





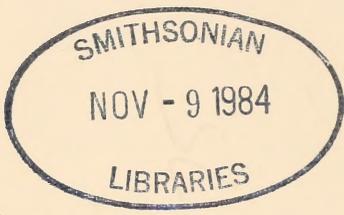
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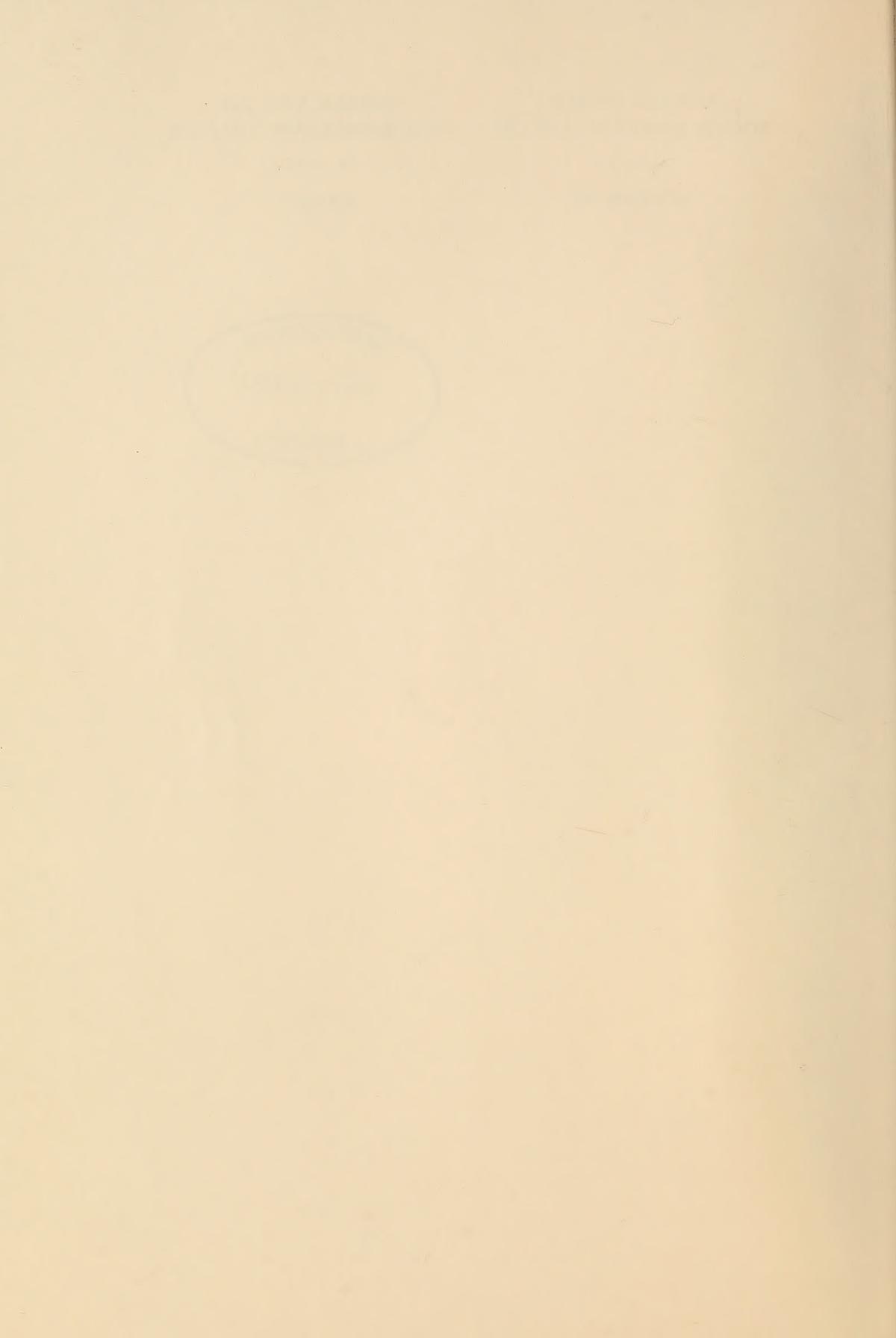
ANNALS OF THE
SOUTH AFRICAN MUSEUM

ANNALE VAN DIE
SUID-AFRIKAANSE MUSEUM

VOLUME 92

BAND 92





ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 92 BAND



THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2.5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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Examples (note capitalization and punctuation)

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

(continued inside back cover)

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Volume 92 Band
April 1983 April
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PRIMARY TYPE SPECIMENS OF MARINE
MOLLUSCA (EXCLUDING CEPHALOPODA)
IN THE SOUTH AFRICAN MUSEUM

By
ELIZABETH GILES
&
TERRENCE GOSLINER

Cape Town Kaapstad

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PRIMARY TYPE SPECIMENS OF MARINE MOLLUSCA
(EXCLUDING CEPHALOPODA)
IN THE SOUTH AFRICAN MUSEUM

By

ELIZABETH GILES

&

TERRENCE GOSLINER

South African Museum, Cape Town

[MS accepted 2 November 1982]

ABSTRACT

A list of type specimens of marine Mollusca contained in the collections of the South African Museum is presented. Three hundred and thirty-seven species are included in this list.

