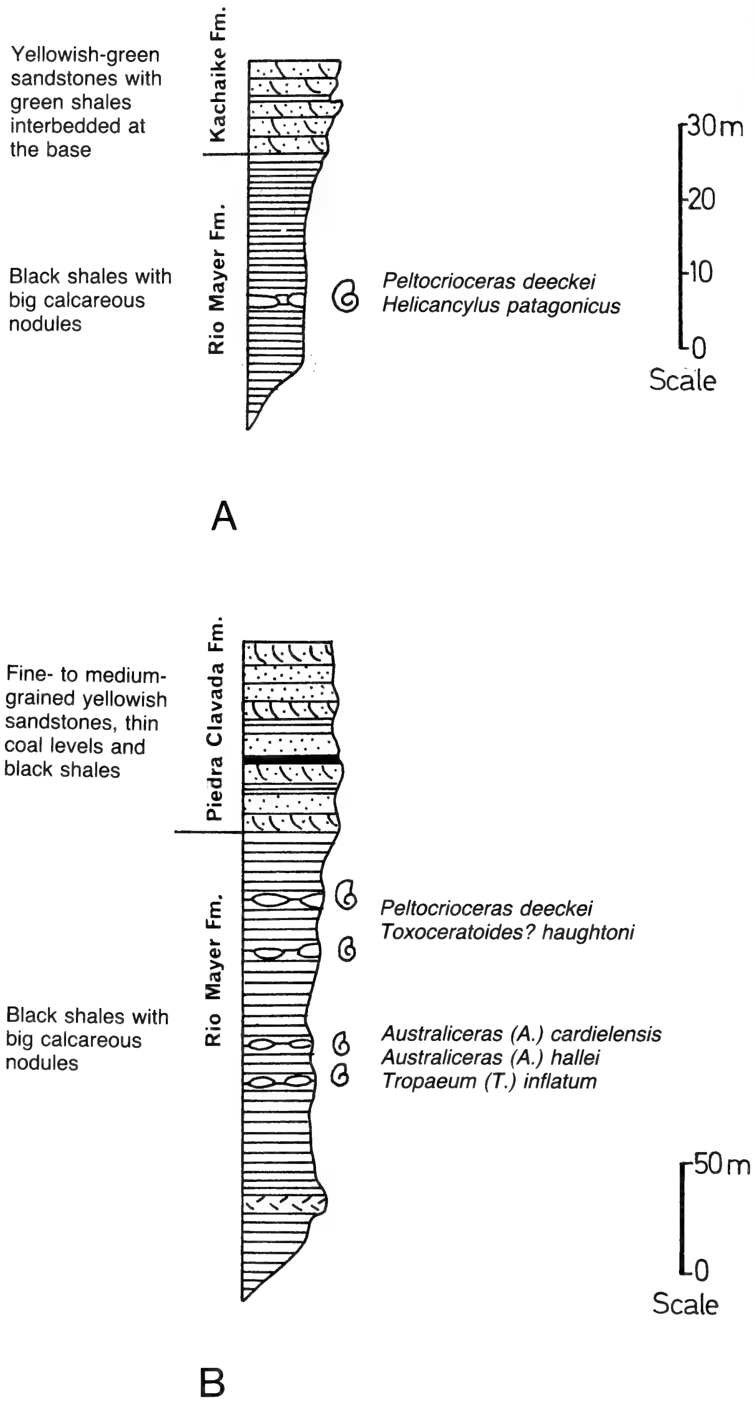

Fig. 6. Stratigraphical sections. A. La Muralla, Lake San Martín. B. Río Cardiel, Lake Cardiel.

The Río Mayer Formation consists of a monotonous succession of black shales, poorly to strongly indurated, sometimes yellowish due to alteration, with many levels of calcareous nodules. The size of the nodules ranges from a few centimetres up to more than a metre in diameter. All the fossils are preserved in these nodules. Different, small-scale facies may be present locally. They are indicated in Figures 2 to 6, in which the various fossiliferous horizons are also shown.

The Río Mayer Formation usually rests conformably on marine and continental sandstones of the Springhill Formation. In some sections, however, the unit directly overlies the Jurassic Complejo El Quemado volcanics.

In the northern area the Río Mayer Formation is conformably overlain by the sandstones of the Río Belgrano Formation (Ramos 1979), whilst to the south, in the Andean region, it is succeeded by the Kachaike Formation. This last unit is characterized by marine to continental interbedded sandstones and tuffs (Riccardi 1971). In the extra-Andean region the Piedra Clavada Formation, a mainly shallow marine sequence composed of sandstones, shales and tuffs, rests upon the Río Mayer Formation (Ramos 1982).

HISTORY OF PALAEONTOLOGICAL RESEARCH

In 1912 Stolley described two specimens of *'Ancyloceras' patagonicum* amongst other cephalopods. The material on which Stolley based his study was collected by Halle (1913), who also studied the palaeoflora and stratigraphy of the Cretaceous deposits near Bahía de La Lancha, Lake San Martín.

A few years later, Bonarelli & Nágera (1921) published the results of their geological and palaeontological expedition to Lake San Martín. Amongst other invertebrate fossils they described and figured two specimens, *Leptoceras* gr. *silesiacum* Uhlig and *Leptoceras* sp. indet., that were typical of the 'Level with *Leptoceras*' or 'Level c' in their biostratigraphic subdivision of the Lower Cretaceous.

A complete regional study dealing with the geology of the western part of the Province of Santa Cruz was carried out by Piatnitzky (1938). This author also gave short descriptions and illustrations of the most relevant faunas, including one specimen of *Leptoceras* sp. from Arroyo de la Mina and another of *Ancyloceras patagonicum* from Río Cardiel.

After Piatnitzky there were no major palaeontological contributions until 1968 when Riccardi, in an unpublished thesis, described and figured the Lower Cretaceous invertebrate faunas of Bahía de La Lancha, with a detailed study of the stratigraphy of this area. Riccardi (1968) described a series of crushed specimens of *'Ancyloceras' patagonicum*. He also gave an exhaustive account of the representatives of this group, not only in the Austral Basin, but also in other regions of the world.

Finally Leanza (1970), in a monograph dealing with the Cretaceous ammonite faunas of the Austral Andes, described and figured one specimen of

Helicancylus cf. *patagonicus* (Stolley) and also referred Bonarelli & Nágera's *Leptoceras* to the genus *Acrioceras*, proposing two new species: *A. nagerai* and *A. bonarellii*.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Zittel, 1884

Order AMMONOIDEA Zittel, 1884

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily ANCYLOCERATACEAE Gill, 1871

Family **Ancyloceratidae** Gill, 1871

Subfamily Helicancylinae Hyatt, 1894

Discussion

Casey (1961: 76) grouped in the subfamily Helicancylinae a series of small ancyloceratids in which the sculpture is simplified on the terminal hook. He included three Aptian genera, *Helicancylus* Gabb, *Toxoceratoides* Spath, and *Tonohamites* Spath, while three Barremian genera, *Acrioceras* Hyatt, *Lytocrioceras* Spath, and *Leptoceras* Uhlig, were provisionally assigned to the subfamily.

Casey (1961: 77) also extensively discussed the nomenclatorial problems that involved the type-genus *Helicancylus* Gabb, 1869. Gabb (1869) included in *H. aequicostatus* a series of fragmentary specimens from which he believed a complete specimen could be reconstructed. These consisted of an initial helix, a shaft, and a body chamber; this last fragment was previously referred to *Ptychoceras aequicostatus* Gabb, 1864 (pl. 13 (fig. 20)). Anderson (1938: 215) indicated that the material referred to *H. aequicostatus* by Gabb (1869) included at least three species. He restricted the name *Helicancylus* to the helical part, redescribing it as *H. gabbi* (Anderson 1938: 222, pl. 79 (figs 4–5)). He proposed the new generic name *Hamiticeras* for the original *Ptychoceras aequicostatus* Gabb, 1864 specimen, and for the specimen figured later by Gabb (1869, pl. 25 (figs c–f)). The latter was assigned to *Hamiticeras pilsbryi* and proposed as the type-species of the genus. Casey (1961) pointed out that *Ptychoceras aequicostatus* is the type-species of *Helicancylus* and that it is congeneric with *Hamiticeras pilsbryi*. Thus the latter genus became a synonym of *Helicancylus*.

The present author disagrees with Casey and partially agrees with Anderson, in that the original *Helicancylus* comprises three different genera. The helical fragment shows no relation to any of the other specimens and is here excluded from the subfamily. The helical coiling of the specimen recalls *Helicancyloceras* Klinger & Kennedy, 1977, and even more *Kutatissites* Kakabadze, 1970 (= *Simionescites* Avram, 1976*b*), being similar in particular to *Kutatissites princeps* (Avram, 1976*b*, pl. 3 (fig. 1a–c)) and *K. rachathasensis* Kakabadze, 1981 (pl. 11 (fig. 3a–c)). Although Casey (1961) considered the helical fragment as 'irrelevant to the interpretation of *Helicancylus*', it can be seen from recent literature that this is not so. Its inclusion in the genus and even in the subfamily only leads to misconceptions. This was the case with Thieuloy (1976), who referred *Kutatissites* to the subfamily Helicancylinae when comparing it with 'the helical part of *Helicancylus*'. The large ancyloceratid *Kutatissites* can hardly be placed in a subfamily that groups 'those diminutive ancyloceratids in which the sculpture is simplified on the terminal hook' (Casey 1961: 76).

With reference to the shaft and body-chamber fragments assigned to *Helicancylus* by Gabb (1869) and to *Hamiticeras* by Anderson (1938), it is here believed that *Hamiticeras pilsbryi*, type-species of *Hamiticeras*, is not congeneric with *Ptychoceras aequicostatus*, type-species of *Helicancylus*. It is proposed to consider both as valid genera. *Helicancylus* will be discussed later; *Hamiticeras* can be diagnosed as follows: 'Small size. Shaft straight and final hook long, almost parallel to the shaft. Ornament of the phragmocone consists of strong trituberculate and thin intermediate ribs. Final hook with sharp, high, non-tuberculate ribbing.' To *Hamiticeras* can be referred *H. pilsbryi* from the Upper Aptian (*Argonauta* zone) of California (Anderson 1938) and from the Caucasus (Drushchits & Kudryavtsev 1960: 295, pl. 11 (figs 6a–b, 7a–b)), and *Hamiticeras* sp. (Avram 1976*a*, pl. 2 (fig. 1 only)) from the Upper Aptian of the Carpathian mountains (Romania).

After Casey's (1961) monograph, some authors adopted his classification (Day 1974; Thomson 1974; Klinger & Kennedy 1977; Martínez 1982), while others (Murphy 1975; Förster 1975; Etayo Serna 1979; Kakabadze 1981) assigned the different genera to the family Ancyloceratidae, without any reference to the subfamilies.

More complicated is the history of the assignation of the Barremian genera *Acrioceras, Leptoceras* and *Lytocrioceras*. Sarkar (1955) described and illustrated a series of species of *Acrioceras* and *Leptoceras*, and reviewed the original material of *Lytocrioceras*. He expanded the original conception of *Acrioceras* Hyatt, proposing four new subgenera. They were mainly based on the coiling and on the ornament:

Acrioceras (Acrioceras) s.s.: coiling acrioceratid; ornament with tuberculate ribs.
Acrioceras (Paraspinoceras) (Breistroffer): coiling acrioceratid; non-tuberculate ribs.
Acrioceras (Aspinoceras) (Anderson): coiling aspinoceratid; non-tuberculate ribs.
Acrioceras (Protacrioceras) Sarkar: coiling aspinoceratid; tuberculate ribs.

(See Figure 7 for the different types of coiling.)

Unfortunately Sarkar (1955) based his revision on material of D'Orbigny and from other collections of the nineteenth century, which lack precise stratigraphic data. According to Sarkar (1955: 26) *Acrioceras* ranges from the Hauterivian to the Lower Aptian. He described one species of *Leptoceras* and redescribed the type of *Lytocrioceras jauberti* (Astier, 1851: 25, pl. 9 (fig. 17)) but no photographic illustration was given.

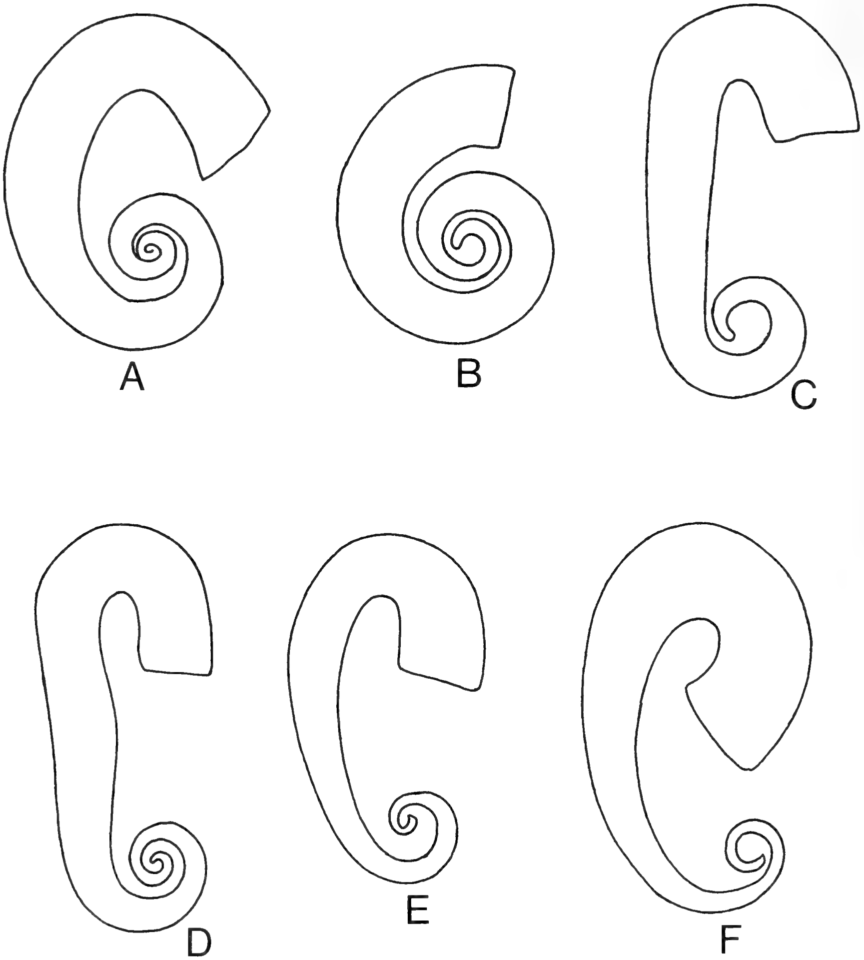

Fig. 7. Different types of coiling referred to in the text. A. Aspinoceratid. B. Crioceratitid. C. Acrioceratid. D. Ancyloceratid. E. Toxoceratid. F. Labeceratid.

Wright (1957: L211) maintained *Aspinoceras* as a valid genus and included *Paraspinoceras* as a doubtful synonym of *Lytocrioceras*. He interpreted *Helicancylus* in the sense of Anderson (1938) and regarded *Tonohamites* and *Toxoceratoides* (the latter with doubt) as synonyms of *Hamiticeras*. While Thomel (1964) accepted Sarkar's (1955) revision of *Acrioceras*, Wiedmann (1962) dissented and regarded all four subgenera as synonyms of *Acrioceras* s.l. Manolov (1962: 531) proposed the new subfamily Leptoceratinae for a group of small Barremian forms that he considered to be early representatives of the family Ancyloceratidae. He also pointed out the close relationship between all these forms. His subfamily comprised *Leptoceras* Uhlig, *Karsteniceras* Royo y Gómez, *Veleziceras* Wright, and *Eoleptoceras* Manolov. Manolov (1962) furthermore questioned the occurrence of *Leptoceras* in the Berriasian (Nikolov 1960), as that genus is unknown from the Valanginian and Hauterivian. Thieuloy (1966), however, maintained that the true *Leptoceras* occurs in the Berriasian and erected the new genus *Leptoceratoides* for the homeomorphic Barremian forms. Dimitrova (1970) proposed a completely new arrangement of the Cretaceous heteromorphs, spreading the different genera united in the Helicancylinae by Casey (1961) into a number of families and subfamilies. Although she based her study on suture lines, she did not accept Wiedmann's (1966) suborder Ancyloceratina, which included all Cretaceous ammonoids with quadrilobate primary suture. Dimitrova's (1970) proposal was generally avoided by later authors, except for Avram (1976*a*), who followed her classification.

As interpreted here, the subfamily Helicancylinae comprises the Aptian genera *Helicancylus* Gabb, *Hamiticeras* Anderson, *Tonohamites* Spath, and *Toxoceratoides* Spath, and the Barremian *Acrioceras* Hyatt and *?Lytocrioceras* Spath. The last genus is very enigmatic and as far as can be established it is only known from the single specimen of the type-species. The Barremian genus *'Leptoceras'* (= *Leptoceratoides*) has been referred to a different stock (Manolov 1962; Wiedmann 1973).

In Patagonia, the subfamily Helicancylinae is represented by *Helicancylus, Toxoceratoides*, and *Tonohamites*.

Genus *Helicancylus* Gabb, 1869

Type-species. Ptychoceras aequicostatus Gabb, 1864, from the Aptian of California, by original designation (Gabb 1869).

Diagnosis

Coiling variable, usually with a straight or curved shaft and a final hook. Ornament on the shaft consists of ribs of equal size, each one bearing one to three rows of tubercles. Final hook with single, non-tuberculate ribs. Suture line with bifid saddles and asymmetrical, trifid lobes.

Discussion

As interpreted here, *Helicancylus* differs from *Toxoceratoides* by the total lack of intercalatory ribbing and the presence of tubercles on every rib of the shaft as well as the simple ribbing on the final hook. *Toxoceratoides* shows strong trituberculate and fine intercalatory ribs on the shaft and sharp ribs springing in bundles from umbilical tubercles on the final hook (Casey 1961; Klinger & Kennedy 1977).

Tonohamites is easily distinguished from *Helicancylus* by the rounded, non-tuberculate ribs on the shaft and the strong, rounded or flat ribbing on the final hook. *Hamiticeras* Anderson has similar ornament on the final hook but shows strong trituberculate ribs separated by thin intermediaries on the shaft.

According to Casey (1961: 93) the only European record of *Helicancylus* was the Upper Aptian *'Hamites'* sp. figured by Jacob & Tobler (1906, pl. 2 (figs 10–11)). Besides this material, which most probably belongs to the genus, several species can be assigned to it, although some are included tentatively. They are as follows:

Ancyloceras elatum von Koenen (1902: 375, pl. 38 (fig. 8a–c), pl. 40 (fig. 2a–b), pl. 45 (fig. 9), pl. 53 (figs 6–7)).
Toxoceratoides? elatum (von Koenen) (Kemper 1976, pl. 33 (fig. 1)).
Ancyloceras fustiforme von Koenen (1902: 384, pl. 49 (figs 4–5, 7, 9), pl. 53 (figs 8–9)).
Toxoceratoides cf. *fustiformis* (von Koenen) (Casey 1961: 83, pl. 17 (fig. 4)).
Hamiticeras aequicostatum (Gabb) (Anderson 1938: 216, pl. 37 (figs 2–2a, 3), pl. 79 (fig. 6)).
Hamiticeras philadelphium Anderson (1938: 216, pl. 79 (figs 2–3)).
Ancyloceras patagonicum Stolley (1912: 11, pl. 1 (figs 3–3a, ?2–2a)).
Acrioceras bonarellii Leanza (1970: 207, fig. 6 (1)).
Genus uncertain. Group of *'Ancyloceras' patagonicum* Thomson (1974: 19, pl. 3 (figs c, g–h)).

'Ancyloceras' elatum von Koenen was doubtfully referred to *Toxoceratoides* by Kemper (1976), who also figured one fragmentary specimen. This species as well as *'Ancyloceras' fustiforme* von Koenen, assigned to *Toxoceratoides* by Casey (1961) are here both included in *Helicancylus* (see p. 290).

The group of *'Ancyloceras' patagonicum* referred to an indeterminate genus by Thomson (1974) can also be placed in *Helicancylus*. Thomson compared the suture line of *'Hamiticeras' aequicostatum* (illustrated by Anderson 1938, pl. 79 (fig. 6)) with that of the lectotype of *'Ancyloceras' patagonicum*. He noted that 'The suture of *"Hamiticeras"* is more complex and has a narrow external saddle, a broad trifid first lateral lobe and a slightly smaller second lateral lobe' (Thomson 1974: 20). He concluded that the *'A.' patagonicum*-group most probably represented a new genus.

The suture line of the lectotype of *'A.' patagonicum*, as illustrated by Thomson (1974, text-fig. 4b) appears very similar to that of the Patagonian material studied here and referred to *Helicancylus patagonicus*. Both are figured (Fig. 9D–G) for comparison. Recently Thomson (1982) included the Patagonian material in *Helicancylus*, but in open nomenclature.

Occurrence

Helicancylus occurs in the Aptian of Antarctica (Thomson 1974), California (Gabb 1869; Anderson 1938), England (Casey 1961), Germany (Von Koenen 1902; Kemper 1976), Patagonia (Stolley 1912; Riccardi 1968; Leanza 1970), and Switzerland (Jacob & Tobler 1906) (Fig. 8).

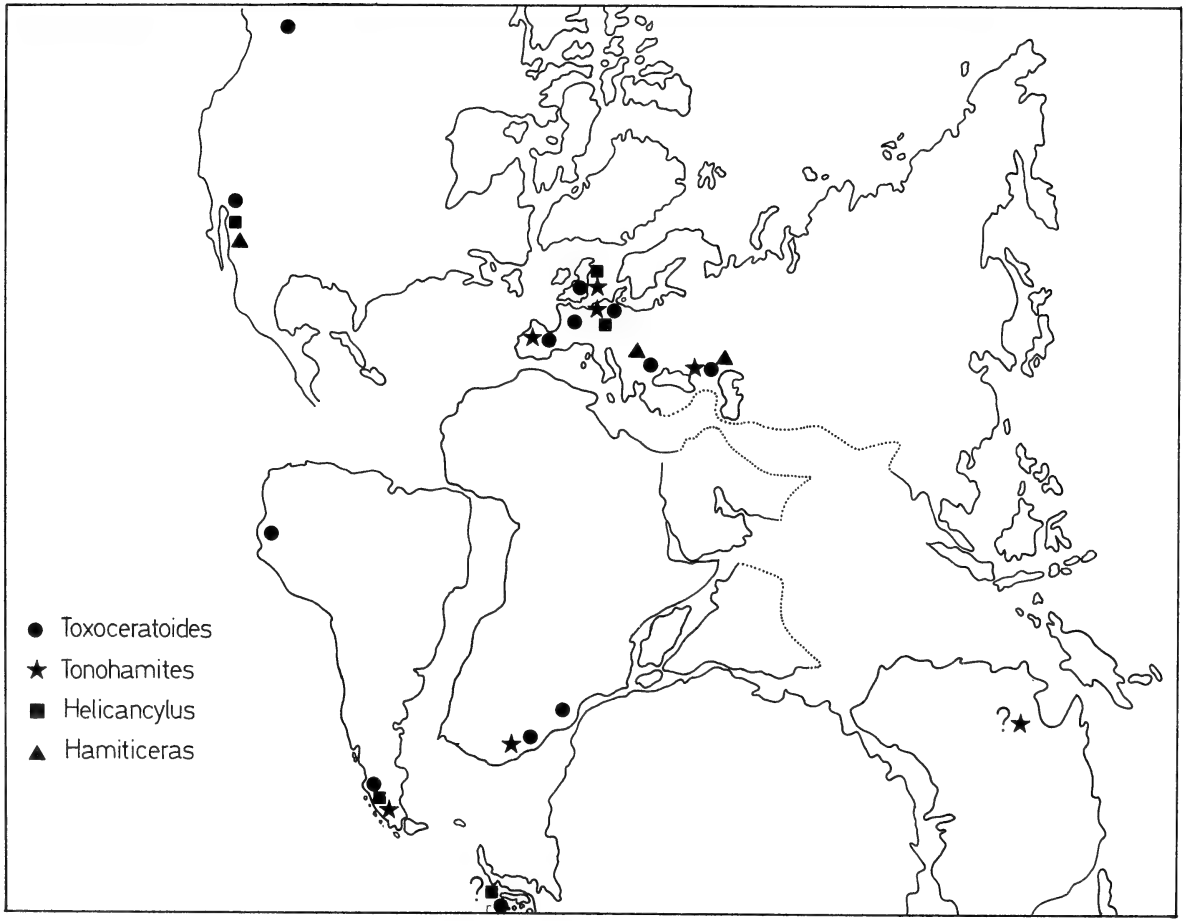

Fig. 8. Palaeobiogeographical distribution of the four Aptian genera of Helicancylinae.

The report of *Helicancylus furcata* Kakabadze from the Aptian of the Soviet Union (Kakabadze 1981) is not accepted here. Kakabadze interpreted the genus in the sense of Anderson (1938), referring to the initial helix only.

Helicancylus patagonicus (Stolley, 1912)

Figs 9A–G, 10, 11A–C, 12A–F, 19A–B

Ancyloceras patagonicum Stolley, 1912: 11, pl. 1 (figs 3–3a, ?2–2a).
non *Ancyloceras patagonicum* Stolley: Howarth, 1958: 4, pl. 1 (fig. 4).
non *'Ancyloceras' patagonicum* Stolley: Riccardi, 1968 *(pars)*, pl. 21 (fig. 1).
non *Helicancylus* cf. *patagonicus* Leanza, 1970: 205, fig. 4 (1).
non *'Ancyloceras' patagonicum* Stolley: Thomson, 1974: 19, pl. 3 (figs c, g–h).

Lectotype

The specimen figured by Stolley (1912, pl. 1 (fig. 3–3a)). Original at Riksmuseum N Mo. 117877, Stockholm, by subsequent designation Thomson (1974: 19).

Material

CPBA 11062 from La Muralla, Lake San Martín; CPBA 10898, 10848, 10844 and ?10887 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

The most complete specimen, CPBA 11062 (Fig. 11A–C), shows ancyloceratid coiling, with a nearly straight shaft and a recurved crozier. The early stage of growth is unknown.

The whorl section is initially compressed (Wh/Wb = 1,13–1,20), subovoid, with rounded dorsum and venter and flat to gently inflated flanks. With increasing diameter, the whorl section becomes more rounded and on the final hook it is nearly circular (Fig. 9A–C).

Ornament on the shaft consists of prominent, narrow, obliquely prorsiradiate, tuberculate ribs. They are separated by interspaces wider than themselves. They pass with a slight forward curvature over the dorsum, sometimes showing duplications, and are distinctly interrupted over the venter. All the ribs bear at least two rows of tubercles, one siphonal and the other ventrolateral. In some specimens there is also a third row of small dorsolateral tubercles.

Towards the end of the shaft the tuberculation gradually disappears and on the final hook the ornament consists of radial, simple, sharp ribs. They cross the venter without interruption. On the dorsum they are reduced to striae with a forward curvature.

The suture line is quite simple, with trifid lateral, umbilical and internal lobes; the first is broad and slightly asymmetrical (Fig. 9E–G).

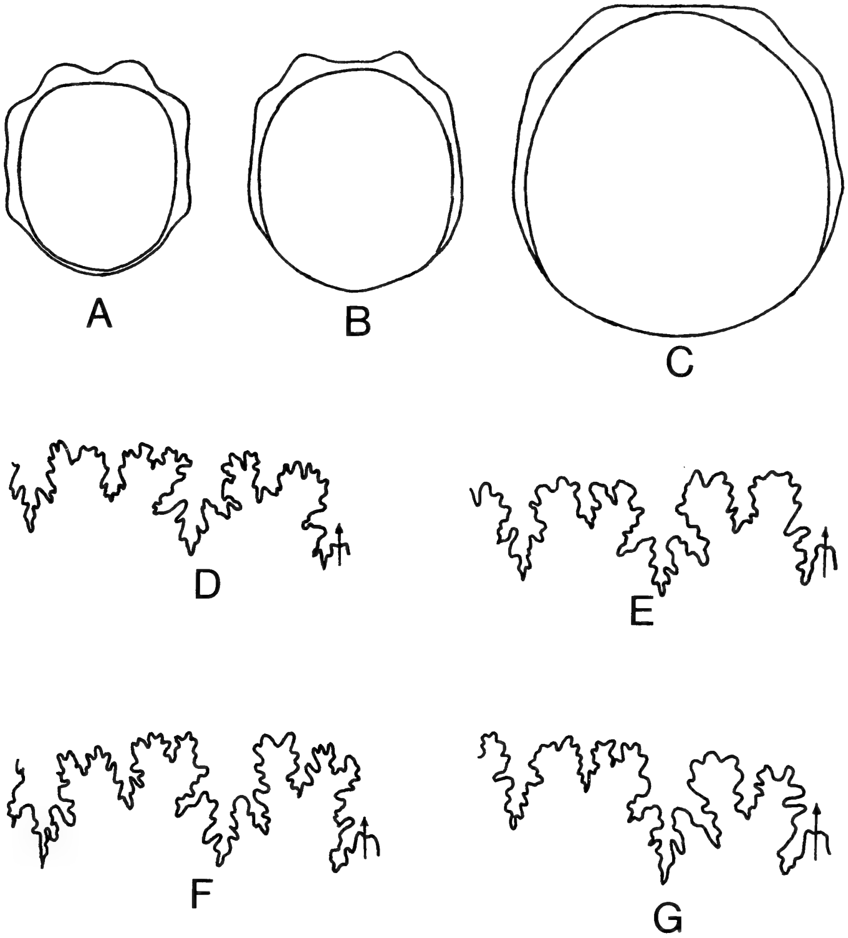

Fig. 9. *Helicancylus patagonicus* (Stolley). A–C. Whorl section of CPBA 11062. × 2,5. D. Suture line of lectotype (after Thomson 1974). E–F. Suture line of CPBA 11062. × 4. G. Suture line of CPBA 11087. × 4.

Dimensions

Specimen	H_M	H_O	H_m
Lectotype*	20,0	14,0	13,0
CPBA 11062	16,0	11,0	9,0
CPBA 10848	14,0	—	11,0
CPBA 10844	20,0	—	16,0
CPBA 10887	10,0	—	4,0

* Deposited at the Riksmuseum N Mo. 117877 (Stockholm). Measurements taken from Stolley's (1912, pl. 1 (fig. 3–3a)) original photograph.

Discussion

When Stolley (1912) proposed this species, he described two fragmentary specimens. He was in doubt whether to refer both to the same species, but pointed out that the difference in ornament was no greater than that in other species of *'Ancyloceras'* known from the Lower Cretaceous of northern Germany. As far as can be seen from the original illustrations, the main difference between Stolley's two specimens is the degree of curvature of the shaft, rather than the ornament. The small specimen figured by Stolley (1912, pl. 1 (fig. 2–2a)) is here doubtfully referred to the species. According to Thomson (1974) both may belong to different genera.

Helicancylus patagonicus (Stolley) differs from *H. bonarellii* (Leanza) in the coiling and in the ornament. In the former, the coiling is ancyloceratid, with a straight shaft and a recurved crozier, and a slow increase in the whorl section. In the latter, the coiling is open crioceratitid or toxoceratid, with a rapid increase in the whorl section, especially on the final hook. Besides, in *H. bonarellii* the ribs are rounded, closely spaced, and with feeble tubercles, while in *H. patagonicus*

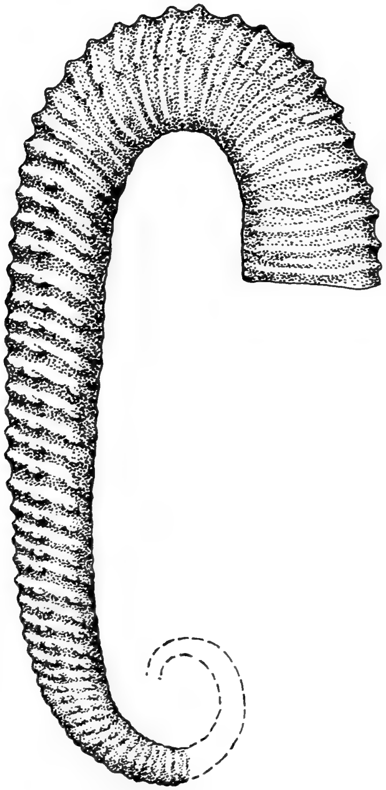

Fig. 10. Reconstruction of *Helicancylus patagonicus* (Stolley).
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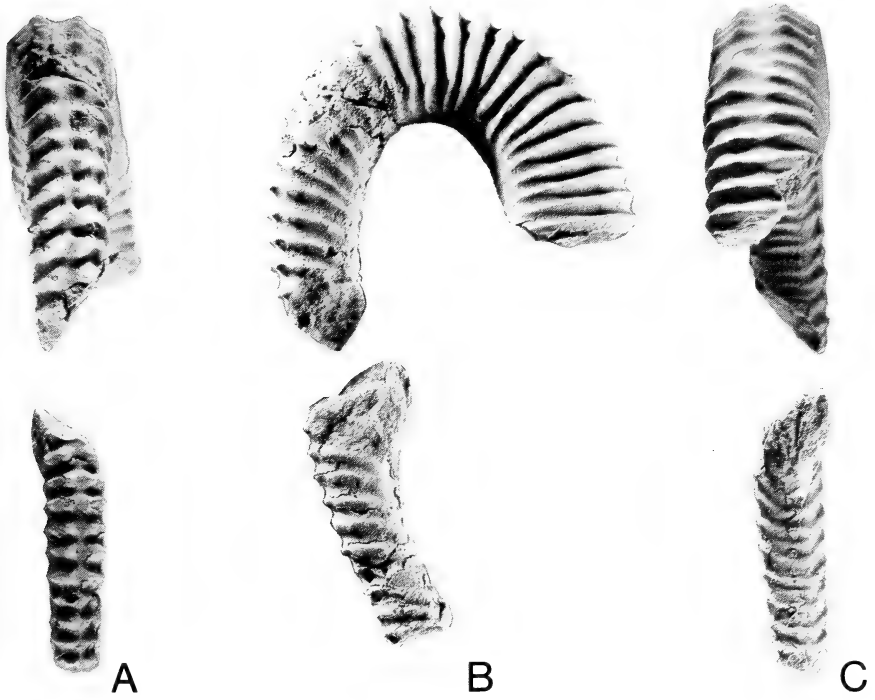

Fig. 11. *Helicancylus patagonicus* (Stolley). CPBA 11062 from La Muralla. × 1.

they are high and sharp, with well-developed tuberculation, and they are separated by wider interspaces.

The Antarctic material figured by Howarth (1958, pl. 1 (fig. 4)) as *'Ancyloceras' patagonicum* or by Thomson (1974, pl. 3 (figs c, g–h)) as group of *'A.' patagonicum* seems to be more related to *H. bonarellii*.

Helicancylus aequicostatus Gabb differs from *H. patagonicus* in the whorl section, ornament, and suture line. The former species has a subtrapezoid whorl section with flat dorsum, shaft ornamented with dense rounded ribs that cross the venter without interruption and bear faint siphonal tubercles only. The suture line in *H. aequicostatus* is more incised than in the Patagonian species, with a narrow ventral saddle (Anderson 1938: 217, pl. 37 (figs 2–3), pl. 79 (fig. 6)).

Helicancylus philadelphium (Anderson) is very closely related to *H. aequicostatus*. Although Anderson (1938) did not compare them, it seems that a row of faint ventrolateral tubercles in the former species is the only different feature.

The European species *H. fustiformis* and *H. elatum* described by Von Koenen (1902) are known from fragmentary specimens only. Although Von Koenen's descriptions are precise, he described each fragment in detail and it is difficult to interpret each species as a whole.

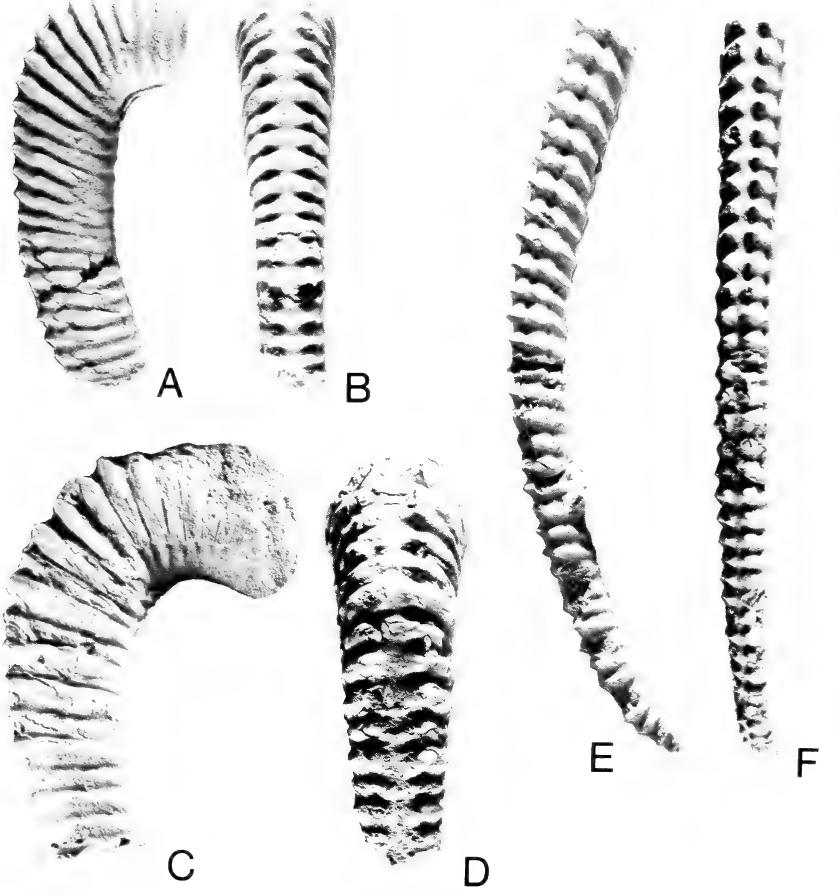

Fig. 12. *Helicancylus patagonicus* (Stolley). A–B. CPBA 10844. C–D. CPBA 10848. E–F. CPBA 10887. All from Puesto La Señalada. All × 1.

Helicancylus elatum (von Koenen) (1902: 375, pl. 38 (fig. 8a–c), pl. 40 (fig. 2a–b), pl. 45 (fig. 9), pl. 53 (figs 6–7)) has a rapid increase in the whorl section, and fine dense ribs that are trituberculate on the shaft and bend of the crozier. *Helicancylus fustiformis* (von Koenen) (1902: 384, pl. 41 (figs 4–5, 7a–c, 9a–b), pl. 53 (figs 8a–b, 9a–b)) is mostly known by small shaft fragments with subcircular whorl section and trituberculate ribs. Casey (1961: 83, pl. 17 (fig. 4)) described a fragmentary specimen as *Toxoceratoides* cf. *fustiformis*, pointing out that this species is very similar to *T. royerianus* but with tubercles in every rib.

In Patagonia, Piatnitzky (1938, pl. 6 (figs 31–32)) figured a fragment of a shaft of *'Ancyloceras' patagonicum*. It may belong to this species because of its well-marked tubercles, although the ribbing is quite dense.

The small specimen referred to *Helicancylus* cf. *patagonicus* by Leanza

(1970) has bi- or trifurcate ribs arising from an umbilical tubercle on the bend of the crozier. It is here referred to *Toxoceratoides nagerai*.

It is interesting to discuss the range of this species. Halle (1913) collected one specimen, illustrated by Stolley (1912, pl. 1), in sandstones referred to his division 6, in Calafate Stream (fig. 2–2a), and another from the summit of a high ridge on the south side of a stream (today known as Bajo Comisión Stream) also in his division 6. This informal lithologic unit is at present known as Kachaike Formation, of Upper Aptian to Albian age.

When describing Halle's material, Stolley (1912) compared it with European species of Upper Neocomian to Lower Aptian age, but concluded that *'Ancyloceras' patagonicum* might be of Upper Aptian age. This idea was ratified in his description of *?Oppelia (Adolphia)* sp. in the same publication. Thomson's (1974: 20) reference to an Upper Neocomian or Lower Aptian age of this species seems to be a misreading of Stolley's work.

All the material described here was collected in the uppermost section of the Río Mayer Formation, in a level characterized by the abundance of giant specimens of *Peltocrioceras deeckei* (Favre). This fact partially corroborates Riccardi's (1968) opinion that *'A.' patagonicum* was not present in Halle's division 6, but only in his division 5 (at present the Río Mayer Formation). Unfortunately, this statement was based on a negative fact: that after Halle, no one has collected specimens of this species in the Kachaike beds, but always in the Río Mayer Formation. Another problem is that Riccardi (1968) described as *'A.' patagonicum* what is here referred to *Helicancylus bonarellii* and *H. patagonicus*. The former species is actually restricted to the upper section of the Río Mayer Formation in a level *below* that of *Peltocrioceras deeckei*, while *H. patagonicus* occurs *with* it.

Further problems arise with the statement by Halle (1913) that *'A.' patagonicum* occurs above a level with a well-preserved taphoflora in Bajo Comisión Stream. According to Baldoni & Ramos (1981) this apparent position is just topographic. They pointed out that this species occurs in the middle section of the Río Mayer Formation at that locality. The present author had the opportunity to study the specimen of *'A.' patagonicum* of Baldoni & Ramos (1981). It does not belong to *Helicancylus patagonicus* but to *Toxoceratoides nagerai* (see Fig. 17A–B), which actually occurs in the middle section of the Río Mayer Formation at the Puesto Bajo Comisión locality, well below the level with the flora.

At the locality La Muralla, which seems to be very close to the place where Halle collected his second specimen of *'A.' patagonicum*, this species is associated with *Peltocrioceras deeckei*. They were found in the uppermost section of the Río Mayer Formation. Although the latter species does not provide a precise age, its association with *Eogaudryceras (Eogaudryceras) hertleinei* (Wiedmann) at Puesto La Señalada and with *Acantohoplites (Nolaniceras) uhligi* (Anthula) at Vega Montes de Oca, together with stratigraphical evidence, points to an Upper Aptian age for the horizon of *Peltocrioceras deeckei* (Aguirre Urreta 1985).

The author also had the opportunity to study one beautifully preserved specimen of *Helicancylus patagonicus* collected by Piatnitzky. The latter stated (1936) that the specimen was found loose in the Cerro Pelado, in the Río Cardiel area. At that locality only the lower member of the Piedra Clavada Formation (Ramos 1982, fig. 2) is exposed. The lithology of the nodule in which the specimen is preserved confirms its origin. The Piedra Clavada Formation overlies the Río Mayer Formation comformably and has its chronological equivalent in the Kachaike Formation.

All this indicates that *Helicancylus patagonicus* is associated with *Peltocrioceras deeckei* and that it appears at some higher horizons. It means that we cannot rule out its possible presence in the Kachaike Formation, as was already stated by Halle (1913).

Helicancylus bonarellii (Leanza, 1970)

Fig. 13A–F

Leptoceras gr. *silesiacum* Uhlig: Bonarelli & Nágera, 1921: 18, fig. 3.
Leptoceras sp. Piatnitzky, 1938: 79, pl. 4 (fig. 20).
?Ancyloceras patagonicum Stolley: Howarth, 1958: 4, pl. 1 (fig. 4).
'Ancyloceras' patagonicum Stolley: Riccardi, 1968 *(pars)*, pl. 21 (fig. 1).
Acrioceras bonarellii Leanza, 1970: 209, fig. 6 (1).
Paraleptoceras singulare Leanza, 1970: 209, fig. 8 (5).
?'Ancyloceras' patagonicum Stolley: Thomson, 1974: 19, pl. 3 (figs c, g–h).

Holotype

The specimen figured by Bonarelli & Nágera (1921, fig. 3). Geological Survey Collection DNGM 9308 from locality Bahía de La Lancha (here referred to as La Federica), Lake San Martín, Río Mayer Formation. ?Upper Aptian.

Material

Apart from the holotype, MLP 17094–96 (collected by A. Riccardi), CORD–Pz 4360 (collected by M. Flores), MLP 16018a–b (collected by H. Arbe), CBPA 11065–6 from the same level and locality as the holotype. Río Mayer Formation. ?Upper Aptian.

Description

All the available specimens are crushed or preserved as impressions. Coiling is variable. On most of the specimens it is toxoceratid, but in some it is open crioceratitid with the whorls not touching. The most complete specimen (Fig. 13A) shows a small open spire followed by a gently curved shaft and a final recurved crozier. Nothing can be said about the whorl section as the specimens are extremely crushed.