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INTRODUCTION

The molluscan collections housed in the South African Museum have provided the basis for numerous systematic investigations and extensive studies by well-known malacologists such as G. B. Sowerby, J. R. Tomlin, and W. H. Turton. In 1958 K. H. Barnard initiated his work on the molluscan fauna, based largely on material obtained from the dredging operations of the R.S. *Pieter Faure*.

As a result of these research activities spanning more than a century, many primary type specimens have been deposited in the collections of the South African Museum. In his posthumously published faunal list of South African molluscs Barnard (1974) noted some of the type material but a complete list has not been published.

The designation of type specimens was not indicated in most of the works of the above-mentioned authors and their status has been largely determined on the basis of review of K. H. Barnard's research notes, which involve correspondence with most of his predecessors as well as his own work.

Localities and data are given as they appear in the original publications or have been supplemented by information contained in catalogues of the molluscan holdings in the South African Museum.

SPECIES LIST

Class POLYPLACOPHORA

Family *Acanthochitonidae*

- Acanthochiton turtoni* Ashby, 1928: 79, pl. 6 (figs 1–4)
 = *Acanthochitona garnoti* (Blainville): Barnard, 1963*d*: 328.
 Holotype: SAM–A32649. Valve of holotype.
 Locality: Port Alfred; no depth or date.
 Collected by: Col. W. Turton.

Family *Lepidopleuridae*

- Lepidopleurus chariessa* Barnard, 1963*d*: 332, fig. 29h.
 Syntypes: SAM–A9338. Two shells, disarticulated.
 Locality: off Cape St. Blaize; 125 fm.; 1899.
 Collected by: R.S. Pieter Faure.

Family *Chitonidae*

- Chiton ashbyi* Barnard, 1963*d*: 343, fig. 29m.
 Holotype: SAM–A9337. Middle valve of holotype.
 Locality: off Cape Infanta; 46 fm.; 10 July 1900.
 Collected by: R.S. Pieter Faure.
- Chiton barnardi* Ashby, 1931: 46, pl. 6 (figs 74–76), pl. 7 (fig. 77).
 Holotype: SAM–A5331. Shell.
 Paratype: SAM–A6590. One valve.
 Locality: Mozambique Island (?Inhaca); no depth; 1912.
 Collected by: K. H. Barnard.
- Chiton (Hanleya) sykesi* Sowerby, 1903: 225, pl. 5 (fig. 13)
 = *Lepidopleurus sykesi* (Sowerby): Ashby, 1931: 15, pl. 2 (figs 16–19).
 Syntypes: SAM–5342. Two, girdle on slide.
 Locality: off Cape Point; 210 fm.; 11 June 1900.
 Collected by: R.S. Pieter Faure.

Family *Ischnochitonidae*

- Chaetopleura pomarium* Barnard, 1963*d*: 335, fig. 29i.
 Holotype: SAM–A9339. Shell with animal.
 Locality: western Cape Peninsula; no depth or date.
 Collected by: University of Cape Town.

Ischnochiton delagoaensis Ashby, 1931: 40, pl. 6 (figs 63–66).

Holotype: SAM–A6589. Valves, disarticulated.

Locality: Delagoa Bay; no depth; 1912.

Collected by: K. H. Barnard.

Ischnochiton hewitti Ashby, 1931: 33, pl. 5 (figs 50–53).

Holotype: SAM–A6757. Median valve of holotype.

Paratypes: SAM–A33953. Eight valves.

Locality: Mouille Point, Table Bay; intertidal; 1900.

Collected by: R. M. Lightfoot.

Class GASTROPODA

Subclass PROSOBRANCHIA

Family Pleurotomariidae

Pleurotomaria africana Tomlin, 1948: 2, pl. 1.

Holotype: SAM–A29663. Shell.

Locality: 29°48'S 31°23'E; 366 m; 21 July 1931.

Collected by: R.S. *Africana II*.

Family Scissurellidae

Scissurella africanae Barnard, 1963*b*: 13.

Holotype: SAM–A29933. Shell.

Locality: 30°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. *Africana II*.

Scissurella tabulata Barnard, 1964*c*: 21.

Holotype: SAM–A9335 (not A9345). Shell with operculum.

Locality: off Cape Natal; 804 m; 4 April 1901.

Collected by: R.S. *Pieter Faure*.

Family Fissurellidae

Glyphis spreta Smith, 1901: 104, pl. 1 (fig. 18)

= *Diodora spreta* (Smith): Tomlin, 1932: 160.

Syntypes: SAM–2459. Three shells.