Ornament consists of fine, simple, rounded ribs, separated by interspaces narrower than the ribs. On the initial spire rib density is about four per whorl height, on the shaft or at mid-growth stage (in specimens with crioceratitid coiling) it is about five, and at the final stage nine ribs are present per whorl

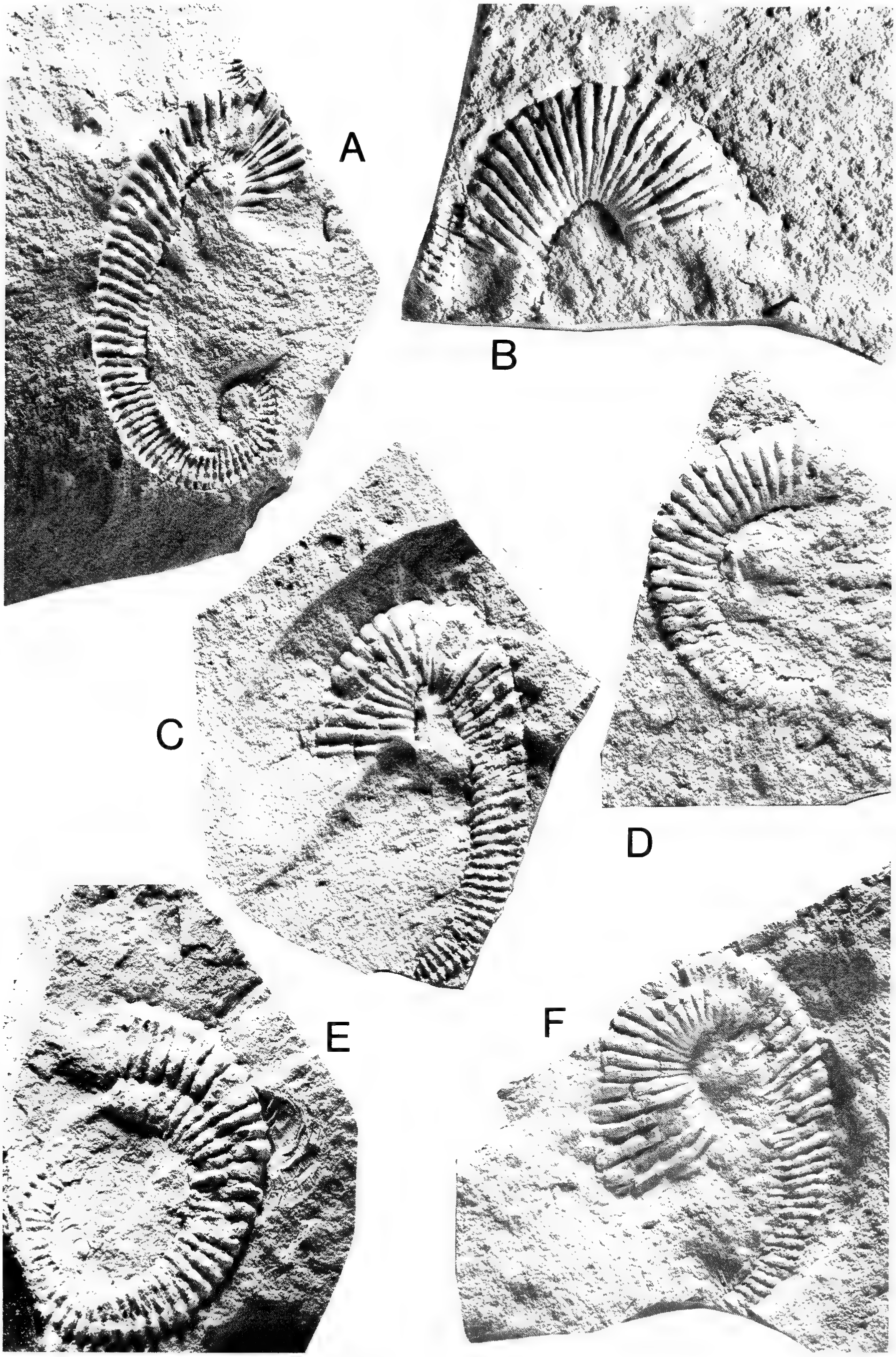

Fig. 13. *Helicancylus bonarellii* (Leanza). A. MLP 17094. B. CPBA 11065. C. MLP 16018a. D. MLP 16018b. E. MLP 17095. F. MLP 17096. All from La Federica. All × 1.

height. The ribs bear tubercles, but not only their number but also their appearance and disappearance are extremely variable. When present at the early stage, the tubercles are only ventral. As size increases, the ribs also show small ventrolateral and even smaller umbilical tubercles.

On the final hook the tuberculation gradually disappears and the ornament consists of simple, rounded radial ribs, which cross the venter apparently without interruption.

The suture line is unknown.

Dimensions

Specimen	*L*	H_M	H_O	H_m
MLP 17094	56,0	10,0	9,5	1,0
MLP 17096	50,0	17,0	9,0	4,0
MLP 16018*a*	53,0	13,0	8,5	4,0
MLP 17095*	47,0	16,5	—	5,5
MLP 16018*b*	38,0	7,0	—	3,0
DNGM 9308	—	20,0	13,0	6,0

* Specimens with crioceratitid coiling.

Discussion

Leanza (1970), when proposing this species, indicated that it belonged to the *'Leptoceras' silesiacum* group. He also pointed out that according to Anderson (1938) the species had to be referred to the genus *Acrioceras* Hyatt. Riccardi (1968) had already stated that Uhlig (1883) never included *'Crioceras' silesiacum* in his subgenus *Leptoceras*. It is irrelevant to discuss here the generic affinities of Uhlig's species, but it differs from the Patagonian material in the coiling and in the ornament of the shaft and final hook (Uhlig 1883: 142, pl. 28 (fig. 4)).

Helicancylus bonarellii differs from *H. patagonicus* in its smaller size and in its crioceratitid or toxoceratid instead of the latter's ancyloceratid coiling. The ornament of the former species consists of rounded, dense ribs with weak tubercles.

As stated before, the specimens illustrated by Thomson (1974, pl. 3 (figs c, g–h)) and referred to an indeterminate genus of the group *'Ancyloceras' patagonicum*, as well as the material figured by Howarth (1958, pl. 1 (fig. 4)) as *'A.' patagonicum*, show more similarities with *H. bonarellii* than with *H. patagonicus*. It is interesting to point out the close morphological resemblance between some specimens of *Antarcticoceras antarcticum* Thomson (1974: 20, pl. 3 (figs i–k, m–n)) and those of *H. bonarellii* with crioceratitid coiling.

Antarcticoceras antarcticum was first referred to an unknown genus of the subfamily Helicancylinae (Thomson 1971: 158) and afterwards to an uncertain family (Thomson 1974). Thomson was in doubt whether to assign this taxon to the Crioceratitidae or to the Ancyloceratidae. He stated that in the morphology of the shell the genus seems to be allied to the Crioceratitidae, but it also has some non-crioceratitid features such as ribbing of similar size, a rather simple suture line and a high dorsolateral tubercle.

Further research on the possible relationships between the Antarctic specimens of *'Ancyloceras' patagonicum, Antarcticoceras antarcticum*, and the Patagonian *Helicancylus bonarellii* might be worthwhile.

Genus *Toxoceratoides* Spath, 1924

Type-species. Toxoceras royerianum d'Orbigny, 1842, from the Lower Aptian of France, by original designation (Spath 1924: 78).

Diagnosis

Coiling ancyloceratid or toxoceratid. Ornament of initial spire and shaft consists of trituberculate and intermediate ribs. On the final hook the ornament is simpler, with single ribs intercalated with others that bi- or trifurcate from an umbilical tubercle. Suture line with bifid saddles and trifid lobes.

Discussion

Spath (1924: 78) erected this genus without giving any diagnosis. Wright (1957: L212) doubtfully regarded *Toxoceratoides* as a synonym of *Hamiticeras*, taking into account that the type-species of the former genus was only known by fragments that do not allow a proper description.

Drushchits & Eristavi's (1958) first diagnosis of *Toxoceratoides* referred only to the coiling, suture line, and ornament of the shaft. Casey (1961: 77) accepted the validity of the genus and characterized it as: 'Coiling ancyloceratid or leptoceratid; may commence with a very small helix. Phragmocone ornamented as in *Ancyloceras*, with periodic trituberculate ribs. Final hook with close, narrow, sharp ribbing which bifurcates or trifurcates irregularly from an umbilical tubercle. Suture line as in *Ancyloceras*.'

Although Casey stated the presence of leptoceratid coiling in his diagnosis none of the species he refers to this genus actually shows it. The term 'leptoceratid coiling' is difficult to interpret as *Leptoceras* includes species with crioceratitid as well as open coiling. Thus it is preferable to use the term toxoceratid instead of leptoceratid coiling (Fig. 7E).

None of the species referred to *Toxoceratoides* shows any trace of an initial helix, except for a doubtful record of Day (1974: 13). Day identified three fragments as *Toxoceratoides?* sp. The present author had the opportunity to see plaster casts of two of them. The ornament as well as the coiling do not fit in *Toxoceratoides* and they may be inner whorls of a big ancyloceratid (e.g. *Peltocrioceras*). The third fragment, as seen in the illustration (Day 1974, pl. 1 (fig. 2)), shows a partially preserved initial helix followed by a shaft ornamented with narrow, close, non-tuberculate, sharp ribs—a feature not common in *Toxoceratoides*. Therefore the presence of an initial helix is ruled out in the present diagnosis of *Toxoceratoides*. If this feature proves to be present, it would be necessary to analyse the taxonomic position of this genus again, as the presence of an initial helix is a typical feature of the nearly contemporaneous Heteroceratinae (Klinger 1976).

Klinger & Kennedy (1977: 307) partially accepted Casey's diagnosis; they pointed out the close relationship between *Toxoceratoides* and *Tonohamites*, and stated that species like *Tonohamites decurrens*, with strong trituberculation on the shaft, link both genera.

Later, Etayo Serna (1979: 20) proposed the subgenus *Colomboceratoides*, type-species *Toxoceratoides (Colomboceratoides) renzoni*, with the following diagnosis: 'Coiling as in *Toxoceratoides* but differs from the latter genus by the development of sculpture characterized by a retarded development of the subdue lateral trituberculation: early ribs without tubercles, followed by the appearance on both sides of venter of slender spines, subsequently lateral tubercles appear and much later the nipple-like peridorsal tubercles show up. The suture line is much simplified, it has massive subrectangular saddles and subtrifid L.'

According to Kakabadze (1981: 129) this subgenus is superfluous as its main characteristics are the same as those present in *Toxoceratoides*. The only apparent difference is the delayed appearance of the trituberculation, but this is a very variable character and it does not seem to have any specific value.

Toxoceratoides differs from *Tonohamites* mainly in the ornament of the final hook. In the latter genus tuberculation on the shaft is usually reduced but, as stated by Klinger & Kennedy (1977), species like *Tonohamites decurrens*, with a strong trituberculate phragmocone, show the close relationships between these two genera.

Hamiticeras has a *Toxoceratoides*-like shaft, but the final hook is long, parallel to the shaft, and the ribs are sharp, strong, single, and wide-spaced. These features are sufficient to distinguish the genera.

It is very difficult to find complete specimens of *Toxoceratoides*, perhaps due to their small size and open coiling. This has led to the erection of a large number of species in this genus. Some of these are monotypic or based on fragments, while others were erected in the nineteenth century and never restudied. There is no complete agreement between different authors as to which features are of specific value. The only distinct characteristics for specific separation are the coiling, whorl section, and the ornament of the body chamber. To a lesser degree, the ornament of the shaft can be used; little can be said about the initial spire as it is virtually unknown.

Species referred to or possibly belonging to *Toxoceratoides* are:

T. biplex (von Koenen) (1902: 381, pl. 41 (figs 3, 10a–b, 11a–b)).
T. biplicatum (von Koenen) (1902: 379, pl. 41 (figs 2a–b, 8a–b)).
T. caucasicus (Kasansky) (1914: pl. 1 (fig. 8a–c)).
T. corae Murphy (1975: 33, pl. 5 (figs 1, 5)).
T. emericianum (d'Orbigny) (1842: 487, pl. 120 (figs 5–9)).
T.? greeni Murphy (1975: 33, pl. 5 (figs 2–3, 6)).
T.? haughtoni Klinger & Kennedy (1977: 310, figs 59A–D, 60A–I, 61A–C, 62A–D, 63, 64A–C, 65A–B, 66B, 79A–B).

T. krenkeli Förster (1975: 160, pl. 4 (figs 1–2), text-fig. 33a–b).
T. nagerai (Leanza) (1970: 206, fig. 5 (1)).
T. obliquatus (Young & Bird) (1828: 278, pl. 18 (fig. 11)).
T. proteus (Spath) (1930: 461, pl. 16 (fig. 7)).
T. (Colomboceratoides) renzoni Etayo Serna (1979: 20, pl. 6 (fig. 19), text-fig. 3O–P).
T. rochi Casey (=*Ancyloceras royerianum* Roch, 1927: 30, pl. 1 (fig. 4)).
T. rotundus (Phillips) (1875: 264, pl. 1 (fig. 24)).
T. royerianus (d'Orbigny) (1842: 481, pl. 118 (figs 7–11)).
T. saulae Murphy (1975: 31, pl. 4 (figs 4, 6)).
T. seminodosus (Roemer) (1841: 93).
T. sheperdi (Spath) (1924: 173, figs 5–6).
T. starrkingi (Anderson) (1938: 207, pl. 59 (fig. 4–4A), pl. 45 (fig. 4A)).
T. subproteus Casey (1980: 651, pl. 103 (fig. 3)).
Toxoceratoides sp. 1 Murphy (1975: 35, pl. 6 (figs 1–2, 11)).
Toxoceratoides? sp. 2 Murphy (1975: 35, pl. 3 (fig. 6), pl. 6 (figs 5–6)).
Toxoceratoides sp. nov. Thomson (1974: 16, pl. 3 (figs a, d)).
Ancyloceras (Acrioceras) aff. *starrkingi* Anderson (Jeletzky 1964: 66, pl. 19 (fig. 2A–C)).
Toxoceratoides sp. 1 Martínez (1982: 140, pl. 24 (fig. 3a–c), text-fig. 21).
Toxoceratoides sp. 2 Martínez (1982: 141, pl. 24 (fig. 4a–d), text-fig. 22).
Toxoceratoides sp. 3 Martínez (1982: 142, pl. 24 (fig. 5a–d)).

Toxoceratoides biplicatum (von Koenen), referred to *Toxoceratoides* by Klinger & Kennedy (1977: 307), with bifurcate and ventrally tuberculate ribs on the shaft, is doubtfully included in this genus. According to Murphy (1975) *Ancyloceras (Acrioceras)* aff. *starrkingi* described by Jeletzky (1964) does not belong to Anderson's species and may be new.

Occurrence

Toxoceratoides occurs in Germany (Von Koenen 1902), Antarctica (Thomson 1974), Canada (Jeletzky 1964), Colombia (Etayo Serna 1979), Spain (Martínez 1982), California (Anderson 1938; Murphy 1975), France (D'Orbigny 1842; Roch 1927), England (Spath 1924, 1930; Casey 1961, 1980; Howarth 1962), Mozambique (Krenkel 1910; Haughton & Boshoff 1956; Wachendorf 1967; Förster 1975), Romania (Avram 1967*a*), south-western USSR (Kakabadze 1981), Zululand (Klinger & Kennedy 1977) and Patagonia (Leanza 1970; present paper).

Reports of *Toxoceratoides* from Australia are not accepted here. *'Ancyloceras' taylori* Etheridge, referred to *Toxoceratoides* by Whitehouse (1926), is believed to be a *Tonohamites* species, as discussed later in this paper. The fragments described by Day (1974) as *Toxoceratoides?* sp. seem to belong to more than one genus, but not to *Toxoceratoides*.

According to Casey (1961) *Toxoceratoides* ranges from the Upper Barremian to the Lower Aptian (*deshayesi* zone), and it appears to be replaced by

Tonohamites at the top of the Lower Aptian (*bowerbanki* zone). However, more recent publications (Klinger & Kennedy 1977; Etayo Serna 1979) show that *Toxoceratoides* ranges up to the Upper Aptian. In Patagonia this genus is present in deposits of Lower and Upper Aptian age.

Toxoceratoides nagerai (Leanza, 1970)

Figs 14, 15A–C, 16A–D, 17A–D

Leptoceras sp. indet. Bonarelli & Nágera, 1921: 19, fig. 4.
Helicancylus cf. *patagonicus* (Stolley): Leanza, 1970: 205, fig. 4 (1).
Acrioceras nagerai Leanza, 1970: 206, fig. 5 (1).

Holotype

An external mould found in a loose calcareous nodule in the bed of Fósiles River, Lake San Martín (Bonarelli & Nágera 1921: 19). It seems that the holotype is lost, but plaster casts are available (Geological Survey Collection DNGM 9297).

Material

Apart from a plaster cast of the holotype, CPBA 10880–81 from Río Cardiel; CPBA 10843 from Puesto La Señalada; CPBA 10830, 11061 from Puesto Bajo Comisión; and CORD–Pz 4368 from La Federica, Lake San Martín (collection Dr M. Flores). Río Mayer Formation. Lower–Upper Aptian.

Description

The very early stage of growth is unknown. The coiling is toxoceratid with an open initial spire followed by a slightly arcuate shaft and a recurved terminal hook (Fig. 14).

The whorl section is initially subquadrate or suboctagonal if measured over the trituberculate ribs (Fig. 15A–B). It is equidimensional or slightly compressed (Wh/Wb = 1,00–1,07) with a nearly flat dorsum and moderately curved flanks converging to a rounded venter. With increasing diameter, the whorl section becomes more rounded. On the body chamber it is nearly circular with inflated flanks converging to a broad rounded venter (Fig. 15C).

At the smallest diameter (3 mm) ornament consists of single, rounded ribs, bearing a small ventral tubercle and separated by wider interspaces. At a slightly larger diameter (6 mm), the ribs become differentiated and the ornament consists of alternating tuberculate ribs and non-tuberculate intermediaries, both of equal strength. With increasing diameter the tuberculate ribs become stronger and ventrolateral tubercles appear. One to five intermediate non-tuberculate ribs are present at this stage. At a larger diameter (10 mm) the ornament comprises fine intermediaries and strong trituberculate ribs, with small umbilical tubercles. The ribs pass straight, or bend forward in a gentle arc, over the dorsum and run prorsiradiate over the flanks; while the thin intermediaries cross the venter without interruption, the strong trituberculate ribs end on the ventral tubercle. Some ribs are duplicated over the dorsum and unite at the umbilical tubercle,

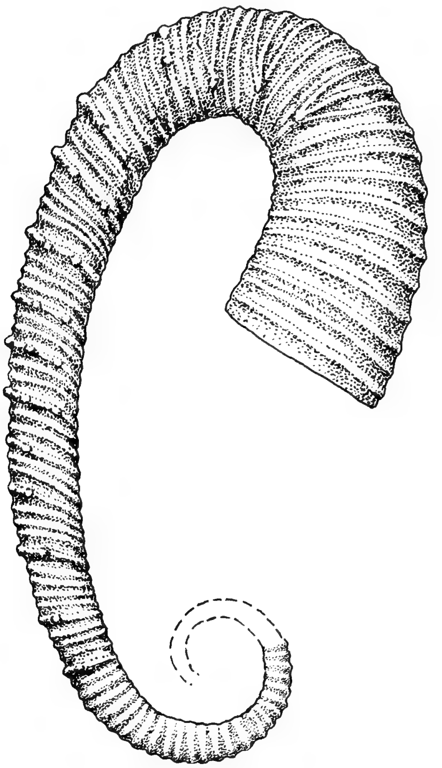

Fig. 14. Reconstruction of *Toxoceratoides nagerai* (Leanza).

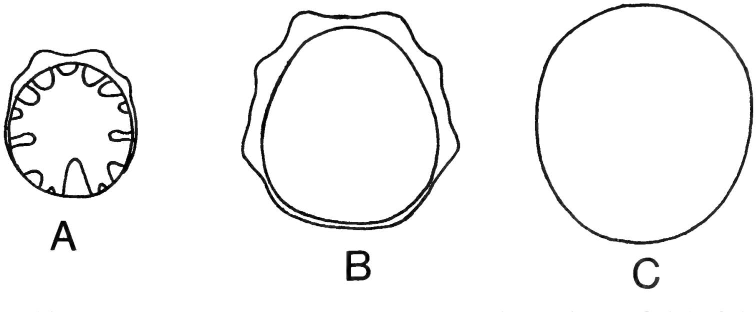

Fig. 15. Whorl section of *Toxoceratoides nagerai* (Leanza). A. CPBA 10881. B. CPBA 10843. C. CPBA 10880. All × 2.

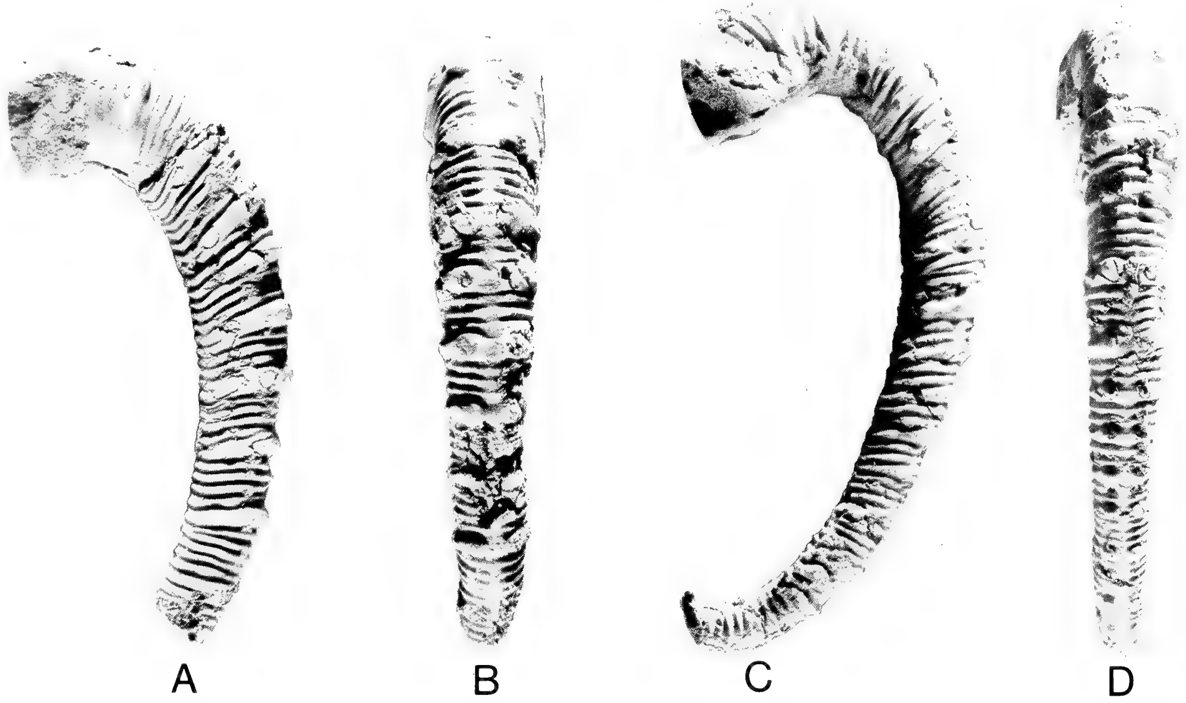

Fig. 16. *Toxoceratoides nagerai* (Leanza). A–B. CPBA 10880. C–D. CPBA 10881. Both specimens were found in the same calcareous nodule at Río Cardiel. All × 1.

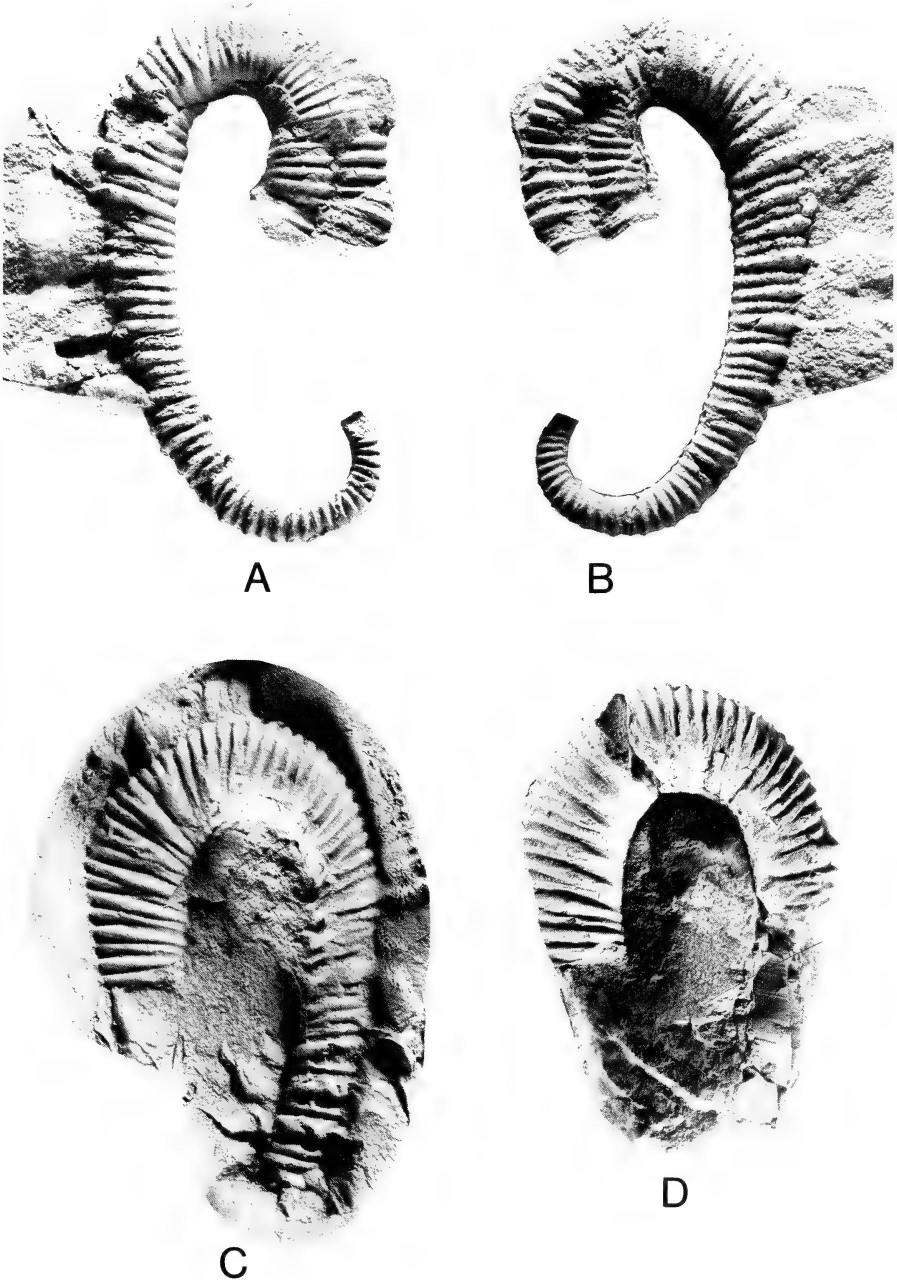

Fig. 17. *Toxoceratoides nagerai* (Leanza). A–B. CPBA 10830 from Puesto Bajo Comisión. C. Resin cast of CPBA 10843 from Puesto La Señalada after removing the calcite infilling the phragmocone. D. CPBA 10843. All × 1.

while others bifurcate on the umbilical wall and cross the flank as two fine intermediaries.

At the end of the shaft and beginning of the hook, the lateral and ventral tubercles disappear and the ornament changes to narrow, simple, sharp ribs that pass radially around the whorl and to ribs arising in groups of two or three from an umbilical tubercle. On the final hook these tubercles also disappear and the ribbing is simple.

The suture line is quite simple with trifid internal, umbilical, and lateral lobes.

Dimensions

Specimen	*L*	H_M	H_O	H_m
DNGM 9297	*c.* 80,0	22,0	9,0	5,5
CPBA 10880	*c.* 90,0	16,0	—	8,0
CPBA 10881	*c.* 88,0	14,0	—	5,5
CPBA 10830	69,0	*c.* 18,0	9,0	3,0

Discussion

Leanza (1970: 206) referred this species to the genus *Acrioceras*, pointing out that it belongs to the *'Ancyloceras' tabarelli* group (Uhlig 1883: 114, pl. 28 (fig. 2)). He also stated that the curved shaft resembles that of *'Ancyloceras' silesiacum* illustrated by Uhlig (1883: 142, pl. 28 (fig. 4)). Uhlig (1883), however, did not refer the latter species to *'Ancyloceras'* but to *'Crioceras'*. In any case, although *Acrioceras tabarelli* shows superficial similarities with *Toxoceratoides nagerai*, the coiling and ornament of the latter species plead for its attribution to *Toxoceratoides*.

Toxoceratoides royerianus has a depressed whorl section, with a flat dorsum and a shaft ornamented with alternate strong trituberculate ribs and fine intermediaries (Casey 1961: 80, pl. 6 (fig. 2a–b), pl. 17 (fig. 3a–b), text-fig. 30a–h), while *T. nagerai* has a compressed to equidimensional whorl section and more intermediate ribs on the shaft. Besides, the suture line of the first species is very incised, while in the latter it is quite simple.

Toxoceratoides rochi Casey is very close to *T. royerianus*, but differs from that species and from *T. nagerai* by the presence of very strong ribs on the final hook with very weak umbilical tubercles (Roch 1927: 30, pl. 1 (fig. 4)).

Toxoceratoides saulae Murphy, 1975, differs from *T. nagerai* mainly in having an ovoid, depressed whorl section and coarser trituberculate ribs on the end of the shaft.

Toxoceratoides krenkeli Förster (1975, pl. 4 (figs 1–2)) has a more depressed whorl section, mainly trituberculate ribs on the shaft with few intermediaries and coarse ribbing on the final hook.

Toxoceratoides proteus (Spath) shows lateral tubercles on the final hook from which the bifurcate ribs arise (Casey 1961: 82, pl. 10 (fig. 2a–c)). This feature allows an easy separation from all the other known species of the genus.

The shaft of *T. starrkingi* (Anderson) bears some resemblance to that of *T. nagerai*, but the final hook has not only umbilical but also lateral and ventral tubercles (Anderson 1938: 207, pl. 59 (fig. 4–4A), pl. 65 (fig. 4A)).

Tonohamites decurrens has a *Toxoceratoides*-like shaft, which resembles that of *Toxoceratoides nagerai*, especially in the number of fine intermediate ribs. However, both species are easily distinguished by the ornament of the final hook. In the former, there are radial, broad and rounded single ribs (Casey 1961: 80, pl. 5 (fig. 3a–b), pl. 21 (fig. 2)), while in *T. nagerai* the ribbing on the final hook is sharp, narrow and with some umbilical tubercles.

Leanza (1970, fig. 4 (1)) described a fragmentary specimen of *Helicancylus* cf. *patagonicus*. He stated the close similarities with Stolley's (1912, fig. 3–3a) *'Ancyloceras' patagonicum*. Although Leanza's specimen is poorly preserved, it shows umbilical tubercles on the bend of the hook, as well as bi- and trifurcate ribs. These features are not present in *Helicancylus patagonicus* and Leanza's specimen is therefore referred to *Toxoceratoides nagerai*.

Toxoceratoides cf. *biplex* (von Koenen, 1902)

Figs 18C–D, 19C

Compare:

Ancyloceras? biplex von Koenen, 1902: 381, pl. 49 (figs 10a–b, 11a–b).
Toxoceratoides cf. *biplex* (von Koenen): Casey, 1961: 83, pl. 20 (fig. 6).

Material

CPBA 10910 from Puesto Bajo Comisión, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

One specimen is available, consisting of the end of the shaft and final hook, and preserved as an internal cast partially covered with the original shell.

The whorl section on the earliest preserved part, which coincides with the end of the phragmocone, is depressed (Wh/Wb = 0,83), ovoid, with a flat dorsum, a broadly rounded umbilical edge, strongly inflated flanks, and a broadly rounded venter. The maximum width is at the dorsal third of the flanks. On the final hook the whorl section is more rounded, slightly depressed (Wh/Wb = 0,93) with a narrower dorsum, moderately inflated flanks converging to a rounded venter (Fig. 18C–D).

Ornament consists of fine, sharp, dense ribs. They run prorsiradiate over the flanks. On the bend of the crozier there are frequent low-angle bifurcations near the umbilical margin. On some ribs, slight tubercle-like elevations are present at the umbilical edge. Over the dorsum the ribs are reduced to striae with a forward flexure. The upper half of the flanks as well as the venter are heavily abraded, but it seems that the ribs cross the venter without interruption, and at the distal end they are simple, dense and radial.

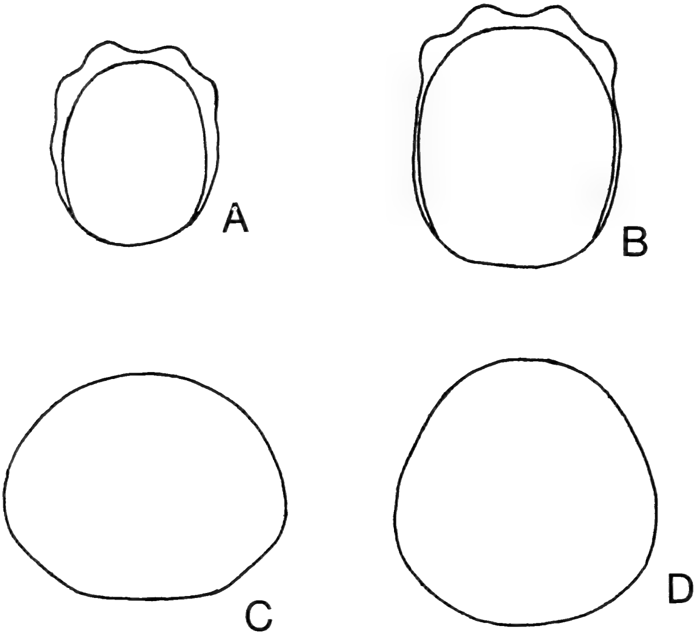

Fig. 18. A. Whorl section of *Toxoceratoides? haughtoni* Klinger & Kennedy, CPBA 10901. × 2. B. Whorl section of *Toxoceratoides?* sp., CPBA 11049. × 2,5. C–D. Whorl sections of *Toxoceratoides* cf. *biplex*, CPBA 10910. × 2,5.

Discussion

The single specimen compares well with that of Von Koenen (1902, pl. 49 (figs 10b–11b)) in ornament and whorl section, although the latter is more depressed and with the maximum width on the dorsal half of the flank. Von Koenen (1902: 381) indicated the presence of lateral tubercles, but did not illustrate these. In the Patagonian specimen faint elevations can be seen occasionally on some ribs where the original shell is still preserved.

Drushchits & Kudryavtsev (1960: 295, pl. 39 (fig. 3a–c)) described and figured two fragmentary specimens of *Leptoceras biplex* von Koenen. The presence of strong bituberculate ribs on the shaft and bifurcate ribs on the bend of the crozier casts doubt on the specific assignation of these specimens. According to Förster (1975: 162) the Russian material may belong to *Toxoceratoides fustiformis*. As the latter species does not have umbilical tubercles on the bend of the crozier and the shaft is ornamented with trituberculate ribs, it is doubtful that the Russian material can be assigned to *T. fustiformis* or to *T. biplex*.

Casey (1961: 83, pl. 20 (fig. 6)) referred a small fragmentary specimen to *T.* cf. *biplex*, which resembles the one here described. According to him, the most characteristic feature of this species is the presence of 'fine, sharp, wiry ribbing'.

Toxoceratoides? haughtoni Klinger & Kennedy, 1977

Figs 18A, 19H–J

Toxoceratoides? haughtoni Klinger & Kennedy, 1977: 310, figs 59A–D, 60A–I, 61A–C, 62A–C, 64A–C, 66B, 79A–B.

?Toxoceratoides (Colomboceratoides) renzoni Etayo Serna, 1979: 20, pl. 6 (fig. 19), text-fig. 3O.

Holotype

SAS 64/T_1 from locality 168, Mfongozi Creek, northern Zululand, Aptian III–IV (Upper Aptian). South African Geological Survey Collection, Pretoria. Collected by H. Klinger, 1970.

Material

CPBA 10901 from La Horqueta, Cardiel River (collection Lic. G. Marín), and CPBA 10849 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

Both specimens are fragments of curved shafts. The whorl section is initially subcircular, slightly compressed (Wh/Wb = 1,07) with a feeble convex dorsum and rounded flanks converging to a flattened venter. As size increases the whorl section becomes more laterally compressed (Wh/Wb = 1,25) (Fig. 18A).

At the smallest diameter (Wh = 7,5 mm) ornament consists of single rounded ribs, slightly prorsiradiate and with rounded ventral tubercles, which are marginal to a siphonal depression. At this stage small ventrolateral tubercles can also be seen. At a diameter of 10 mm there are two kinds of ribs; some are fine, non-tuberculate, and the others are strong, high with ventrolateral and ventral tubercles. Both types alternate regularly. While the first type crosses the venter without interruption, the second one ends on both sides of a siphonal depression. Both cross the dorsum straight or slightly curved and run prorsiradiate over the flanks.

Some of the strong ribs duplicate from the ventrolateral tubercle and on the lower flank and dorsum they form two fine ribs, while between the ventrolateral and ventral tubercle there is only a single flat and broad rib. At large diameters, the intercalatory ribs disappear.

The suture line cannot be traced on the present material.

Discussion

The shaft fragments correspond well with those of Klinger & Kennedy (1977). These authors assigned this species to *Toxoceratoides* with doubt because of the peculiar ornament of the early whorls as well as the absence of simple ribbing on the recurved crozier. According to Klinger & Kennedy (1977) those atypical features serve to distinguish *T.? haughtoni* from other species assigned to

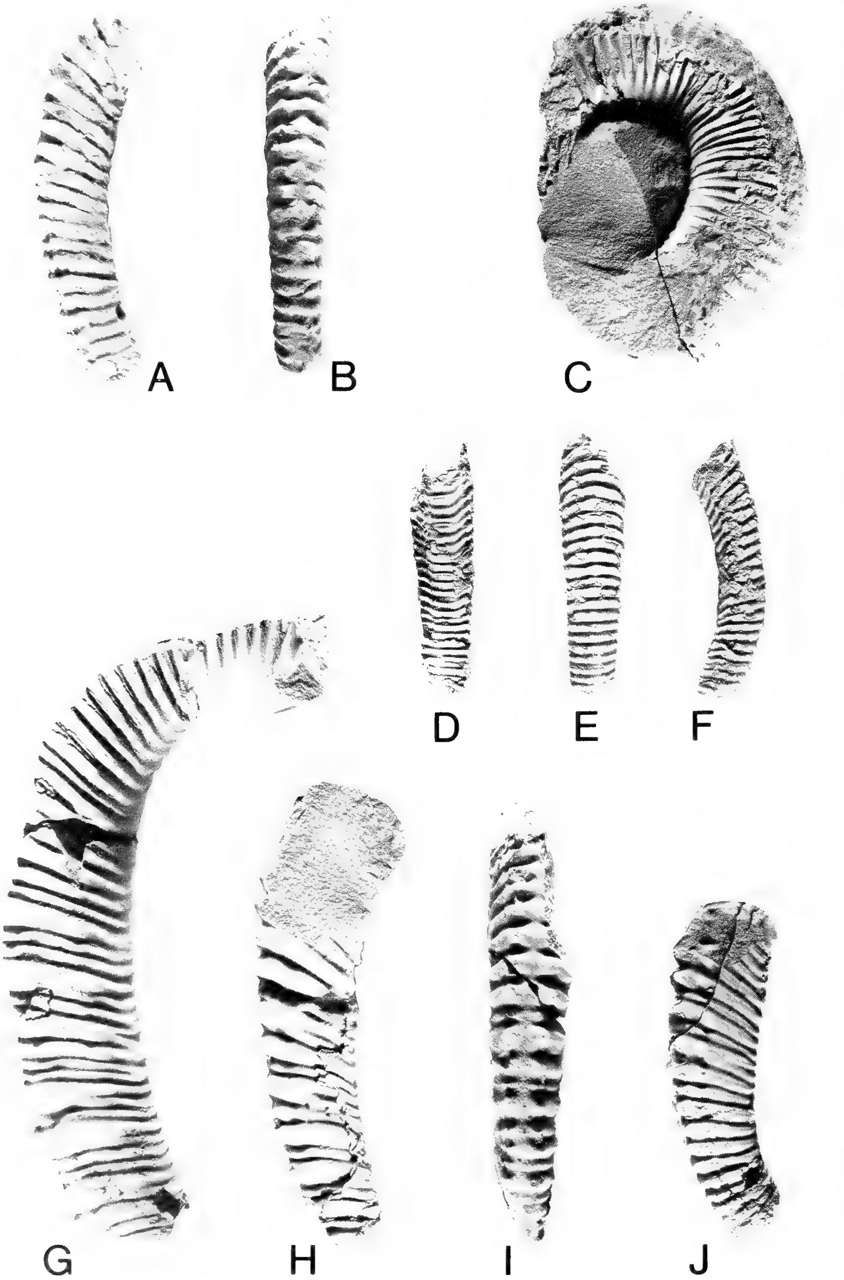

Fig. 19. A–B. *Helicancylus patagonicus* (Stolley), CPBA 10898 from Puesto La Señalada. C. *Toxoceratoides* cf. *biplex*, CPBA 10910 from Puesto Bajo Comisión. D–F. *Tonohamites aequicingulatus* (von Koenen), CPBA 11897 from Loma Pelada. G. *Toxoceratoides?* sp., CPBA 11049 from Puesto La Señalada. H–J. *Toxoceratoides? haughtoni* Klinger & Kennedy. H–I. CPBA 10849 from Puesto La Señalada. J. CPBA 10901 from La Horqueta. All × 1.

this genus. Unfortunately neither the early whorls nor the final hook are preserved in the Patagonian material.

Toxoceratoides krenkeli is to some extent a comparable species, as the ornament on the shaft is similar to that of *T.? haughtoni*. However, the former species has a depressed whorl section and the tuberculation appears at a very small diameter (Förster 1975; Klinger & Kennedy 1977).

Etayo Serna (1979) proposed a new subgenus and new species of *Toxoceratoides: T. (Colomboceratoides) renzoni*. The ornament and whorl section of the single fragment of this species shows close similarities to *T.? haughtoni*, so that *T. renzoni* may be a junior synonym.

Occurrence

Toxoceratoides? haughtoni occurs in the Upper Aptian of Zululand and Patagonia.

Toxoceratoides? sp.

Figs 18B, 19G

Material

CPBA 11049 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

The single fragment is 80 mm long and comprises the upper part of the shaft (55 mm) and the beginning of the final hook. The ventral region is heavily abraded.

At the smallest diameter ($Wh = 14$ mm) the whorl section is ovoid, laterally compressed ($Wh/Wb = 1{,}27$) with a feeble convex dorsum, slightly curved flanks and rounded venter. The whorl section, measured over a tuberculate rib, is subhexagonal (Fig. 18B). As size increases, the whorl section becomes more rounded.

The shaft is ornamented with strong tuberculate ribs and thin non-tuberculate intermediaries, which are arranged in an irregular pattern. Both types cross the dorsum with a forward curvature, are prorsiradiate over the flank and straight over the venter, where the strong ribs are interrupted. The ribs show two rows of tubercles: one ventral and the other ventrolateral. On the upper part of the shaft some bear a third row of small tubercles near the umbilical edge.

As in *Toxoceratoides? haughtoni*, some of the strong ribs are duplicated at the ventrolateral tubercle and cross the dorsum as two fine single ribs; between the tubercles they are broad and flat. Only the dorsolateral part of the end of the shaft and the beginning of the crozier is preserved. The ornament consists of single, fine, narrow, dense, non-tuberculate ribs. There is no indication of umbilical tuberculation.

The suture line, partially exposed, shows relatively high elements and it is quite incised, with trifid lateral, umbilical, and internal lobes.

Discussion

Generic allocation of the specimen is difficult as it shares characteristics of *Toxoceratoides* and *Tonohamites*.