Locality: Mossel Bay; intertidal; 1898.

Collected by: Miss Powrie.

Emarginula koon Kilburn, 1978: 439, pl. 5.

Paratype: SAM–A33924. Shell.

Locality: Shelly Beach near Port Shepstone; November 1965.

Collected by: R. Cock.

Emarginula natalensis Barnard, 1963d: 297, fig. 23.

Syntypes: SAM-A9325. Three shells, worn.

Locality: off Cape Morgan; 141 m; 26 July 1901.

Collected by: R.S. Pieter Faure.

Emarginula oppressa Barnard, 1963d: 298, fig. 24a

= *Emarginella oppressa* (Barnard): Kilburn, 1978: 446, pl. 8 (fig. b).

Holotype: SAM-A9330. Shell.

Locality: off Cape Natal; 98 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Emarginula pulchreclathrata Tomlin, 1932: 162, fig. 4

= *Emarginula agulhasensis* Thiele: Kilburn, 1978: 433, pl. 2a-b.

Holotype: SAM-A3617. Shell.

Locality: Saldanha Bay; 98 m; 13 March 1902.

Collected by: R.S. Pieter Faure.

Emarginula thorektes Kilburn, 1978: 440, pl. 6a-c.

Paratype: SAM-A9323. Shell.

Locality: off Cape Morgan; 141 m; 26 July 1901.

Collected by: R.S. Pieter Faure.

Emarginula vadum Barnard, 1963d: 297, figs 23d-24b.

Holotype: SAM-A9329. Shell.

Locality: off Cape Vidal; 146-183 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Parmaphorella barnardi Tomlin, 1932: 164, fig. 5

= *Tugali barnardi* (Tomlin): Kilburn, 1978: 452, pl. 11 (figs b-d).

Holotype: SAM-A3623. Shell.

Locality: off Cape Point; 344 m; 27 February 1902.

Collected by: R.S. Pieter Faure.

Puncturella (Vacerrrena) christiaensi Kilburn, 1978: 448, pl. 9 (figs c-e).

Paratype: SAM-A33925. Shell.

Locality: off Sodwana Bay; 50 m; 1975.

Collected by: R.V. Meiring Naude.

Family Trochidae

Angaria lacunosa Barnard, 1963d: 283.

Holotype: SAM-A9281. Shell.

Locality: off Natal; no depth or date.

Collected by: R.S. Pieter Faure.

Bassilissa gelida Barnard, 1963b: 440, fig. 8b.

Holotype: SAM-A9720. Shell, radula, slide.

Locality: 33°26'S 16°33'E; 2 380 m; August 1959.

Collected by: F. H. Talbot on board R.S. *Africana II*.

Calliostoma circus Barnard, 1969: 653, fig. 27b.

Holotype: SAM-A30032. Shell with operculum, radula slide.

Locality: off Cape Point; no depth or date.

Collected by: commercial trawler.

Calliostoma glaucophaos Barnard; 1963b: 442, fig. 8c.

Syntypes: SAM-A9830. Two shells with opercula, radula slide.

Locality: 33°52'S 16°51'E; 2 520–2 810 m; December 1959.

Collected by: F. H. Talbot on board R.S. *Africana II*.

Calliostoma (Lischkeia) granoliratum Sowerby, 1903: 222, pl. 5 (fig. 7)

= *Calliotropis granolirata* (Sowerby): Thiele, 1925: 48.

Holotype: SAM-A5296. Shell with operculum.

Paratype: SAM-A33690 (previously A5296). Shell.

Locality: off Cape Point; 665 m; 12 June 1900.

Collected by: R.S. *Pieter Faure*.

Calliostoma iridescens Sowerby, 1903: 223, pl. 5 (fig. 4).

Holotype: SAM-A5294. Shell.

Locality: off Cape Natal; 101 m; 24 December 1900.

Collected by: R.S. *Pieter Faure*.

Calliostoma perfragile Sowerby, 1903: 222, pl. 5 (fig. 3).

Holotype: SAM-A5275. Shell.

Locality: off Cape Point; 282–304 m; 18 April 1900.

Collected by: R.S. *Pieter Faure*.

Calliotropis chenoderma Barnard, 1963d: 263, fig. 16c.

Syntype: SAM-A9296. Shell.

Locality: off Cape St. Blaize; 229 m; 21 December 1899.

Syntype: SAM-A9297. Shell.

Locality: off Cape Morgan; 86 m; 25 July 1901.

Collected by: R.S. *Pieter Faure*.

Calliotropis persculpta (Sowerby): see *Solariella persculpta* p. 7.

Calliotropis pompe Barnard, 1963c: 440, fig. 8b.

Syntypes: SAM-A9883. Two shells, one with operculum.

Locality: off Cape Point, 34°42'S 16°54'E; 1 725–1 789 fm.; December 1959.

Syntype: SAM-A9795. Shell.

Locality: off Cape Point, 33°50'S 16°30'E; 1 450–1 660 fm.; December 1959.

Collected by: F. H. Talbot on board R.S. *Africana II*.

Gibbula beckeri Sowerby, 1901: 214, pl. 22 (fig. 22).

Paratype: SAM-A3321. Shell.

Locality: Port Alfred; intertidal; 1915.

Collected by: H. Becker.

Gibbula (Enida) perspectiva Sowerby, 1900: 6, pl. 1 (fig. 17).

Paratype: SAM-A3320. Shell.

Locality: Pondoland; intertidal; 1915.

Collected by: H. Becker.

Guttula blanda Barnard, 1963d: 265, fig. 17.

Holotype: SAM-A7424. Shell, radula slide.

Locality: off Cape Point; 1 270 m; 20 August 1903.

Collected by: R.S. *Pieter Faure*.

Minolia adarticulata Barnard, 1963d: 235, fig. 11f.

Syntypes: SAM-A9277. Two shells.

Locality: off Hood Point, East London; 90 m; 15 July 1901.

Collected by: R.S. *Pieter Faure*.

Minolia cycloma Barnard, 1964c: 18, fig. 2c–d.

Holotype: SAM-A9279. Shell.

Locality: off Tugela River, Natal; 67 m; 9 January 1901.

Collected by: R.S. *Pieter Faure*.

Minolia congener Sowerby, 1903: 223, pl. 5 (fig. 2)

= *Solariella laevis* (von Martens): Barnard, 1963d: 239, fig. 10c.

Syntypes: SAM-A5257. Two shells with opercula.

Locality: off Cape St. Blaize; 67 m; 22 October 1900.

Collected by: R.S. *Pieter Faure*.

Seguenzia fatigans Barnard, 1963b: 13, pl. 2 (figs 10–11).

Syntypes: SAM-A29930. Two shells.

Locality: 27°48'S 47°19'E; 875 m; 22 June 1961.

Collected by: R.S. *Africana II*.

Seguenzia simplex Barnard, 1963d: 265, fig. 16a.

Syntypes: SAM-A7421. Four shells (one juvenile); radula slide.

Locality: off Cape Point; 1 280 m; 20 August 1903.

Collected by: R.S. *Pieter Faure*.

- Solariella beckeri* Sowerby, 1901: 214, pl. 22 (fig. 21)
= *Solariella laevissima* (von Martens): Barnard, 1963d: 239, fig. 10c.
Paratype: SAM-A3323. Shell.
Locality: Kowie (Port Alfred); no depth; 1915.
Collected by: H. Becker.
- Solariella dowi* Barnard, 1963b: 13, pl. 2 (figs 10–11).
Syntypes: SAM-A29932. Two shells.
Locality: 27°48'S 47°19'E; 875 m; 22 June 1961.
Collected by: R.S. *Africana II*.
- Solariella franciscana* Barnard, 1963d: 243, figs 10e–11b
= *Spectamen franciscana* (Barnard): Kilburn, 1977: 178.
Holotype: SAM-A3615. Shell with operculum, radula slide.
Locality: off Cape St. Francis; 137 m; 19 February 1902.
Collected by: R.S. *Pieter Faure*.
- Solariella gilchristi* Barnard, 1963d: 242, fig. 11d.
Syntypes: SAM-A3605. Two shells.
Locality: off Buffalo River; 564 m; 24 April 1901.
Collected by: R.S. *Pieter Faure*.
- Solariella macleari* Barnard, 1963d: 241, fig. 11c.
Syntypes: SAM-A7417. Four shells, one apex, two opercula, radula slide.
Locality: 'off Cape Point N 89°E, 36 miles'; 1 280 m; 20 August 1903.
Collected by: R.S. *Pieter Faure*.
- Solariella palirrous* Barnard, 1963a: 12, pl. 2 (figs 7–8).
Holotype: SAM-A29931. Shell broken.
Locality: 36°48'S 52°08'E; 400 m; 9 July 1961.
Collected by: R.S. *Africana II*.
- Solariella persculpta* Sowerby, 1903: 223, pl. 5 (fig. 8)
= *Calliotropis persculpta* (Sowerby): Thiele, 1925: 48.
Syntype: SAM-A5251. Shell.
Locality: off Cape Natal; 800 m; 4 April 1901.
Collected by: R.S. *Pieter Faure*.
- Solariella turbynei* Barnard, 1963d: 243, fig. 11a.
Holotype: SAM-A9276. Shell.
Locality: off Cape Point; 246 m; 17 February 1902.
Collected by: R.S. *Pieter Faure*.
- Turcica helix* Barnard, 1964c: 21, fig. e.
Holotype: SAM-A9295. Shell.
Locality: off Cape Vidal; 146–183 m; 27 February 1901.

Paratype: SAM-A9256. Shell, broken.

Locality: off Umkomaas; 73 m; 31 December 1900.