The absence of umbilical tubercles on the bend of the crozier and the ornament of single ribs are features of *Tonohamites* rather than of *Toxoceratoides*. However, in the former genus the ribs are usually broad and rounded, not thin and sharp as in the Patagonian specimen. The shaft ornament is more *Toxoceratoides*-like, but not typical if compared with species like *Toxoceratoides royerianus* (Casey 1961: 78, pl. 6 (fig. 2)) or *T. krenkeli* (Förster 1975: 160, pl. 4 (figs 1–2)). Besides, *Tonohamites decurrens* has the shaft ornamented as in *Toxoceratoides*, which shows the close relationship between both genera, as stated by Klinger & Kennedy (1977: 319).

The only feature that allows a comparison with another species is the longitudinal duplication of the strong ribs. This character is also present in *Toxoceratoides? haughtoni*. Both species differ markedly in the ornament of the bend of the crozier.

Finally, *Tonohamites* and *Toxoceratoides* show a typical ancyloceratid pattern in the suture line, with bifid saddles and trifid lobes, but the former usually has low, simple elements while in the latter the suture line may be more incised with relatively higher elements.

Based on the suture line and to a lesser extent on the ornament of the shaft, the present fragment is referred with doubt to *Toxoceratoides*, aware that the ornament of the final hook is atypical.

Genus *Tonohamites* Spath, 1924

Type-species. Tonohamites decurrens Spath, 1924, from the Lower Aptian of Germany, by original designation.

Diagnosis

Coiling toxoceratid or labeceratid. Ribbing usually rounded, tuberculation may be present, but the tubercles are weak and mostly confined to the venter. On the body chamber the ribs are simple, strong, rounded or flat and non-tuberculate. Suture line simple, with bifid saddles and trifid lobes.

Discussion

The type-species of this genus is difficult to interpret, and nomenclatural problems are involved. Casey (1961: 84) extensively discussed this point. Wright (1957: L212) regarded *Tonohamites* as a synonym of *Hamiticeras*, while Casey (1961: 84) maintained the genus and gave the first diagnosis.

The type-species of *Tonohamites* does not show the main features present in other species assigned to this genus. In fact, the ornament of the shaft, with strong trituberculate ribs, closely resembles that of *Toxoceratoides* and isolated fragments can hardly be distinguished. However, the ornament of the body chamber of *Tonohamites*, with broad, rounded, or flat ribs, allows an easy separation from *Toxoceratoides*, which shows fine, sharp, single ribs intercalated with bi- or trifurcate ones arising from umbilical tubercles on the final hook.

Hamiticeras Anderson, as interpreted here, differs from *Tonohamites* in its coarse trituberculate and intermediate ribs on the shaft and its long, parallel final hook with radial, sharp, high ribbing.

Helicancylus Gabb, redefined here, is easily distinguished from *Tonohamites* by the complete lack of minor ribbing, and the presence of tubercles on every rib on the shaft and on the recurved crozier.

According to Klinger & Kennedy (1977), Casey (1961) referred the following species to *Tonohamites*:

Tonohamites decurrens Spath (1924: 85). (Lectotype is the specimen illustrated by Von Koenen 1902, pl. 33 (fig. 2, and the lower part of fig. 3a).)
Tonohamites aequicingulatus (von Koenen) (1902: 394, pl. 37 (figs 5a–c, 6a–e)).
Tonohamites? hunstantoniensis Casey (1961: 90, pl. 21 (fig. 1a–d)).
Tonohamites koeneni Casey (1961: 89). (Holotype is the specimen illustrated by Von Koenen 1902, pl. 33 (fig. 3a, upper part only).)
Tonohamites limbatus Casey (1961: 89, pl. 21 (fig. 3a–b), pl. 22 (figs 3a–c, 4)).
Tonohamites? eichwaldi (Jasykow) (*in* Sinzow 1872: 36, pl. 6 (figs 7–9)).
Tonohamites? undosus (von Koenen) (1902: 393, pl. 35 (fig. 13a–f)).

It is interesting to mention that Casey (1961) noted similarities between some fragments of *Tonohamites aequicingulatus* and *Hamites? undosus* von Koenen. He also indicated that the latter species is only known by a small fragment of the shaft and that it is really difficult to decide whether it is a separate species. Finally, Casey decided to join all the fragments as belonging to a single, variable species and placed *T.? undosus* as a possible synonym of *T. aequicingulatus*.

To the list given above must be added *Tonohamites? caseyi* Klinger & Kennedy (1977: 324, figs 46, 49) and perhaps *Tonohamites? taylori* (Etheridge). Etheridge (*in* Jack & Etheridge 1892: 498, pl. 42 (fig. 13)) described and figured one specimen of *'Ancyloceras' taylori* showing a tightly coiled initial spire followed by a straight shaft, both ornamented with simple annular ribs. Later the same author (Etheridge 1909: 162, pl. 49 (figs 3–6)) included that fragment with other specimens and described them all as *'Crioceras' taylori*.

The type specimen of *'Ancyloceras' taylori* was placed in *Toxoceratoides* by Whitehouse (1926), who figured a small additional fragment, while the specimens of *'Crioceras' taylori* were included in the Albian genus *Labeceras* Spath.

Finally Day (1974: 14) noted that *'Ancyloceras' taylori* might be placed more suitably in *Tonohamites* than in *Toxoceratoides*. This view is supported by the *Tonohamites*-like ornament of the small fragment illustrated by Whitehouse (1926: pl. 36 (fig. 5)).

Kakabadze (1981) recorded *Tonohamites picteti* (Ooster) from the Lower Aptian of southern USSR. As he did not describe nor figure the specimens, it is not possible to decide if they belong to this genus or not. Ooster's (1857, pl. 50 (figs 1–6)) type specimen of *'Ancyloceras' picteti* does not resemble *Tonohamites*.

Specific differentiation within the genus *Tonohamites* is rather difficult, especially when dealing with fragments. It is based mainly on the coiling, ornament, and whorl section.

Occurrence

Tonohamites occurs in the Lower Aptian of Germany (Von Koenen 1902), Spain (Martínez 1982), England (Casey 1961), and ?southern USSR (Kakabadze 1981). It also occurs in the Upper Aptian of Madagascar (Collignon 1962) and Zululand (Klinger & Kennedy 1977). This is the first record from Patagonia (see Fig. 8).

Tonohamites aequicingulatus (von Koenen, 1902)

Fig. 19D–F

Hamites aequicingulatus von Koenen, 1902: 394, pl. 37 (figs 5a–c, 6a–e).
Tonohamites aequicingulatus (von Koenen): Casey, 1961: 87, pl. 9 (figs 2a–b, 3a–b, 4), text-fig. 32. Klinger & Kennedy, 1977: 322, figs 38C, 68A–E, 88D.
Tonohamites sp. aff. *aequicingulatus* (von Koenen): Collignon, 1962: 14, pl. 221 (fig. 960).

Lectotype

The original of Von Koenen (1902, pl. 37 (fig. 5a–c)) from the Lower Aptian of northern Germany, by subsequent designation of Casey (1961: 87).

Material

CPBA 11897 from Loma Pelada, Tucu-Tucu. Río Belgrano Formation. Lower Aptian.

Description

The small part of a shaft, 35 mm long and preserved as an internal cast, is partially covered with the original shell.

The whorl section is ovoid, depressed ($Wh/Wb = 0,75–0,77$), with flat dorsum, slightly convex flanks, and broadly rounded venter. Ornament consists of annular, rounded ribs. They are nearly radial on the dorsum and prorsiradiate on the flanks. There are four ribs within a distance equal to the whorl diameter. In the early stage some ribs bear siphonal, lateral and umbilical tubercles; these are very small and rounded and disappear with increase in size.

The partially exposed suture line is simple with asymmetrical lateral lobe.

Discussion

As Casey (1961: 88) noted, this species is only known from fragments. The Patagonian specimen resembles both the European (Von Koenen 1902; Casey 1961) and Zululand (Klinger & Kennedy 1977) material. The only apparent difference between those specimens and the present fragment is that in the latter some early ribs bear three rows of tubercles, whilst the figured specimens show none or a ventral row only (Von Koenen 1902, pl. 37 (fig. 5); Casey 1961, pl. 9 (fig. 2b), text-fig. 32b).

The Madagascan specimen figured by Collignon (1962, pl. 221 (fig. 960)) shows a more rounded whorl section and the ribs are stronger. It has tentatively been referred to this species.

Tonohamites decurrens Spath has strong trituberculate ribs separated by intermediaries on the shaft (Casey 1961: 86, pl. 21 (fig. 2), pl. 5 (fig. 3a)). *Tonohamites limbatus* Casey has a slightly compressed subrectangular whorl section and strongly prorsiradiate, narrow ribs (Casey 1961: 89, pl. 20 (figs 3a–c, 4)).

According to Klinger & Kennedy (1977: 322) the body chamber of *T. koeneni* Casey resembles that of *T. aequicingulatus*, but the latter species shows ventral tubercles on the shaft.

Martínez's (1982: 142, pl. 24 (fig. 6a–b), text-fig. 23) small shaft fragment referred to *Tonohamites* sp. has comparable ornamentation and whorl section. It differs, however, in its more simple suture line at the same diameter.

Occurrence

Tonohamites aequicingulatus is known from the Aptian of Germany (Von Koenen 1902) and Lower Aptian (*bowerbanki* zone) in England (Casey 1961). The Madagascan and Zululand specimens are from the Upper Aptian (Collignon's (1962) *Aconeceras nisus* and *Melchiorites melchioris* zone, and Kennedy & Klinger's 1975 Aptian III–IV—see Klinger & Kennedy (1977)).

CONCLUDING REMARKS

The most important results of this study are:

— The redefinitions of *Helicancylus* (type-genus of the subfamily Helicancylinae) and of *Hamiticeras* clarify the systematics of the subfamily Helicancylinae.

— *Helicancylus*, as here interpreted, accommodates some species (one of which is *Helicancylus patagonicus*) of hitherto uncertain affinities.

— The systematic study allows the recognition of three genera of this subfamily in the Austral Basin: *Helicancylus, Toxoceratoides* and *Tonohamites*. They are recorded for the first time in this basin. Seven species have been identified.

— The representatives of this subfamily are locally common in several horizons of the Río Mayer Formation and in one level of the Río Belgrano; all are of Aptian age. Their recognition means an important increase in our knowledge of the Aptian biostratigraphy of the northern part of the Austral Basin.

— The identified fauna facilitates the correlation with previously known assemblages, especially from western Europe and south-eastern Africa.

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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:
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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) . . .'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
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e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably 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. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

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.

MARÍA BEATRIZ AGUIRRE URRETA

APTIAN AMMONITES FROM THE ARGENTINIAN AUSTRAL BASIN. THE SUBFAMILY HELICANCYLINAE HYATT, 1894

x 1

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ANNALS
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(a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
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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
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
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(i) *Abbreviations*, where these are numerous.

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions 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.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters. If Letraset is used authors are requested to use Helvetica-style lettering, if possible.

The number of the figure should be lightly marked in pencil on the back of each illustration.

5. REFERENCES cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid., idem, loc. cit., op. cit.* are not acceptable):

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

'Smith (1969) describes . . .'
'Smith (1969: 36, fig. 16) describes . . .'
'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al*. 1927) . . .'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc., to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.
For journal article give title of article, title of journal in italics (according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number in parentheses, pagination (first and last pages of article).

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 la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.

Fischer, P. H., Duval, M. & Raffy, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.

Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **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 ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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UPPER BARREMIAN HETEROCERATINAE (CEPHALOPODA, AMMONOIDEA) FROM PATAGONIA AND ZULULAND, WITH COMMENTS ON THE SYSTEMATICS OF THE SUBFAMILY

By

MARÍA BEATRIZ AGUIRRE URRETA
&
HERBERT CHRISTIAN KLINGER

Cape Town Kaapstad

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By

María Beatriz Aguirre Urreta

Departamento de Geología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina

&

Herbert Christian Klinger

Department of Invertebrate Palaeontology, South African Museum, Cape Town

(With 26 figures)

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ABSTRACT

Representatives of the ammonite subfamily Heteroceratinae from the province of Santa Cruz, Patagonia, Argentina, include *Heteroceras (H.) elegans* Rouchadzé and *Colchidites vulanensis* Egojan *australis* Klinger, Kakabadze & Kennedy. Examination of this material and that of Zululand casts doubt on the current systematic concepts applied within the subfamily, shows distinct size-related dimorphism in *Colchidites*, and further illustrates the scope of intraspecific variation.

CONTENTS

Ann. S. Afr. Mus. **96** (8), 1986: 315–358

INTRODUCTION

The Upper Barremian ammonite subfamily Heteroceratinae Spath, 1922, is best known from the south-western part of the U.S.S.R. Recent description of abundant representatives of this heteromorph group from Zululand, South Africa (Klinger 1976; Klinger *et al.* 1984) has shown distinct faunal similarities with the Caucasus; a trend that continues well into the Aptian, as indicated by other heteromorph ammonite groups (Förster 1975*a*, 1975*b*; Klinger & Kennedy 1977). Blasco *et al.* (1980) recorded the first occurrence of the heteroceratine genus *Colchidites* from Tucu Tucu in the province of Santa Cruz, Patagonia, Argentina. Since then, more material was collected by Aguirre Urreta in Patagonia for comparison with the Zululand and Caucasian material. Also, additional material from Zululand became available.

This material casts doubt on the current systematic concepts applied in the subfamily and displays the extensive range of intraspecific variation within the group. In addition, size-related dimorphism is demonstrated in the group for the first time.

LOCATION OF SPECIMENS

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

SAM = South African Museum, Cape Town
BMNH = British Museum (Natural History), London
GIAS = Geological Institute, Academy of Science, Georgian S.S.R., Tbilisi
CPBA = Cátedra de Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires
UP = Geology Department, University of Pretoria (Boshoff collection)
SAS = Geological Survey, Pretoria, South Africa

FIELD LOCALITIES

Patagonia

Most of the Patagonian material was collected at two localities: Chorrillo del Medio and Loma Pelada, situated in the central-western province of Santa Cruz, approximately 48°25′S 72°00′W (Fig. 1). These were described by Aguirre Urreta (1983) and details of the sections are shown in Figure 2. Only one specimen was collected at locality Cerro Cornillos, situated south of the former, 10 km north of Lake San Martín, approximately 48°47′S 72°23′W.

Zululand

All the Zululand material was collected at locality 170 of Kennedy & Klinger (1975: 302, fig. 11), cliff and gully sections 2 km north-west of Mlambongwenya Trading Store on the north side of the Mlambongwenya Stream, 27°10′10″S 32°10′13″E. Details of the section are shown in Figure 3, which is a composite for this locality and extends over several hundred metres. It corresponds to Haughton's (1936: 293) localities L_7–L_{13}.

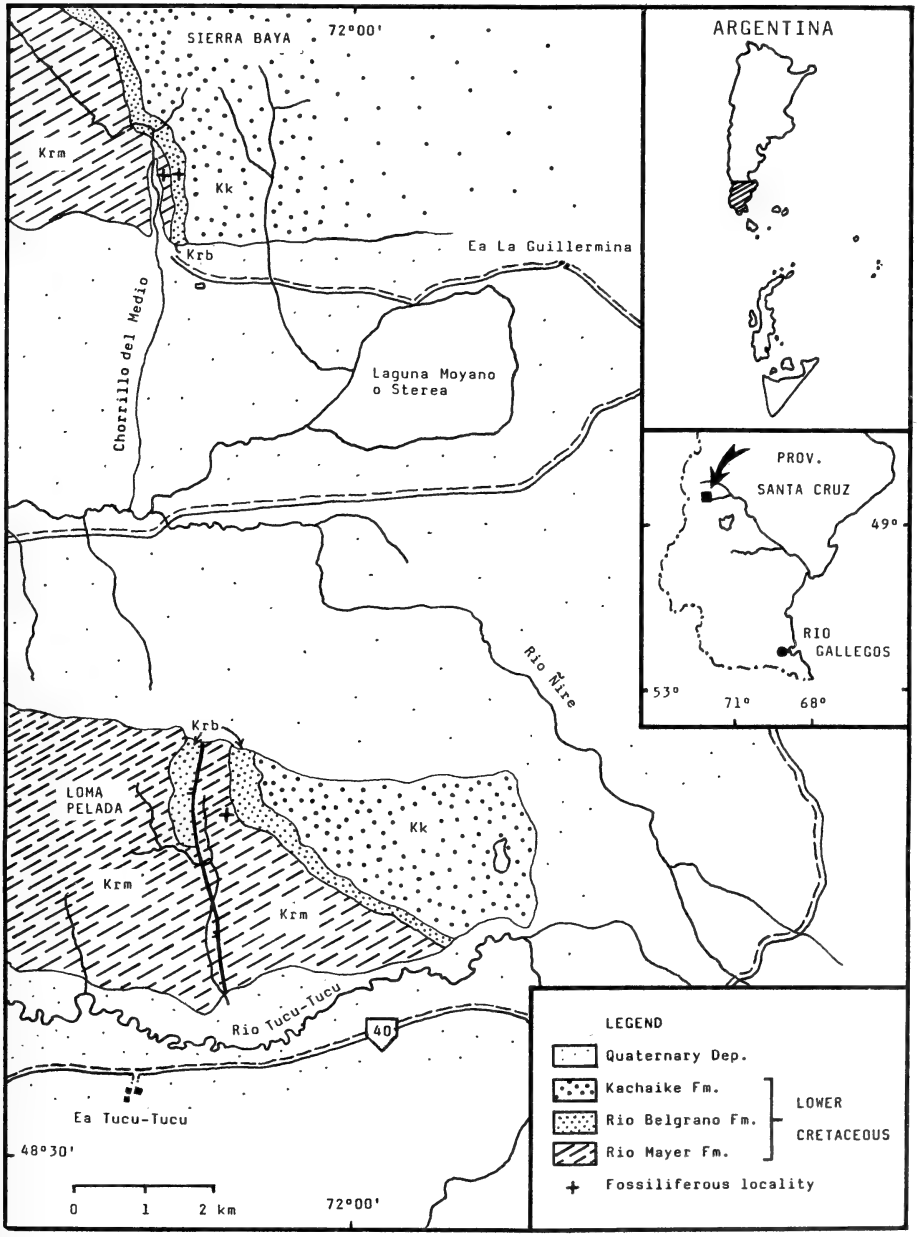


Fig. 1. Locality map of Patagonian exposures.

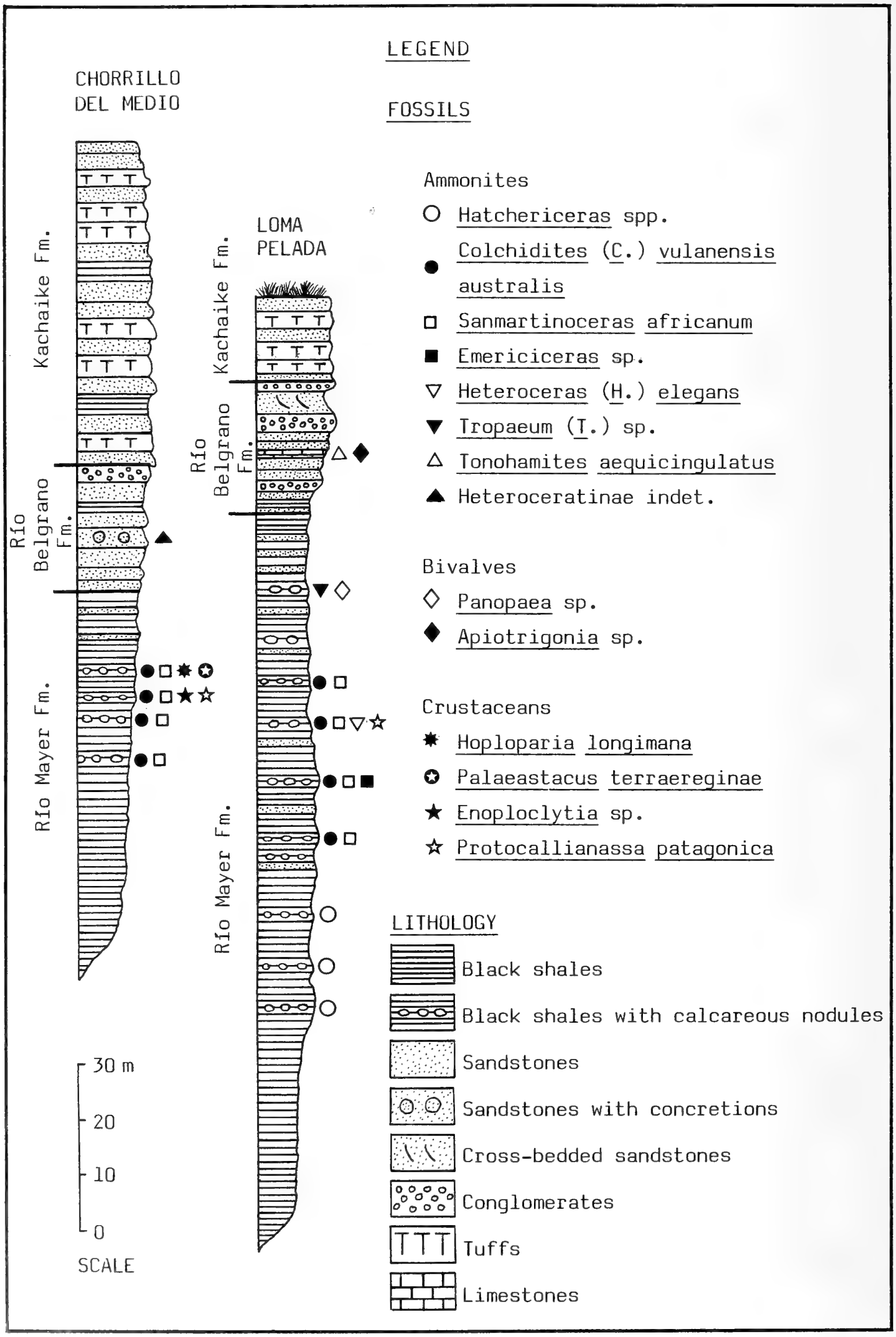
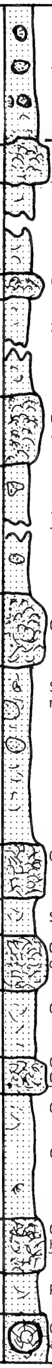


Fig. 2. Stratigraphic section at Loma Pelada and Chorrillo del Medio, Patagonia.



44 & 45	At least 10m o buff concretion Ancyloceras, Tr
43	Prominent concr Tropaeum and ot
42	1·6m poorly ex
41	Concretions wit
40	2m poorly expo
39	Concretions wit ancyloceratid f
38	1·5m silts wit The APTIAN/BARR
37	Concretions wit
36	Silts with scat molluscs, inclu
35	Concretions crow
34	Silts
33	Concretions crow occasional acone
32	Glauconite-rich
31	Concretions with Colchidites and
30	Grey-buff, burro Grey-buff, burro
29	Concretions with Heteroceras and
28	Poorly exposed s
27	Concretions with and trigoniids.

Fig. 3. Stratigraphic

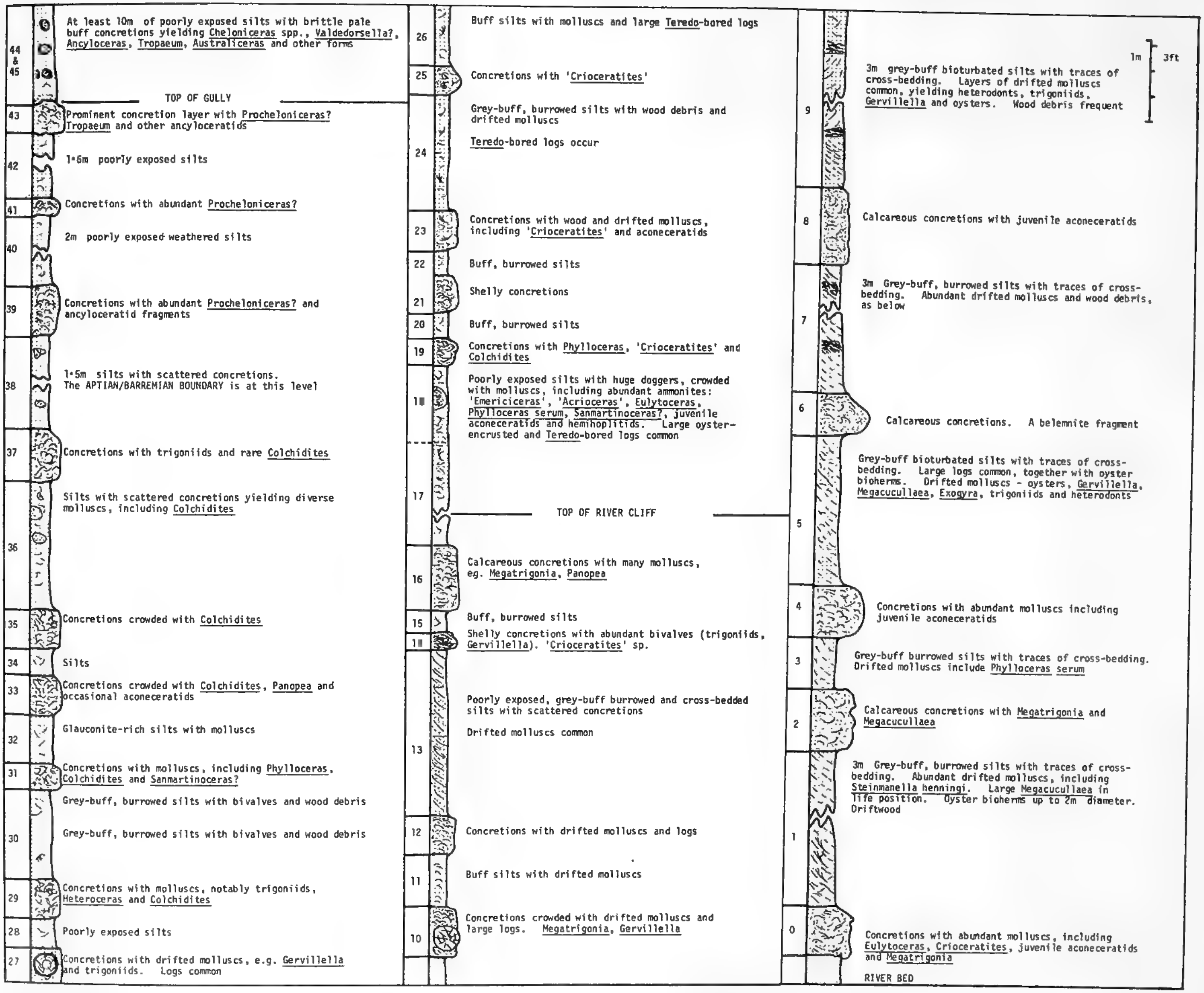


Fig. 3. Stratigraphic section at locality 170, Mlambongwenya Creek, Zululand. Reproduced with permission of British Museum (Natural History), London.

Note should be taken of the different lithologies. In Zululand the fauna occurs in a near-shore facies of silts and sandstones with abundant plant material, including well-preserved impressions of *Zamites recta* and *Cladophlebis dundrodiensis*. In Patagonia the dominant lithologies are anoxic black shales, with several levels of calcareous nodules in which the fossils are preserved.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullmann & Wiedmann 1970 for a recent review) is followed in the present work.

I = internal lobe; U = umbilical lobe; L = lateral lobe; E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Phylum **MOLLUSCA** Cuvier, 1797
Class CEPHALOPODA Zittel, 1884
Order AMMONOIDEA Zittel, 1884
Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily ANCYLOCERATACEAE Gill, 1871
Family **Heteroceratidae** Spath, 1922
Subfamily Heteroceratinae Spath, 1922

The subfamily Heteroceratinae Spath, 1922, has a virtually world-wide distribution (see e.g. pp. 322, 325) but is best known from the south-western part of the U.S.S.R. (Georgia, Caucasus and Turkmenia) through the monographical studies of Djanélidzé (1926), Rouchadzé (1933), Eristavi (1955), Egojan (1965), Kotetishvili (1970) and Kakabadze (1967, 1971*a*, 1975); especially the latter. The systematics of the subfamily are based mainly on the work of Rouchadzé (1933), and subsequently elaborated by Kakabadze (1967, 1971*a*, 1975). According to Kakabadze (1967, 1971*a*, 1971*b*, 1975) the group is elevated to familial level, and consists of two subfamilies that are further subdivided as follows:

Heteroceratinae Spath, 1922	Colchiditinae Kakabadze, 1967
Heteroceras (Heteroceras) d'Orbigny, 1850	*Imerites* Rouchadzé, 1933
Heteroceras (Argvethites) Rouchadzé, 1933	*Eristavia* Kakabadze, 1967
Hemibaculites Hyatt, 1900	*Colchidites* Djanélidzé, 1926
	Paraimerites Kakabadze, 1967

With the exception of *Hemibaculites*, which is an enigmatic genus and of uncertain affinities, all the above genera are closely related, both morphologically and phylogenetically.

Division at subfamilial level is based on coiling. In Heteroceratinae an initial helix is immediately followed by an uncoiled section, which may either be a straight shaft or a broadly curved section, ending in a recurved hook of which the shafts may be parallel or divergent. In the Colchiditinae an initial helix is followed by a planispirally coiled section of variable duration, which embraces the initial helix, finally uncoiling into a shaft and recurved hook. In some forms an uncoiled section has not yet been recorded, and it is suspected that they may reach maturity in the planispirally coiled stage.

As discussed earlier (Klinger 1976: 8) division into separate subfamilies as advocated by Kakabadze is considered superfluous.

Differentiation at generic or subgeneric level is based mainly on the presence or absence of tuberculation. *Heteroceras* s.s. is non-tuberculate throughout, whereas *H. (Argvethites)* has a pair of ventral tubercles on the shaft. *Colchidites* is non-tuberculate throughout; *Paraimerites* has a pair of variably developed ventral tubercles on part of the planispiral section and *Eristavia* and *Imerites* are both quadri-tuberculate on part of the planispiral whorls. *Eristavia* differs from *Imerites* in having intercalatory and bifurcating ribs; the latter originate at the ventrolateral tubercles and continue over the dorsum.

Within the genera *Heteroceras* and *Colchidites*, several species groups have been recognized. These were already identified by Rouchadzé (1933) and subsequently either retained or elevated in rank by Kakabadze (1967, 1971*a*, 1975). Within *Heteroceras* s.s. Rouchadzé (1933) recognized two species groups: *Heteroceras astieri* d'Orbigny and *Heteroceras helicoceroides* Karsten (misspelled *heliceroides*). The group of *H. astieri* includes large forms with a high helix, and axis of coiling oblique to the dorso-ventral symmetry of the shell. The shaft is long and curved, with a recurved crozier. The group of *H. helicoceroides* includes small forms with the axis of coiling of the helix oblique to the plane of symmetry of the shell, with a slender, straight shaft and relatively long recurved crozier. *Heteroceras (Argvethites)* is similar in size to the latter species group, but differs by the possession of a row of ventral tubercles on the shaft, and often a siphonal depression on the crozier.

In *Colchidites*, Rouchadzé (1933) identified three species groups:

(1) *Colchidites* gr. ex *intermedius* Djanélidzé, with a well-developed helical stage consisting of 5–8 whorls, a poorly developed planispiral part not exceeding one whorl, and a well-developed shaft and hook.

(2) *Colchidites* gr. ex *colchicus* Djanélidzé, with 4–7 whorls in the helical stage, one or two planispiral whorls, and a relatively well-developed uncoiled part.

(3) *Colchidites* gr. ex *shaoriensis* Djanélidzé with a low helix consisting of 2–3 whorls and a well-developed planispiral section with two or more whorls. An uncoiled part has as yet not been found in this species group.

According to Kakabadze (1975) these three species groups of *Colchidites* form a phylogenetic sequence, demonstrating yet another trend towards recoiling amongst heteromorphs (cf. Wiedmann 1969)—starting with *Heteroceras* at the one end, and ending at the other with a near-ammonitic coiled, streamlined form, *C.* gr. ex *shaoriensis*, which in turn may have given rise to the 'normally' coiled Deshayesitidae. It is unknown whether similar species groups and trends are present in *Paraimerites*, as only one, monotypical uncoiled species, *P. brevihelicoides* Kakabadze, is known. No uncoiled forms are known in either *Imerites* or *Eristavia*. Both genera appear stratigraphically before *Paraimerites* and *Colchidites* from a common ancestor with *Heteroceras*, but range into the uppermost Barremian with *Paraimerites* and *Colchidites*.

The validity of this classification will be discussed below on the basis of the Patagonian and Zululand material.

Fig. 4. Lumachelle with *Colchidites* from locality 170, Mlambongwenya Creek, Zululand. Note the co-occurrence of fine and coarsely ribbed forms. SAM–PCZ6393. × 0,65.

Genus *Heteroceras* s.s. d'Orbigny, 1850

Type-species. Turrilites emerici d'Orbigny, 1842, from the Upper Barremian of south-western France.

Diagnosis

Open-coiled heteromorphs with an initial helix followed by a straight or curved shaft and recurved crozier. Coiling in helix dextral or sinistral, with whorls tightly coiled or scarcely in contact. Ornament on helix consists of sinusoidal, single ribs. On the shaft and on the bend of the crozier, there are single, bifurcating and intercalatory ribs. These cross the dorsum with a slight forward curvature, sometimes duplicating there, and straight over the venter. In some, a slight siphonal depression may interrupt ribbing over the venter on part of the shaft and/or crozier. Suture line rather simple with low elements.

Occurrence

Heteroceras s.s. occurs in south-western U.S.S.R. (Georgia, Caucasus, Turkmenia) (Rouchadzé 1933; Eristavi 1955; Egojan 1965; Kotetishvili 1970; Kakabadze 1975), Bulgaria (Nikolov 1964; Dimitrova 1967), Hungary (Fülöp 1964), Czechoslovakia (Silesia) (Uhlig 1883), France (d'Orbigny 1842, 1850, 1851; Kilian 1888*a*, 1888*b*), California (Murphy 1975), Colombia (Karsten 1858, 1886; Royo y Gómez 1945), Canada (Jeletzky 1970), Japan (Obata & Ogawa 1976; Obata *et al.* 1976), Zululand (Klinger 1976; Klinger *et al.* 1984; herein), Patagonia (herein).

It has also been listed in Algeria (Blayac 1905; Simionescu 1905), Morocco (Roch 1930), Tunisia (Burollet *et al.* 1983), Tanzania (Spath 1930), Spain (Simionescu 1905) and Romania (Simionescu 1905). Reference to this genus in Peru seems to be due to geographic misinterpretation of Karsten's (1856, 1886) works.

Many unsubstantiated references to *Heteroceras* are probably misidentifications of Upper Cretaceous nostoceratids.

Heteroceras (Heteroceras) elegans Rouchadzé, 1933

Figs 5, 10E–I

Heteroceras elegans Rouchadzé, 1933: 232, pl. 13 (fig. 4), text-fig. 36. Eristavi, 1955: 118. Kakabadze, 1975: 89, pl. 3 (figs 1, 3–5), pl. 8 (fig. 5).
Heteroceras astierianum d'Orb.: Drushchits & Eristavi, 1958, pl. 49 (fig. 3).
Heteroceras (H.) sp. aff. *H. (H.) astieranum* d'Orbigny: Klinger, 1976: 11, pl. 1 (figs 1–2), text-figs 5a–c, 6a.
Heteroceras (Heteroceras) elegans Rouchadzé: Klinger, Kakabadze & Kennedy, 1984: 44, figs 2A–F, 3A–G, 4A–C.

Type

Lectotype by subsequent designation (as holotype) by Kakabadze (1975) is the specimen figured by Rouchadzé (1933, pl. 13 (fig. 4)) from western Georgia, Goresha, Upper Barremian zone of *Colchidites securiformis*, housed in the collections of the Geological Institute of the Academy of Science, Georgian S.S.R., cat. no. GIAS 350/1016.

Material

CPBA 11898–11900 from Loma Pelada, Tucu Tucu, CPBA 11121 from Cerro Cornillos, Lake San Martín, Patagonia, Río Mayer Formation, Upper Barremian, and SAS H54/29hi, BMNH C80025a–c, 80026a–b, 80028–9 from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Description

The helix consists of 4–5 contiguous whorls, coiled either dextrally or sinistrally. The last helical whorl passes directly into the straight to slightly curved shaft. The recurved crozier is relatively long, and nearly parallel to the shaft.

The whorl section in the helix is subcircular; on the shaft it varies from slightly compressed to depressed, and on the crozier it becomes equidimensional to subquadrate.

Ornament on the helix consists of fine, single, sinusoidal ribs. Ribbing on the shaft is usually single and slightly prorsiradiate, but at the end of the shaft and in the bend of the crozier bifurcating ribs are common. On the final part of the crozier the ribs are single, slightly curved and separated by interspaces wider than themselves.

A siphonal depression is present in some, but not all of the Zululand and Patagonian specimens (cf. Fig. 5A). It may already occur on the shaft, or only on the crozier, or on both. Ribs may be slightly thickened here, but no distinct tubercles develop.

Comparison

The Patagonian and Zululand material compares favourably with the specimens of *H. (H.) elegans* figured from western Georgia (Rouchadzé 1933; Kakabadze 1975; Klinger *et al.* 1984). According to Kakabadze (1975: 66) a siphonal depression occurs in the majority of tuberculate heteroceratids, i.e., *H. (Argvethites)*. Our material shows that this feature also occurs at random in non-tuberculate forms, and seems to be of very low taxonomic value.

The specimens here described also resemble the single helix and shaft fragment referred to *Heteroceras* aff. *astieri* by Obata & Ogawa (1976, pl. 4 (fig. 5)).

Heteroceras (H.) elegans differs from *H. (H.) helicoceroides* (Karsten) by the presence of chevron-like ornament on the venter of the latter—a rather *Hemibaculites*-like feature.

In *H. (H.) eristavii* the helix does not pass directly into the shaft; the latter is shorter and the recurved crozier forms a very tight bend (Kakabadze 1975: 90, pl. 4 (figs 1, 3), pl. 5 (fig. 5), pl. 8 (fig. 7)).

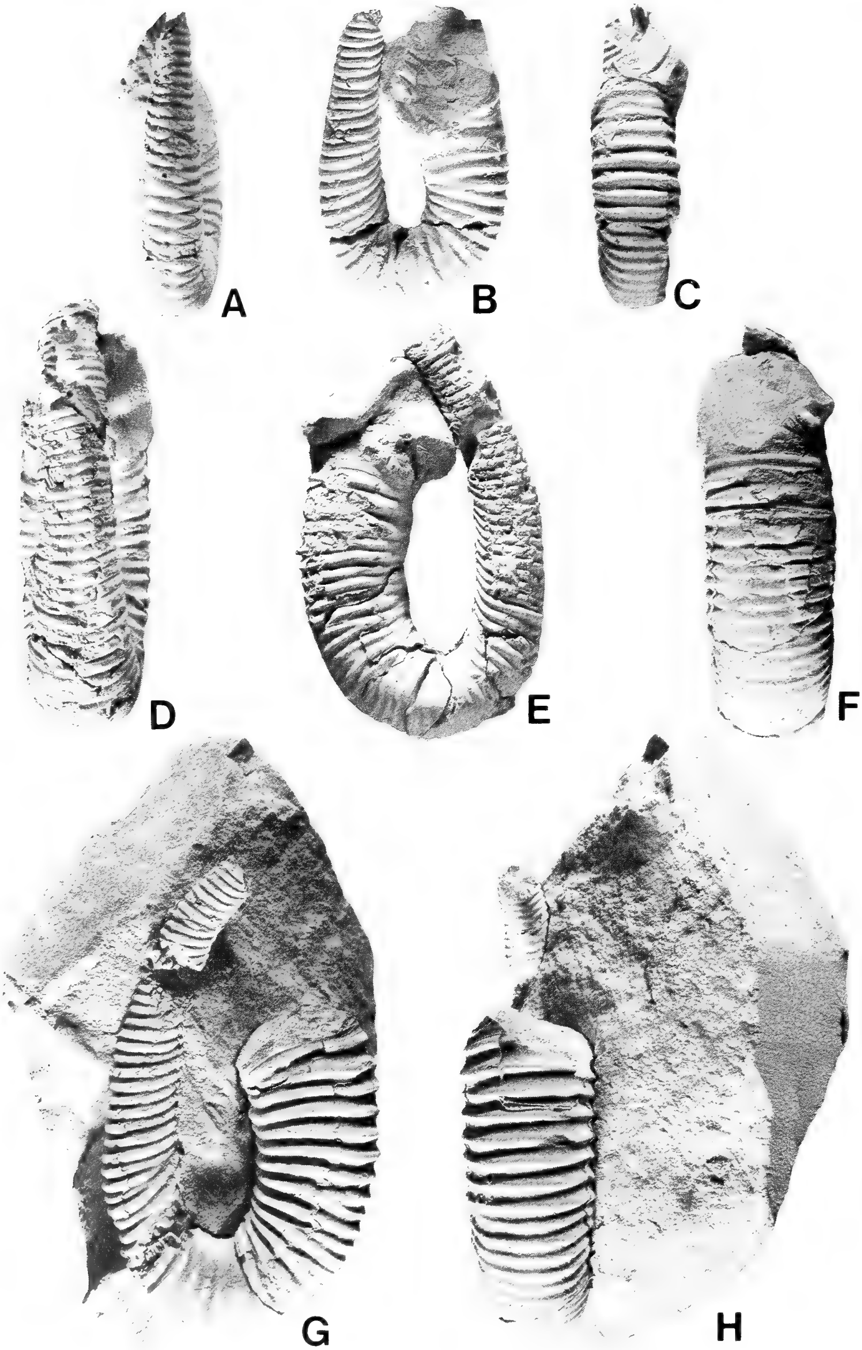


Fig. 5. *Heteroceras (Heteroceras) elegans* Rouchadzé, 1933. A–C.CPBA 11898. D–F. CPBA 11121. G–H. SAS H54/29hi. All × 1.

Heteroceras (H.) vermiforme Rouchadzé is only known from fragments. It is a very small species, with fine ribbing and an open, recurved crozier (Rouchadzé 1933, pl. 13 (fig. 5); Kakabadze 1975, pl. 3 (figs 6–8), pl. 4 (fig. 2)).

According to Kakabadze (1975: 92), *H. (H.) isocostata* Kakabadze is related to *H. (H.) elegans*, but differs in its greater size, stronger ornament on the helical part and the presence of bifurcating ribbing at the beginning of the shaft.

Occurrence

Upper Barremian of northern Caucasus, western Georgia, Zululand and Patagonia.

Genus *Colchidites* Djanélidzé, 1926

Type-species. Colchidites colchicus Djanélidzé, 1926, from the Upper Barremian of Georgia.

Diagnosis

Three distinct coiling modes occur during ontogeny—an initial helical spire consisting of between two and eight whorls, followed by a planispiral, discoidal section coiled more or less at right angles to the spire, which in turn may or may not end in a straight shaft with recurved crozier. Ornament consists of non-tuberculate, single, dichotomizing or intercalatory ribs.

Occurrence

Colchidites occurs in south-western U.S.S.R. (Turkmenia, Caucasus, Georgia) (Djanélidzé 1926; Rouchadzé 1933; Eristavi 1955; Drushchits & Kudryavtsev 1960; Kotetishvili 1970; Kakabadze 1971*a*), France (Kilian 1888*a*, 1888*b*), Turkey (Pelin & Thieuloy 1975), Colombia (Royo y Gómez 1945; Etayo Serna 1964), Patagonia (Blasco *et al.* 1980; herein); Zululand (Klinger 1976; Klinger *et al.* 1984). Myczynski's (1977) record of *Colchidites* sp. aff. *C. colchicus* from Cuba is accepted with reservation. The illustrated specimen is a poorly preserved, very small open-coiled heteromorph with no initial helix.

Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy, 1984

Figs 4, 6–9; 10A–D, J; 11–25, 26A–D

Colchidites sp. A Klinger, 1976: 16, pl. 1 (figs 6–7), pl. 3 (fig. 1), text-figs 5g, 6f–g.
Colchidites sp. B Klinger, 1976: 17, pl. 3 (fig. 2), text-fig. 5h.
Colchidites aff. *C. colchicus* Djanélidzé: Blasco, Nullo & Ploszkiewicz, 1980: 45, pl. 1 (figs 1–8).
Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy, 1984: 45, figs 6A–F, 7A–F, 8A–L, 9A–N.