Collected by: R.S. *Pieter Faure*.

Turcica konos Barnard, 1964c: 20, fig. 3f.

Syntypes: SAM-A9257. Four shells (two adult, one immature, one broken).

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. *Pieter Faure*.

Turcica salpinx Barnard, 1964c: 19, fig. 3a-d.

Syntype: SAM-A9252. Shell, adult, broken.

Locality: off Cape Morgan; 40 m; 26 July 1901.

Syntypes: SAM-A9253. Five shells (three broken, two juvenile).

Locality: off Hood Point; 90 m; 15 July 1901.

Collected by: R.S. *Pieter Faure*.

Family Liotiidae

Brookula coronis Barnard, 1963b: 12, pl. 2 (figs 5-6).

Syntypes: SAM-A29929. Nine shells.

Locality: 36°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. *Africana II*.

Leptothyra echomenus Barnard, 1963b: 12, pl. 2 (figs 3-4).

Syntypes: SAM-A29928. Five shells.

Locality: 36°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. *Africana II*.

Leptothyra sola Barnard, 1963d: 231, fig. 9e.

Holotype: SAM-A9288. Shell, probably juvenile.

Locality: probably Algoa Bay; no depth or date.

Collected by: R.S. *Pieter Faure*.

Leptothyra syngenes Barnard 1963b: 11, pl. 2, figs 2, 4.

Syntypes: SAM-A29927. Twelve shells, some broken.

Locality: 36°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. *Africana II*.

Rufulana sextula Barnard, 1963d: 232, fig. 9f.

Syntypes: SAM-A29634. Three shells.

Locality: probably Algoa Bay; 55 m; 10 November 1898.

Collected by: R.S. *Pieter Faure*.

Family **Turbinidae**

Astraliium (Cyclocantha) gilchristi Sowerby 1903: 221, pl. 5 (fig. 6)

= *Astrea gilchristi* (Sowerby): Barnard 1963*d*: 221, fig. 7c.

Syntype: SAM-A5219. Shell.

Locality: off Scottburgh; 168 m; 7 March 1901.

Collected by: R.S. Pieter Faure.

Calcar rhyssopoma Barnard, 1964*b*: 17, fig. 2a-b.

Syntypes: SAM-A9285. Fourteen shells, one operculum, radula slide.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Turbo boswellae Barnard, 1969: 652, fig. 27a.

Holotype: SAM-A30031. Shell, operculum, radula slide.

Locality: off Cape Point; 366 m; no date.

Collected by: commercial trawler.

Turbo foveolatus Barnard, 1963*d*: 216, fig. 6.

Syntypes: SAM-A9284. Five shells.

Locality: 34°05'S 25°52'E; 95 m; 14 November 1898.

Collected by: R.S. Pieter Faure.

Family **Rissoidae**

Amphithalamus muiri Barnard, 1963*a*: 188, fig. 15d.

Syntypes: SAM-A9262. Eleven shells.

Locality: Still Bay; intertidal zone; no date.

Collected by: T. Muir.

Family **Vitrinellidae**

Cochliopsis catherinae Barnard 1963*a*: 180, fig. 35a.

Holotype: SAM-A9221. Shell.

Locality: 34°27'S 25°42'E; 473 m; 14 November 1898.

Paratype: SAM-A9341. Shell.

Locality: 33°50'S 25°54'E; 61 m; 11 November 1898.

Collected by: R.S. Pieter Faure.

Cochliopsis tugelae Barnard, 1963*a*: 180, fig. 35b.

Holotype: SAM-A9282. Shell.

Locality: off Tugela River; 26 m; 16 January 1901.

Collected by: R.S. Pieter Faure.

Vitrinella inclinans Barnard 1963a: 179, fig. 35c.

Syntypes: SAM-A29680. Six shells with animals, one operculum.

Locality: 34°27'S 25°45'E; 463 m; 19 November 1898.

Collected by: R.S. Pieter Faure.

Family **Turritellidae**

Turritella chrysotoxa Tomlin, 1925: 315, fig. 3a.

Syntype: SAM-A3561. Shell.

Locality: off Illovo River; 50 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Turritella kowiensis Sowerby, 1900: 6, pl. 1 (fig. 12)

= *Turritella carinifera* form *kowiensis* (Sowerby): Barnard, 1963a: 166.

Syntypes: SAM-A3315. Two shells.

Locality: Kowie, Port Alfred; no depth; 1915.

Collected by: H. Becker.

Turritella salisburyi Tomlin, 1925: 314, fig. 36

= *Turritella sanguinea* Reeve: Barnard, 1963a: 169.

Syntype: SAM-A5113. Shell.

Syntype: SAM-A33952. Shell.

Locality: off East London; 95 m; 12 July 1901.

Collected by: R.S. Pieter Faure.

Family **Vermetidae**

Vermetus (Stoa) corralinaceus Tomlin, 1939: 145, pl. 12 (fig. 4).