Type

Holotype is SAS 3304/L54 from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Material

CPBA 11784, 11786, 11789, 11791, 11797–11803, 11805–6, 11809–11, 11814–18, 11821–23, 11829–30, 11839–47, 11849, 11851, 11856–61, 11863, 11865–67, 11874, 11876, 11878, 11884–5, 11888, 11901–2, all from Loma Pelada, Tucu Tucu (Bald Mountain of Hatcher 1903: 139) and CPBA 11828, 11838, 11848, 11852, 11894–6, all from Chorrillo del Medio, Tucu Tucu, Province of Santa Cruz, Patagonia, Río Mayer Formation, Upper Barremian; SAS L54/36h, L54/3288, BMNH C80013, 80015–20, 80022–25, SAM–PCZ6388–92, and more than 50 uncatalogued specimens, including blocks of colchiditid lumachelle, all from locality 170, Mlambongwenya Creek, northern Zululand, Makatini Formation, Upper Barremian.

Description

Dimorphic colchiditid with an initial helix consisting of at least five whorls, surrounded by one or two or more planispiral whorls. No uncoiled section is present.

The whorls of the helix are tightly coiled and impressed; they are either dextral or sinistral. Of 57 specimens, 30 are dextral and 27 sinistral. The most complete specimen (Fig. 6E) shows five whorls in the helix, thus the actual number may be as high as six or seven. The apical angle of the helix varies between 42 and 64 degrees. The axis of coiling of the helix is oblique to the plane of coiling of the planispiral section, forming an acute angle of between 31 and 42 degrees. The apex of the helix rests on the umbilical edge of the planispiral section. The whorl section in the helix is slightly depressed, subquadrate with rounded edges.

Ornament on the helix consists of sharp, narrow, sinusoidal ribs, which coalesce in twos or threes at the umbilical edge. Density varies between 24 and 32 per whorl.

Coiling in the first half of the planispiral whorl is irregular, with lateral deviations, but then becomes regular. In most specimens the planispiral whorl embraces the helix tightly, leaving no openings. The first planispiral whorl is higher than wide (Wb:Wh = 0,97–0,83), but the whorl section varies considerably from subrectangular to subcircular in different specimens. The ornament also shows a wide range of variation. In some specimens the ribs are high and sharp, slightly sinusoidal, usually simple, separated by wide interspaces, with rib density between 20 and 22. In others, the ornament consists of dense, rounded, sinusoidal ribs, which are simple or bifurcate from midflank. Bifurcations are asymmetrical on either side of the flanks, and are not arranged in a regular pattern. Rib density varies between 32 and 36. However, between these extremes there is a complete series of intermediate forms, so that separation on these grounds alone is impossible.

Some specimens are adult after one planispiral whorl at a diameter of about 50 mm. There are distinct apertural modifications consisting of strong, widely spaced prominent ribs. These are here interpreted as microconchs. Other

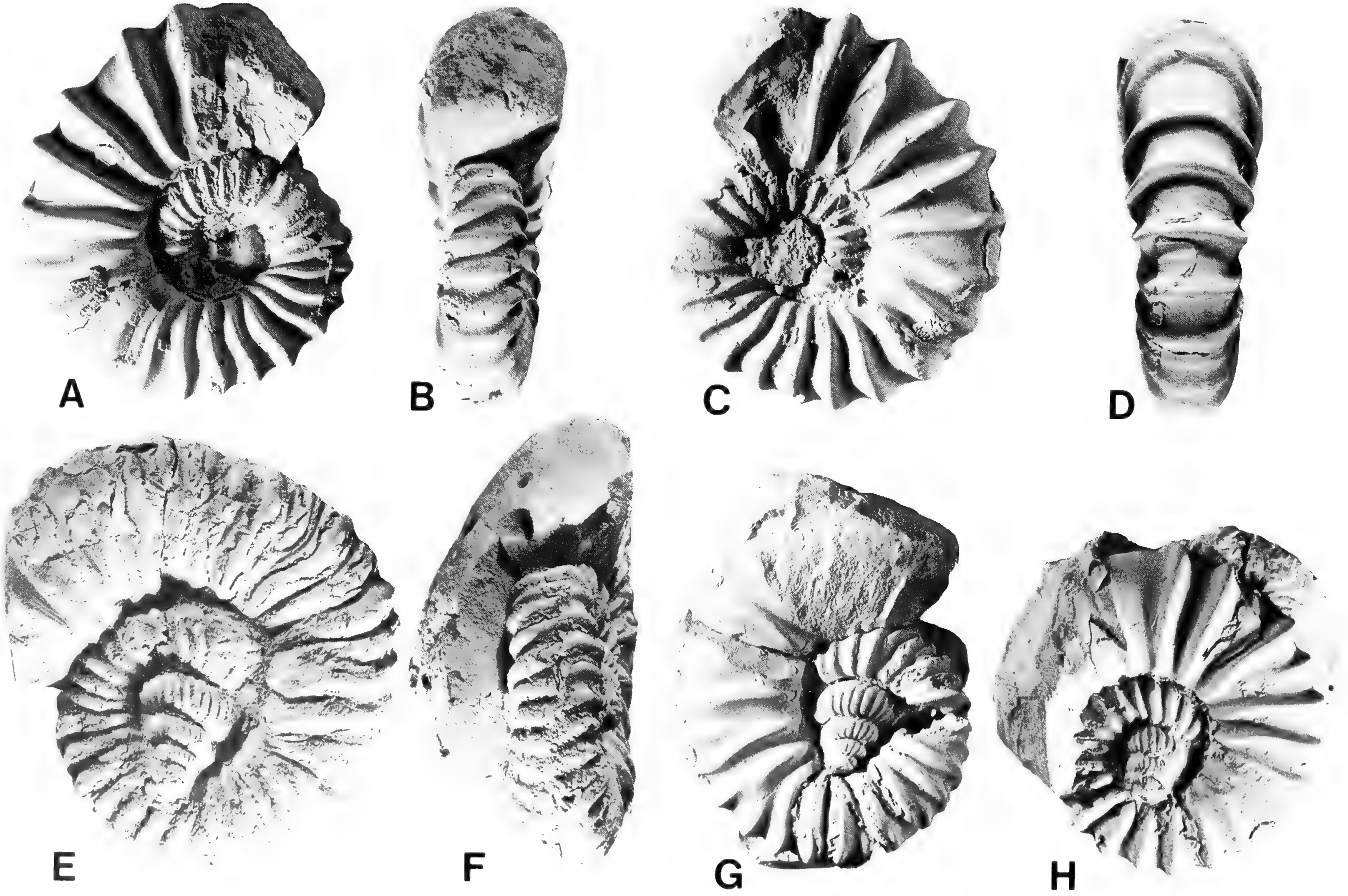


Fig. 6. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch with apertural modification. CPBA 11876. E–F. Microconch. CPBA 11842. G–H. Microconch with apertural modification. CPBA 11823. All × 1.

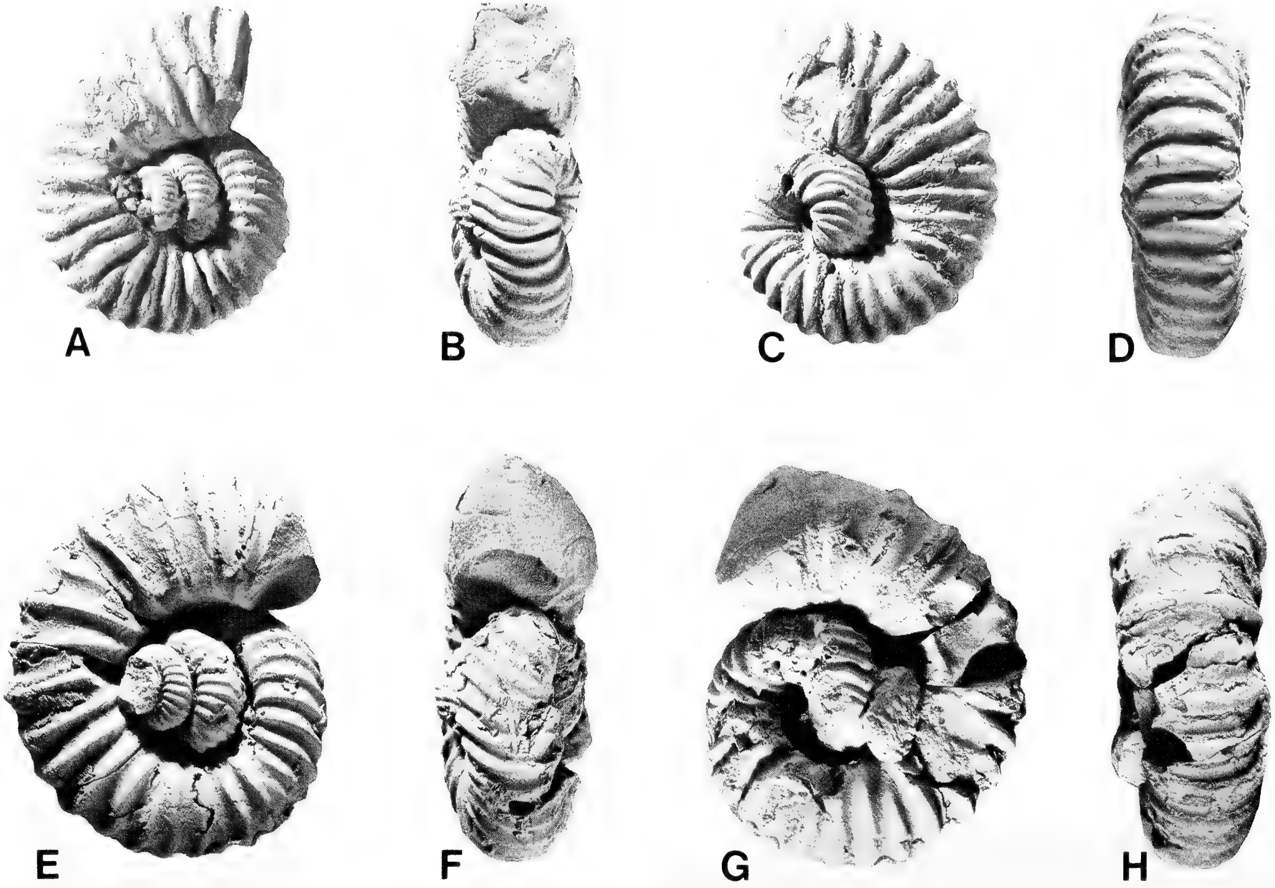


Fig. 7. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11815. E–H. Microconch. CPBA 11863. All × 1.

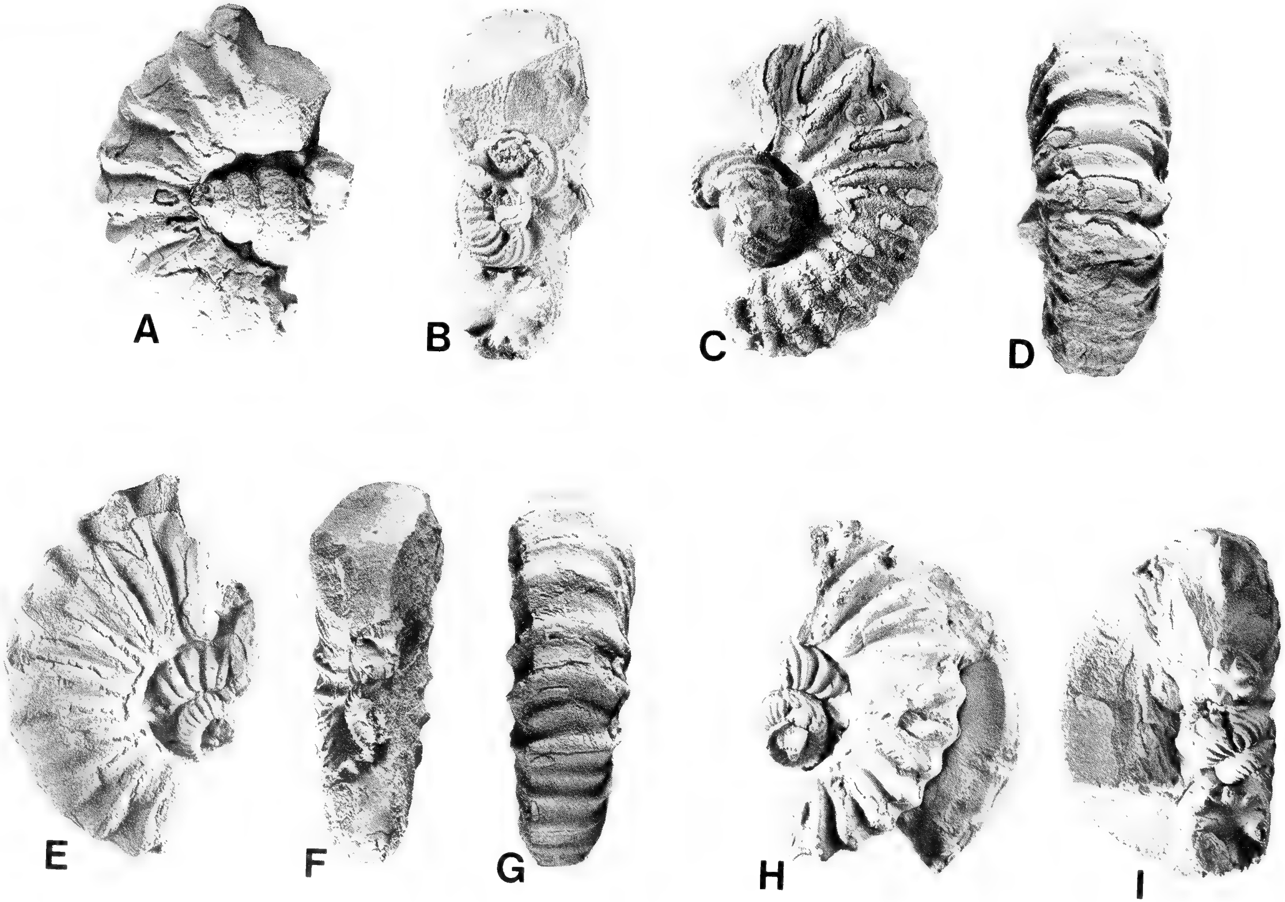


Fig. 8. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11861. E–G. Microconch. CPBA 11816. H–I. Microconch. CPBA 11789. All × 1.

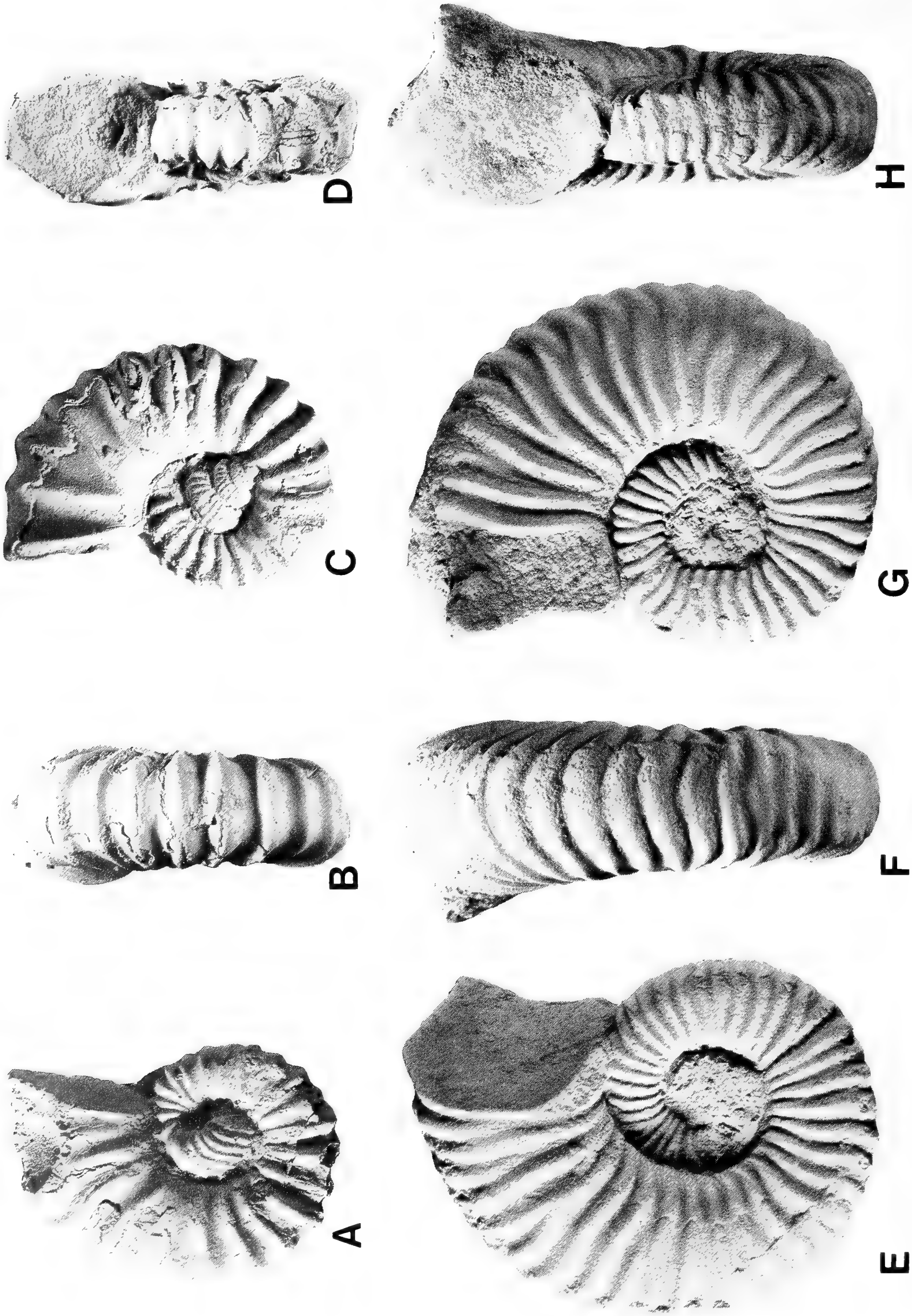


Fig. 9. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–D. Microconch. CPBA 11846. E–H. Immature macroconch? CPBA 11894. All × 1.

specimens have more than two planispiral, still septate whorls. It is estimated that fully grown specimens must have had at least two and a half to three planispiral whorls at a diameter of 300 mm. No signs of uncoiling or uncoiled fragments are known.

Ornament on the planispiral section is very variable, but generally tends to weaken on the outer whorls, becoming nearly smooth in some specimens.

Dimensions

Specimen	D	W_h	W_b	W_h/W_b	U
Holotype	44,2	18,0 (0,40)	17,0 (0,38)	1,06	15,5 (0,35)
L54/36h	91,0	38,0 (0,42)	31,0 (0,34)	1,22	31,0 (0,34)
C80022	37,0	16,5 (0,44)	15,0 (0,40)	1,10	12,0 (0,32)
C80016	51,5	21,0 (0,41)	21,0 (0,41)	1,00	19,0 (0,37)
C80018	54,0	25,0 (0,46)	21,5 (0,40)	1,16	20,0 (0,37)
C80015	50,0	23,0 (0,46)	23,0 (0,46)	1,00	18,0 (0,36)
C80017	53,0	22,0 (0,41)	21,0 (0,40)	1,05	18,0 (0,34)
PCZ6389	112,0	46,0 (0,41)	34,0 (0,31)	1,35	— —
CPBA 11848	37,0	15,0 (0,41)	12,5 (0,34)	1,20	12,0 (0,32)
CPBA 11828	35,0	16,5 (0,46)	16,0 (0,44)	1,03	12,0 (0,33)
CPBA 11821	36,5	14,5 (0,40)	13,5 (0,37)	1,07	12,0 (0,33)
CPBA 11817	41,0	17,0 (0,41)	16,5 (0,40)	1,03	12,0 (0,29)
CPBA 11809	45,5	18,5 (0,41)	16,0 (0,35)	1,15	— —
CPBA 11815	45,0	18,0 (0,40)	16,0 (0,36)	1,13	14,0 (0,31)
CPBA 11851	47,5	19,5 (0,41)	16,0 (0,37)	1,22	15,0 (0,32)
CPBA 11839	40,0	15,0 (0,38)	15,0 (0,38)	1,00	12,5 (0,31)
CPBA 11800	39,0	16,5 (0,42)	15,0 (0,38)	1,10	13,0 (0,33)
CPBA 11791	53,5	21,0 (0,39)	19,0 (0,36)	1,11	22,0 (0,41)
CPBA 11830	54,0	20,5 (0,38)	20,0 (0,37)	1,03	21,0 (0,39)
CPBA 11867	48,5	20,0 (0,41)	20,0 (0,41)	1,00	14,5 (0,30)
CPBA 11894	60,0	25,0 (0,42)	22,0 (0,37)	1,14	21,0 (0,35)
CPBA 11797	160,0	65,0 (0,41)	48,0 (0,30)	1,35	50,0 (0,31)

Comparison

Most of our material compares favourably with Egojan's (1965) original figured specimens, especially as far as the large size of the macroconchs is concerned. The Zululand material was separated from the Caucasian material at subspecific level by Klinger *et al.* (1984) on account of the broader and flatter venter of the planispiral section, but on the basis of the present material we doubt if even this is necessary.

Egojan (1965: 120) compared *C. vulanensis* to *C. djanelidzei* Rouchadzé but the two species differ on account of the disparate number of whorls in the helical section; *C. djanelidzei* only has 2–3 as compared to 6–7 in *C. vulanensis australis*.

Occurrence

Colchidites vulanensis s.l. occurs in the Upper Barremian of the Caucasus, Zululand and Patagonia.

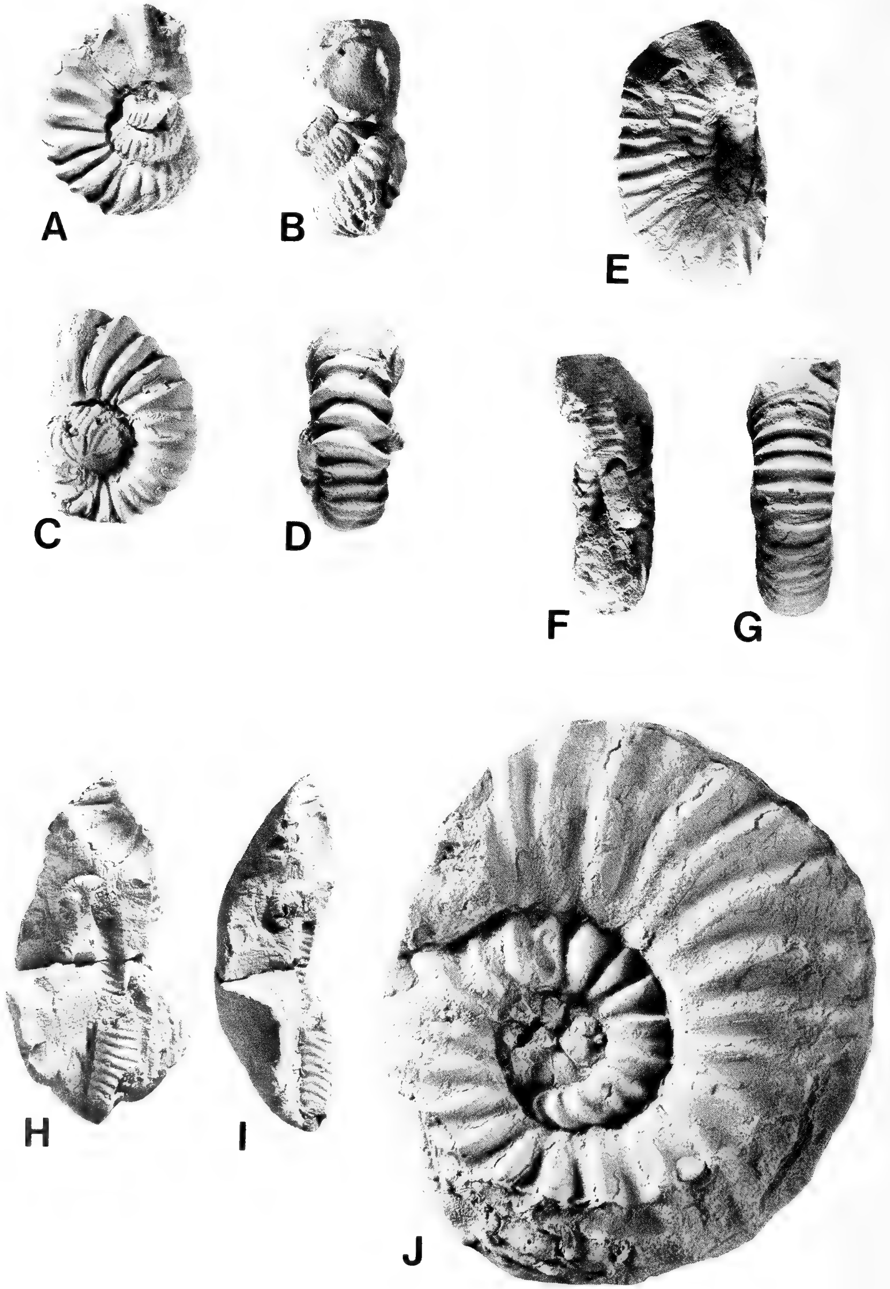


Fig. 10. A–D. *Colchidites vulanensis australis*. Coarsely ribbed microconch. CPBA 11821. E–G. *Heteroceras (H.) elegans* Rouchadzé, 1933. CPBA 11900. H–I. *Heteroceras (H.) elegans* Rouchadzé, 1933. CPBA 11899. J. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Immature macroconch? CPBA 11784. All × 1.

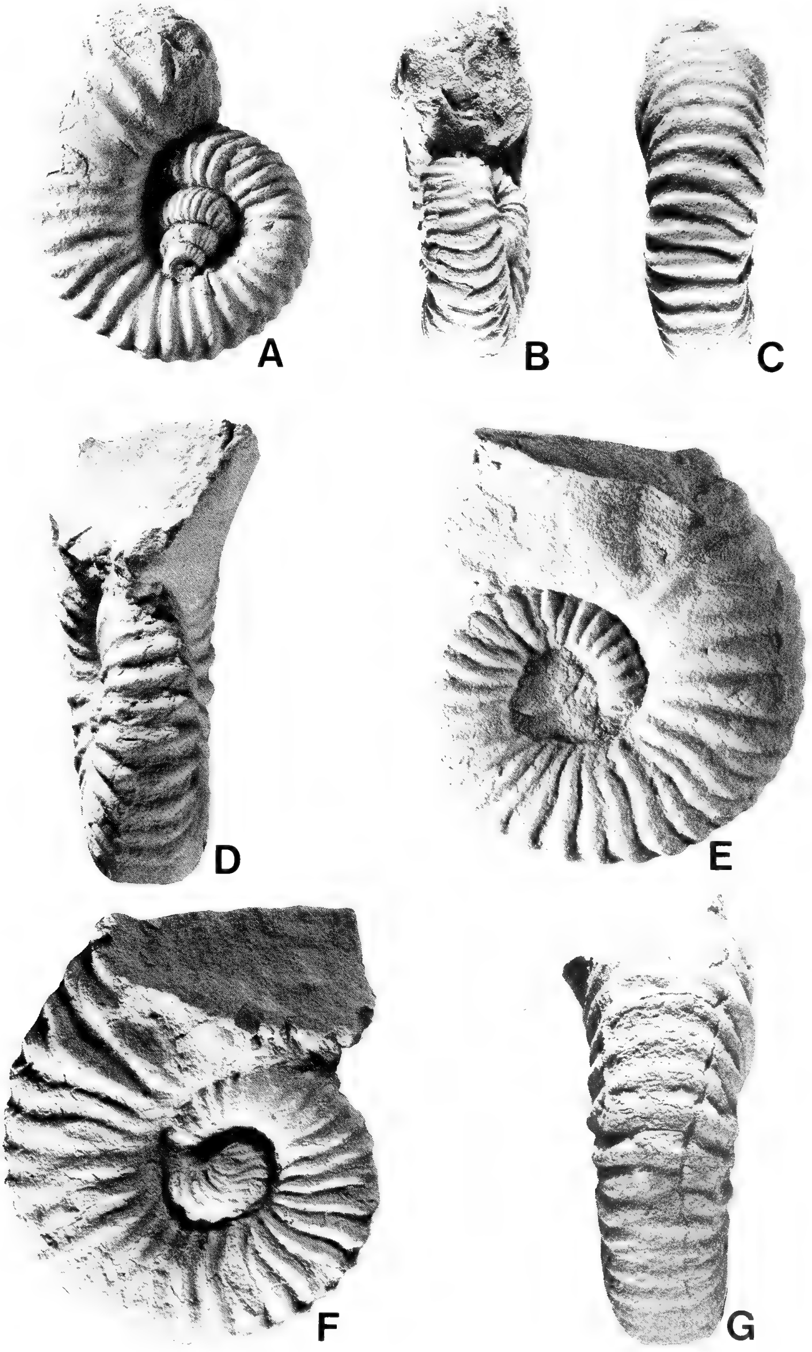


Fig. 11. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. A–C. Holotype. SAS 3044/L54. D–G. Immature macroconch? CPBA 11838. All × 1.

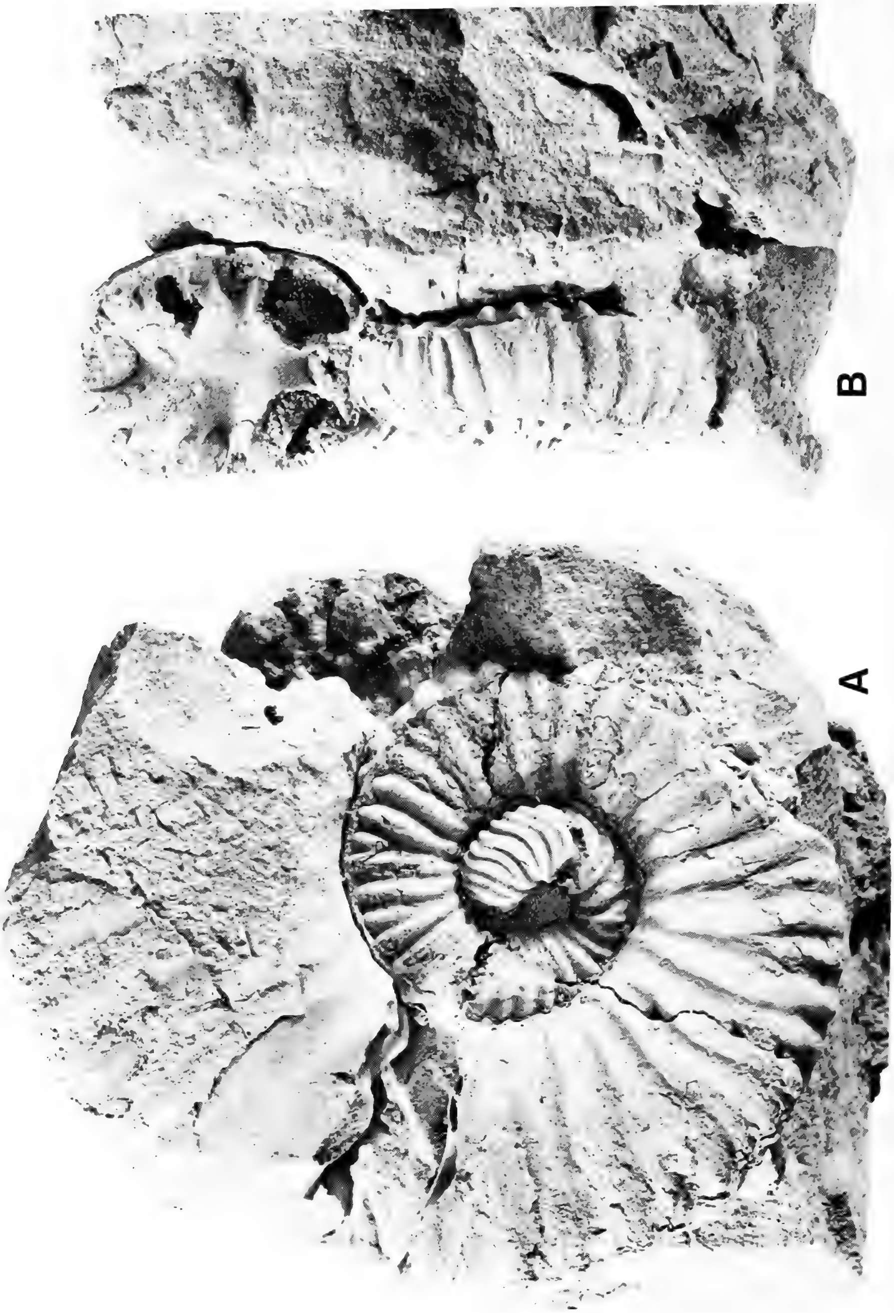


Fig. 12. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAS L54/36h. × 1.

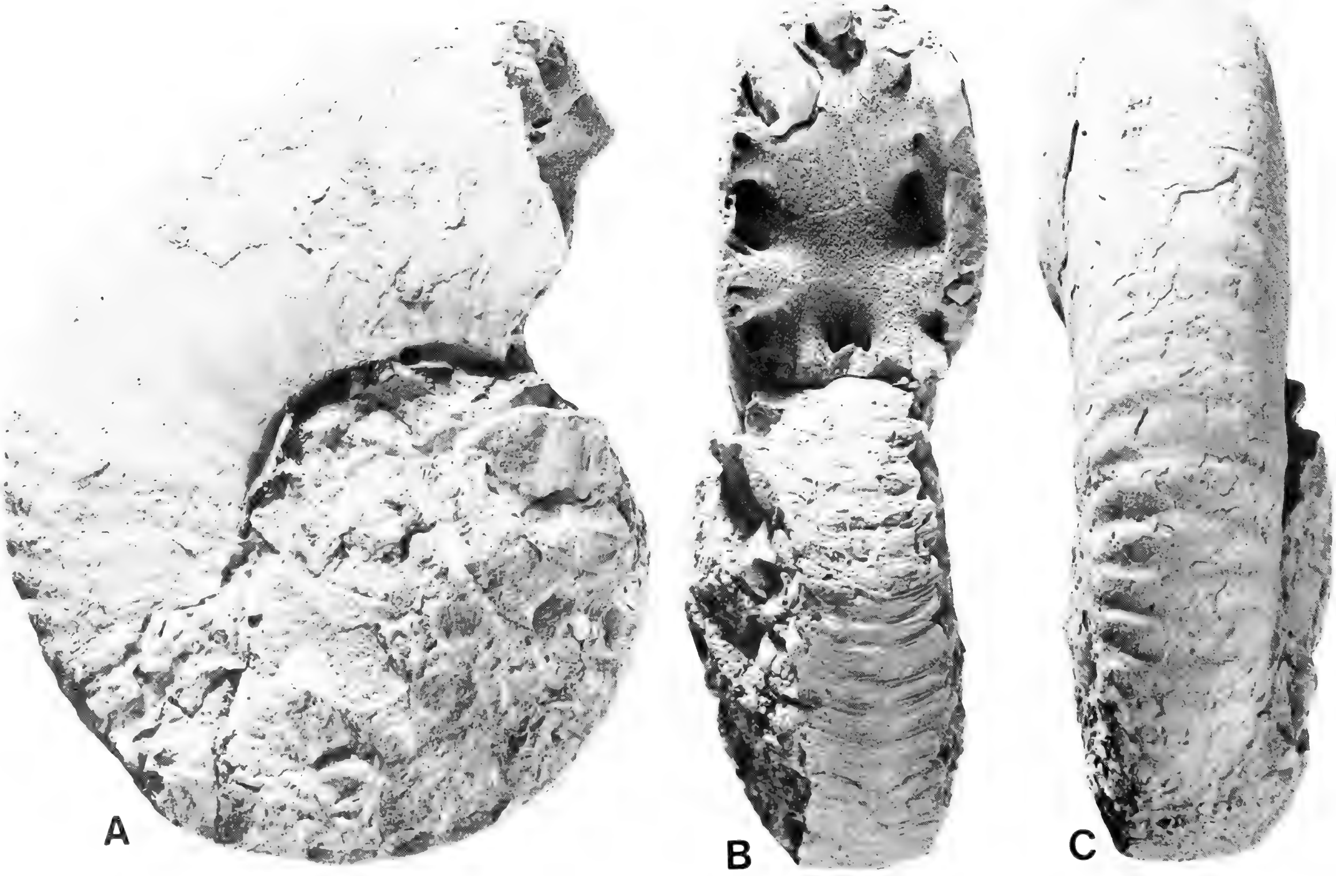


Fig. 13. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6389. × 1.

Fig. 14. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM-PCZ6388. × 0,65.

Fig. 15. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6388. × 0,65.

Fig. 16. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. SAM–PCZ6388. × 0,65.

Fig. 17. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11896. × 1.

Fig. 18. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11896. × 1.

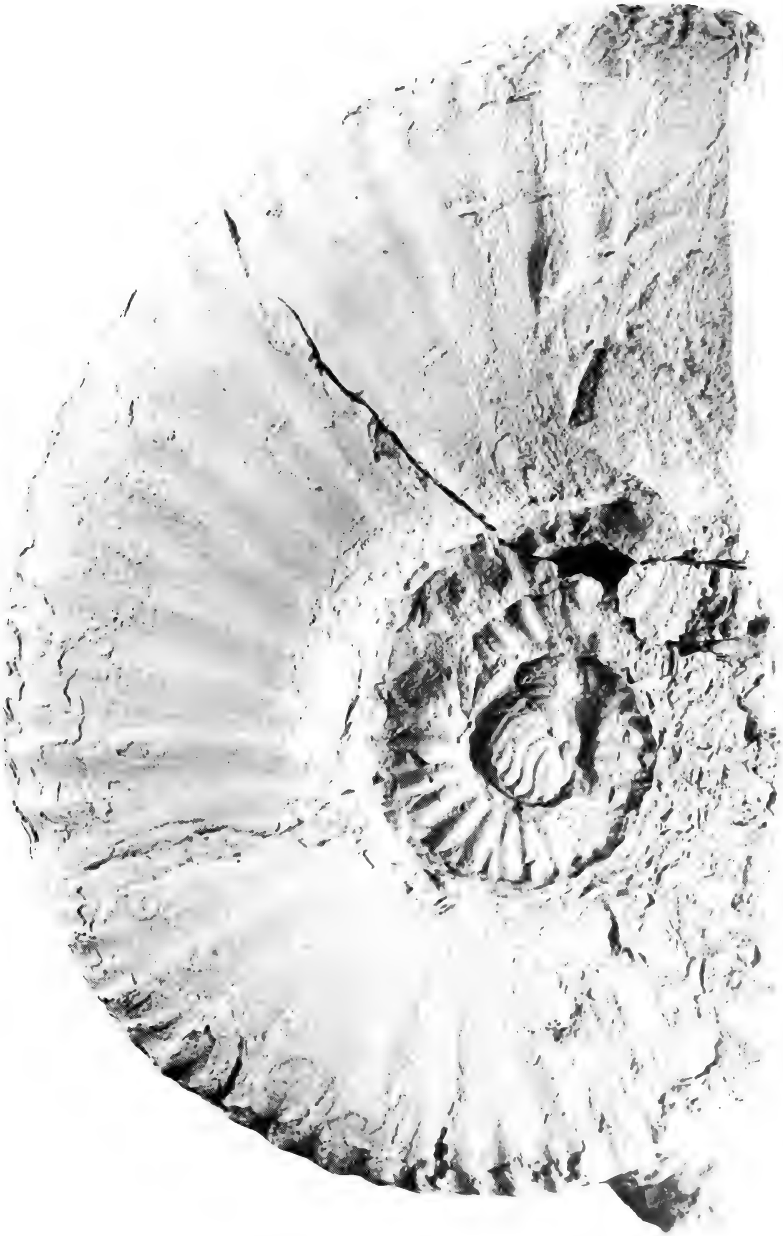


Fig. 19. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11797. × 1.

Fig. 20. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11797. × 1.

Fig. 21. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11799. × 1.

DISCUSSION

Validity of genera and species groups

Description of the Patagonian and Zululand material raises a number of questions that cast doubt on the current systematic concepts employed within the Heteroceratinae, and these merit discussion.

The first concerns the tripartite division of *Colchidites* into species groups *C. intermedius*, *C. colchicus* and *C. shaoriensis*. This was originally conceived by

Rouchadzé (1933) and retained by Kakabadze (1971*a*). Egojan (1965), however, had already cast doubts on the correct allocation of *C. vulanensis*. The well-developed planispiral part places it in the group of *C. shaoriensis*, whereas the well-developed helix places it more suitably in *C. colchicus*. These same doubts were raised by Klinger (1976) and Klinger *et al.* (1984) and two alternatives were proposed: either an uncoiled section was never developed; or, the Zululand assemblage was an ontogenetically segregated population, with the representatives of the discoidal stage inhabiting the shallow, near-shore water, and the uncoiled ancyloceratid forms inhabiting the deeper parts of the basin. The discovery of microconchs with complete apertures, however, clearly rules out the

Fig. 22. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11799. × 1.

Fig. 23. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch. CPBA 11829. × 1.

presence of an uncoiled section in *C. vulanensis australis*. Thus, as far as the number of whorls in the helix and planispiral sections are concerned, *C. vulanensis australis* fits none of the three recognized species groups. Instead, it more closely resembles representatives of *Paraimerites* or *Imerites*. With the exception of *Paraimerites brevihelicoides* Kakabadze, a monotypical species, none of the

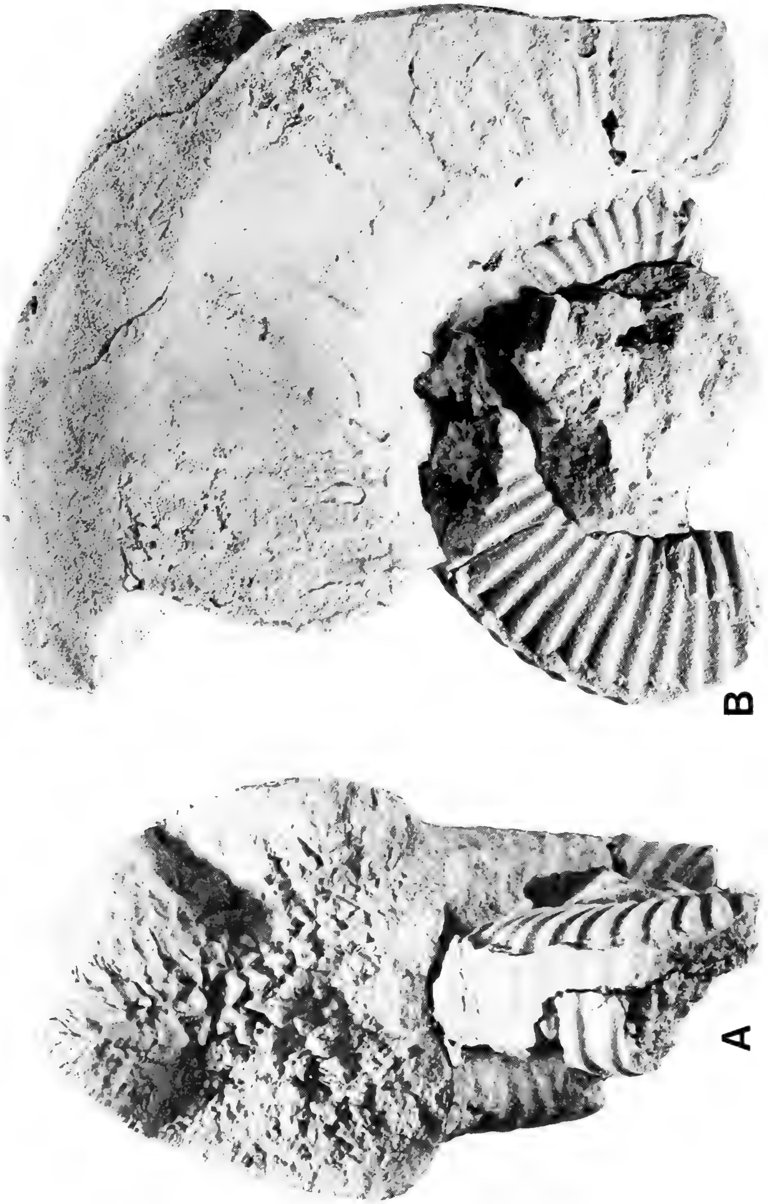


Fig. 24. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch with subtrigonal whorl section. SAM-PCZ6390. × 1.