Paratypes: SAM-A31494. Two blocks of tubes, radula slide.

Locality: Oudekraal, west Cape Peninsula; no depth or date.

Collected by: University of Cape Town.

Vermetus periscopium Barnard, 1963a: 146, fig. 30a.

Paratypes: SAM-A29925. Four shells, one operculum, four animals, radula slide.

Locality: 29°46'S 31°17'E; 110–130 m; 23 April 1958.

Collected by: University of Cape Town.

Vermetus quincunx Barnard, 1963a: 148, figs 28c, 29b–c.

Syntypes: SAM-A29814. Large mass, numerous fragments, protoconchs, two opercula, radula slide.

Locality: 34°27'S 25°42'E; 470 m; 19 November 1898.

Collected by: R.S. Pieter Faure.

Family **Cerithiidae**

Alabina telamon Barnard, 1963a: 138, fig. 26d.

Holotype: SAM-A29676. Shell.

Locality: off Tugela River; 118–146 m; 11 January 1901.

Collected by: R.S. Pieter Faure.

Family **Cerithiopsidae**

Cerithiella natalensis Barnard, 1963a: 126.

Holotype: SAM-A9045. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Cerithiella nonnitens Barnard, 1963a: 127, fig. 23g.

Holotype: SAM-A9047. Shell.

Locality: off Cove Rock, East London; 146–183 m; 30 July 1900.

Collected by: R.S. Pieter Faure.

Cerithiella (Stilus) subuliapex Barnard, 1963b: 10, pl. 1 (fig. 8).

Holotype: SAM-A29924. Shell.

Locality: 27°48'S 47°19'E; 875 m; 22 June 1961.

Collected by: R.S. Africana II.

Cerithiella taylori Barnard, 1963a: 126, fig. 23i.

Holotype: SAM-A9711. Shell.

Locality: 33°26'S 16°33'E; 2 260–2 370 m; August 1959.

Collected by: R.S. Africana II.

Cerithiella vidalensis Barnard, 1963a: 127.

Holotype: SAM-A9046. Shell.

Locality: off Cape Vidal; 146–183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Cerithiopsis rota Barnard, 1963a: 124, fig. 23a–c.

Holotype: SAM-A9043. Shell.

Locality: 34°25'S 44°33'E; 61 m; 10 November 1898.

Collected by: R.S. Pieter Faure.

Family **Finellidae**

Cerithidium fragrans Barnard, 1963a: 139, fig. 15c.

Syntypes: SAM-A29679. Five shells, fossils.

Locality: raised beach, Little Brak River; no date.

Collector unknown.

Family **Abyssochrysidae**

Abyssochrysos tomlini Barnard, 1963a: 143, fig. 27f

= *Abyssochrysos melvilli* (Schepman): Houbrick, 1979: 10, figs 7d, f, i, 8.

Lectotype: SAM-A9101. Shell.

Paralectotype: SAM-A33950 (previously A9109). Shell.

Locality: off Cape Natal; 535 m; 4 April 1901.

Collected by: R.S. Pieter Faure.

Abyssochrysos melanoides Tomlin, 1927: 78. figs 1-3.

Syntype: SAM-A5116. Shell.

Locality: off Cape Point; 1 462-2 724 m; 21 July 1903.

Syntypes: SAM-A33951 (previously A5116). Twelve shells, four opercula, one radula.

Collected by: R.S. Pieter Faure.

Family **Triforidae**

Trifora ? axialis Barnard, 1963b: 10, pl. 1 (fig. 7) (*sic*).

Syntypes: SAM-A29923. Two shells.

Locality: 36°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. *Africana II*.

Trifora bactron Barnard, 1963a: 115, fig. 20c.

Holotype: SAM-A9077. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Paratype: SAM-A9076. Shell.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Trifora baculus Barnard, 1963a: 115, fig. 20b.

Holotype: SAM-A9078. Shell.

Locality: off Sandy Point north of Cape Morgan; 93 m; 14 August 1901.

Collected by: R.S. Pieter Faure.

Trifora dagama Barnard, 1963a: 112, fig. 19f.

Syntype: SAM-A9073. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Trifora morgani Barnard, 1963a: 111, fig. 19a.

Holotype: SAM-A9079. Shell, broken.

Locality: off Sandy Point north of Cape Morgan; 93 m; 14 August 1901.

Collected by: R.S. Pieter Faure.

Trifora natalensis Barnard, 1963a: 112, fig. 19c.

Syntype: SAM-A9071. Shell.

Locality: off Umhloti River; 73 m; 18 December 1900.

Syntype: SAM-A9072. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Trifora scala Barnard, 1963a: 115, fig. 19d.

Syntype: SAM-A9074. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Syntype: SAM-A9075. Shell.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Family Pyramidellidae

Odstomia tugelae Barnard, 1963a: 93, fig. 15b.