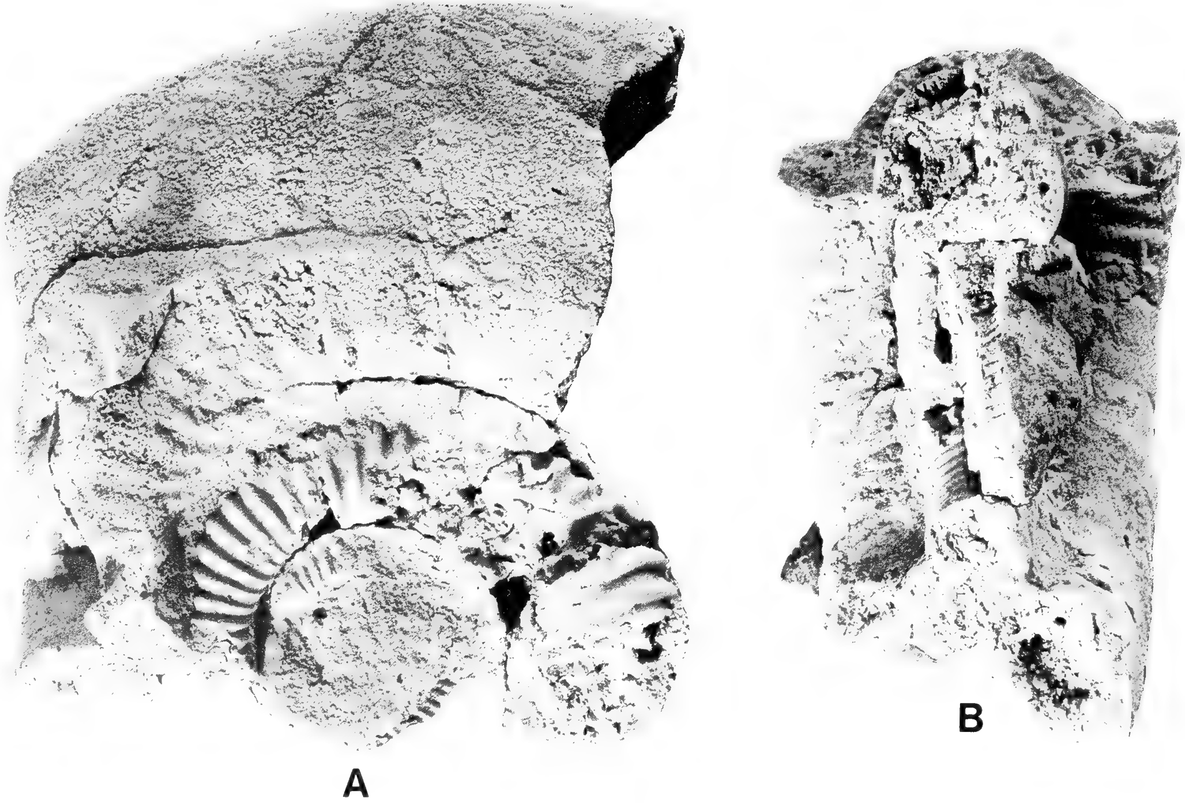


Fig. 25. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. Macroconch with subtrigonal whorl section. SAM–PCZ6390. × 1.

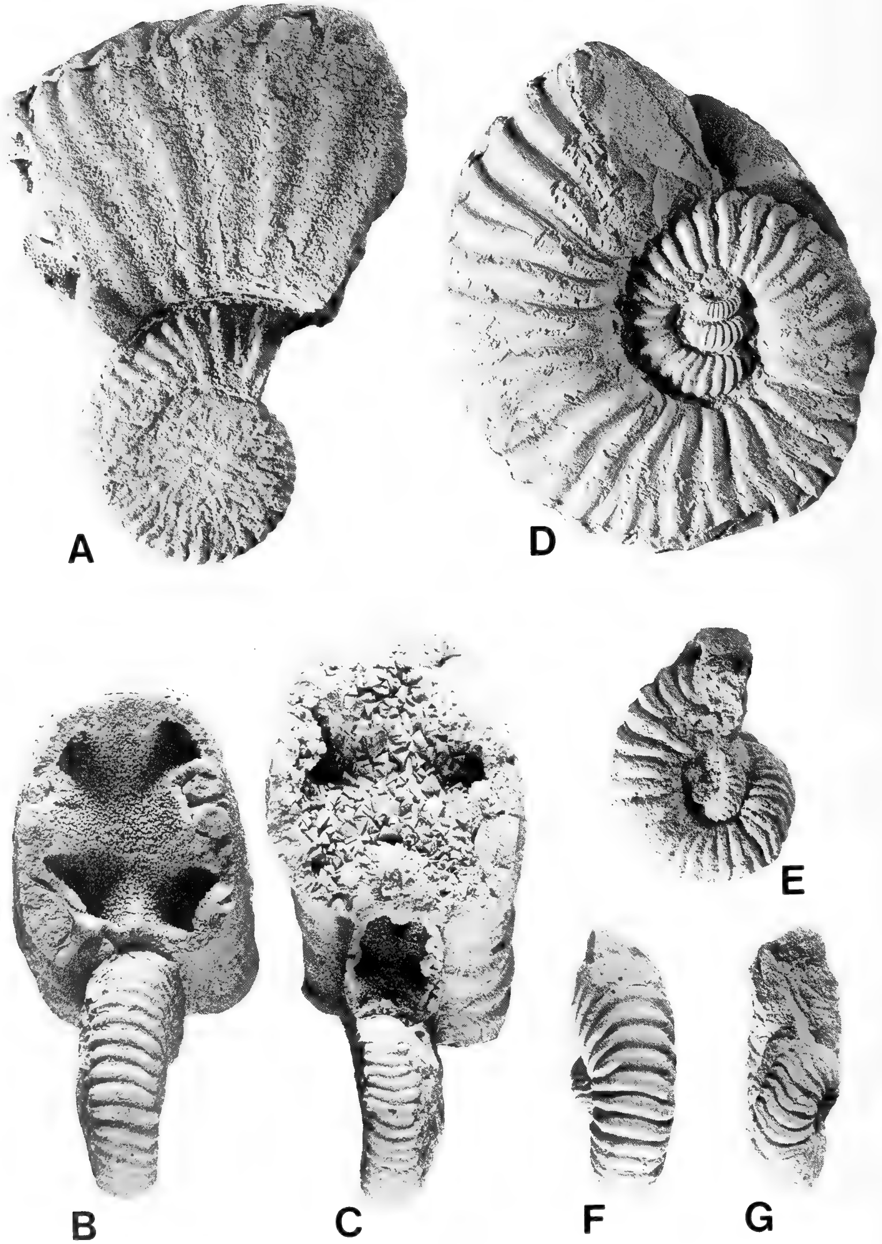


Fig. 26. A–C. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. SAS L54/3288. D. *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy, 1984. CPBA 11805. E–G. *Paraimerites haughtoni* Klinger, Kakabadze & Kennedy, 1984. SAS L54/D5. All × 1.

other species referable to either *Paraimerites* or *Imerites* has an uncoiled section. Affinities of *C. vulanensis australis* with *Paraimerites* or even *Imerites* become more obvious in specimens with distinct quadrate to rectangular whorl section. Here the ribs are slightly flared near the venter, and the ventrolateral edges of these may easily be interpreted as tubercles. Also, there is a slight thickening of the ribs on the ventrolateral flanks that coincides with a slight forward flexure and/or bifurcation of the ribs. This could be interpreted as incipient *Imerites* ornament.

Having established that *Colchidites vulanensis australis* does not fit the traditionally accepted tripartite division of genus *Colchidites*, but instead shows more affinities toward *Paraimerites* and *Imerites*, division at generic level may be scrutinized.

Differentiation within the subfamily Heteroceratinae at generic or subgeneric level is based mainly on the presence or absence of tubercles, as outlined above (p. 320). The presence or absence of tubercles has been used extensively in the classification of other heteromorph taxa. In most cases this is an objective, unambiguous criterion and easy to apply, and forms the mainstay of heteromorph taxonomy. Recent work on various heteromorph groups, especially the *Hamites–Protanisoceras–Anisoceras* plexus (Casey 1961; Wiedmann 1962; Wiedmann & Dieni 1968; Scholz 1979), the Turrilitinae (Klinger & Kennedy 1978; Scholz 1979), Baculitidae (Cooper & Kennedy 1977; Scholz 1979), etc., has made it painfully obvious how divided workers are in assessing the importance of tuberculation. Thus the tuberculate forms of the baculitid genus *Lechites* are accorded subgeneric rank by Cooper & Kennedy (1977) while the same are merely regarded as subspecific variants of the non-tuberculate species by Scholz (1979). Indeed, Scholz (1979) has shown that in some heteromorph groups (*Lechites*), tubercles may appear iteratively, and that the proportion or absence of tuberculate to non-tuberculate forms may differ in different geographic regions. In addition, transitions occur between tuberculate and non-tuberculate forms, e.g. *Hamites praegibbosus* Spath and *Protanisoceras* gr. ex *blancheti* (cf. Casey 1961: 94) where allocation to one genus or another becomes subjective and a matter of opinion.

Bearing these data in mind, we provisionally accept the criterion of presence or absence of tubercles in the systematics of the subfamily Heteroceratinae. Thus those colchiditid specimens without distinct tubercles are referred to genus *Colchidites*, and those with a pair of siphonal rows, to *Paraimerites*, even though the coiling strategies do not fit the diagnoses as applied to the material from south-western U.S.S.R.

These same criteria are applied to differentiating between *Heteroceras* s.s. and *H. (Argvethites)*. According to Kakabadze (1975: 66) a siphonal furrow on the shaft occurs mainly in tuberculate forms, i.e., *H. (Argvethites)*. However, a siphonal furrow occurs in two of the non-tuberculate specimens of *H. (H.) elegans* from Argentina. In addition, siphonal furrows are known from other unrelated heteromorph groups, e.g. *Toxoceratoides* (Aguirre Urreta 1986), *Hamites (Stomohamites) virgulatus* (see Wiedmann & Dieni 1968, pl. 5 (fig. 2), text-figs 21–22) and thus seem to be of no or little taxonomic significance.

Sexual dimorphism

Dimorphism has not been discussed previously in Heteroceratinae. In other groups of ammonites it has been well documented over the past two decades (see e.g. Makowski 1963; Westermann 1969; Kennedy & Cobban 1976; Callomon 1981; Donovan *et al.* 1981; Wright 1981 for discussions), but evidence has come mainly from Jurassic forms—the notable Cretaceous exception being some scaphitids (see Cobban 1969). Callomon (1981) mentioned that sexual dimorphism in the Cretaceous remains largely to be explored, especially amongst the Ancyloceratina. Unfortunately, apart from the above-mentioned scaphitids, data here are still very scant. Dimorphism has been demonstrated in the baculitid genus *Sciponoceras* (see Kennedy & Juignet 1983: 17 for summary) and *Lechites* (Cooper & Kennedy 1977) and suggested in *Hamites* by Cooper (unpublished data, see Kennedy & Juignet 1983: 12).

Dimorphism in Heteroceratinae was only found in the austral representatives of *Colchidites vulanensis*, but we suspect that it may also be present in *Heteroceras*. The two species groups recognized within *Heteroceras*, *H.* gr. ex. *helicoceroides* and *H.* gr. ex. *astieri* may possibly be dimorphic pairs.

Intraspecific variation

Finally, the Patagonian and Zululand material illustrates the extent of intraspecific variation magnificently. Admittedly, coarsely and finely ornamented forms can be identified, as can forms with quadrate whorl sections approaching *Paraimerites* ornament; but these are all connected by transitions, so that it would be futile to separate these at any formal level. This variation also casts doubt on the validity of the great number of species referred to the genera *Heteroceras* and *Colchidites*, as listed below. Egojan (1965) had already commented on the disparate number of species to specimens in the Georgian collections but, without direct access to this material, we have to refrain from definite comments on the synonymies.

SUMMARY

The ammonite subfamily Heteroceratinae is represented in Patagonia by *Colchidites vulanensis australis* Klinger, Kakabadze & Kennedy and *Heteroceras (H.) elegans* Rouchadzé, both species also known from Zululand and the Caucasus. The representatives of *Colchidites vulanensis australis* demonstrate dimorphism in the genus: microconchs mature at diameters of about 50 mm and one planispiral whorl; and macroconchs with more than two planispiral whorls still septate at diameters exceeding 150 mm. The microconchs show apertural modifications in the planispiral section, clearly ruling out the possibility of an uncoiled section. The ratio of helical to planispiral coils, plus the absence of an uncoiled section in *C. vulanensis australis* fits none of the three species groups

traditionally accepted within the genus *Colchidites*, but instead shows greater affinity with *Paraimerites* or *Imerites*. Comparison with other heteromorph groups shows that the presence or absence of tubercles may be of very little taxonomic significance, and in cases, be ambiguous. Siphonal depressions occur in various unrelated heteromorph groups, and seem to be of no taxonomic significance. The wide range of intraspecific variation as seen in the Patagonian and Zululand material casts severe doubt on the validity of the multitude of species erected for the material from the south-western U.S.S.R., and suggests that systematics can be greatly simplified.

LIST OF SPECIES OF *HETEROCERAS (HETEROCERAS)* AND *COLCHIDITES*

Species described in open nomenclature are omitted. Most of the references listed below provide descriptions and/or figures of the species concerned.

Genus and subgenus *Heteroceras* d'Orbigny, 1850
(= *Lindigia* Karsten, 1858)

Type-species. Turrilites emericianus d'Orbigny, 1842, by subsequent designation Meek (1876: 477).

Heteroceras emericianum (d'Orbigny) (1842: 580, pl. 141 (figs 3–6); 1851: 220, pl. 3 (fig. 1); Kakabadze 1971*a*: 48, pl. 3 (fig. 2)). Upper Barremian of France.

Heteroceras emericianum (d'Orbigny) var. *costata* Rouchadzé (1933: 242, pl. 15 (fig. 3); Kakabadze 1971*a*: 49, pl. 3 (fig. 1)). Upper Barremian of western Georgia and northern Caucasus.

Heteroceras astierianum d'Orbigny (1851: 219, pl. 4 (fig. 1); Kilian 1888*a*: 430, pl. 3 (fig. 2); 1888*b*: 687, pl. 21 (fig. 1a–b); Dimitrova 1967: 65, pl. 37 (fig. 2); Kakabadze 1975: 86, pl. 1 (fig. 1a–b), pl. 2 (fig. 1), pl. 8 (fig. 2)). [= *Heteroceras imericum* Rouchadzé (1933: 230, pl. 13 (figs 1–2), text-fig. 34).] Upper Barremian of Bulgaria, Caucasus, France and western Georgia.

Heteroceras bifurcatum d'Orbigny (1851: 221, pl. 3 (figs 2–3); Kilian 1888*a*: 432, pl. 3 (fig. 3); Nikolov, 1964: 124, pl. 4 (figs 1–2), pl. 5 (fig. 5a–b); Dimitrova 1967: 64, pl. 39 (fig. 2)). Upper Barremian of Bulgaria and France.

Heteroceras bifurcatum d'Orbigny var. *trifurcata* Kilian (1888*a*: 432). Upper Barremian of France.

Heteroceras devii Rouchadzé (1933: 231, pl. 13 (fig. 3), text-fig. 35; Kakabadze 1975: 87, pl. 1 (fig. 2), pl. 2 (fig. 3), pl. 8 (fig. 1)). Upper Barremian of western Georgia.

Heteroceras elegans Rouchadzé (1933: 232, pl. 13 (fig. 4), text-fig. 36; Kakabadze 1975: 89, pl. 3 (figs 1a–b, 3–5), pl. 8 (fig. 5); Klinger *et al.* 1984: 44, figs 2A–F, 3A–G, 4A–C). Upper Barremian of western Georgia, northern Caucasus, Zululand and Patagonia.

Heteroceras eristavii Kakabadze (1975: 90, pl. 4 (figs 1a–b, 3), pl. 5 (fig. 5), pl. 8 (fig. 7)). Upper Barremian of western Georgia.

Heteroceras haugi Karakasch (1907: 144, pl. 26 (fig. 2)). Upper Barremian of Crimea.

Heteroceras helicoceroides (Karsten) (1858: 103, pl. 1 (fig. 5a–c); 1886: 27, pl. 1 (fig. 5a–c); Royo y Gómez 1945: 466, text-fig. 3). Upper Barremian of Colombia.

Heteroceras isocostata Kakabadze (1975: 91, pl. 4 (fig. 5a–b)). Upper Barremian of western Georgia.

Heteroceras jeletzkyi Murphy (1975: 36, pl. 7 (fig. 4)). Upper Barremian of California.

Heteroceras kotetishviliae Kakabadze (1975: 88, pl. 1 (fig. 4)). Upper Barremian of western Georgia.

Heteroceras tardieui Kilian (1888*a*: 433, pl. 4). Upper Barremian of France.

Heteroceras tskaltuboensis Kakabadze (1975: 87, pl. 2 (fig. 2), pl. 8 (fig. 3)). Upper Barremian of western Georgia.

Heteroceras vermiforme Rouchadzé (1933: 233, pl. 13 (fig. 5); Kakabadze 1975: 90, pl. 3 (figs 6–8), pl. 4 (fig. 2a–b). Upper Barremian of western Georgia.

Genus *Colchidites* Djanélidzé, 1926
(= *Heteroceras (Santandericeras)* Royo y Gómez, 1945)

Type-species. *Colchidites colchicus* Djanélidzé, 1926.

Colchidites colchicus Djanélidzé (1926: 256, pl. 1 (fig. 1); Kakabadze 1971*a*: 54, pl. 6 (figs 1–2)). Upper Barremian of western Georgia.

Colchidites colchicus Djanélidzé var. *phasiensis* Rouchadzé (1938: 169, pl. 5 (figs 5–6), text-fig. 21; Kakabadze 1971*a*: 56, pl. 8 (fig. 1)). Upper Barremian of western Georgia.

Colchidites colchicus Djanélidzé var. *renngarteni* Rouchadzé (1938: 169, pl. 5 (fig. 4), text-fig. 20; Kakabadze 1971*a*: 55, pl. 7 (fig. 1), text-fig. 23). Upper Barremian of western Georgia.

Colchidites apolinarii (Royo y Gómez) (1945: 468, pl. 74 (fig. 1a–b), pl. 75 (fig. 1), text-figs 4–5; Etayo Serna 1968: 59, pl. 1 (figs 4, 6), pl. 2 (figs 1–2), text-figs 3B, 4,4; Kakabadze 1971*a*: 59, pl. 9 (fig. 2a–c)). Upper Barremian of Colombia.

Colchidites atsharensis Rouchadzé (1933: 246, pl. 17 (fig. 2), text-fig. 16; Kakabadze 1971*a*: 76, pl. 9 (fig. 4), pl. 18 (fig. 2a–b), text-fig. 46). Upper Barremian of western Georgia and western Turkmenia.

Colchidites belaiaensis Kakabadze (1971*a*: 66, pl. 15 (fig. 2a–c)). Upper Barremian of northern Caucasus.

Colchidites bethleviensis Kakabadze (1971*a*: 56, pl. 5 (fig. 4a–c), text-figs 24–25). Upper Barremian of western Georgia.

Colchidites colleti Rouchadzé (1933: 249, pl. 18 (fig. 2), text-fig. 48; Kakabadze 1971*a*: 69, pl. 14 (fig. 1), text-fig. 39). Upper Barremian of western Georgia.

Colchidites colleti Rouchadzé var. *shaoriensis* Rouchadzé (1938: 170, pl. 6 (fig. 3)). Upper Barremian of western Georgia.

Colchidites cuneicostatus Kakabadze (1971*a*: 57, pl. 8 (fig. 2a–c), text-figs 26–27). Upper Barremian of western Georgia.

Colchidites djanelidzei Rouchadzé (1933: 247, pl. 17 (fig. 1), text-fig. 47; Kakabadze 1971*a*: 77, pl. 18 (fig. 1a–b), text-fig. 47). Upper Barremian of western Georgia.

Colchidites elissoae Kakabadze (1971*a*: 60, pl. 5 (fig. 3), text-figs 28–29). Upper Barremian of western Georgia.

Colchidites ellipticus Rouchadzé (1933: 252, pl. 20 (fig. 1); Drushchits & Kudryavtsev 1960: 296, pl. 40 (fig. 5a–b); Kakabadze 1971*a*: 64, pl. 11 (fig. 2a–b), pl. 12 (fig. 1a–b), text-fig. 35). Upper Barremian of western Georgia and northern Caucasus.

Colchidites ellipticus kvadaurensis Rouchadzé (1933: 253, pl. 20 (figs 33–34); Kakabadze 1971*a*: 65, pl. 5 (fig. 2), text-fig. 36). Upper Barremian of western Georgia.

Colchidites eristavii Kotetishvili (1970: 80, pl. 12 (fig. 3a–c); Kakabadze 1971*a*: 59, pl. 9 (fig. 2a–c)). Upper Barremian of western Georgia.

Colchidites gamkrelidzei Rouchadzé (1933: 251, pl. 19 (fig. 2), text-fig. 50; Kakabadze 1971*a*: 63, pl. 10 (fig. 2a–b), text-figs 33–34). Upper Barremian of western Georgia.

Colchidites intermedius Djanélidzé (1926, fig. 14; Kakabadze 1971*a*: 51, pl. 4 (fig. 3)). (Non *Colchidites intermedius* in Rouchadzé 1933: 239, pl. 14 (fig. 6), text-fig. 40.) Upper Barremian of western Georgia.

Colchidites kakabadzei Kotetishvili (1970: 81, pl. 13 (fig. 3); Kakabadze 1971*a*: 75, pl. 17 (fig. 1a–c)). Upper Barremian of western Georgia.

Colchidites kakhadzei Rouchadzé (1938: 170, pl. 6 (fig. 4), text-fig. 23; Kakabadze 1971*a*: 61, pl. 10 (fig. 1a–b), text-fig. 30). Upper Barremian of western Georgia and south-eastern France.

Colchidites kutatissiensis Kakabadze (1971*a*: 53, pl. 5 (fig. 1), text-figs 21–22). Upper Barremian of western Georgia.

Colchidites latecostatus Rouchadzé (1933: 246, pl. 16 (fig. 3), text-fig. 45); Kotetishvili 1970: 83, pl. 14 (fig. 1a–b); Kakabadze 1971*a*: 75, pl. 16 (fig. 1a–b)). Upper Barremian of western Georgia.

Colchidites leenhardti (Kilian) (1888*b*: 688, pl. 20 (fig. 3), pl. 21 (fig. 2); Kakabadze 1971*a*: 52, pl. 3 (fig. 3)). Upper Barremian of south-eastern France and western Georgia.

Colchidites longicostatus Kakabadze (1971*a*: 71, pl. 19 (fig. 6), text-fig. 42). Upper Barremian of western Georgia.

Colchidites longus Rouchadzé (1933: 240, pl. 14 (fig. 7), pl. 15 (fig. 1), text-fig. 41; Kakabadze 1971*a*: 50, pl. 4 (fig. 4)). Upper Barremian of western Georgia.

Colchidites multicostatus Kakabadze (1971*a*: 67, pl. 12 (fig. 3a–c), text-fig. 38). Upper Barremian of western Georgia.

Colchidites ratshensis Rouchadzé (1933: 254, pl. 20 (fig. 6); 1938: 170, pl. 4 (fig. 6); Kakabadze 1971*a*: 72, pl. 12 (fig. 5a–b), pl. 14 (figs 2, 4–5), text-figs 43–44). [= *Colchidites nicortsmindensis* Rouchadzé (1933: 255, pl. 20 (fig. 7); Tovbina 1963: 110, pl. 3 (fig. 5)).] Upper Barremian of western Georgia and Turkmenia.

Colchidites ratshensis Rouchadzé var. *kopetdaghensis* Tovbina (1963: 111, pl. 3 (fig. 6); Kakabadze 1971*a*: 73, pl. 12 (fig. 2)). Upper Barremian of Turkmenia.

Colchidites rionensis (Simonovich, Batsevich & Sorokin) (1875: 173, pl. 6 (fig. 1a–b); Rouchadzé 1933: 243, pl. 15 (figs 4–5), text-fig. 43; Kakabadze 1971*a*: 74, pl. 13 (fig. 1), text-fig. 45). Upper Barremian of western Georgia.

Colchidites rotundus Rouchadzé (1933: 241, pl. 15 (fig. 2), text-fig. 42; Drushchits & Kudryavtsev 1960: 296, pl. 37 (fig. 2a–b); Kakabadze 1971*a*: 49, pl. 3 (fig. 4), text-fig. 19). Upper Barremian of western Georgia and northern Caucasus.

Colchidites rouchadzei Eristavi (1955: 121; Kakabadze 1971*a*: 51, pl. 4 (fig. 1)). Upper Barremian of western Georgia.

Colchidites sarasini Rouchadzé (1933: 250, pl. 18 (fig. 3), pl. 19 (fig. 1), text-fig. 49; Kakabadze 1971*a*: 62, pl. 11 (fig. 1a–c), text-figs 31–32). Upper Barremian of western Georgia and Lower Aptian? of north-western Caucasus.

Colchidites securiformis (Simonovich, Batsevich & Sorokin) (1875: 166, pl. 4 (fig. 3a–b); Rouchadzé 1938: 168, pl. 4 (fig. 5); Kotetishvili 1970: 84, pl. 10 (fig. 4); Kakabadze 1971*a*: 81, pl. 17 (fig. 4), pl. 19 (fig. 2), text-fig. 53). Upper Barremian of western Georgia.

Colchidites shaoriensis Djanélidzé (1926, pl. 1 (fig. 2); Kakabadze 1971*a*: 79, pl. 14 (fig. 3), pl. 19 (fig. 3), text-fig. 50). Upper Barremian of western Georgia and western Turkmenia.

Colchidites tenuicostatus Kakabadze (1971*a*: 82, pl. 17 (fig. 2), pl. 19 (fig. 4), text-fig. 54). Upper Barremian of western Georgia.

Colchidites tinae Eristavi (1955: 121, pl. 4 (fig. 11); Kakabadze 1971*a*: 52, pl. 4 (fig. 2)). Upper Barremian of western Georgia.

Colchidites tovbinae Kakabadze (1971*a*: 80, pl. 17 (fig. 3), text-fig. 51). Upper Barremian of western Georgia.

Colchidites trifurcatus Kakabadze (1971*a*: 66, pl. 12 (fig. 4a–b), text-fig. 37). Upper Barremian of northern Caucasus.

Colchidites tzotnei Rouchadzé (1933: 254, pl. 20 (fig. 5), text-fig. 51; Kakabadze 1971*a*: 68, pl. 13 (fig. 2a–c)). (Non *Colchidites tzötnei* in Dimitrova 1967: 65, pl. 26 (fig. 2)). Upper Barremian of western Georgia.

Colchidites veleurensis Kakabadze (1971*a*: 83, pl. 19 (fig. 5), text-fig. 55). Upper Barremian of western Georgia.

Colchidites vulanensis Egojan (1965: 119, pl. 1 (figs 1a–b, 3), pl. 2 (figs 1–2); Kakabadze 1971*a*: 70, pl. 15 (fig. 1), text-fig. 41). Upper Barremian of north-western Caucasus.

Colchidites vulanensis Egojan *australis* Klinger, Kakabadze & Kennedy (1984: 45, figs 6A–F, 7A–F, 8A–L, 9A–N). Upper Barremian of Zululand and Patagonia.

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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:
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semicolon separates more than one reference by the same author
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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.

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) . . .'
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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

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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. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

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.

MARÍA BEATRIZ AGUIRRE URRETA
&
HERBERT CHRISTIAN KLINGER

UPPER BARREMIAN HETEROCERATINAE (CEPHALOPODA, AMMONOIDEA) FROM PATAGONIA AND ZULULAND, WITH COMMENTS ON THE SYSTEMATICS OF THE SUBFAMILY

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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions 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.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters. If Letraset is used authors are requested to use Helvetica-style lettering, if possible.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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

'Smith (1969) describes . . .'
'Smith (1969: 36, fig. 16) describes . . .'
'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al.* 1927) . . .'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc., to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.
For journal article give title of article, title of journal in italics (according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number in parentheses, pagination (first and last pages of article).

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 la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
Fischer, P. H., Duval, M. & Raffy, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.
Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.
Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **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 ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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EVIDENCE FOR THE LOW-ALTITUDE ORIGIN OF THE CAPE MOUNTAIN BIOME DERIVED FROM THE SYSTEMATIC REVISION OF THE GENUS *COLOPHON* GRAY (COLEOPTERA, LUCANIDAE)

By

S. ENDRÖDY-YOUNGA

Cape Town Kaapstad

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By

S. Endrödy-Younga
Transvaal Museum, Pretoria

(With 31 figures)

[*MS accepted 31 March 1986*]

ABSTRACT

The Cape high-mountain stag beetles have been studied during the past five years. They are recognized as representatives of a biome restricted today to the high-altitude ranges of the mountains. This biome is often referred to as a mountain relict. An evaluation of the kinship relations of the *Colophon* species presented a distribution pattern where closely related species are isolated on mountain ranges separated by wide stretches of low-altitude plainland. These plains are now uninhabitable for *Colophon* species. It was concluded that the present high-mountain biome evolved on the low-lying plainland during a period when the environmental conditions there were similar to those of the high altitudes today. Thus the high-mountain biome is not an autochtonous relict, but is in refuge in an area to which it has retreated after its area of origin became uninhabitable due to aridification and temperature increase.

The systematic revision and cladistic analysis of the genus *Colophon* includes the descriptions of two new species, *C. barnardi* and *C. montisatris*.

The discussions are introduced by sections on speciation, environment–organism relationships and interspecific competition.

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Ann. S. Afr. Mus. **96** (9), 1988: 359–424, 31 figs.

INTRODUCTION

The Coleoptera Department of the Transvaal Museum, Pretoria, has adopted historic biogeography as a central theme of research. During the past ten years geographic areas that are of significance in the biohistory of the subcontinent have been selected for fieldwork.

While tracing the origin of the Namib Desert biome, the west-coast area was investigated from the Namib Desert to the winter-rainfall area in the south. Simultaneously the faunal contacts of isolated indigenous forest areas in the Drakensberg and southern Cape mountain ranges were studied. All observations so far lead towards the conclusion that the roots of our primordial fauna are southern in their origin. The Gondwana origin and post-Gondwana radiation of some of our oldest faunal elements from south to north have been discussed previously (Endrödy-Younga 1978). An historic contact between the Cape and south-western biogeographic zones (Endrödy-Younga 1978) also became evident, but was this by derivation or by simultaneous evolution under distinct zonation of environmental conditions? It was clear that the next logical step was to learn more about the oldest stratum of the Cape biome, the Gondwana relicts.

As a starting point, Barnard's (1929, 1932*a*, 1932*b*) studies on the lucanid genus *Colophon* were selected. Barnard and his fellow members of the Mountain Club discovered a number of species of this genus living exclusively in high-altitude mountain habitats of the southern Cape. He compared this distribution pattern to that of the isopod crustacean genus *Phreatoicus* (Barnard 1929). In doing so, he was the first to base on evidence from the invertebrate fauna the suggestion that all the high-mountain organisms—and not only the vegetation—are members of a distinct biome of common origin, and that this habitat has historic significance.

Barnard's hypothesis (1929: 180) attributed geological ages to the inhabiting of mountains, and explained the fragmentation of populations by fragmentation of the mountains. While a time scale thus visualized is exceedingly long, it would in any case solve only a few of the problems. Nevertheless, the relict character of the high-mountain biome is still widely accepted today.

Intensive collections of invertebrates have been made at and around known habitats of *Colophon* species, in a search for phylogenetic and geographic connections between the faunal elements. This fieldwork and its evaluation are still in progress.

Fig. 1. *Colophon montisatris* sp. nov. Male in its natural environment in the Swartberg Range.

It was not my intention to revise the 'marker' genus *Colophon* until one of the species collected in 1978 proved to be undescribed (Fig. 1). As the revision progressed, the problems relating to the faunal history grew alarmingly, but the solution presented itself when the results of the cladistic analysis of the species were compared with their present-day distributions.

The derivation of the conclusions is lengthy and the time for reading is limited for everyone. The paper is therefore presented in the reductive style. Thus I start with my statements *in medias res*, with ample references to the succeeding sections, where the reasoning can be followed and checked.

PAST COOL TEMPERATE AND HUMID CLIMATE IN THE CAPE, AND LOWLAND ORIGIN OF THE HIGH-MOUNTAIN BIOME

Many components, plants and animals, live today exclusively in the alpine regions of the Cape mountains. As all organisms are persistent in environmental conditions to which they have adapted during their speciation (see p. 367), the present high-mountain conditions must be largely the same as they were when the component taxa evolved. There are two possible reasons for this situation: either the biota live where they have evolved (autochtonous) and the conditions in the area have not changed markedly, or the biota evolved somewhere else where the conditions were similar to those where they live now and the biota changed geographic position due to a shift of climatic zonation. In the first case the whole biome represents a relict, and in the second it is in refuge (see p. 370).

The conclusion that the high-mountain biome has been translocated from its area of origin, which was the country of low elevation around and between the mountains, has been reached by the following sequence of hypotheses and observations.

(a) If the biome is autochtonous, a clinal type of character transformation would be expected along the Swartberg and Langeberg ranges. Dispersion and subsequent speciations could occur only along the gradients of the ranges. Under these circumstances distant isolated conspecific populations cannot occur.

(b) Conspecific populations split between mountains ranges are not known in *Colophon*, although some populations are separated by deep passes (*C. primosi*), or by hilly country, far below their present altitude (*C. stokoei*). Different species of the monophyletic genus are, however, separated from each other by extensive plains, of which the most striking example is *C. westwoodi* on Table Mountain. Distantly isolated conspecific populations are well known among plants, e.g. *Protea pruinosa* occurs on Blesberg (in the middle of the Swartberg) and in the Cedarberg. The same can also be expected in other invertebrates, as Barnard pointed out in the isopod genus *Phreatoicus* (1929: 182).

(c) The cladistic analysis of *Colophon* species (see p. 374) indicates that species of closest kinship relation might occur today in different mountain ranges. *Colophon whitei* and *C. montisatris* sp. nov. live at the eastern distribution limits of the genus in the heights of the Swartberg. Species from which they cannot be derived (*C. primosi* and *C. neli*) block their west-to-east route of mountain dispersion. Their closest kins, both in the apomorphic (*C. izardi*) and the plesiomorphic condition (*C. thunbergi* and *C. barnardi* sp. nov.), inhabit sections of the Langeberg, on the other side of the Little Karoo.

(d) The only hypothesis that resolves the problem is that the high-mountain biome evolved around the mountain ranges, where most of the evolutionary lineages have also been separated (in some cases down to the extant species). Considering the persistence of species in their native climatic conditions (see p. 367), the climate of the Little Karoo and a part of the Great Karoo (see p. 363) is expected to have been approximately as humid and as cool in the past as the alpine regions of the Cape mountains today. In order to attain these conditions in the surrounding Karoo, the regional temperature would have to drop to a level that would result in a high-altitude snow cover throughout most of the year.

Due to gradual aridification and temperature increase the low-lying country became uninhabitable, but at the same rate the climate of the mountains became hospitable. Populations of *Colophon* species and their ecological allies gradually moved to higher altitudes in the mountains. Those species that had no access to high mountains became extinct when their refuges became uninhabitable.

The ancestral *Colophon* population had ample space for dispersion, particularly when they gained access to the Little and Great Karoo. The speciating populations could form a mosaic-type distribution on the open flat country. The dispersion-*cum*-speciation process was not necessarily along a gradient, as it would have been if it had occurred on a mountain range. Phylogenetically distant species would then be able to find refuge on the same range, e.g. from either side (see kinship of species on the Swartberg). Similarly, the distribution of conspecific populations of closely related species could split and shift towards different ranges (*Protea pruinosa* on Cedarberg and Swartberg, or *Colophon whitei* and *C. montisatris* sp. nov. on Swartberg and *C. thunbergi* and *C. izardi* on Langeberg).

(e) The role of competition as a driving force for species to occupy alien biotopes, at least in the animal kingdom, is rejected (see p. 368). Interspecific 'competition' might have a certain role in the food chain; thus the appearance of hitherto absent predators might accelerate the extinction of their prey.

CLIMATE AND VEGETATION OF THE PAST LOWLAND HABITATS

The concept of persistence of organisms in their native environmental conditions (see p. 367) suggests that their original requirements had to be similar to those prevailing at present in the alpine regions, i.e. considerably more humid and considerably cooler than they are now in the southern parts of the Great Karoo. The similarity of native conditions of different species is expressed clearly by the altitudes at which they were taken in the different ranges. In the Swartberg range the species occupy only the highest altitudes (approximately 2 000 m), and are absent from any lower intervening sections. In the Langeberg, however, they are less restricted to the heights of the peaks within their distribution areas (from 1 300 m up). Of these two ranges the northern (Swartberg) is the drier, with less frequent cloud cover, higher summer temperatures, and a long dry spell in summer. The relevant altitudes in both ranges (and even lower altitudes) are regularly snow covered during two to three months in winter. The lowest zone on Table Mountain that is occupied by a *Colophon* species is below 1 000 m.

Field observations (see p. 372) revealed that adults are active in any period of the summer months but appear only under optimal weather conditions. All specimens were sighted (in both Swartberg and Langeberg ranges) in the morning or afternoon hours, mostly in thick fog, and on one occasion (Langeberg) in light rain (Fig. 2). Specimens were seen in the late afternoon hours in the spreading shade of peaks in clear weather, but not during sunny noon hours as Barnard mentioned (1929: 178).

Their high humidity requirement is quite evident from the habitat data and field observations. The low temperature as a factor of native conditions is more difficult to test directly. There is, however, some circumstantial evidence to suggest that low temperature was also part of the native climate.

If high humidity was the sole requirement, *Colophon* species could inhabit the forests that are, in places, within a few kilometres of their present habitats.

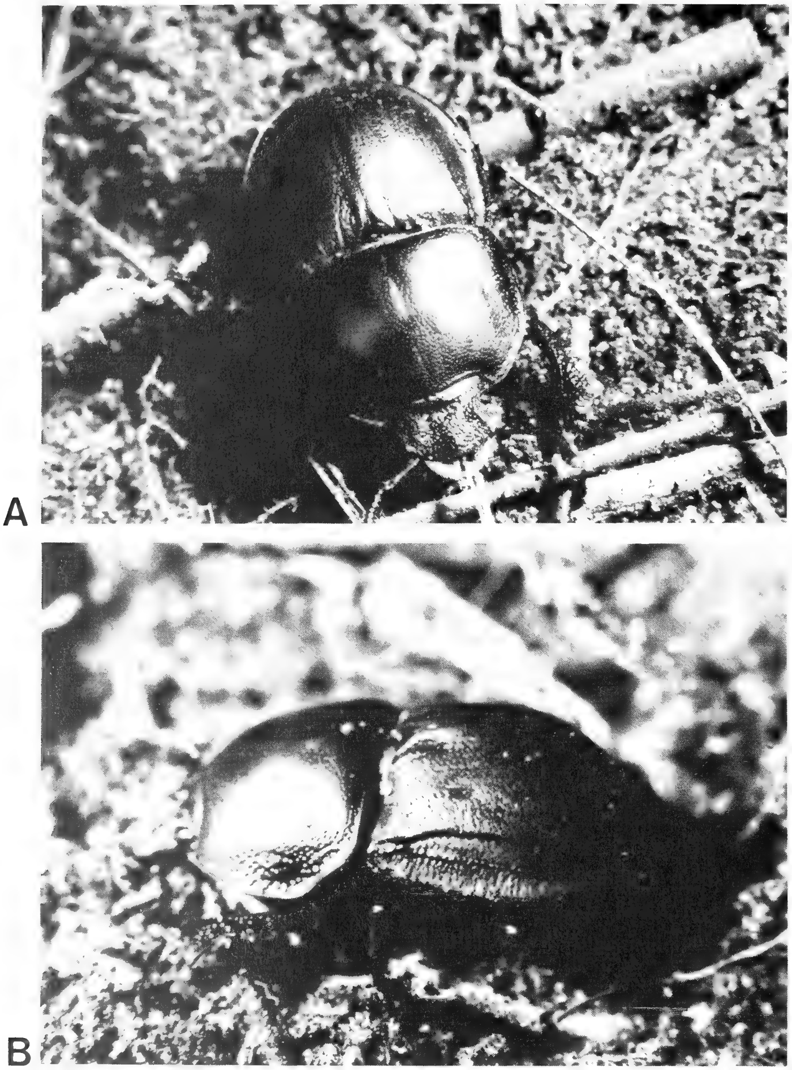

Fig. 2. A–B. *Colophon izardi* Barnard, female. The first live *Colophon* specimen photographed. A. Dorsal view. B. Lateral view.

The forest habitat, however, is alien to *Colophon* and apparently much more so than the low temperatures of humid alpine altitudes and the regular snow cover. Thus to accept low temperature, *Colophon* required little or no adaptation, i.e. deviation from its native condition.

The Northern Hemisphere glacial faunal fluctuation, as observed by Coope (1979) in the British Isles, suggests a rather strong temperature adherence of the coleopterous fauna (see p. 368).

THE ASPECT OF ABSOLUTE TIME

The study of *Colophon* does not offer any direct evidence (see p. 377) of the time when the habitat shift from the lowland to the alpine habitats occurred. However, the *Colophon* species are strictly associated with the fynbos vegetation type, and are restricted to its stratum of alpine altitudes with the implied climatic conditions. Dated changes in the extent of the fynbos vegetation could provide such evidence.

The first evidence (to my knowledge) of lowland fynbos far outside the present distribution area was identified recently by Scholtz (1985), who found *Protea* pollen deposits at 30°22′S 18°26′E.

The climatic change accompanied by the habitat shift to the mountain heights seems to be a Plio–Pleistocene event coloured by several waves of lesser climatic fluctuations (see Brain 1981). The close kinship of isolated *Colophon* species and many known fragmented conspecific populations in other groups of organisms (see p. 362) strongly support this hypothesis. Australian researchers have come to similar conclusions with regard to their local conditions.

THE GEOGRAPHIC EXTENT OF PAST HUMID AND COOL TEMPERATE CLIMATE

Global climatic zonation was not of the same intensity throughout the Earth's history; it is conceivable, however, that it always had an effect on the climate of the subcontinent. It can thus be assumed that the cool temperate conditions became reduced northwards in the middle of the area.

Present distribution records of *Colophon* demarcate the area between the Great Karoo and the southern coastal flats as the area where the evolution of the genus took place. The unrelated western species (*C. primosi*, *C. neli*) of the Swartberg range, blocking the dispersion range of the two apomorphic species (*C. whitei* and *C. montisatris* sp. nov.) (see p. 377 and Fig. 1), suggest that the former two species might have reached their present positions from the Great Karoo. We do not know, however, how far to the north of the Great Karoo was originally inhabited by *Colophon*. Recent visits to some heights of the Witteberg and Cedarberg ranges yielded no trace of *Colophon*, although these ranges have well-developed fynbos vegetation. The ancestral stock of *Colophon* was associated with the extremely cool and humid type of flatland fynbos in the south-western corner of the Cape, and did not necessarily disperse with it into its ecologically marginal northern types. Nevertheless, it is possible that some of its populations shifted northwards when aridification first commenced in the central Karoo.

Past occupation of the southern coastal plains is uncertain. The ancestral species of the genus were certainly already apterous, non-wood-boring (in the larval stage), and likely to be associated with open (low and scattered canopy) fynbos-type vegetation. Areas that were taken over by dense forest vegetation in more humid periods have thus been excluded from the past distribution of *Colophon*.

OBSERVATIONS AND BACKGROUND STUDIES

In the present paper a monophyletic group of stag beetles is studied. The relationships between the 14 recognized species were established by cladistic analysis. The cladogram thus obtained is compared with the present distribution of the species and conclusions are drawn as to what environmental conditions might have facilitated the dispersion of populations to reach their present loci.

Before entering the discussion the premises of this study need to be outlined. Some of them are widely accepted and sufficiently described; others, however, have been neglected or even sharply disputed as valid forces of evolution.