Holotype: SAM-A9225. Shell.

Locality: off Tugela River; 65–80 fm.; 11 January 1901.

Collected by: R.S. Pieter Faure.

Turbonilla bathybias Barnard, 1963a: 89.

Syntypes: SAM-A9175. One shell, one apex.

Locality: off East London; 400–450 fm.; 17 April 1901.

Collected by: R.S. Pieter Faure.

Turbonilla? bifilosa Barnard, 1963a: 90, fig. 15a.

Holotype: SAM-A9220. Shell.

Locality: 34°05'S 25°55'E; 122 m; 1 November 1898.

Collected by: R.S. Pieter Faure.

Turbonilla deprofundis Barnard, 1963a: 89, fig. 14b.

Holotype: SAM-A9157. Shell.

Locality: off East London; 400–450 fm.; 17 April 1901.

Collected by: R.S. Pieter Faure.

Turbonilla tugelae Barnard, 1963a: 88, fig. 14f.

Syntypes: SAM-A9153. Shell, apex.

Locality: off Tugela River; 14 fm.; 16 January 1901.

Collected by: R.S. Pieter Faure.

Family Epitoniidae

Acrilla analogica Barnard, 1963a: 106, fig. 18g–h.

Holotype: SAM-A9026. Protoconch with nine whorls.

Locality: 36°40'S 21°26'E; 366 m; 17 July 1906.

Paratype: SAM-A9229. Shell, broken.
 Locality: 34°27'S 25°42'E; 467 m; 14 November 1898.
 Collected by: R.S. *Pieter Faure*.

Acrilla natalis Barnard, 1963a: 105, fig. 18e-f.
 Syntypes: SAM-A9028. Two shells, broken.
 Locality: off Cape Natal; 99 m; 14 December 1900.
 Collected by: R.S. *Pieter Faure*.

Scala blaisei Barnard, 1963a: 102, fig. 18a
 = *Epitonium blaisei* (Barnard): **comb. nov.**
 Holotype: SAM-A9025. Shell.
 Locality: off Cape St. Blaize; 228 m; 21 December 1899.
 Collected by: R.S. *Pieter Faure*.

Scala bonaspei Barnard, 1963a: 104, fig. 17b
 = *Epitonium bonaspei* (Barnard): **comb. nov.**
 Syntypes: SAM-A9761. Two shells with opercula, proboscis, jaws, radula
 of larger specimen on slide.
 Syntype: SAM-A9793. Shell.
 Locality: off Cape Point; 3 120-3 260 m; December 1959.
 Collected by: R.S. *Africana II*.

Scala illovoensis Barnard, 1963a: 101, fig. 18b
 = *Epitonium illovoensis* (Barnard): **comb. nov.**
 Holotype: SAM-A9023. Shell.
 Locality: off Illovo River; 50-55 m; 31 December 1900.
 Collected by: R.S. *Pieter Faure*.

Scala mathildopsis Barnard, 1963b: 9, pl. 1 (fig. 5)
 = *Epitonium mathildopsis* (Barnard): **comb. nov.**
 Syntypes: SAM-A29921. Six shells.
 Locality: 27°48'S 47°19'E; 875 m; 22 June 1961.
 Collected by: R.S. *Africana II*.

Scala munda Barnard, 1969: 649, fig. 24b
 = *Epitonium mundum* (Barnard): **comb. nov.**
 Holotype: SAM-A30552. Shell.
 Locality: off Cape Point; 1 250 m; 20 August 1903.
 Paratypes: SAM-A7419. Three shells.
 Locality: off Cape Point; 1 280 m; 20 August 1903.
 Collected by: R.S. *Pieter Faure*.

Scala tenebrosa Sowerby, 1903: 220, pl. 4 (fig. 6)

= *Epitonium tenebrosum* (Sowerby): **comb. nov.**

Syntype: SAM-A3599. Shell.

Locality: off Cape St. Blaize; 67 m; 22 October 1900.

Collected by: R.S. Pieter Faure.

Family Mathildidae

Mathilda salve Barnard, 1963a: 176, fig. 34.

Holotype: SAM-A9139. Shell.

Locality: off Cape St. Blaize; 229 m; 21 December 1899.

Paratype: SAM-A9141. Apex of seven whorls, no protoconch.

Locality: off Glendower Beacon, Port Alfred; 183 m; 26 July 1901.

Collected by: R.S. Pieter Faure.

Family Architectonicidae

Fluxina solarium Barnard, 1963b: 11, pl. 2 (fig. 1).

Holotype: SAM-A29926. Shell.

Locality: 27°48'S 47°19'E; 875 m; 22 June 1961.

Collected by: R.S. *Africana II*.

Heliacus numulus Barnard, 1963a: 163, fig. 31e.

Holotype: SAM-A9125. Shell.

Locality: off Cape Morgan; 141 m; 26 July 1901.