SPECIATION

The genetic process of evolution will not be discussed, but rather the status and fate of populations that can or cannot lead to a speciation event. Phyletic gradualism, which proposes sympatric speciation and an accumulation of imperceptible changes as a means of speciation, is rejected (Mayr 1942; critique in Hennig 1966; Paterson 1978). The accepted alternative pattern is that of punctuated equilibria (Hennig 1966; Eldredge & Gould 1972; Paterson 1978). According to this pattern, speciation is an event and not a continuous process; the species are real entities and not subjective fabrications of the observer when he slices convenient sections of the phenetic continua. The species retain their genetic identities for a long period of time relative to the short period of the speciation event leading to them. They do not transform in themselves, but cease to exist when the last population representing them becomes extinct in time. Their genetic continuity is manifested in their daughter species (if formed), or their lineages become extinct with the last surviving species. The physical precondition of any speciation event is the accidental formation of population fragments. Such fragments might speciate (should they survive) if their populations are sufficiently small, the environmental conditions of their new habitats are sufficiently different, and they remain in isolation from other populations for a sufficiently long period of time. It is evident that these rather independent conditions would seldom coincide. Thus the frequency of speciation events will depend both on the genetic constitution of the species involved and on the lability of climatic conditions, aggravated or eliminated by the other components of the environment. The same environmental changes would affect populations of different species (with respect to 'isolation' and speciation) quite differently. This observation emphasizes that 'isolation' hardly depends on the magnitude of the environmental differences, but primarily on the genetically determined reaction of the organism (see also p. 367).

CLADISTIC METHOD OF TRACING KINSHIP

It is claimed that phenetic similarity, if evaluated correctly, reflects the degree of kinship. The theory formulated by Hennig (1966) has an ever-growing literature where the methodology of cladistic analysis is adequately described.

Here only some of the basic premises of the cladistic theorem will be recalled. The analysis is based on the occurrence of the same derived characters (synapomorphies) in two or more species. It means that those species that show the highest numbers of synapomorphies, i.e. the latest acquired stages of the transformation of the phenotypic characters, have the closest kinship. This also implies that the weighting of characters is not a part of the evaluation. Actually, the common occurrence of a normally infraspecific character in the phenetic spectrum of two species would indicate the closest, sister-species relationship (Endrödy-Younga 1981).

THE ORGANISM–ENVIRONMENT RELATIONSHIP

At every single speciation event a set of adaptive characters becomes fixed within the genetic spectrum of a newly established species. The ultimate 'reason' for speciation is to provide the forthcoming generations with a set of inherited characters that enables the individuals to cope with the environmental conditions into which they are born, without the necessity of ever repeating adaptation.

For any organism to survive it is absolutely essential to possess a basic set of adaptations as an inherited genetic asset to cope with the 'normal' or average fluctuations of its native habitat. Thus its apparently limited adaptive capacity is left open to cope with changes within its environment. If this were not the case, any new-born land organism, even today, would first have to adapt to conditions on land, leaving little chance ever to enter complex environmental situations. Terrestrial life would still be struggling for survival along the coastlines.

If speciation is a complex genetic response to a new set of environmental conditions into which the new population fragment was forced, it is easy to understand that the speciated population will be conservative in its further habitat selection; in other words it will stick to its native habitat.

Thus no population will enter a habitat alien to its native type, a habitat for which it is not equipped in its adaptation complex. A population might, however, be stranded in such a habitat by accident; thus it is much rather a 'shipwreck' than a 'colonizer' population. For example, parts of populations of a forest-dwelling species will not endeavour to enter and colonize the surrounding savannah habitats, but may be 'shipwrecked' on them if the forest, which the species was inhabiting, first became fragmented, then gradually disappeared due to climatic changes. The classical island 'colonizers' (e.g. of Hawaii) are in this sense no less 'shipwrecks'. They all reach the islands accidentally and have to encounter the new situation with their various capacities for adaptation.

It is evident that the balance between the magnitude of difference under the native and the new environmental conditions on the one hand, and the adaptive capacity of the population involved on the other, will determine whether the 'shipwreck' population will be able to adapt and survive, or will become extinct. The magnitude of adaptive capacity is a specific character, expressed in habitat utilization with specialists and generalists as the two extremes.

The ever-changing environment is a permanent stress on the organic world that might be countered in two different ways. Either the tolerance to such changes increases infinitely in the organism, resulting in a few infinitely flexible forms, or parts of the organic world specialize to one or other type of condition, resulting in increasing diversity. Apparently an infinite flexibility could not be attained and the mechanism to adapt to particular conditions has developed. The species with its genetically fixed adaptation complex is a foothold (and apparently the only one) to a further change that the environment might provoke.

The inherited adaptation asset is the tool of survival for the individual in its native environment, and the fixation of new adaptations through speciation is the mechanism of the biota to survive the stress of the ever-changing environment.

The key statement to the present theory is specific habitat conservatism (see above). Clear evidence for this statement was provided by Coope (1979), who studied the coleopterous fauna of peat accumulations deposited through a number of successive glacial and interglacial periods. It was found that practically identical assemblages of species disappeared and reappeared with the fluctuations of the glacial periods. At present, in the middle of an interglacial, most of the species known from the glacial peat deposits in England are known to be extant in their cool-climate refuges as far away as in central Asia. There is no evidence of phenetic transformation according to the phyletic model of speciation, and it is reasonable to expect that the same species will reappear again if glaciation were to recur.

It can be concluded that in speciation a new, adjusted habitat preference will be attained along with other simultaneously fixed characters. The species will stick to its acquired habitat, as its whole set of adaptations refers to that particular habitat and not to any other. As a result the species will readily extend its distribution area if its habitat is expanding spatially (due to climatic change), but its distribution will again contract if the climatic trend is reversed.

COMPETITION

Interspecific competition as a driving force of evolution in the animal kingdom is emphatically rejected.

The term competition was introduced in biology for situations where individuals exert pressure on one another in order to obtain more (enough) of their environmental necessities. These necessities range from food and breeding ground to the most general term of 'Lebensraum'. It is claimed that by this action entire populations might be driven into other, less advantageous habitats. It is also often implied that such enforced habitat changes, leading to speciation, represent an important factor of evolution. Without trying to comment on rare and isolated cases (such as sessile benthonic animals) of habitat change for this reason and possible speciation resulting from it, I believe that the course of evolution rests on the balance of the organism–environment relation, as discussed before. In other words, evolution does not 'benefit' from competition, and least of all from that within biota of the same trophic level.

What does interspecific competition imply? It is evident that those individuals whose demands in the 'Lebensraum' are the most similar would be in the fiercest competition against each other. This is undoubtedly the case between conspecific individuals, which share characters including that of identical habitat requirement. Thus it is only logical that competition should act most strongly within the species rather than between species.

Undoubtedly, there is interspecific competition in the plant kingdom, e.g. if a dense-canopy tree grows in the midst of a carpet of sun-loving plants, it will successfully compete with them because neither can change position in order to move out of the disadvantageous sphere of influence of the other. The outcome will be that some of the badly affected individuals would die in the shaded area. But assume that in time the entire deep-soil, well-irrigated flat area is taken over by the forest; would the herbaceous plants of this habitat gradually move onto the shallow soil of the over-drained hillside?

It is certain that one of the advantages achieved in the animal kingdom by the 'invention' of locomotion was that animals capable of it can 'step aside' if another individual enters their sphere of interest.

The concept of interspecific competition in zoology was certainly borrowed from botany. All sorts of distribution patterns, unclarified situations of balance in ecosystems, and behavioural differences in cohabiting species were simply explained as results of competition. To illustrate the above, the Namib Desert biome may be cited as an example.

It is found that congeneric species have slightly different habitat preferences on the dunes; it could be claimed that interspecific competition keeps them apart. I believe that the native microhabitat of the different species is reflected in their present habitat selection. The allopatric speciation areas of many species involved is proven (Endrödy-Younga 1982). The same applies to the high-mountain biome under discussion.

In the desert biome several tenebrionid species might live together in the same hummock or on the same dune; some of them are diurnal, others nocturnal. It has been claimed that the activity pattern of the different species has shifted apart due to competition. The time pattern is, however, a generic or more often a tribal character (Eurychorini and Caenocrypticini are nocturnal, Zophosini and Adesmiini diurnal, in their sometimes continent-wide distribution area). Thus the activity pattern is a much older genetic character of the evolutionary lineages than the co-habitation of a few of their extant representatives that might be thought to compete.

It is claimed in this paper that competition is not a driving force of evolution or dispersion of biota. Unusual pressure on an ecosystem by the importation of new species as a result of various causes, ranging from human importation to continental collision, might be expected. This might drastically alter the composition of the fauna (e.g. Marsupialia in South America), but mainly in the direction of extinctions. We have little evidence that rapid speciation has ever started in an indigenous fauna owing to the arrival of successfully competing biota.

Competition in the food chain could be another possibility. It can be claimed that the prey species move out into an alien habitat to avoid the pressure of predator(s). I have not heard, however, of antelopes vacating the savannah and moving into the forest due to the activity of lions. The competition between predator species for a limited quantity of prey could still be a possibility. In this case, however, conspecific individuals have identical habitat and prey selection, but members of other predator species do not. It would be more likely that the excess population of the predator that upset the balance would be eliminated than that another prey species would be badly affected. Thus neither the difference in habits nor habitat selection between predator species is due to competition. Cheetahs have similar habits and habitats throughout their distribution areas and these are different from those of lions, whether or not they occur together. Probably the best support for this is provided by examples of biological control; pests and predators live together in an oscillating equilibrium without either becoming extinct. Even human influence can tip the balance only if new predators or parasites are introduced, but not by the propagation of the indigenous ones.

WHEN IS A BIOME A RELICT, AND WHEN IS IT IN REFUGE?

The term relict is used equally for biota and for habitats if they are isolated remnants of earlier periods of larger distributions and habitat continua. Thus it has a clear implication in time. Does the term relict, however, mean unequivocally that biota were left behind *in situ* where they evolved and that the relict habitat of today formed a part of the earlier continuum? In other words, has the term relict a similarly clear spatial implication?

It has been seen (p. 367) that species persist in environmental conditions that were associated with their speciation; in other words, species are conservative in their habitat selection. In an ever-changing environment the biota are forced to follow the spatial shifting of climatic zonation. Parts of populations might be left behind *in situ* where conditions are persistent: e.g. gallery forests remaining from a forest belt during an arid period. Such a gallery forest is, in time and space, a relict habitat and its biota might consist largely of relict populations, i.e. relicts in the sense of time and space.

Climate zones might, however, together with their persistent biota, sweep through areas that were previously under the regime of different climatic zones. Under particular conditions such a moving biome might be stranded in a geographic position distant from its original position, where it no longer exists. Such a habitat and its biota are relicts in the temporal sense, but not in the spatial sense. They were left behind from an earlier epoch, but not *in situ*. In other words, these biota are not autochtonous.

The term for such translocated relict habitats is refuge habitat or *refugium*, and applies equally to the biota characterizing them. There is terminological difficulty in describing in one word the biota or species in a refuge habitat, and this might have been the reason why they are simply called ‘relicts’ without distinction.

It will be shown in the following section that the distinction between relict and refuge habitats and their biome is crucial to the understanding of the history of an area where relicts, in the broad sense, occur. It will also be shown that the biota of the Cape high mountains are in refuge, and do not represent a relict in the spatial sense.

OBSERVATIONS ON LIVE SPECIMENS

Very little is known of the biology of the *Colophon* species, and observations are restricted to a few live specimens in nature (Fig. 3) and in captivity.

In October 1977 several high-mountain areas were visited, both in the Swartberg and Langeberg ranges. Although on that occasion no live specimens were seen, it was possible to mark two sites for further studies. The indications of the prospective sites (one in each range) were fragments of dismembered specimens of *Colophon* beetles found in debris and under stones. Large numbers of ground-traps with preservative were set in both areas but they yielded no specimens of *Colophon*, although later several specimens were sighted within a few metres of operating traps. It was concluded that none of the baits used, including fermenting banana, had any attraction for these species. During three subsequent years the two selected sites were visited five times. On three occasions live specimens were seen and observed; each time some of the specimens were taken live to Pretoria, where they were observed for periods of up to 84 days. Our scanty knowledge comes from these field and laboratory observations of live specimens.

Fig. 3. *Colophon izardi* Barnard, male, in its natural environment in the Langeberg Range.

The native habitat in terms of habitat diversity is markedly different for the two species observed. The habitat of the Swartberg species, *Colophon montisatris* sp. nov., was demarcated in a tiny area of about 400 m horizontally and 20 m vertically. Outside this area not even fragments of specimens could be found, despite the fact that no obvious change in any of the environmental conditions could be seen. However, the Langeberg species, *C. izardi*, was found at sites 8 km apart and differing in altitude by about 400 m. The same species is known from five additional localities at increasing distances from the observation area. Although a detailed evaluation of environmental differences between the altitude extremes is not available, the differences in other parameters, such as soils, vegetation, exposure, etc., seemed to be considerable between the high open crest and the broad valley between two crests.

The striking difference between the *Colophon* habitats on the two mountain ranges is obviously due to their general climatic situation. The Swartberg population appears to occupy the last remnant of a habitat still acceptable to it, and it is likely that it is on the verge of natural extinction unless the regional climate soon turns more humid and cooler, thus extending spatially its native habitat. This is a classical 'bottle-neck' situation, providing selective pressure for a trapped population to speciate. Indeed, the climate of the Swartberg is drier and warmer compared to the Langeberg; rain and mist are less regular in the summer months. The same altitudes at which *Colophon* lives in the Langeberg (down to 1 400–1 600 m) are very dry after December in the Swartberg, where the peak of activity of beetles in general has already passed. In the Langeberg the mist zone is lower, and although dry spells might occur there too, the climate is more humid throughout the summer. *Colophon* specimens were seen live in both localities in February too, but with the described difference in their altitude range.

I am of the opinion that *Colophon* species in general have a much less-restricted seasonality of adult activity than Barnard (1929: 178) suggested. Barnard recorded, for example, *C. izardi* in October and November, and I have seen them in December and February; thus the adult activity period covers the whole summer at that altitude. The habitats might often be covered in snow until August or September, persisting from March or April. The surface activity of adults is likely to be triggered by optimal conditions at any time during the summer and is not restricted to any particular period of it. The pattern of scattered days of surface activity of an individual is likely to last through several years. This opinion might be supported by specimens, particularly females, that have the anterior tibiae strongly eroded. This degree of wear also occurs in Tenebrionidae, but only in species that could be kept in captivity for many years.

According to observations *Colophon* species are decidedly diurnal in activity. On all occasions when live specimens were sighted 'observation shifts' were organized, in order to scan the area with powerful lamps throughout the night. However, not a single *Colophon* was sighted, although hundreds of other Coleoptera were collected. Observation on live captive specimens confirms the diurnal activity.

The optimal weather conditions for surface activity can also be defined. Five specimens of *Colophon montisatris* sp. nov. were sighted within an hour, in thick fog after sunset (Swartberg, February 1979). One specimen of *C. izardi* was seen (Langeberg, December 1977—the very first live specimen) at about 16h00 in drizzling rain and biting cold wind. All other specimens were seen in late afternoon hours, often after sunset but before dark. Barnard (1929: 178) mentions 06h00–08h00 as the collecting hours of most of his specimens, and records as exceptional two specimens that were collected 'at midday in hot sun, though amongst low vegetation'. Nevertheless, it is clear that these beetles prefer the cool and humid periods of summer days, when their refuge habitat is not under snow. Again this is an indication of the climatic conditions of their lowland native habitat.

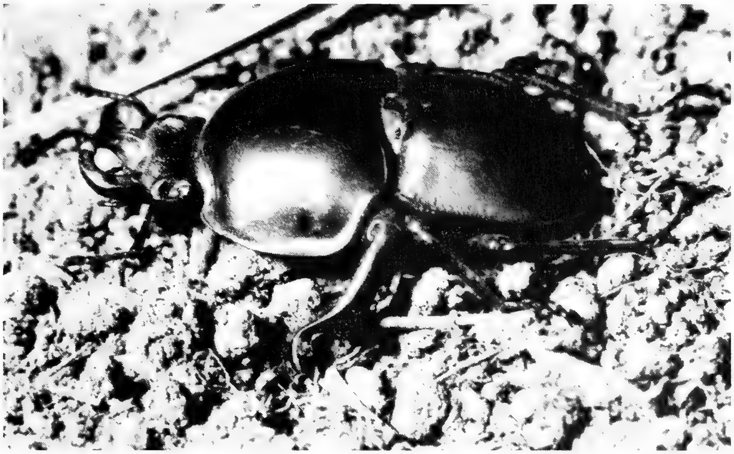

Fig. 4. *Colophon montisatris* sp. nov., male. This specimen's activity was observed for over an hour.

Circumstantial evidence suggests that *Colophon* species have a subterranean life, where their larvae feed on the roots of plants. On two occasions males of two species (*C. izardi* and *C. montisatris* sp. nov.) were observed undisturbed for over an hour. I had hoped that they would lead me to a female (that of *C. montisatris* sp. nov. was not yet known at that time), or would chew on something, dig in, or withdraw to their own burrow when it became dark; they did absolutely nothing. Their slow movement seemed to be entirely undirected and aimless and revealed nothing at all of their habits (Fig. 4). Specimens in captivity did not accept any food provided for them; this included a range of plants from their habitat, obtained from the Botanical Gardens, Pretoria. None of the captive specimens were observed to feed (seven specimens, over periods ranging from 15 to 84 days) unless on the vegetation debris that was richly supplied in the soils brought with them.

CLADISTIC ANALYSIS OF THE *COLOPHON* SPECIES

As will be explained (p. 381), the higher classification of this group can only be clarified in conjunction with a comprehensive revision of the whole family. At this stage we have to be satisfied with the recognition of the genus as a monophyletic group. The general structure displayed by all 14 species suggests that this group is not only monophyletic but forms one single genus.

The 14 species form two distinct groups indicated by the symmetry of the aedeagus and the single correlated character found, i.e. the level of the clypeal margin (see p. 385). However, separate genera could not be allocated to these species groups, as one of them—comprising the plesiomorph species—apparently does not possess any apomorphic character states among the numerous characters studied.

The two species groups are interpreted as two distinct evolutionary lineages within the genus. The first group, comprising the plesiomorph species, is a result

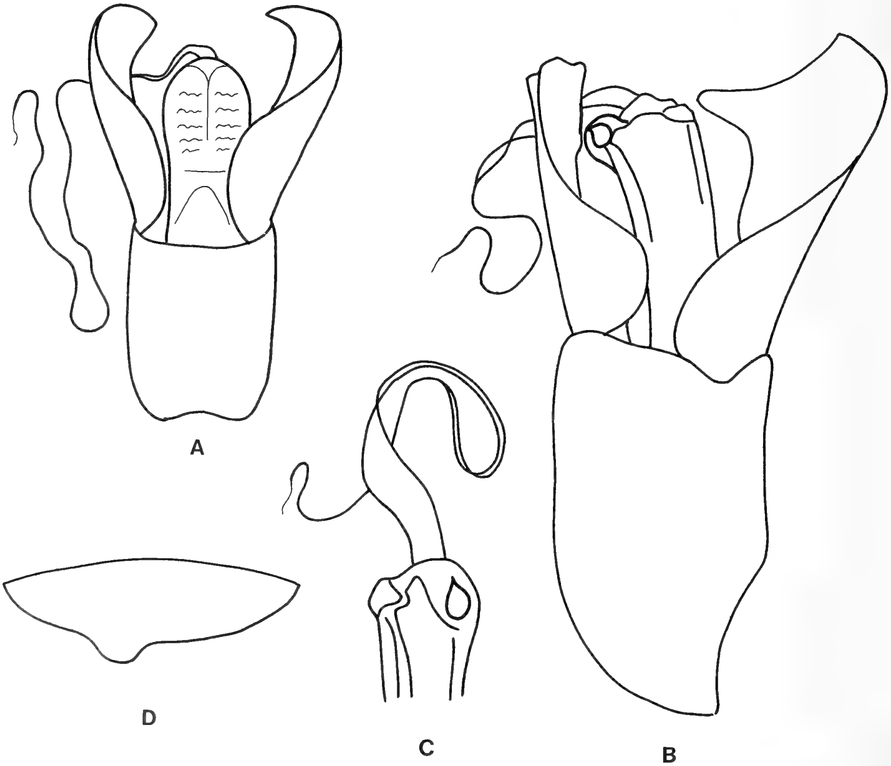

Fig. 5. Lineage characters in the genus *Colophon*. A. Symmetrical aedeagus in the plesiomorphic lineage, as in *C. haughtoni* Barnard. B. Asymmetrical aedeagus in the apomorphic lineage, as in *C. primosi* Barnard. C. Apical portion of penis with the non-rectractable inner sack as in *C. primosi* Barnard. D. Asymmetrical anal sternite in *C. montisatris* sp. nov., typical for the males of the apomorphic lineage.

of the first cleavage and possesses as apomorphies only those characters that ensure the generic position of *Colophon* itself. The generic apomorphies can only be recognized through out-group comparison, but at this stage we do not know what should be considered as an out-group for *Colophon*. However, the existence of true generic-level apomorphies (applicable to all species included) is confidently postulated. The phenetic distinctness of the Cape stag beetles proves their integrity at least at generic level. The problem is indeed to find a relative to them at all.

The two evolutionary lineages represented by the two species groups can be characterized as follows. *Plesiomorphic lineage*—Aedeagus of symmetrical type, parameres very nearly identical or symmetrical; anal sternite evenly rounded posteriorly. Penis feebly sclerotized with distinct transverse undulation on the shaft (Fig. 5A). Clypeus meets labrum on an even level. *Apomorphic lineage*—Aedeagus of asymmetrical type, right paramere strongly dilated towards apex and forms a sharp hook at its inner margin, left paramere slender and without inner hook (Fig. 5B). Anal sternite correspondingly asymmetrical at its posterior margin, emarginate to the right of its median axis so as to provide space for the enlarged right paramere at ejection (Fig. 5D). Penis well sclerotized with very distinct and asymmetrical apical portion (Fig. 5C). Anterior margin of clypeus raised above the level of labrum at their suture.

The symmetrical structure of the penis is a key and irrefutable character to denote the plesiomorphic position in the lineage of species that share this character.

The above group characters are not used in the following analysis, which is based on the transformation series given below. The analysis of each lineage is carried out separately. Often the same characters are used, and are sometimes represented in both transformation series in the manner: absence to presence (plesiomorph group), presence to distortion (apomorph group).

Transformation series in the plesiomorphic lineage

1. Apico-ventral process of anterior tibia small to *large*.
2. A longitudinal crest at the ventral side of anterior tibia more or less uniform and moderate over whole length to *sharply raised* in its basal section.
3. Apico-ventral process of anterior tibia in central position to *shifted to inner margin*.
4. Dorsal process of mandible absent to *present*.
5. Ventral process of mandible concealed to *free standing* and prominent.
6. Lateral margin of pronotum evenly curved along whole length to deeply *emarginate* before reaching posterior lateral angle.
7. Anterior margin of pronotum immarginate at its median section to *continuously marginate*.
8. Gula flat along whole length to *sharply concave* (lateral view).
9. Prosternal apophysis simple to forming a *sharp tubercle* at its caudal (intercoxal) end.

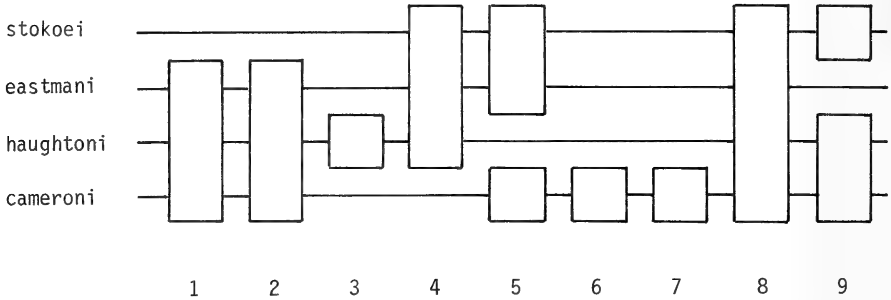

Fig. 6. Tabulated record of apomorphies in the plesiomorphic lineage of the genus *Colophon*. Figures below the histograms refer to characters evaluated in the text.

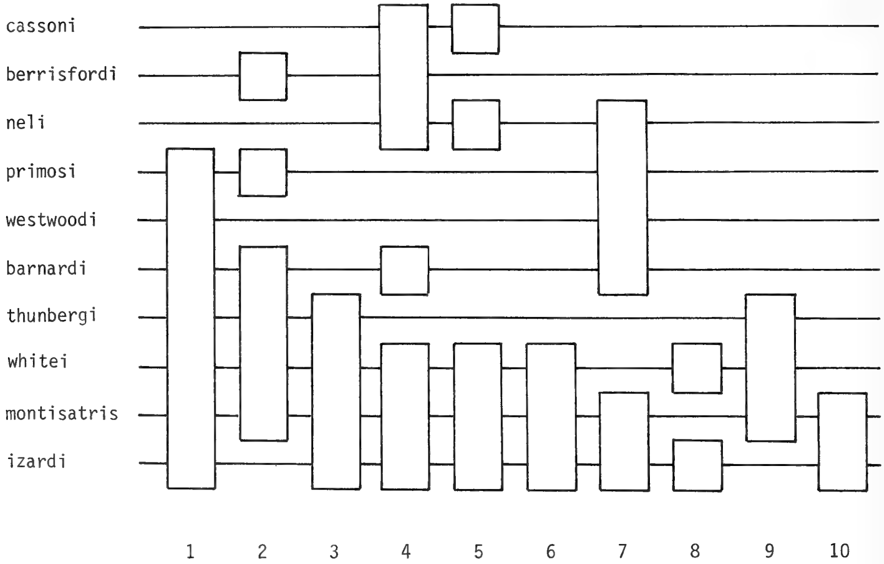

Fig. 7. Tabulated record of apomorphies in the apomorphic lineage of the genus *Colophon*. Figures below the histograms refer to the characters evaluated in the text.

Transformation series in the apomorphic lineage

1. Apico-ventral process of anterior tibia present, reducing to *absent*.
2. Inner angle of anterior tibia rounded to forming a *prominent process*.
3. Anterior tibia straight to *bent inward*.
4. Longitudinal ventral elevation of anterior tibia flat and rounded to *sharply crested*.
5. Lateral margin of anterior tibia with several spaced teeth, through trifid to *bifid* apical portion.
6. Anterior tibia evenly curved at external margin to a deep *U-shaped emargination* in pre-apical position.

7. Dorsal process of mandible present to *absent*.
8. Ventral process of mandible in basal, to *median* or *apical* position.
9. Lateral margin of pronotum moderately to *sharply* and *deeply emarginate* posteriorly.
10. Gena evenly rounded behind eye to a distinct *postgenal protuberance*.

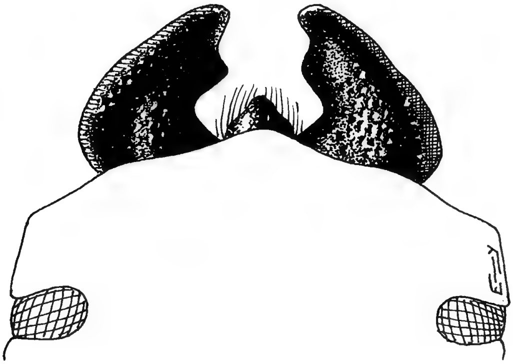

Fig. 8. Simple female mandibular structure in *Colophon westwoodi* Gray. The mandibles are very similar in females of all *Colophon* species.

Where applicable, the very uniform display of character states in females was used for out-group comparison in deciding on the polarity of the transformation series. Females generally, but notably in Lucanidae, are more conservative in phenetic changes and thus can be considered in most characters to be close to a hypothetical ancestor (Figs 8, 14A). In some other characters, stages uniformly displayed by the symmetrical-aedeagus lineage, were considered as plesiomorphic states in the genus, e.g. the presence of an apico-ventral process of the anterior tibia and the presence of a dorsal process of the mandible.

The synapomorphies, as displayed in the plesiomorphic and in the apomorphic lineages of species respectively, are shown in Figures 6 and 7. From these data a cladogram was constructed (Fig. 9). On the branches the numbers of synapomorphies are marked in squares and the numbers of autapomorphies in circles, indicating the position of terminal species.

THE PRESENT-DAY DISTRIBUTION OF *COLOPHON* SPECIES COMPARED WITH THEIR EVOLUTION

It is assumed that *Colophon*, as a monophyletic genus, had a single ancestral species. From this ancestral population, by the repeated speciation of marginal population fragments, an increasing number of species has evolved. In a slow-moving, wingless and terrestrial type of organism such as *Colophon*, the process of dispersion must have been slow and the chances of population fragmentation,

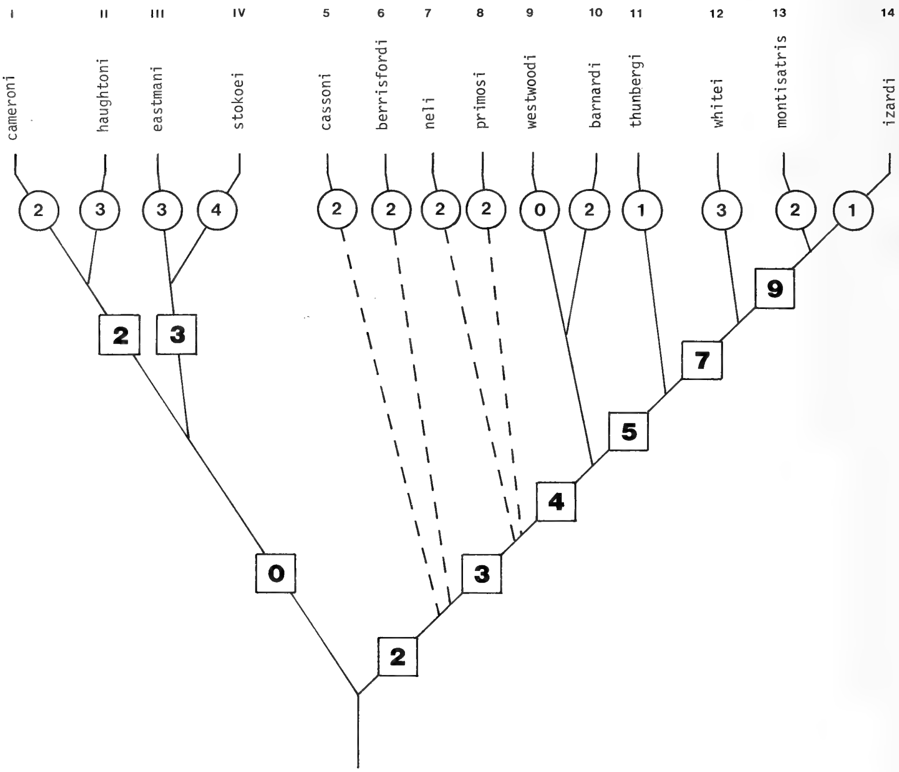

Fig. 9. Cladogram of *Colophon* species. Figures in squares show the numbers of synapomorphies found; figures in circles show the numbers of autapomorphies found in the individual species.

affecting spatially advanced marginal populations, rather good. If the character transformations in species of such a group of apterous organisms are studied along a geographical gradient, a clinal pattern will usually be found. This is only to be expected as the phenetic reflection of a chain of subsequently forming daughter species. Similar observations have also been made on apterous tenebrionids (Endrödy-Younga 1982).

The assumption that *Colophon* and its entire high-mountain biome is an *in situ* relict of past climatic epochs should be dramatically proved by the phenetic cline of *Colophon* species along the mountain ranges where they live. It would be expected that consecutive east–west sections of the Swartberg and Langeberg ranges should be occupied by species of closest kinship in the sequence of their specific character transformations.

However, the actual situation is very different from that expected. The plesiomorph group of species occupies the mountain ranges in the south-western corner of the area (Fig. 10). Most of the apomorphic species occupy the east–west ranging Swartberg and Langeberg mountains, but one (*C. westwoodi*) lives

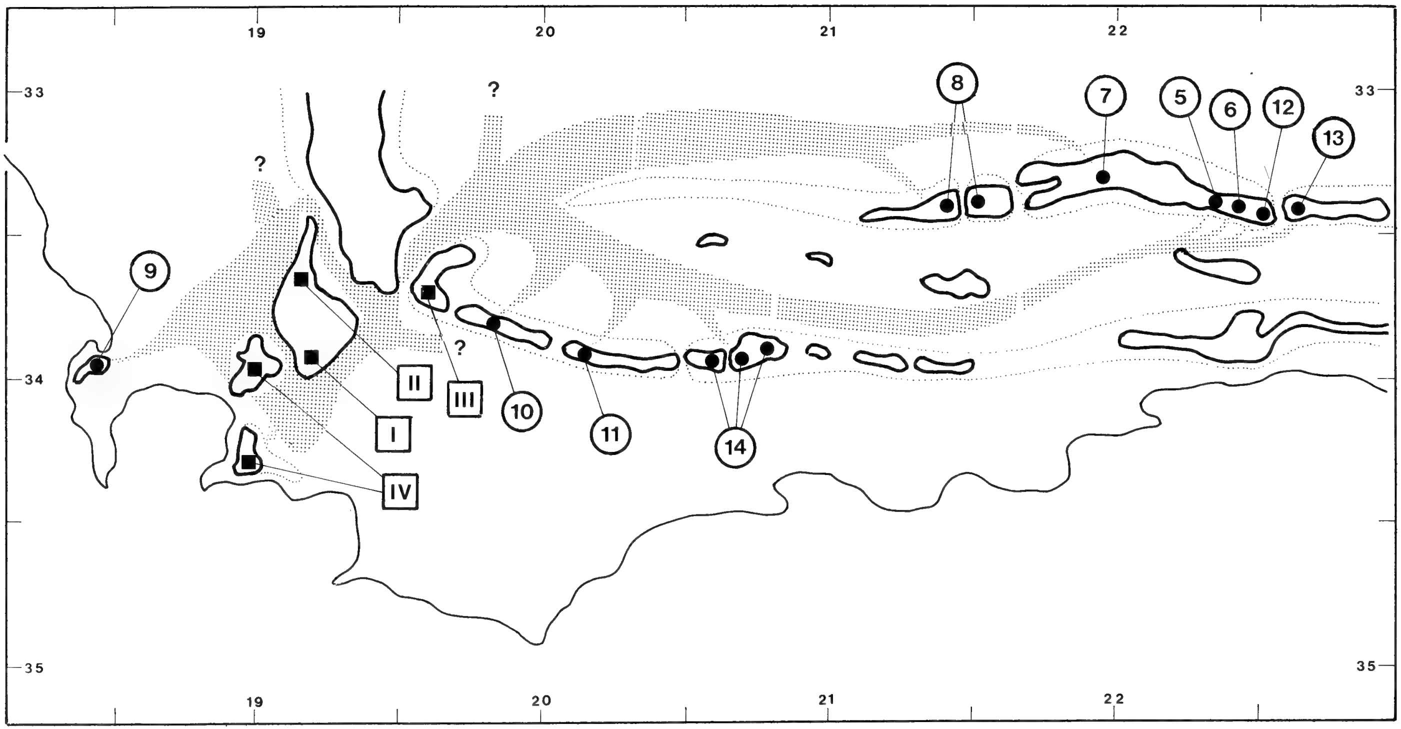

Fig. 10. Hypothetical dispersion and present-day distribution of the *Colophon* species. Roman figures represent the species of the plesiomorphic lineage, arabic figures the species of the apomorphic lineage (see Fig. 9 for names).

on Table Mountain, where it is isolated at the western extremity of the mountain groups occupied exclusively by the plesiomorph species.

Similarly, the three terminal apomorphic species of the apomorphic species group are separated at the east end of the major mountain ranges: *C. whitei* and *C. montisatris* sp. nov. on the Swartberg and *C. izardi* on the Langeberg, with the arid Little Karoo between them.

Thus the dispersion and speciation of the *Colophon* stock could not have occurred on and along the mountain ranges but only on the lowland situated around the mountains. At the end of the humid and cool temperate climatic period, when the presently inhabited altitudes of the mountains were under snow most of the year, an intricate mosaic pattern of *Colophon* species inhabited the low-altitude country. Because of the gradual changes towards a dry and hot summer, the populations withdrew to the nearest mountains where they could persist under their native conditions. It is likely that several species retreated into areas that could provide only temporary shelter. Populations that became stranded in hilly country of insufficiently high altitudes could not survive during continuing aridification.

The phylogenetic position of *Colophon primosi* and *C. neli* raises further problems. They belong undoubtedly to the apomorphic species group of the genus; however, they cannot be derived from the same ancestral stock as all other species of this group. There is a strong indication that the dispersion and speciation of the *C. whitei–C. izardi* lineage proceeded eastwards between the main mountain ranges. It is unlikely, however, that the ancestry of *C. primosi* and also of *C. neli* followed the same route. It is conceivable that the ancestral territories of those latter lineages occupied sections of the southern Karoo, north of the Swartberg range. The same geographical situation can also be the reason why only those two species have survived wheras their closest relatives, having no access to nearby mountains for retreat, became extinct.

SYSTEMATIC REVISION OF THE GENUS *COLOPHON*

THE HISTORY OF STUDIES

The first *Colophon* specimens must have been collected around the turn of the eighteenth and nineteenth centuries by unknown travellers. The genus, with its first known species, *C. westwoodi*, was described by Gray in 1832; locality, date or collector of the type-specimen (in the British Museum (Natural History), London) are not known. A second, similarly old specimen in the Hope Museum, examined by Parry in 1870, bears no information regarding its origin, but was already labelled as a 'type' in Parry's time. Gray (1832) knew, however, only of one male.

The second species, *C. thunbergi*, described by Westwood (1855), is dedicated to the notable traveller and naturalist C. P. Thunberg, who visited the western Cape in the 1790s. There is no evidence that he actually collected the specimen in question, but a passage in his diary (1793) coincides with the locality of a specimen of *C. thunbergi* in Oberthur's collection (Muséum national d'Histoire naturelle, Paris), referring to the Swellendam section of the Langeberg range. These hints led Barnard to the discovery of a population of this controversial species at the Zuurbrak Peak in 1932 (Barnard 1932*b*).

Dr K. H. Barnard revived interest in these curious beetles. As a curator, and after Péringuey, the director of the South African Museum, Cape Town, he was not only a keen student of aquatic zoology but also a devoted mountaineer. It is only to be expected that the curious high-mountain dwellers would not long evade his interest. As far as can be ascertained, the first specimens of *Colophon* collected by Barnard were those found in 1916 in the Hottentots Holland Mountains. They proved to be different from the two known species and were described as *C. stokoei* Barnard, 1929. The second record came from Dr S. Haughton, who collected a single male of yet another unknown species in the Matroosberge in 1917—*C. haughtoni* Barnard, 1929, dedicated to its collector. Thus encouraged, Barnard's mountaineering colleagues paid attention to these curious beetles during their excursions, and their efforts are reflected in Barnard's dedications of new species collected. All nine of Barnard's species are named after members of the Mountain Club of South Africa. (I have completed the eminent list by naming one of the new species after the former President of the Club, Dr K. H. Barnard.)

In his first paper on *Colophon*, Barnard (1929) described five new species: *C. stokoei*, *C. haughtoni*, *C. cameroni*, *C. izardi* and *C. primosi*, and made the first character evaluation in the genus, pointing out the main specific characters of the male mandibles, anterior tibiae, and aedeagi. Studying the aedeagi, he first discovered that the taxonomic position of the genus under the subfamily Lampriminae is, at least, doubtful.

A plate with photographs of all species of *Colophon*, including those to be published in a forthcoming scientific paper, was published in a popular article (Barnard 1932*a*). Although the names to be used accompanied the photographs, this article cannot be considered as the place of publication (see *International Code of Zoological Nomenclature 1964*: Article 12). The proposed names became available in a subsequently published scientific paper (Barnard 1932*b*), where descriptions of *C. neli*, *C. whitei*, *C. cassoni*, *C. berrisfordi* and *C. eastmani* were given.

THE POSITION OF THE GENUS *COLOPHON* IN LUCANIDAE

The genus *Colophon* was until very recently associated with Southern Hemisphere subfamilies of the Lucanidae. McLeay (1819) recognized the subfamilies Chiasognathinae and Lampriminae as separate subfamilies. Following this classification, Didier & Séguy (1953) placed *Colophon* under Lampriminae. The same classification was maintained by Landin (1955) and Brinck (1956). For a long period of time these two subfamilies (both Southern Hemisphere) were combined under the name Chiasognathinae, and *Colophon* was considered a member of it (Parry 1864; Handlirsch 1908; Van Roon 1910; Jeannel 1942). Thus the actual affiliation of the genus has not changed.

Lacordaire (1856), who recognized Chiasognathinae and Lampriminae, placed *Colophon* under the subfamily Lucaninae, or '*lucanides vrais*'. All classifications mentioned so far were based on differently evaluated external characters, in particular those of males that are strongly subjected to secondary sexual character transformations.

The first author to examine the male genitalia of *Colophon* species was Barnard (1929), who was by no means a specialist of Lucanidae. Nevertheless he, referring to Sharp & Muir (1912), observed that these genitalia are distinctly more like the Lucaninae than the Lampriminae-type, and shed the first doubt on the association of this South African genus with the Lampriminae. His noteworthy discovery was disregarded by several subsequent authors.

In 1960 Holloway published her study on a wide range of species of the family Lucanidae comparing, among other characters, the structures of male genitalia. She categorically excluded *Colophon* from Lampriminae, and placed the genus under Lucaninae as Lacordaire (1856) and Barnard (1929) had done, although on a more intuitive basis.

Being concerned with the relationship and origin of the genus *Colophon*, I have repeated Holloway's study on less extensive, but representative, material from South America, Africa and Australia, including species classified under the subfamilies Chiasognathinae, Lampriminae and Lucaninae. I agree that according to Holloway's (1960) classification *Colophon* does not belong to either of the Southern Hemisphere subfamilies, but to the cosmopolitan Lucaninae. Nevertheless, the problems of relationship and origin remain unresolved. It became evident that there is no evolutionary link between *Colophon* and the other, old-world stock genera of African Lucanidae. Thus, although *Colophon* belongs to the subfamily Lucaninae, it seems not to be derived from its African old-world lineages, nor could the latter be derived from the stock of *Colophon*. Although no conclusive studies were made in this direction, some of the Southern Hemisphere genera of the subfamily Lucaninae (such as *Pholidotus* McLeay in Brazil, and *Rhyssonotus* in Australia) seem to be more closely related to *Colophon* than any of the African genera.

Thus the Gondwana origin of *Colophon* can be maintained under its classification in Lucaninae, but the problems in the evolution of the subfamily are compounded. Holloway (1960) envisaged the necessity of further subdivision of the subfamily to resolve diversity problems. Such a study might also clarify the problems surrounding origin, evolution and dispersion within the group.

MATERIAL EXAMINED

In the course of the present study nearly all *Colophon* specimens known to be deposited in collections were re-examined. In all 136 complete specimens and numerous fragments were seen, some of the latter being listed below under primary and secondary types. The material included four primary and 38 secondary type specimens, 46 further specimens and numerous fragments from the South African Museum, Cape Town; eight primary and 18 secondary type specimens and eight further specimens from the British Museum (Natural History), London; the type specimen of *C. thunbergi* from Oxford; and one primary and 10 secondary type specimens and 11 further specimens and fragments in the collection of the Transvaal Museum, Pretoria. By kind courtesy of the South African Museum, some of the duplicates could be deposited in the Transvaal Museum, Pretoria.

The value of fragments, which are more frequently found than intact or live specimens, was fortunately already realized by Barnard. Some fragments, such as male heads and anterior tibiae, are perfectly characteristic of the species they represent. Barnard had already made use of such fragments in his character evaluations and listed them in his species descriptions. Indeed, in several instances the single, or few, intact specimens alone would not permit conclusive recognition of specific characters and individual variations. In this paper more importance than usual is given to fragments; where appropriate they are designated as paralectotypes and have been marked accordingly.

In listing material examined the locality data have been taken from the actual specimens labels, hence various inconsistencies in spelling, etc. Any additional information added is placed within square brackets.

KEY TO *COLOPHON* MALES

1 (8) Edge of clypeus in flush with labrum. Aedeagus of symmetrical type, left and right parameres closely similar. Penis less sclerotized with distinct transverse undulation, apical portion symmetrical (Fig. 5A). Apical sternite symmetrical at apical margin.

2 (3) Mentum with sharply raised anterior portion forming one or two (bilateral) rounded elevations or a deep aciculate anterior surface; sickle-shaped mandibles with ventral process at base only (Fig. 17A). Anterior tibia emarginate before apico-lateral dilation (Fig. 20C). 21–27 mm. Western Cape mountains .... *C. stokoei* Barnard

3 (2) Mentum flat or moderately and evenly convex.

4 (5) Apex of mandible and pre-median dorsal process connected by a flattened shiny surface (Fig. 11B). Ventral process of mandible broadly obtuse-angled. Prosternal apophysis without any process on posterior portion. (Anterior margin of pronotum not furcate-marginate.) Anterior tibia slightly and evenly curved and dilated (Fig. 14D); apico-ventral process extremely large, cylindrical and perpendicular to tibia. 20–23 mm. Western Cape mountains .... *C. haughtoni* Barnard

5 (4) Dorsal process of mandibles more or less cylindrical, not forming a flat inner surface; position more or less postmedian.

6 (7) Ventral process of mandible well developed and situated in basal position. It is flat, acute-angled, without forward-pointing cylindrical process. Dorsal process in median position, apex symmetrically truncate (Fig. 11A). Anterior tibia evenly but somewhat more dilated (Fig. 14B). 16–26 mm. Western Cape mountains .... *C. cameroni* Barnard

7 (6) Ventral process of mandible indistinct, situated in a basal position not surpassing mentum. Dorsal process about median in position, narrow, cylindrical, perpendicular to main arm (Fig. 11C). Anterior tibia distinctly arcuate at apical portion (Fig. 14E), ventral crest evenly and sharply elevated from base, abruptly contracted postmedially, forming a right angle (Fig. 14F). Apico-ventral process entirely in inner marginal position, also visible in dorsal view (Fig. 14E). 17–22,5 mm. Western Cape mountains. . . . . *C. eastmani* Barnard

8 (1) Anterior margin of clypeus sharply elevated above the level of labrum. Aedeagus of asymmetrical type, left and right parameres strongly dissimilar, the left one angularly dilated (Fig. 5B). Penis strongly sclerotized, surface smooth with longitudinal lateral margination, apex asymmetrical (Fig. 5C).

9 (10) Mandibles long, beak-like and prognathous with matching inner margin (Fig. 21B), together with legs orange-brown in contrast to black body; small ventral processes in basal position. Anterior tibia straight, evenly dilated with four sharp lateral teeth (Fig. 20A). 28–35 mm. Swartberg range. . . . . *C. primosi* Barnard

10 (9) Mandibles arcuate, black.

11 (12) Anterior tibia narrow, rectangularly bent inward in apical third (Fig. 27F). Ventral process of mandibles in apical position; apex of main arm in closed position of mandibles forms a circle with ventral process (Fig. 29C). Pronotum about as long as broad, normally with a pair of red dots on disc (Fig. 31). 21,8–25,3 mm. Langeberg range. . . . . *C. izardi* Barnard

12 (11) Anterior tibia straight or bent at varying angles, but not rectangularly bent or filiform.

13 (14) Anterior tibia flat and oblong with parallel margins, about three times longer than broad (Fig. 27A); ventral crest sharp at basal half of length, ending here abruptly, forming a rectangle. Apico-ventral process large. Mandible with ventral process only (Fig. 21A). 15–19 mm. Swartberg range. . . . . *C. neli* Barnard

14 (13) Tibia not regularly oblong.

15 (16) Frons behind clypeal declivity with a rounded elevation. Main arm of mandibles broadly truncate and slightly bifid at apex, with rounded dorso-median elevation. Dorsal process reduced to a tiny basal knob. Basally situated ventral process small, hardly surpassing labrum (Fig. 24A). Anterior tibia moderately arcuate and dilated with four or five often irregular lateral processes (Fig. 20B). 21–25 mm. Table Mountain. . . . . *C. westwoodi* Gray

16 (15) Frons flat in middle or finely concave at clypeal declivity.

17 (20) Mandible without dorsal process.

18 (19) Anterior tibia very strongly dilated from base to apical four-fifths, then abruptly reduced into a U-shaped emargination before rising into bifid apico-lateral process (Fig. 27B). Pronotum deeply emarginate posteriorly, posterior angle rectangular. 23–27,8 mm. Swartberg range. .... ***C. montisatris*** sp. nov.

19 (18) Basal three-fifths of anterior tibia almost straight and parallel in dorsal view, apical dilation trifid, not contracted before dilation (Fig. 20E). Posterior third of pronotum contracted, but lateral margin here not concave, posterior angle of pronotum obtuse-angled, ampliate lateral margin of disc rounded. 21 mm. Langeberg range. ***C. barnardi*** sp. nov.

20 (17) Mandibles with dorsal and ventral processes.

21 (22) Anterior tibia very strongly dilated from base to deep pre-apical emargination of lateral margin; apico-lateral process narrow and bifid (Fig. 27D). Dorsal process of mandibles in median position forming an oblong surface with pointed angle at its inner apical corner; the whole process is sunk below the dorsal level of the main arm. Ventral process with its forward-pointing apex is positioned between the apex of main arm and dorsal process (Fig. 29A). 26–31 mm. Swartberg range. .... *C. whitei* Barnard

22 (21) Anterior tibia not strongly dilated laterally, tibia semi-parallel, expanding evenly to apical process. Dorsal process of mandibles is not an oblong structure.

23 (24) Ventral process of mandibles is produced sharply forward; it is narrow and cylindrical. According to the shape and position of the dorsal processes this species is known in two sympatric morphs (Fig. 17B, C). More than 18 mm. Western Cape mountains. ...... *C. cassoni* Barnard

24 (23) Ventral process of mandibles forms a forward-upward slanting ridge from base, its corners are rounded obtuse-angled (Fig. 19). Dorsal process pointed triangular. Length about 21 mm. Swartberg range. .... *C. berrisfordi* Barnard

DESCRIPTIONS OF THE SPECIES

THE PLESIOMORPH GROUP OF SPECIES

The common characters of the species forming this group are the symmetrical type of aedeagus (Fig. 5A) and evenly arcuate posterior margin of anal sternite in males. A correlated character is the structure of the forehead, where the margin of the clypeus is level with the labrum (in males). Phenetic characters do not show the split into the two main lineages in females.

The parameres in this species group are nearly similar, symmetrically arcuate at their apex, with the left paramere also simple (enlarged in the species of the apomorphic group). Penis less sclerotized than in the apomorphic species, with characteristic undulation on the shaft. Apex evenly and symmetrically rounded, ending in the long flagellum of the ductus ejaculatorius. Minor differences were seen between species in minute details of the aedeagus; however, these will not be described, as no particular importance was attributed to them in the evaluation. External characters of males were found to be sufficiently constant and much more evident than those of the aedeagi. In *C. stokoei*, the only species where considerable variability of characters could not be evaluated conclusively (individual or subspecific), there are not enough males known to provide the support of genital characters.

Colophon cameroni Barnard, 1929

Figs 11A, 12, 14B

Colophon cameroni Barnard, 1929: 172, fig. 7; 1932*a*: 23, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 309, 320. Holloway, 1960: 335.

Diagnosis

Black, medium size; mandible with large dorsal and small ventral processes. Anterior tibia almost straight, ventral crest sharply elevated basally, flat apically with apico-ventral process. Aedeagus of symmetrical type.

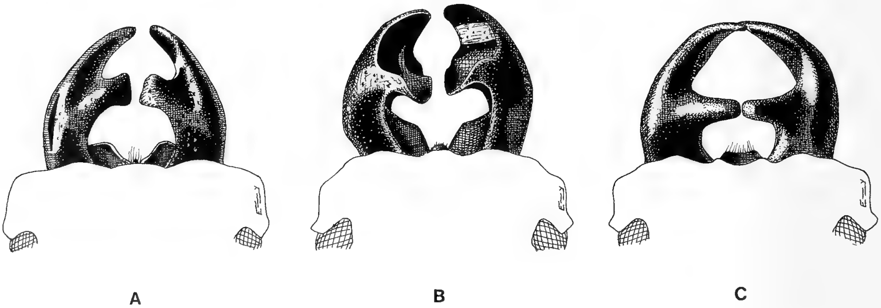

Fig. 11. Male mandibular structure in *Colophon* species. A. *C. cameroni* Barnard. B. *C. haughtoni* Barnard. C. *C. eastmani* Barnard.

Description

Male. Head broad and short, slightly tapering in front of eyes; rounded ocular canthi high, vertex flatly depressed between. Frons steeply deflected towards clypeus, which is level with flat and broad labrum. Punctation finer and denser near ocular canthi than at vertex. Mandibles prognathous, finely and evenly arcuate, pointed apex not bent inward. Dorsal process large, slightly raised above the level of main arm; slightly forward-pointing, truncate apex slightly dilated. Ventral process short and broad at base of mandible, rounded apex rectangular or obtuse-angled (Fig. 11A). Mentum more than twice as broad as long, corners narrowly rounded, anterior margin arcuately truncate. Gular sulcus shallow.

Pronotum distinctly broader than elytra, lateral margins semi-parallel (hardly converging forward) in median third, more convergent in anterior third, posteriorly not emarginate. Lateral and basal margins margined, anterior margin smooth. Punctation very fine and scattered.

Elytra smooth, densely shagreened and very finely punctate, wanting distinct subhumeral carina.

Anal sternite only slightly asymmetrical.

Anterior tibia straight, evenly dilated from base to apex; bifid apico-lateral process short and broad, not marked off basally by deep insinuation of lateral margin (Fig. 14B). Ventral crest sharply elevated in basal two-thirds, gradually flattened anteriorly; apico-ventral process small.

Aedeagus of symmetrical type. Penis feebly sclerotized, apex symmetrical and smoothly rounded, shaft sharply and deeply wrinkled transversely. Parameres

Fig. 12. *Colophon cameroni* Barnard, male; paralectotype; length 24,5 mm.

relatively symmetrical, right paramere broader, apex more pointedly turned inward; left paramere narrower, inward-turning apex short and rectangular.

Female. No female is known from the type locality.

Length

Male: 25 mm (range, estimated from heads, 16–26 mm).

Distribution

Western Cape, Hex River Mountains.

Material examined

Males: 3 complete specimens, 1 anterior part of body, 24 heads and 10 anterior legs. Females: 3 complete specimens, 2 bodies and 1 head. Lectotype ♂, paralectotype ♀ (complete); 1 ♂ and 1 ♀ (complete), 4 ♂ heads (paralectotypes) in British Museum (Natural History), London. All other specimens in South African Museum, Cape Town.

Lectotype. ♂: Waai Hoek Mts., 5 000 ft. [= 1 524 m], 1.1.1925, K. H. Barnard, in British Museum, London.

Paralectotypes. 1 complete ♂, 7 ♂ heads and 5 ♂ anterior legs: Waai Hoek Mts., 5 600 ft.[= 1 707 m], [April] 1928, K. H. Barnard in South African Museum, Cape Town; 1 complete ♀, Waai Hoek Mts., 5 600 ft. [= 1 707 m], in British Museum, London. 17 ♂ heads (13 in South African Museum, 4 in British Museum): Fonteintjieberg, Worcester distr., 6 500 ft. [= 1 982 m], [March] 1929, K. H. Barnard.

Additional material. 1 ♂, 1 ♀, Milner Ridge Peak, Hex River Mountains, 6 000 ft.[= 1 829 m], January 1934, K. H. Barnard, in British Museum, London. 1 ♂, 2 ♀ (specimens found dead) and 2 ♂ anterior legs: Great Winterhoek top, 6 800 ft. [= 2 073 m], August 1929, K. H. Barnard, in South African Museum. 3 ♂ anterior legs: Witzenberg range, Tulbagh, 1932, F. Berrisford, in South African Museum.

Variability

There is a considerable size variation in the 21 ♂ heads measured. They range between 4 and 6 mm, measured between transverse sulcus of vertex and apex of mandibles. No allometric variation was found. A limited individual variation could be observed in the angle of the basal process of mandibles, and in the apical curvature of mandibles, as well as in the length of the ventral elevation of anterior tibia. Nevertheless, the Waai Hoek and Fonteintjiesberg specimens are certainly conspecific.

A pair from Milner Ridge Peak, Hex River Mountains (see above) represent the smallest specimens [♂ 16 mm, ♀ 17 mm). Head length of male (measured as above) is only 3,7 mm. In this male the mandibular structure is similar but the dorsal processes are narrower and are not dilated at their apex; ventral process flat, obtuse-angled. Elytra in both specimens with faint and short subhumeral elevation. Anterior tibia similar, but elevation of ventral crest less than half of tibial length.

Colophon haughtoni Barnard, 1929

Figs 11B, 13, 14D

Colophon haughtoni Barnard, 1929: 171, fig. 6; 1932*a*: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 308, 320.

Diagnosis

Black; pronotum and elytra more shiny than in the other species. Medium size. Pronotum immarginate anteriorly. Anal sternite moderately asymmetrical, aedeagus of symmetrical type.

Description

Male. Head broadly oblong. Genal margin in front of eye distinctly emarginate. Ocular canthus high but rounded, vertex evenly concave in between, steeply deflected in middle to broad and finely emarginate clypeus, which is on the same level as the labrum. Punctation of vertex distinct, somewhat denser laterally. Mentum broad, semicircular. Transverse gular sulcus broad and rather shallow. Mandibles moderately long, evenly arcuate from base to apex. Apex appears as split, inner dorsal portion being curved backwards to form a broad concave surface between the two apices. Dorsal process absent. Ventral process small and obtuse-angled at base of mandibles (Fig. 11B).

Pronotum broadest at about the basal third of its length, evenly arcuate anteriorly in one, roundly arcuate to apical angle in another specimen. Prebasal section of lateral margins contracted but not emarginate. Posterior angle obtuse. Anterior margin of pronotum immarginate. Disc very finely and sparsely punctate, punctures somewhat larger laterally. Base of prosternal apophysis without a trace of callous elevation.

Elytra short and broad, not much narrower than pronotum. A short humeral crest at base distinct and, particularly in one of the two males, a faint longitudinal striation discernible.

Anal sternite moderately asymmetrical.

Anterior tibia arcuate, moderately dilated towards apex with an apical and a pre-apical triangular process, which appears in some other species as the bifid apico-lateral process (Fig. 14D). Ventral crest sharp and elevated in basal two-thirds, flattened pre-apically, forming a very large conical process perpendicular to tibia.

Aedeagus of symmetrical type. Penis feebly sclerotized together with apical portion. Parameres (right) unarmed pre-apically, apical portion of parameres nearly symmetrical.

Female. Shape of pronotum and elytra, and sculptural features of latter, similar to that of males.

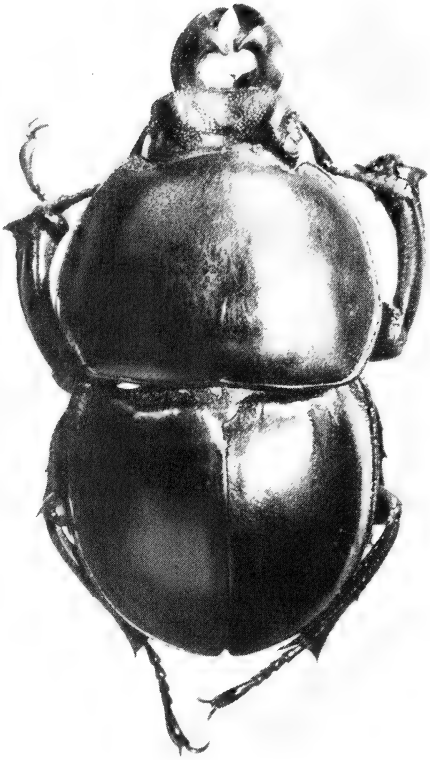

Fig. 13. *Colophon haughtoni* Barnard, male; length 23 mm.

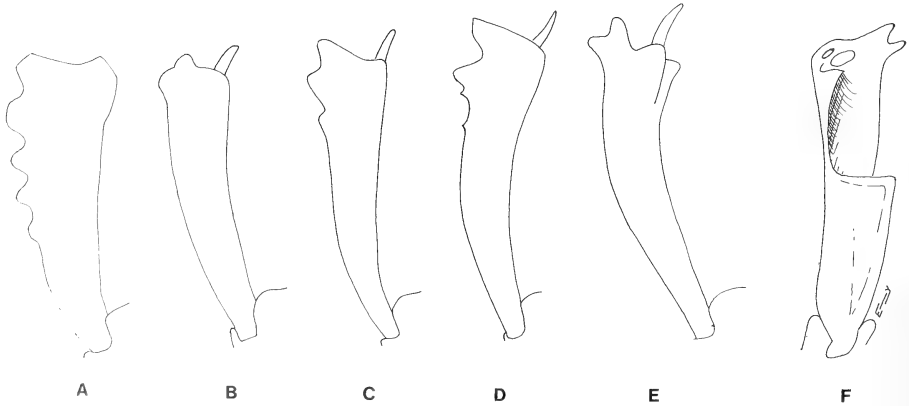

Fig. 14. Anteror tibiae in *Colophon* species. A. *C. primosi* Barnard, female. B. *C. cameroni* Barnard, male. C. *C. cassoni* Barnard, male. D. *C. haughtoni* Barnard, male. E. *C. eastmani* Barnard, male. F. *C. eastmani* Barnard, male in semi-ventral view.

Length

Males 20–23 mm, female 18 mm.

Distribution

Hex River Mountains.

Material examined

Holotype. ♂: Matroosberg, Hex River Mountains; 1917, S. H. Haughton; in British Museum (Natural History), London.

Additional material. 2 ♂, 1 ♀: Matroosberg, Hex River Mountains; January 1941, K. H. Barnard, in South African Museum, Cape Town. 2 ♀ (found dead): Groot Hoek Peak, Hex River Mountains; September 1933; K. H. Barnard, in British Museum, London.

Colophon eastmani Barnard, 1932

Figs 11C, 14E–F, 15

Colophon eastmani Barnard, 1932*b*: 174, fig. 6. Didier & Séguy, 1953: 76. Brinck, 1956: 309, 320.

Diagnosis

Medium-sized black species. Mandible with dorsal process in middle and ventral process basally. Clypeus is flush with labrum, pronotum immarginate anteriorly. Anterior tibia in male moderately arcuate with bifid apico-lateral process. Anal sternite moderately asymmetrical, aedeagus of symmetrical type.

Description

Male. Head transversely oblong. Genal margins in front of eye emarginate, not converging. Ocular canthi large, broad and rounded, vertex evenly concave in between, anteriorly straight or shallowly sinuate. Vertex steeply deflected to clypeus. Clypeus broadly truncate or finely emarginate; flush with broad and flat triangular labrum. Disc finely and rather sparsely punctate. Mandible evenly arcuate, sickle-shaped apex pointed, perpendicular dorsal process behind middle with large rounded apex. Ventral process very short, pointed, obtuse-angled; in closed position of mandibles concealed by labrum (Fig. 11C). Mentum flat, twice as broad as long, laterally evenly arcuate. Transverse gular sulcus deep, anteriorly vertical.

Pronotum moderately broader than elytra, broadest between middle and posterior third of length; lateral margins almost evenly arcuate between lateral angles, posteriorly flattened but not emarginate, posterior angle rounded obtuse-angled. Pronotum anteriorly immarginate. Punctation hardly visible on disc, more distinct laterally.

Anal sternite forms a small callus at margin, which is almost in middle; hardly asymmetrical.

Fig. 15. *Colophon eastmani* Barnard, male; paralectotype; length 22 mm.

Anterior tibia moderately arcuate inward, slightly dilated, apico-lateral process produced, bifid (Fig. 14E, F). Ventral crest sharp, gradually elevating to abrupt end in front of middle; apico-ventral process small, triangular, forward-pointing, visible in dorsal view (Fig. 14E, F).

Aedeagus of symmetrical type. Penis feebly sclerotized. Parameres not quite symmetrical.

Female. Unknown.

Length

Male 17–22,5 mm (lectotype 22,5 mm).

Distribution

Western Cape mountains.

Material examined

6 ♂ (dead), 2 ♂ heads, 10 ♂ anterior legs.

Lectotype. ♂: Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in British Museum, London.

Paralectotypes. 1 ♂: Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in British Museum, London. 3 ♂ (partially fragmented), 2 ♂ heads, 10 ♂ anterior legs; Keeromberg (Worcester), Sept. 1930; K. H. Barnard, in South African Museum, Cape Town.

Additional material. 1 ♂ (fragmented): Dassieberg, Robertson, 5 550 ft. [= 1 692 m]; January 1936, K. H. Barnard; South African Museum.

Colophon stokoei Barnard, 1929

Figs 16, 17A, 20C–D

Colophon stokoei Barnard, 1929: 168, figs 3–5. Didier & Séguy, 1953: 77. Brinck, 1956: 308, 320.

Diagnosis

A species with symmetrical type of aedeagus and anal sternite; clypeus flush with labrum. Mandibles without dorsal process, anterior tibiae arcuate, apically bifid in front of lateral emargination. Mentum prominently thickened.

Remarks

A range of variations was described as 'local variation' by Barnard, who marked the different types as 'f. typ. [forma typica], var. A, B, C, and D'. Considering the large and fragmented distribution area of *C. stokoei*, the marked differences could indicate subspecifically distinct populations. The locality records, however, seem to contradict such a situation. One of Barnard's reasons for not attaching specific or subspecific value to any of these variations could have been the inconclusive distribution patterns drawn from the available records. Some of the locality data, often provided by laymen, are considered as doubtful (e.g. the Blesberg record of *C. whitei*, see p. 417), and no further records have become known since Barnard's (1929) description. Though I doubt that some of the considerable differences are due only to individual variations, I refrain from drawing any conclusions due to the inadequacy of the material. The differences will be briefly discussed and the varieties are denoted below by the same letters as used by Barnard.

Description

Male. Head transversely oblong, anterior lateral angle almost pointed, but more obtuse-angled than in *C. westwoodi*. Internal subocular crests rounded but distinct, with tubercle at the anterior inner end of each crest. Frons evenly depressed between tubercles and arcuately slanting to clypeus. Barnard's 'anterior margin of head' refers to the angle of declivity of frons towards clypeus and not to a difference in levels between clypeus and labrum. The shape of frons and its form of declivity show a high degree of variation. It is sharp-edged with an overhanging clypeus in *C. stokoei* var. B. Clypeus meets triangular labrum on the same level.

Mandibles comparatively short and simple, each nearly semicircular, dorsal surface of apical portion furcate. Dorsal process lacking. Ventral process prominent, rectangular (*C. stokoei* var. C) or forward-pointing acute-angled (Fig. 17A).

Mentum very thick with a high degree of variation (simple in all other species). The actual form of mentum is the basis of Barnard's division of the species into varieties. In all varieties mentum evenly elevating from base in lateral view, and forming a vertical line or surface anteriorly. Anterior margin transverse, sometimes more or less tuberculate at either side (*C. stokoei* forma typica and *C. stokoei* var. B), anterior surface broad and large, deeply excavated (*C. stokoei* var. A), or simply roundly pointed (*C. stokoei* var. C and D).

Pronotum evenly arcuate at lateral margins, hardly and only very slightly emarginate near posterior angle. In general appearance moderately enlarged.

Elytra short and broad with distinct variation in proportions. Smooth in most varieties but in the 'holotype' of *C. stokoei* var. C, elytron with two distinct lateral elevations and a rounded inner longitudinal elevation (costae).

Anterior tibia more or less arcuate and dilated towards apex. Apex laterally bifid (*C. stokoei* forma typica, var. A, B and D) with deep U-shaped emargination pre-apically (Fig. 20C) (*C. stokoei* forma typica, var. A and B, less deep in *C. stokoei* var. D); or apico-lateral armature tridentate with indistinct pre-apical emargination (*C. stokoei* var. C) (Fig. 20D). Ventral longitudinal crest distinct, but not sharply raised basally, almost continuous to apex in *C. stokoei* var. C. Apico-ventral process long and narrow in all varieties.

Aedeagus of symmetrical type and similar in all varieties where known (*C. stokoei* forma typica, var. A and C) and all seven dissected specimens. As specific differences in aedeagi can be found between all recognized species of the genus, the similarity of aedeagi in *C. stokei* varieties might indicate their infraspecific status. Dorsal line of left paramere in lateral view emarginate in apical third, and forms an angle where it turns into the finely convex basal two-thirds; in *C. haughtoni* apical portion almost straight, angle flat and indistinct. Right paramere less pointed than in *C. haughtoni*.

Female. Apparently identical between varieties where known (i.e. from localities of *C. stokoei* forma typica, var. B, C and D).

Length

Male 24–27 mm, female 18–22 mm (Barnard (1929)—20–22 mm in males, measured without mandibles).

Distribution

Western Cape mountains from Hottentots Holland to the Stellenbosch and Wellington mountains.

Material examined

10 ♂ (two dismembered and seven dissected), 4 ♀. Of these 2 ♂ and 2 ♀ are in British Museum (Natural History), London; all other specimens in South African Museum, Cape Town.

Type material. The designation of a primary type should actually only be applied to the 'forma typica' described by Barnard as *C. stokoei*; specimens listed under his lettered varieties should not be designated as paralectotypes of the same species. However, I intend to designate primary types for the 'varieties' as well, so as to avoid increasing the existing confusion, not only in the evaluation of the variability of the species but probably also in the given locality records. The label data are quoted exactly from the specimen labels and additional information, partly from Barnard (1929), is given in brackets.

C. stokoei forma typica

Lectotype. 1 ♂: Hott.-Holl. [Hottentots Holland] Mts., 4 000 ft. [4 000–5 000] ft. [= 1 220–1 524 m], Caledon C.C. [Cape Colony], Barnard, [January] 1916; in British Museum, London.

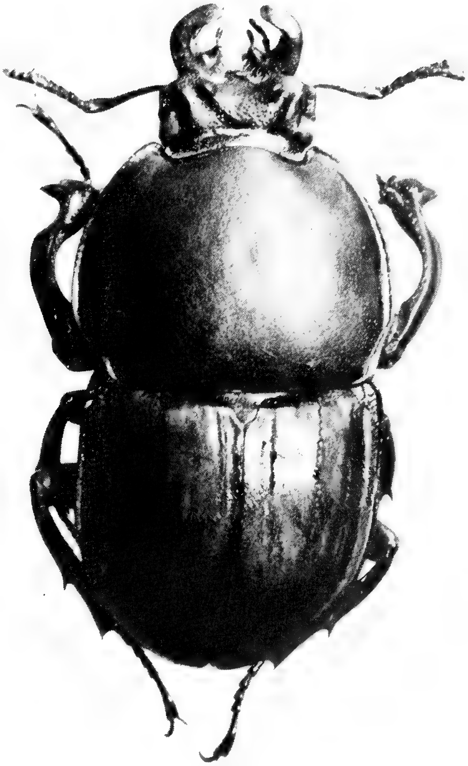

Fig. 16. *Colophon stokoei* Barnard, male; paralectotype of Barnard's forma typica; length 24 mm.

Paralectotype. 1 ♂: data as for lectotype; in South African Museum, Cape Town.

A third male with identical data to the above specimens, but not mentioned in Barnard's (1929) description, is in the South African Museum, Cape Town. It is identical to the 'lectotype' of *C. stokoei* var. A (see below).

C. stokoei var. A.

'Lectotype', ♂: Kleinmond Mt., C.P. [Cape Province]; 1.8.1927, T. P. Stokoe, in the South African Museum, Cape Town.

The identity of this specimen, the second listed by Barnard (1929), is not quite certain, though the area, date and collector agree. The first specimen listed by Barnard as *C. stokoei* var. A could not be found, unless it is the one listed above but bearing different locality. Though both specimens agree with the description of *C. stokoei* var. A, they prove how unreliable the locality data are.

C. stokoei var. B.

Syntypes consisting of 1 ♂ head, 1 ♀ head, 4 ♂ anterior legs (rather dissimilar in details): Plattberg, 3 000 ft. [915 m], Palmiet Riv. Mts., K. H. Barnard, Febr. 1927 [South African Museum]. Syntype, 1 ♀ (dismembered): locality as for other syntypes; in British Museum (Natural History), London.

C. stokoei var. C.

Holotype, ♂: Drakenstein Peak [Stellenbosch District], 4 000 ft. [1 220 m], 2.1.1920; K. H. Barnard [and T. P. Stokoe]; in South African Museum, Cape Town.

C. stokoei var. D.

Syntypes consisting of 1 ♂ head and 3 ♂ anterior tibiae: Up. [Upper] Snoukop, Wellington 4 500 [–5 000] ft. [= 1 372–1 524 m], K. H. Barnard [and R. Primos], [January].

Additional specimens. 1 ♂ (forma typica): Sneeukop, Hottentots-Holland Mts., Somerset West (name of collector illegible), 20.xii,1945. 1 ♂ (forma typica): Bushmans Castle, Berg River Range, Franshoek, Dec. 1943. 1 ♂ (closest to *C. stokoei* var. C, but more slender and straight anterior tibia): Sneeukop, Hottentot-Holland* Mts., 4 500 ft. [1 372 m], 15.xii.1935, K. H. Barnard. 2 ♂ and 2 ♀ (morphologically between *C. stokoei* forma typica and *C. stokoei* var. C): Berg River Range, Emerald Dome, Apr. 1944, K. H. Barnard. 1 ♀ (see Barnard 1929, *C. stokoei* var. C): Helderberg, 5.xii.1926, K. H. Barnard.

THE APOMORPH GROUP OF SPECIES

The common characters of this species group are the strongly asymmetrical shape of the aedeagus and the correspondingly asymmetrical posterior margin of the anal sternite in males. A correlated character expressed in the same form in all the species of this group is the anterior margin of the clypeus being raised above the level of the labrum. As the asymmetry of the aedeagus and the position of the labrum are not functionally related, these correlated apomorphic characters indicate convincingly the monophyletic origin of this well-defined evolutionary lineage.

The parameres in these species are asymmetrically expanded, with the left-hand one in particular forming a large apical or pre-apical triangular process pointing towards the penis. Thus the two parameres form a closed sheath or funnel around the penis in a closed position, probably in order to protect the penis and the long flagellum at penetration at the start of copulation. (Note that the flagellum is not retractile into the penis as it is in the Lampriminae.) The penis is strongly sclerotized, its apical portion asymmetrical. Its integument is firmly sclerotized with longitudinal furrows (Fig. 5B) and is not transversely undulating as in the plesiomorphic species group (Fig. 5A). The posterior margin of the anal sternite is emarginated above the enlarged left paramere and bears a more-or-less (according to species) distinct, rounded projection above the right paramere (Fig. 5D). More or less distinct differences in the structure of the parameres and the penis were observed between species. Although these differences are likely to be constant and specific, a detailed evaluation was not possible owing to the scarcity of the material. While male genital characters might improve the phylogenetic evaluation of the species, their importance in species identification is limited, as male external characters are ample and appear to be specifically constant.

Colophon cassoni Barnard, 1932

Figs 14C, 17B–C, 18

Colophon cassoni Barnard, 1932*b*: 172, fig. 4. Didier & Séguy, 1953: 76. Brinck, 1956: 311, 320.

Diagnosis

Small to medium-sized black species. Male mandibles with dorsal and prominent ventral processes. Aedeagus of asymmetrical type.

Description

Male. Head broadly oblong. Genal margin in front of eye straight, parallel or slightly converging. Anterior margin deeply insinuated and deflected to vertically positioned clypeus. Clypeus narrow, pointed in small specimens, raised above

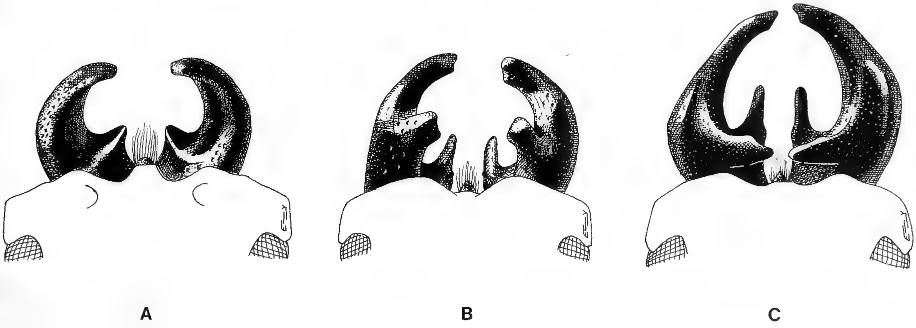

Fig. 17. Male mandibular structure in *Colophon* species. A. *C. stokoei* Barnard (forma typica). B. *C. cassoni* Barnard (forma typica). C. *C. cassoni* m. *recurva* morpha nov.

level of small triangular labrum. Mandibles rather short, main arms curved inwards at varying angles. Apices roundly pointed or truncate, sometimes slightly emarginate. Ventral process sharply produced anteriorly, joining the main arm, slightly sinuate at its inner margin; apex reaches basal third to half of length of mandible. Dorsal process thick, almost cylindrical, rising smoothly from surface of main arm, pointing slightly forward (Fig. 17B). Mandibular armature is subject to allometric variation. Mentum slightly convex, roundly triangular, coarsely punctate. Gular sulcus flat.

Pronotum hardly broader than elytra in specimens seen (all small). Margins semi-parallel in median third, evenly arcuate, converging anteriorly, finely emarginate behind. Pronotum with margination only interrupted in middle of anterior margin. Punctation extremely fine on disc, more distinct at posterior angle.

Elytra smooth, finely punctate, sutural margins smoothly and rather indistinctly elevated.

Anal sternite asymmetrical, without distinct off-centre protuberance of margin (small specimen).

Anterior tibia similar to that of *C. cameroni*; almost straight at inner margin, arcuately dilated towards apex. Bifid apico-lateral process more produced, sometimes with a third rudimentary proximal process (Fig. 14C). Ventral crest sharply elevated at basal two-thirds (some variation in length), arcuately interrupted pre-apically; apico-ventral process rather large; in an inner-side view the process looks as if split from body of tibia.

Aedeagus: right paramere forms a large process at its inner margin; margin between process and apex straight, angularly emarginate between process and base. Left paramere unarmed, wedge-shaped with roundly pointed apex.

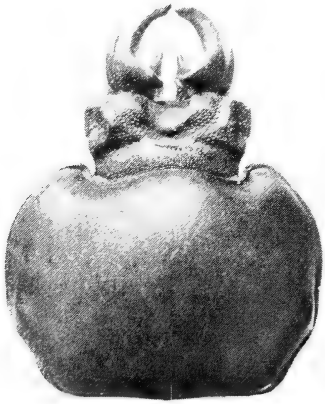

Fig. 18. *Colophon cassoni* Barnard, male; paralectotype, fragment; length 14 mm. An estimated total length of the specimen could be about 23 mm.

Female. Distinguished by the anterior margination (interrupted in middle) of pronotum, emargination of posterior converging portions of pronotal margins, smooth and rather broad fine elevation of sutural margins. Pronotal punctation more distinct than in male.

Length

Male 18 mm (range estimated from size of heads 16–24 mm); female 16–17 mm.

Distribution

Swartberg, the northern range of Cape mountains.

Variability

The mandibular armature of males shows two distinct forms, without any intermediates. Barnard (1932*b*: 172) referred to intermediates but these differed only in thickness and shape of the apex of the dorsal processes (as is often seen in the genus) and not in the position and direction of the processes. No similar dimorphism has been seen in any other species of the genus. However, as no correlated characters could be found and only one complete male is known of each form, the actual value of this unusual difference cannot be evaluated. All specimens and fragments referred to this species were collected on two occasions (1930 and 1932) and both samples include both mandibular forms. It can thus be assumed that the two forms occur sympatrically. For the time being the two varieties will be considered as morphs of the same species (see below).

Colophon cassoni Barnard, 1932 (forma typica)

Fig. 17B

Description

Dorsal process of mandibles in median position, pointing diagonally forward. With mandibles in closed position, the small space bounded laterally by the main arms and apically by the dorsal processes is of an inverted heart-shape (Fig. 17B).

Material examined

Lectotype. ♂: Meiringspoort Berg, Zwartberg Range, K. H. Barnard, Febr. 1932; in British Museum (Natural History), London.

Paralectotypes. 1 ♀ (identity doubtful); Meiringspoort Berg, Zwartberg range, K. H. Barnard, Febr. 1932; in British Museum, London. 21 ♂ heads, 26 ♂ anterior legs; data as for lectotype; in South African Museum, Cape Town. 2 ♀ (identity doubtful), 3 ♂ heads, Meiringspoort Berg, Zwartberg Range, F. Berrisford, 1930; in South African Museum.

Colophon cassoni morpha *recurva* morph. nov.

Fig. 17C

Description

Dorsal process of mandibles in basal position pointing diagonally backward. Space between the apex of mandibles and dorsal processes ovate and much larger (Fig. 17C).

Material examined

Holotype. ♂: Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard; in British Museum (natural History), London.

Paratypes. 2 ♂ heads (data as for holotype); 1 ♂ front body, 2 ♂ heads (data as for holotype, but coll. F. Berrisford, 1930); in South African Museum, Cape Town. ♂ head (data as for holotype) in Transvaal Museum, Pretoria.

Remarks

Barnard's (1932*b*) description gave the data for specimens collected by F. Berrisford as 'Blaauw Punt near Meiring's Poort, Zwartberg Range, 6 500 ft. (F. Berrisford and P. Casson Scott-Hayward), March 1930'. As is often the case, the data published by Barnard are not consistent with those of the labels; there is no doubt, however, that they refer to the same specimens.

The identity of Meiringspoort Berg could not be established among the peaks west of the poort.

Colophon berrisfordi Barnard, 1932

Fig. 19

Colophon berrisfordi Barnard, 1932*b*: 173, fig. 5; 1932*a*: 19, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 311, 320.

Remarks

The holotype (the only specimen known) is a fragment, generally in a fresh condition, consisting of the front part of the body of a male (head with both antennae and pronotum with both anterior legs, one complete with tarsi). The aedeagus and anal sternite, which bear the most important species-group characters, are wanting. Sharp-edged clypeus, elevated above labrum, refers the species to the apomorphic group, as this character is correlated with the asymmetrical type of aedeagus in all known species. Structure of anterior tibia is practically identical with that of *C. cassoni*, and rather similar to that of *C. cameroni*.

Description

Male. Head very similar to that of *C. whitei*, with the sharp and narrow transverse dorsal impression level with eyes; genal canthus in front of eye less dilated. Moderately arcuate mandibles with well-developed premedian dorsal process, and with small tubercle between this process and apex (more distinct on left mandible). Ventro-basal process of mandible forms a forward- and upward-slanting ridge with rounded corners (Fig. 19).

Pronotum sharply margined all round, marginal fossa only flattened at a point in middle of anterior margin. Shape similar to *C. whitei*, surface densely shagreened, punctation extremely fine in middle of disc, gradually more distinct towards lateral margins.

Anterior tibia slightly arcuate, semi-parallel to apical dilation, not contracted pre-apically. Apical dilation armed with three teeth. Ventral crest strongly elevated from base to in front of middle, here almost forming a right angle, arcuately flattened to the base of the small rectangular apico-ventral process. Ventral crest and apico-ventral process are comparable to those of *C. neli* and *C. cassoni*. Inner apical corner of tibia forms a sharp, slightly acute-angled process, not rounded as in *C. neli*.

Female. Unknown.

Length

From apex of mandibles to base of pronotum 13 mm, breadth of pronotum 10,0 mm, suggesting a smaller specimen than the smallest known specimen of *C. whitei*; total length probably in the range of 20–22 mm.

Distribution

Central part of Swartberg Range, west side of Meirings Poort.

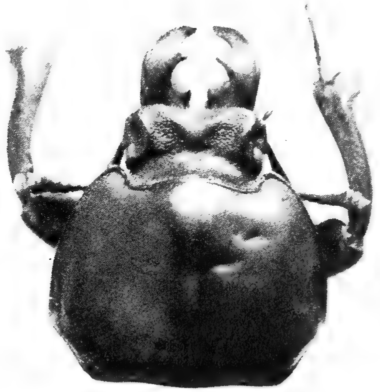

Fig. 19. *Colophon berrisfordi* Barnard, male; holotype, fragment; length 13 mm. An estimated total length of the specimen could be about 21 mm.

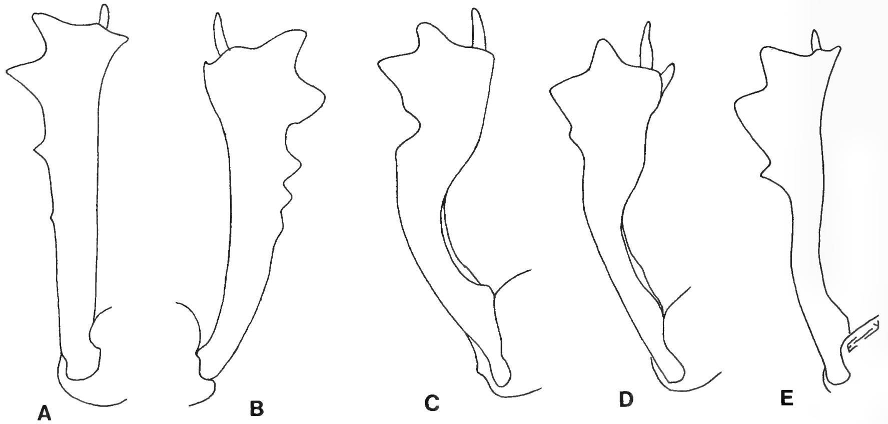

Fig. 20. Male anterior tibiae in *Colophon* species. A. *C. primosi* Barnard. B. *C. westwoodi* Gray. C. *C. stokoei* Barnard forma typica from Bushmans' Castle. D. *C. stokoei* Barnard, holotype of Barnard's var. C. E. *C. barnardi* sp. nov.

Material examined

Holotype. ♂ (anterior part of specimen): Meirings Poort Berg, Zwartberg range, F. Berrisford, 1930; in British Museum (Natural History), London. (Name label in Barnard's hand.)

Colophon neli Barnard, 1932

Figs 21A, 27A

Colophon neli Barnard, 1932*b*: 170, fig. 2; 1932*a*: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

Diagnosis

Colophon neli is the smallest known species of the genus. Black. Mandible lacking dorsal process. Anterior tibia broad, straight and parallel. Clypeus raised above labrum. Anal sternite and aedeagus of asymmetrical type.

Description

Male. Head broadly oblong. Ocular canthus and a pair of anterior elevations at the base of the mandibles rounded. Vertex deflected in a V-shape to clypeus, which is narrow with rounded or emarginate apex and is raised high above narrow triangular labrum. Surface coarsely punctate, particularly in depressions. Mandible simple sickle-shaped, with only prominently pointed ventral process at the base (Fig. 21A). Gular sulcus very flat and shallow.

Pronotum broadest at about basal third of length; lateral margins evenly arcuate, converging anteriorly, finely emarginate towards obtuse-angled posterior angle. Margination only interrupted in middle of anterior margin. A fine punctation of surface visible only near the posterior angle. Base of prosternal apophysis not calloused as in most species.

Elytra conspicuously small in relation to large pronotum, almost circular. Broad sutural margins smooth and raised. No subhumeral callus or other conspicuous longitudinal sculptural elements. The very fine shagreen produces an iridescent sheen on the elytra of fresh specimens (lectotype).

Anal sternite asymmetrical, but does not form an off-centre callus.

Anterior tibia broad from the base, straight and parallel, it forms a short and broad bifid apico-lateral process (Fig. 27A). Ventral crest sharp and well raised basally, then terminates abruptly between half and two-thirds of tibial length, forming a rectangle; after a short stretch of interruption forms a small triangular process near apex.

Aedeagus asymmetrical. Penis strongly sclerotized, apical portion asymmetrically dilated. Right paramere forms a broad triangular process at its inner margin, well removed from apex of paramere; margin between apex and inner process slightly emarginate. Left paramere contracts towards apex, apex rounded.

Female. It resembles *C. cassoni* in raised suture line, which is less distinct than in male. Anterior tibia, however, has an apico-ventral process, which is absent in *C. cassoni*.

Length

Male 15–19 mm, female 15–17 mm.

Distribution

Swartberg Mountains, the northern range of the Cape mountains.

Material examined

7 ♂, 3 ♀, 1 ♂ front body, 14 ♂ heads, 3 ♀ heads, 12 ♂ anterior legs.

Lectotype. ♂: Zwartberg Pass, K. H. Barnard, Nov. 1929; in South African Museum, Cape Town.

Paralectotypes. 3 ♂, 2 ♀, 8 ♂ heads, 9 ♂ anterior legs: Zwartberg Pass, K. H. Barnard, Nov. 1929; in South African Museum, Cape Town. 3 ♂, 1 ♀: Zwartberg Pass, K. H. Barnard, Nov. 1929; in British Museum (Natural History), London.

Additional material. 1 ♂ front body, 6 ♂ and 3 ♀ heads, 3 ♂ anterior legs: Swartberg Pass, Dec. 1968, R. H. Jones and J. H. Potgieter; Transvaal Museum, Pretoria.

Remarks

The altitude data on the labels of some of the type specimens range between 5 500 and 6 000 ft. [1 677 m and 1 829 m], and not 5 500 and 6 500 ft. [1 677 m and 1 982 m] as stated in Barnard's (1932*b*) description.

Colophon primosi Barnard, 1929

Figs 14A, 20A, 21B, 22A–C

Colophon primosi Barnard, 1929: 175, fig. 9; 1932*a*: 19, figs. Didier & Séguy, 1953: 76. Brinck, 1956: 314, 320.

Description

Male. Head broadly oblong, rather similar to that of *C. izardi*, but ocular corner not sharply raised. Vertex only depressed, frons level transversely and only slightly deflected to produced clypeus, which is very highly elevated above the level of flat triangular labrum. Mandibles straight, prognathous, longer and narrower in lectotype from Seven Weeks Poort Berg than in the Blue Berg specimens. Apex uniformly emarginate at inner margin, with sharp inward-turning points (Fig. 21B, 22A, C). Ventral process clearly marked in Blue Berg specimens, more rounded in lectotype. Surface of head distinctly punctate, punctatation of mandibles hardly visible. Labrum slightly transverse, oblong; gular sulcus sharp but rather shallow.

Pronotum with some variations in details; similar but somewhat broader than in *C. izardi*. Punctation, if discernible at all, visible only at lateral and anterior margins.

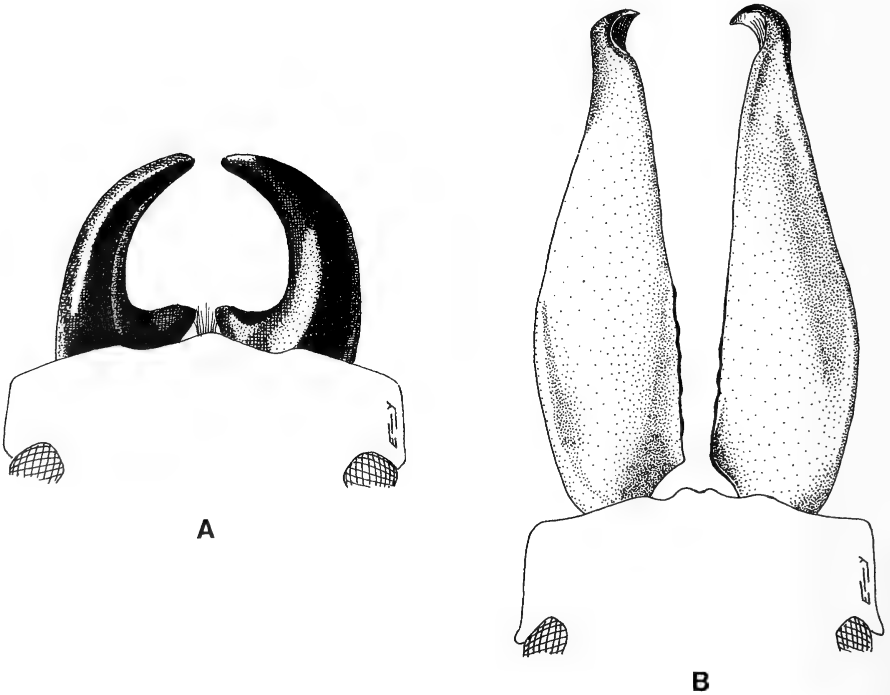

Fig. 21. Male mandibular structure in *Colophon* species. A. *C. neli* Barnard. B. *C. primosi* Barnard.

Elytra more evenly tapered towards apex, less semi-parallel anteriorly than in *C. izardi*; subhumeral carina rounded but very distinct; submarginal lateral depression coarsely corrugated transversely.

Prosternal apophysis hump-like between coxae. Anal sternite asymmetrical, off-centre apex produced in a transversely oblong and flat process.

Anterior tibia very simple, straight, with four lateral teeth and an inner apical tooth (Fig. 20A). Ventral crest serrate and continuous, without apical process. Posterior tibia consistently with a sharp lateral tooth in middle.

Aedeagus of asymmetrical type. Penis strongly sclerotized and asymmetrical. Right paramere armed at inner margin; apex (distal) truncate, acute-angled; left paramere narrower than in *C. izardi*, apical portion parallel with roundly truncate apex.

Thorax, body, elytra, and head (except vertex), black; vertex, mandibles and legs (except tarsi), reddish brown.

Female. Head conspicuously small (Fig. 22B). Black, but coxae, humeri, tibiae and parts of head reddish brown. More convex than in male, lateral corrugation of elytra less distinct. Prosternal process similar; anal sternite sharply punctate, punctures with fine and short hairs; anal sternite in male only finely punctured and bare.

Length

Male 28–35 mm (lectotype 35 mm); length of mandibles 8–10,5 mm (lectotype 10,5 mm); female 20–22 mm.

Distribution

Central section of Swartberg range, northern range of Cape mountains.

Material examined

5 ♂ (3 fresh, 2 damaged) (2 dissected), 7 ♀ (5 fresh, one damaged, one fragmented). Lectotype ♂, 2 ♀ paralectotypes, and additional 3 ♂ and 2 ♀ specimens in South African Museum, Cape Town; 1 ♂ and 2 ♀ paralectotypes in British Museum (Natural History), London. 1 ♀ in Transvaal Museum, Pretoria.

Lectotype. ♂: Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in South African Museum, Cape Town.

Paralectotypes. 1 ♂, 2 ♀: Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in British Museum, London. 2 ♀ (one badly fragmented): Seven Weeks Poort Berg, Ladysmith District, 7 000 ft. [2 134 m], K. H. Barnard, 1928; in South African Museum, Cape Town.

Further material. 1 fresh ♂, 2 damaged ♂, 2 fresh ♀: Blue Berg, Zwartberg range, 1930, F. Berrisford; in South African Museum, Cape Town. 1 ♀: Seven Weeks Poort Berg, 6 300 ft. [1 921 m], 2 Feb. 1986, coll J. Vlok; in Transvaal Museum, Pretoria.

Fig. 22. *Colophon primosi* Barnard. A. Big male; paralectotype; length 35 mm. B. Female; length 22 mm. C. Small male; length 28 mm. The slight allometric variation shown here is the greatest observed in the genus.

Remarks

Colophon primosi is the most peculiar species of the genus, with mandibles not readily derived from any other forms. Other characters, however, secure its place in the genus and also in the apomorphic lineage (asymmetrical aedeagus, raised clypeus).

All specimens of the type series were found dead, some of them very distinctly bleached, leaving Barnard (1929: 176) in doubt in respect of their natural coloration. Three fresh specimens (1 ♂, 2 ♀) of the Blue Berg series were probably found live and confirm the unusual coloration described by him. Male mandibles, anterior part of head, gula and all femora and tibiae light yellow-brown; rest of body, antennae and tarsi black. In females the coloration is similar, except mandibles are black in small specimens.

There is no noteworthy difference between specimens of the Seven Weeks Poort Mountain and Blue Berg samples, which raises some interesting historic biogeographic problems (see p. 362).

Colophon westwoodi Gray, 1832

Figs 8, 20B, 23, 24A

Colophon westwoodi Gray, 1832: 533, pl. 46 (fig. 5). Castelnau, 1840: 173. Westwood, 1855: 194. Parry, 1864: 70. Péringuey, 1901: 3. Van Roon, 1910: 8. Boileau, 1913: 218. Handlirsch, 1924: 695. Barnard, 1929: 166, fig. 1; 1932*a*: 19, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 309, 320.

Diagnosis

Black, medium to large size. Most of anterior margin of pronotum marginate. Mandibles short and strongly curved inward, main arm broadly bifid with rounded protuberance dorsally; ventral and dorsal process in basal position, small and roundly pointed. Anal sternite asymmetrical, aedeagus of asymmetrical type. Anterior tibia finely arcuate, dilated towards apex, with four or five lateral teeth not quite regularly increasing in size distally.

Description

Male. Head broadly oblong, genal margin in front of eyes semi-parallel, occasionally finely emarginate, anterior angle sharp. Anterior margin moderately sinuate between mandibles, a canthus above clypeus sometimes more or less protuberant in middle. Vertex deflected to pre-clypeal canthus, overhanging the clypeus; latter is flush with the base of flat, triangular labrum. A somewhat similar canthus is present only in *C. primosi*. Ocular canthi flat. Vertex with a pair of anterior protuberances and an even more distinct median protuberance. Punctation strong, dense and rather uniform. Mandible short and stout, main arm broad and short, evenly curved in about 90° towards equally broad and bifid apex. There is a large and rounded protuberance of different elevations in the middle of the dorsal surface, close to inner margin. As a small dorsal process is present near the base, it is thought that the dorsal protuberance is not analogous with the

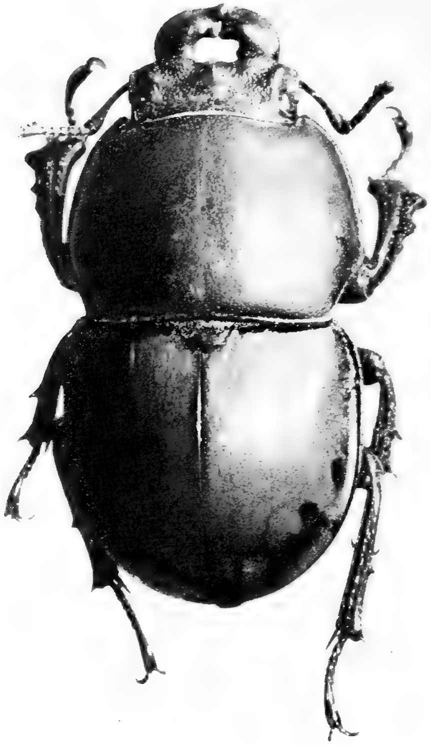

Fig. 23. *Colophon westwoodi* Gray, male; length 20 mm.

dorsal processes of other species (Fig. 24A). Mentum almost flat, about twice as broad as long, slightly converging anteriorly, apex rounded. Transverse gular sulcus flat.

Pronotum even in large males only moderately broader than elytra, rather convex. Broadest in front of basal third, lateral margins evenly arcuate and converging anteriorly, emarginate posteriorly to sharp and rectangular posterior angle. All edges margined, margination only interrupted in middle of anterior margin. Punctation very fine, but sharp, uniformly dense; hardly more distinct laterally.

Elytra about as long as combined breadth, semi-parallel in anterior half of length; do not appear as disproportionately small in relation to the pronotum, as in most other species. Surface smooth and matt-shagreened with eight irregular rows of fine punctures. Lateral submarginal depression more densely, but not more coarsely, punctate.

Anal sternite very distinctly asymmetrical.

Anterior tibia moderately arcuate at inner margin, evenly dilated from base to apex. Lateral margin with four or five progressively larger triangular processes; last two (largest) processes do not appear as a bifid unit (Fig. 20B). Ventral crest continuous from base to apex, not forming an apico-ventral process. Lateral median process of posterior tibia as large and sharp as in intermediate tibia (in other species usually reduced or missing).

Aedeagus of asymmetrical type. Penis strongly sclerotized, apical portion asymmetrically dilated. Right paramere produced to a large inner process; its anterior margin to apex is straight, posterior margin evenly and deeply emarginate towards base. Left paramere narrow with rounded apex.

Female. Distinguished by anteriorly marginate pronotum with sharply pointed rectangular posterior angle.

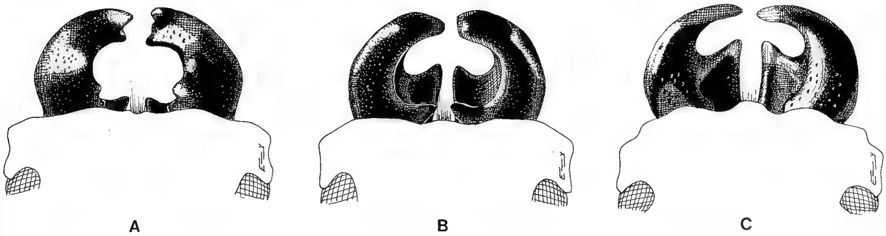

Fig. 24. Male mandibular structure in *Colophon* species. A. *C. westwoodi* Gray. B. *C. thunbergi* Westwood. C. *C. barnardi* sp. nov.

Length

Male 21–25 mm, female 19–24 mm.

Distribution

Table Mountain, Cape Town.

Material examined

14 ♂ and 19 ♀. Holotype and three additional specimens in British Museum (Natural History), London; 24 specimens in South African Museum, Cape Town, and 5 specimens in Transvaal Museum, Pretoria.

Holotype. ♂: no data, ex Vigin's collection, British Museum, London.

Additional material. The other material listed above has been recorded from Devil's Peak, Constantiaberg, Kalk Bay Mountain, and Echo Valley. Live specimens were collected in December, January and February.

Remarks

This was the first species of the genus to be described, and ever since it has been the most frequently collected.

Colophon barnardi sp. nov.

Figs 20E, 24C, 25

Diagnosis

Small black species. Mandibles with ventral process only. Anterior tibia with three apico-lateral teeth. Clypeus raised above labrum. Aedeagus of asymmetrical type.

Description

Male. Medium size, completely black. Head broadly oblong with sharp genal canthus and with rounded and arcuate elevations at the inner margins of eyes. Clypeus slightly produced and sharply elevated over labrum. Surface densely and sharply punctate, integument matt. Mandibles short, sickle-shaped, arcuate through 90 degrees. Dorsal process entirely absent, ventral processes large, their inner margins parallel; apex of processes forward-pointing, acute-angled. Apex of main arms simple (Fig. 24C). Mentum flat, hardly convex transversely, apical margin broadly arcuate. Pregular sulcus deep.

Pronotum evenly convex transversely, more deflected towards posterior than towards anterior margin. All around marginate; submarginal lateral depression very narrow anteriorly, slightly dilated at lateral angle of pronotum. Pronotum broadest at posterior third of length, gradually more arcuately contracted towards anterior lateral angle; pronotum considerably contracted posteriorly, but lateral margin straight to obtuse-angled posterior lateral angle. Disc smooth and matt with scattered punctures at lateral and anterior margins. Base of prosternal apophysis sharply dentate.

Elytra distinctly longer than combined breadth, not particularly small compared to pronotum, narrower than the latter. Humeral angle rectangular, narrowly rounded. Disc convex, submarginal depression broad anteriorly; gradually narrower behind; suture not elevated, marginate or smoother than disc. Surface entirely smooth, without any costal elements, matt with indistinct traces of scattered punctation.

Anterior tibia straight, narrowest at basal quarter of length; dilated in apical half, forming three lateral teeth; inner apical angle sharply produced (Fig. 20E). Ventral crest moderately elevated in basal half, gradually diminishing anteriorly; apico-ventral process absent.

Anal sternite asymmetrical at apical margin, forming a narrow process to the right of median line (ventral view).

Aedeagus of asymmetrical type.

Female. Pronotum slightly narrower, but of similar shape to that of male; disc of elytra similarly smooth (paratype) or with short, subhumeral costal element (allotype).

Length

Male 20 mm, female 20,2–21,0 mm.

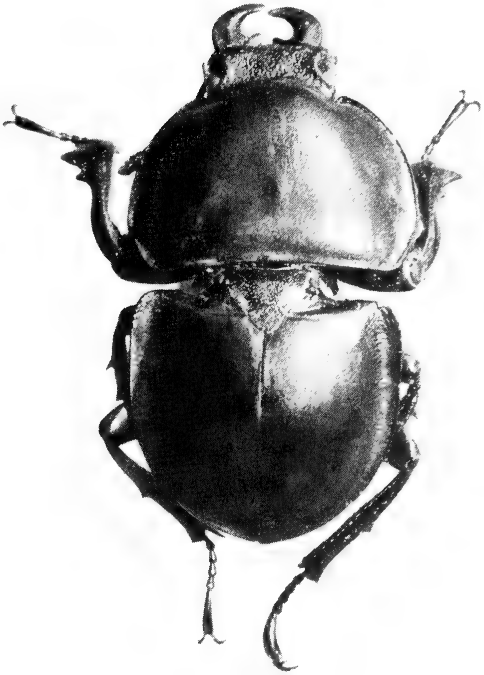

Fig. 25. *Colophon barnardi* sp. nov., male; holotype; length 20 mm.

Material examined

1 ♂, 2 ♀, and 1 ♂ thorax with right leg attached. Holotype ♂ and allotype ♀ in South African Museum, Cape Town; 2 paratypes (1 ♂ thorax, 1 ♀ lacking abdomen) in Transvaal Museum, Pretoria.

Holotype. ♂ (dead): Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

Allotype. ♀ (dead): Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

Paratypes. 1 ♂ thorax, 1 ♀: Leeuw River Peak, Swellendam, April 1941, K. H. Barnard.

All specimens were labelled by Barnard as *C. thunbergi*.

Etymology

This species is named in honour of Dr K. H. Barnard, collector of most of the known specimens of *Colophon* and first reviser of this genus.

Colophon thunbergi Westwood, 1855

Figs 24B, 26

Colophon thunbergi Westwood, 1855: 198. Parry, 1864: 70; 1870: 71; 1872: 83. Boileau, 1913: 217. Barnard, 1929: 167, fig. 2; 1932*b*: 170, fig. 1. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

Diagnosis

Rather large, black species. Mandible with dorsal and ventral processes. Clypeus raised above labrum. Anterior tibia slender and bent at base, dilated with bifid or trifid apico-lateral armature.

Description

The description below is based on the holotype and points out, where necessary, the differences shown by the fragments.

Male. Head broad and short, angularly oblong, anterior angle of gena only slightly obtuse-angled, narrow, anterior margin not indented or emarginate near lateral angle. Anterior margin evenly sinuate in middle. Disc rather sharply raised at inner margin of eye, moderately depressed anteriorly in middle, with a pair of round and indistinct elevations at either side of depression. Punctation consists of rather uniform, moderately large, well-spaced punctures in the middle; integument densely shagreened. Mandibles short and stout, bent more or less at a right angle; dorsal process near base conical; in the fragments less forward-pointing (as figured). Ventral process very broad, with inner corner roundly produced anteriorly, reaching about two-thirds of mandibular length (Fig. 24B). Labrum flat and pointedly triangular, clypeus sharply elevated above its base. Mentum large and flat, oblong, anterior margin truncate. Pregular sulcus evenly concave, not sharply incised.

Fig. 26. *Colophon thunbergi* Westwood, male; length 15 mm. An estimated total length of the specimen could be 25 mm.

Pronotum broadest at about basal third; margins very slightly emarginate or straight, contracting to obtuse-angled basal corner. Margination also complete anteriorly. Pronotum in the holotype evenly rounded disciform, lateral margins evenly arcuate, converging to perfectly rectangular anterior angle. Surface densely shagreened, also very finely punctured at sides.

Elytra semi-parallel at anterior portion, very slightly contracted towards rectangular humeral angle. Surface of disc smooth, densely and finely shagreened and indistinctly punctate. A much reduced subhumeral costa is slightly elevated at basal fifth of length (some further); hardly discernible longitudinal lines are shown only by smoother integument. Dimensions in holotype 11,5 x 11,8 mm.

Anal sternite distinctly asymmetrical, off-centre process flatly rounded.

Anterior tibia bent inward in dorsal view. In holotype almost the whole basal third narrow, apical dilation disciform. Apical armature bifid (Fig. 26). In all fragments the narrow basal portion is shorter, apical dilation more gradual, and the apical armature consists of three triangular processes (in one tibial fragment the proximal process is clearly broken off). Ventral crest continuous between base and apex, evenly and moderately elevated, not raised at base as in *C. barnardi*. In the latter species the tibia is more slender and much straighter.

Aedeagus of asymmetrical type.

Female. The single female in the British Museum, from Zuurbrak Peak, is herein tentatively retained in *C. thunbergi*. It is somewhat different from the two females from Leeuw River Peak that are herein referred to *C. barnardi* (see p. 411). The Zuurbrak Peak female differs from the Leeuw River Peak females in the following characters: ocular canthus sharper, punctation of head coarser and sparser. Elytron in the Zuurbrak specimen is marked by two punctured costae of common subhumeral origin; they reach to about the middle of the elytral length.

Length

Male (holotype) 26 mm.

Material examined

1 ♂ (holotype); 1 ♀ (identity doubtful), in British Museum (Natural History), London. 5 ♂ heads and 5 ♂ anterior legs, South African Museum, Cape Town.

Holotype. ♂: no locality, with labels 'Type Col. 247; *C. thunbergi* and *C. westwoodi* Gray i[n]. litt. in the Hope Museum, Oxford'.

Additional material. 1 ♀ (identity uncertain): Zuurbrak Peak, in British Museum, London. The 5 ♂ heads and 5 ♂ anterior legs are from Zuurbrak Peak, Langeberg Range, near Swellendam; coll. Barnard & Thorne, February 1932; South African Museum, Cape Town. These latter fragments indicate the possible locality of the holotype.

Remarks

The locality of the holotype in the Hope Museum, Oxford, is not known, but morphologically it agrees sufficiently with the fragments collected by Barnard at

Zuurbraak Peak, where *Colophon thunbergi* is sympatric with *C. izardi*. The slight differences found between the holotype and the fragments do not appear to be greater than the range observed among the fragments—with the possible exception of bifid tibial armature in holotype.

Colophon whitei Barnard, 1932

Figs 27D–E, 28, 29A

Colophon whitei Barnard, 1932*b*: 171, fig.3; 1932*a*: 20, figs; 1936: 8. Didier & Séguy, 1953: 17. Brinck, 1956: 311, 320.

Diagnosis

Large black species. Mandible with dorsal and ventral processes. Anterior tibia bent inward, dilated lateral margin deflected and deeply excised before reaching bifid apical armature. Anal sternite and aedeagus of asymmetrical type.

Description

Male. Head broadly oblong with sharp genal canthus. Surface longitudinally elevated at inner margins of eyes, elevations rounded and slightly inward slanting from frons towards base; a similar, broadly funnelling elevation occupies the whole frons. Frons steeply deflected to clypeus. Clypeus broad, flatly emarginate at anterior margin, showing some variation in breadth and depth of emargination; sharp anterior edge of clypeus raised above the level of labrum. Labrum flat, elongately triangular, sometimes briefly bifid at apex. Integument of head more densely and coarsely punctate in depressions than on elevations. Mandibles with dorsal and ventral processes (Fig. 29A); main arm prognathous, usually only

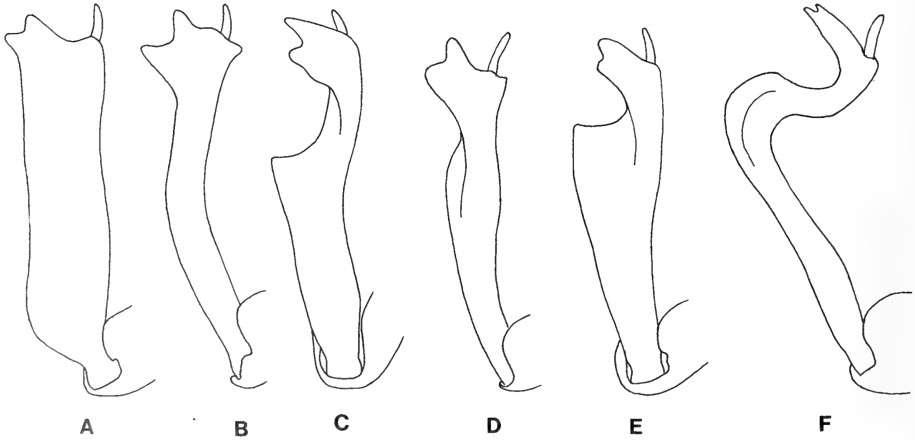

Fig. 27. Male anterior tibiae in *Colophon* species. A. *C. neli* Barnard. B. *C. montisatris* sp. nov. C. *C. montisatris* sp. nov. in lateral view. D. *C. whitei* Barnard. E. *C. whitei* Barnard, lateral view. F. *C. izardi* Barnard.

apical third curved inward through 90 degrees; apices, particularly that of the left mandible, narrow and truncate. In the inner margin of each mandible two processes appear. The ventral process seems to be homologous with that of *C. cassoni*, *C. eastmani* and *C. cameroni*, but the more dorsal one is probably not. This tooth lies in the midline of the mandible's thickness in *C. whitei*, whereas in the other three species it lies flush with the dorsal surface. This mandibular process in semi-dorsal position appears as a unique character among the known species of the genus. The most closely related species, *C. montisatris* sp. nov., entirely lacks this semi-dorsal tooth, although its ventral one is homologous with that of *C. whitei*. The rudimentary semi-dorsal process of *C. barnardi* might be homologous with that of *C. whitei*. Mentum slightly concave, lateral margins parallel, anterior lateral angles narrow; truncate anterior margin slightly produced in middle. Pregular sulcus deep.

Pronotum evenly convex transversely, more deflected to posterior than to anterior margin; broadest at the basal third of length where lateral margins are parallel; margins evenly curved towards produced anterior angle; distinctly emarginate behind; posterior angle obtuse. All margins evenly and sharply bordered, margination only interrupted in a spot in the middle of the anterior margin. Integument smooth but not shiny, with a few fine punctures laterally; disc without, or occasionally with, faint scattered punctures. Base of prosternal apophysis with a small callus. Scutellum triangular with arcuate margins showing some variation in breadth and shape.

Elytra narrower than the widest part of the pronotum but broader than the pronotum at its posterior angles. Humerus narrowly rounded, almost rectangular. Disc convex, submarginal depression broad, integument here more or less distinctly corrugated. Surface otherwise smooth, matt with fine and scattered punctation. Suture line not conspicuously raised, although sometimes smoother and shinier than rest of surface.

Anterior tibia gradually dilated from base, dilation turns gradually into a latero-ventral position; dilation is abruptly reduced at apical quarter where it forms a sharp rectangular corner; apico-lateral corner of tibia is formed by a bifid process (Fig. 27D, E). Median (primary) ventral crest distinct. Inner margin of anterior tibia almost straight. Intermediate tibia with a single, sharply pointed median process; posterior tibia unarmed.

Apical margin of anal sternite strongly asymmetrical in middle.

Aedeagus asymmetrical; right paramere with large inner process; left paramere simple, comparatively broad.

Female. Pronotum narrower than in males, disc similarly smooth, only punctate near lateral margins; a faint longitudinal median impression appears in some specimens. Humeral angle rounded, lateral margins finely arcuate. Surface smooth and matt with scattered, very fine punctures. No distinct costal elements. No reliable differences could be found between females of *C. whitei* and of *C. montisatris* sp. nov.

Fig. 28. *Colophon whitei* Barnard, male; lectotype; length 25,5 mm.

Length

Male 26–31 mm, female 19–22 mm.

Distribution

Central section of the Swartberg (northern range of the Cape mountains), west of Meiringspoort.

Material examined

15 ♂ (3 damaged, 3 bleached, 1 anterior part of body), 5 ♀, intact specimens; 5 ♂ and 2 ♀ heads.

Lectotype. ♂, Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard and C. W. Thorne; South African Museum, Cape Town.

Paralectotypes. 8 ♂ and 5 ♀, Meiringspoort Berg, Zwartberg Range, Febr. 1932, K. H. Barnard and C. W. Thorne. (Of these 7 ♂ and 1 ♀ in South African Museum, Cape Town, and 1 ♂ and 2 ♀ in British Museum, London.) 6 ♂ and 5 ♀ heads: Meirings Poort Berg, Zwartberg Range, [6 500 ft. (= 1 982 m), March] 1931, A. B. Berrisford; 1 ♀ (data as for holotype) does not belong to this species; 1 ♂, 2 ♀: Blesberg, Zwartberg Range, 1930, F. Berrisford (locality probably erroneous; see below), in South African Museum.

Remarks

This and the following species (*C. montisatris* sp. nov., p. 418) are closely related and their separation might have occurred only after the present populations retreated to the high altitudes of the Swartberg Range, on either side of Meirings Poort. It is evident that the common ancestor had a distribution area on the flat at the level of the foot of the mountain, since Meirings Poort cuts through the latter and serves to drain water from the north to the south.

The locality date for the specimens recorded from Blesberg must be regarded as doubtful. These three specimens formed part of Barnard's (1932*b*) type series. However, Blesberg is on the east side of Meiringspoort. The identity of the females could not be ascertained, but the male is certainly conspecific with the rest of the type series of *C. whitei* from the west side of Meiringspoort. Blesberg is the type locality of *C. montisatris* sp. nov., where 10 ♂ specimens (2 anterior parts of body) of that species were collected in 1979 and 1981 without finding any fragments of *C. whitei*. It seems to be almost certain that at least the male specimen of *C. whitei* recorded from Blesberg is incorrectly labelled, and was actually collected on the west side of Meiringspoort. Similar problems were encountered with material of *C. stokoei* (see p. 393), where the possibility of erroneous locality labelling made the final evaluation of *C. stokoei* morphs impossible. It has to be taken into consideration that a considerable portion of *Colophon* specimens were collected by non-entomologist mountaineers.

A female specimen labelled as *C. whitei*, and with the same locality data as the lectotype, does not belong to this species.

Specimens mentioned in the Barnard's (1932*b*) description as collected at Blou Punt (Blaauw Punt) and Spitzkop (both on the west side of Meiringspoort), could not be found in the South African Museum, nor in the British Museum, although there is no record that Barnard disposed of any specimens to any other museums.

Variability

In evaluating the characters of 14 complete males, one pronotum and head, and seven heads, the variability in main characters, such as mandible, mentum and anterior tibia, was found to be minimial. No allometric variation was found between the biggest and smallest specimens, except the relatively greater breadth of pronotum in the larger specimens. In the type series there is a specimen with rather distinct longitudinal striation of elytra, which gives the impression of an ontogenetic anomaly. A certain ontogenetic anomaly is shown in another specimen in which the right mandible is about half normal size, and having reduced but distinct male characters—and not partially hermaphrodite as is found occasionally in Lucanidae. Would the two malformations in 14 specimens indicate the genetic effect of in-breeding in a tiny extant population?

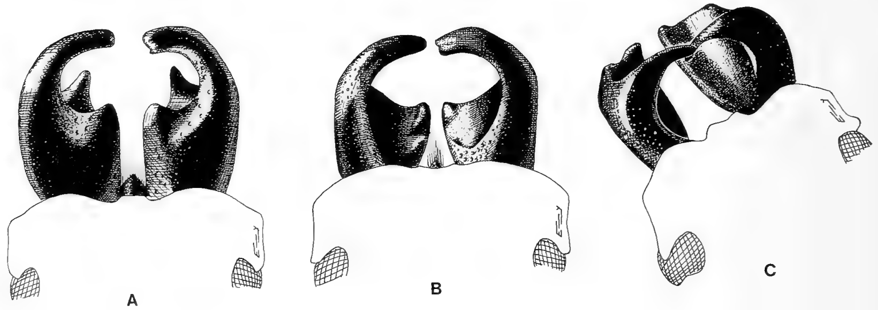

Fig. 29. Male mandibular structures in *Colophon* species. A. *C. whitei* Barnard. B. *C. montisatris* sp. nov. C. *C. izardi* Barnard, semi-lateral view.

Colophon montisatris sp. nov.

Figs 1, 4, 27B–C, 29B, 30A–B

Remarks

Colophon montisatris is a sister species of *C. whitei*. In many respects the new species seems to be the more ancestral and, in its characters, closer to the hypothetical common ancestor. Characters not described below were found to be identical with those described for *C. whitei*.

Description

Male. Declivity of frons towards clypeus not quite vertical; clypeus broader, distinctly emarginate. Labrum similar. Mandibles with ventral process only (the most diagnostic specific character). Main arms of mandibles slightly shorter than in *C. whitei*, not tapering towards broader apex. Ventral process sharply pointed, less produced, and altogether closer to base than in *C. whitei* (Fig. 29B).

Mentum, pronotum and elytra very similar to those of *C. whitei*.

Anterior tibia angularly nicked inward in middle, in dorsal view semi-parallel, not dilated towards apex. Lateral crest more deflected ventrally, narrower, anterior emargination towards bifid apico-lateral process deeper (Fig. 27B, C).

Aedeagus similar to that of *C. whitei*, but left unarmed paramere narrower.

Female. No characters could be found that enable one to distinguish between females of this species and those of *C. whitei*.

Length

Male 23–27,8 mm (breadth 11–14 mm), female 23 mm.

Material examined

10 ♂, 1 ♀ and 2 ♂ anterior bodies. Holotype ♂, allotype ♀ and 6 ♂ paratypes in Transvaal Museum, Pretoria; 1 ♂ paratype each is deposited in the South African Museum, Cape Town, British Museum (Natural History), London, and Natural History Museum, Budapest.

Holotype. ♂, Swartberg Range, Blesberg, 2.III.1979, leg. Endrödy-Younga, E-Y:1556.

Allotype. ♀ (dead), Swartberg Range, Blesberg, 6.III.1981, E-Y:1755.

Paratypes. 4 ♂, Swartberg Range, Blesberg, 2.III.1979, leg. Endrödy-Younga, E-Y:1556. 1 ♂ (dead): Swartberg Range, Blesberg, 6.III.1981,

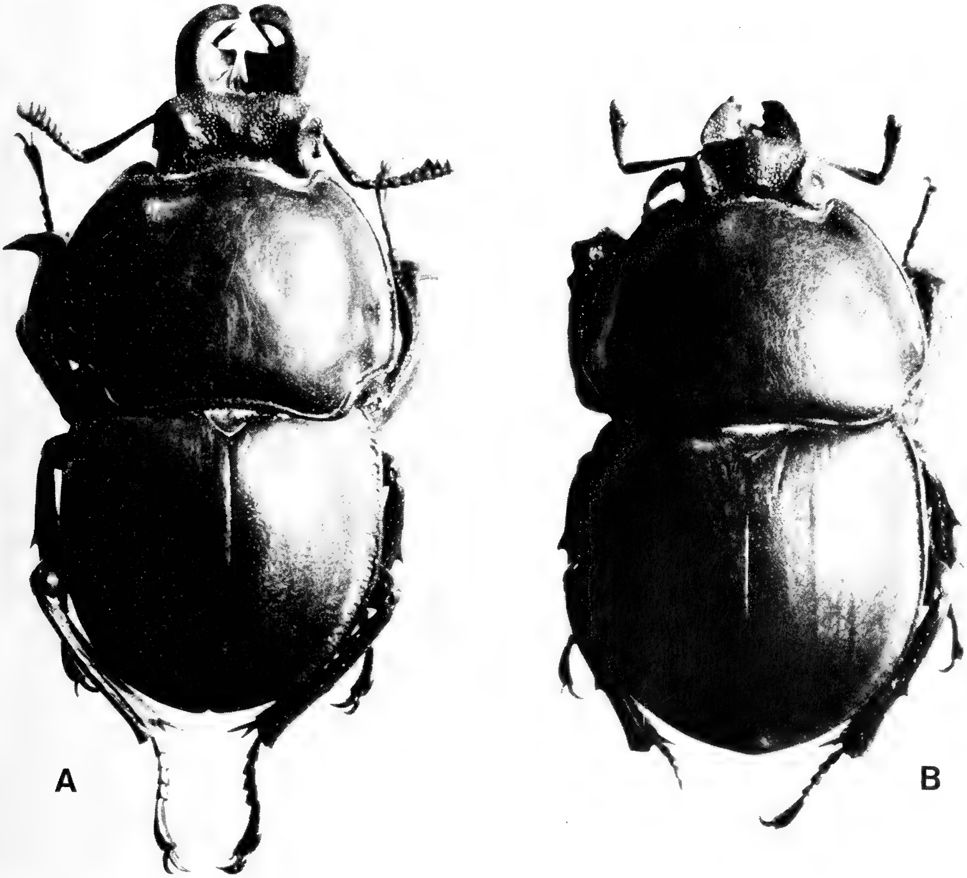

Fig. 30. *Colophon montisatris* sp. nov. A. Holotype, male; length 25 mm. B. Allotype, female; length 23 mm.

E-Y:1755. 1 ♂ (dead) and 1 ♂ anterior body: Swartberg Range, Blesberg, 17.XII.1978, E-Y:1534. 1 ♂ live and 1 ♂ dead, Swartberg Range, Blesberg, 5.III.1981, E-Y:1754. 1 ♂ live, 1 ♂ anterior body, Swartberg Range, Blesberg, 7.III.1981, E-Y:1756, (3 further ♂ seen).

Variation

Allometric variation is evident from the specimens examined. The lengths (in mm) of the ten complete males are: 22,3; 23,9; 24,9; 25,0; 26,9; 27,0; 27,4; 27,5; 27,5; and 27,5. All specific characters can be found on both the smallest and largest specimens, though moderate accentuation of secondary male sexual characters was observed in large specimens. With increase in size mandibles become larger with sharper edges; ventral process, flush with main arm at ventral surface in small specimens, is produced ventrally in large specimens; pronotum becomes broader and proportionately bigger than elytra. There is no distinct difference in anterior tibia between small and large specimens.

Colophon izardi Barnard, 1929

Figs 2, 3, 27F, 29C, 31A–B

Colophon izardi Barnard, 1929: 173, fig. 8; 1932*a*: 20, figs. Didier & Séguy, 1953: 77. Brinck, 1956: 310, 320.

Diagnosis

Male anterior tibia narrow and bent inward at 90 degrees. Armature of male mandibles forms a funnel in closed position. Pronotum in both sexes usually with a pair of red dots.

Description

Male. Head broadly oblong, gena emarginate in front of eye, anterior angle narrow, obtuse-angled. Ocular canthus distinct but rounded, disc broadly depressed in between. Punctation denser and coarser laterally. Frons only slightly deflected towards clypeus, which is visible in dorsal view. Clypeus broad, finely emarginated and sharply raised above level of labrum; labrum flat and broadly triangular. Mandibles very characteristic: main arms simple, sickle-shaped, with flat dorsal surface. Ventral process reaches maximum development in this species; in dorsal view as much produced as main arms, broad from the base, the whole mandibular structure forming a funnel towards clypeus (not towards the mouth, which is beneath) (Fig. 29C). Gula broadly rounded, gular sulcus sharp and deep.

Pronotum as long as elytra, slightly broader than latter, bearing a pair of large, round centrally bilateral reddish-brown patches. Broadest at basal third, flatly and evenly curved anteriorly, evenly tapering behind, not emarginate prebasally. All edges margined, only briefly interrupted in middle of anterior margin. Punctation very fine and scattered but distinct, stronger laterally.

Elytra with fine subhumeral crest, extending from base to middle of elytron.

Anal sternite asymmetrical, produced apex not calloused.

Anterior tibia apomorphic in shape: anterior third bent 90° inward; ventral crest low and continuous, lateral crest dilated pre-apically, then sharply interrupted, emargination between lateral crest and undivided apico-lateral process deeply U-shaped (Fig. 27F).

Aedeagus of asymmetrical type. Penis strongly sclerotized, asymmetrical. Right paramere armed inwards; inner process similar, but apex rectangular and not acute-angled as in *C. whitei*. Left paramere angularly emarginate at inner margin.

Female. Punctation of head, pronotum and elytra much more distinct than in male. Inner margin of anterior tibia evenly curved. Anal sternite symmetrical, densely punctate and finely pubescent, whereas in male it is smooth and bare. Discoidal red patches of pronotum similar to male.

Length

Male 21,8–25,3 mm, female 20–21 mm.

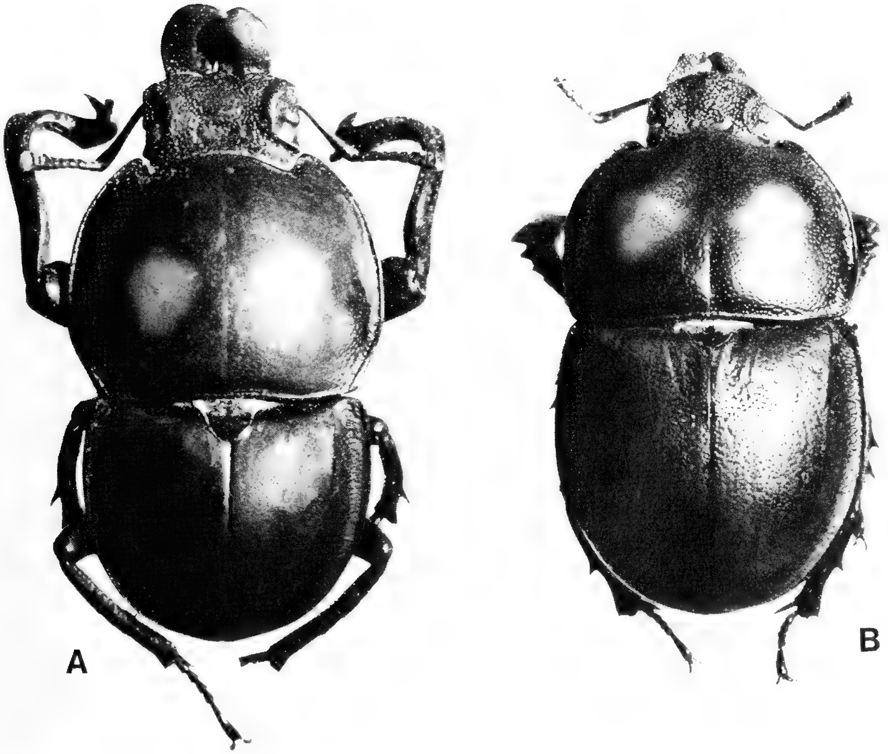

Fig. 31. *Colophon izardi* Barnard. A. Male; length 22,5 mm. B. Female; length 19,5 mm. The first live specimen found during this project.

Distribution

Central section of Langeberg Range, the southern range of the Cape mountains.

Material examined

5 ♂, 5 ♀; 17 ♂ heads, 1 ♀ head; 17 ♂ anterior tibia, 2 ♀ anterior tibia. Complete specimens are in the British Museum (Natural History), London; South African Museum, Cape Town; and Transvaal Museum, Pretoria.

Lectotype. ♂: Lemoenshoek, Heidelberg, C.P., 5 000 ft. [= 1 524 m], K. H. Barnard; British Museum (Natural History), London.

Paralectotypes. 3 ♀: Lemoenshoek, Heidelberg, C.P., 5 000 ft. [= 1 524 m], K. H. Barnard (1 ♀ in British Museum, London; 2 ♀ in South African Museum, Cape Town).

Additional material. 1 ♂: Lemoenshoek, January 1957, T. P. Stokoe. 2 ♂ pronota: Grootberg, Langeberg, 1.XI.1978, Endrödy-Younga, E-Y:1499. 1 ♀: Grootberg, Langeberg, 7.12.1978, E-Y:1527. 3 ♂, 1 ♀: Grootberg, Langeberg, 8.III.1979, E-Y:1562.

Remarks

Some females, due to their entirely black pronota, were excluded from the type series by Barnard, as were some fragments from localities from where no complete males were known. These included 3 ♀, 8 ♂ heads and 7 ♂ anterior legs, Riversdale Mountains, tops of peaks (Kampsche Berg in Barnard's description); 1 ♀, Zuurbrak Peak, Swellendam Dist., 5 000 ft. [= 1 524 m], K. H. Barnard, Oct. 1925; 9 ♂ heads, 1 ♀ head, 10 ♂ and 2 ♀ anterior legs: Tradouw Peak, Swellendam Distr., 4 400 ft. [= 1 341 m], K. H. Barnard, Oct. 1928.

It is remarkable that specimens with red pronotal dots came only from the Lemoenshoek–Grootberg area (11 specimens), and specimens with the pronotum entirely black from Kampsche Berg and Zuurbrak Peak. A final decision on the status of the black specimens is further complicated by the fact that they are all females, which are in any case difficult to identify. However, male mandibles and anterior legs from these localities do not show any difference when compared to the type specimens. Furthermore, one of the male specimens collected live in Grootberg (E-Y:1562) shows a very definite reduction of the red marking of its pronotum. The dots in this specimen are hardly more than 1 mm in diameter and dark reddish brown. Though further material would be of great interest, I have little doubt that the black-pronotum specimens are *C. izardi* Barnard.

ACKNOWLEDGEMENTS

My sincere thanks are due to my colleagues who enabled me to study the valuable material preserved in their respective museums: Dr V. B. Whitehead, South African Museum, Cape Town; Mr M. E. Bacchus, British Museum

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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 preferably 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. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

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.

S. ENDRÖDY-YOUNGA

EVIDENCE FOR THE LOW-ALTITUDE ORIGIN OF THE CAPE MOUNTAIN BIOME DERIVED FROM THE SYSTEMATIC REVISION OF THE GENUS *COLOPHON* GRAY (COLEOPTERA, LUCANIDAE)