Collected by: R.S. Pieter Faure.

Heliacus obolos Barnard, 1963a: 163, fig. 31f-g.

Holotype: SAM-A9127. Shell, broken.

Locality: off Umhloti River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Heliacus petasus Tomlin, 1928: 334, pl. 26 (fig. 4).

Holotype: SAM-A3579. Shell.

Locality: off Scottburgh; 169 m; 7 March 1901.

Collected by: R.S. Pieter Faure.

Family Stiliferidae

Apicalia sowerbyi Barnard, 1963a: 94, fig. 16.

Syntypes: SAM-A9169. Two shells.

Locality: off Hood Point, near East London; 90 m; 15 July 1901.

Collected by: R.S. Pieter Faure.

Family **Fossaridae**

Fossarus translucens Barnard, 1969: 647, fig. 23a.

Holotype: SAM-A30052. Shell.

Locality: Gordon's Bay, False Bay; intertidal; no date.

Collected by: Dr Ackert.

Megalomphalus mosselensis Barnard, 1957: 180, figs b-d.

Holotype: SAM-A29922. Shell, six embryo ex utera, radula slide.

Locality: Mossel Bay; no depth or date.

Collected by: University of Cape Town.

Family **Amaltheidae**

Cheila microstriata Barnard, 1963a: 76, fig. 10j.

Syntype: SAM-A9004. Shell, broken.

Locality: off Durban; 153 m; 17 December 1900.

Syntype: SAM-A9005. Shell.

Locality: off Umhloti River; 73 m; 18 December 1900.

Syntype: SAM-A9006. Shell, broken.

Locality: off Durnford Point, Natal; 164 m; 11 July 1900.

Syntype: SAM-A9342. Shell.

Locality: off Cape Vidal; 146-183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Family **Trichotropidae**

Trichotropis zuluensis Barnard, 1963a: 78, figs 12d-13c.

Syntype: SAM-A9011. Shell, radula slide.

Locality: off Durnford Point, Natal; 165 m; 28 February 1901.

Syntype: SAM-A9012. Shell.

Locality: off Cape Vidal; 146-183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Family **Aporrhaidae**

Aporrhais pesgallinae Barnard, 1963a: 67, fig. 8.

Holotype: SAM-A30248. Shell with animal in alcohol, radula slide.

Locality: 26°23'S 14°17'E; 311 m; 28 October 1948.

Collected by: R.S. *Africana I.*

Family **Naticidae**

Falsilunatia pseudopsila Barnard, 1963a: 64, fig. 7e; 1969: 646, fig. 22.

Holotype: SAM-A9780. Shell with operculum, radula slide.

Locality: off Cape Point; 2 920 m; December 1959.
Collected by: R.S. *Africana II*.

Polynices cleistopsila Barnard, 1963a: 64, fig. 7d.

Syntypes: SAM-A9735. One adult shell, two juveniles, three opercula, radula slide.

Locality: Off Cape Point, 33°36'S 16°15'E; 2 830 m; August 1959.
Collected by: R.S. *Africana II*.

Family Cypraeidae

Cypraea fultoni Sowerby, 1903: 218, pl. 4 (fig. 7).

Holotype: SAM-A5053. Shell.

Locality: South Africa; *ex pisce*; no depth or date.

Collected by: R.S. *Pieter Faure*.

Family Triviidae

Trivia verhoefi Gosliner & Liltved, 1982: 121, figs 1f, 13–16.

Holotype: SAM-A34387. Shell with animal.

Locality: Llandudno, 34°01'S 18°20'E; 25 m; 22 December 1979.

Collected by: G. Verhoef.

Paratype: SAM-A34388. Shell with animal.

Locality: Llandudno; 20 m; 16 March 1980.

Collected by: W. R. Liltved.

Paratype: SAM-A34389. Shell with animal.

Locality: Llandudno, 25 m; 27 March 1980.

Collected by: W. R. Liltved.

Family Ovulidae

Amphiperas beckeri Sowerby, 1900: 5, pl. 1 (fig. 13)

= *Primovula beckeri* (Sowerby): Thiele, 1929; Barnard 1963a: 55, figs 5d–6c.

Paratypes: SAM-A8918. Four shells.

Locality: Kowie, Port Alfred; intertidal; ?1899.

Collected by: H. Becker.

Family Tonnidae

Eudolium aulacoides Tomlin, 1927: 83, fig. 4a.

Holotype: SAM-A3529. Shell.

Locality: off Cape Point; 1 020–1 280 m; 17 September 1903.

Collected by: R.S. *Pieter Faure*.

Family **Cymatiidae**

Thalassocyon bonus Barnard, 1960: 440, fig. 3.

Holotype: SAM-A9714. Shell, operculum broken, radula slide A9810.

Locality: off Cape Point; 2 280–2 380 m; August 1959.

Collected by: R.S. *Africana II*.

Family **Columbariidae**

Columbarium angulare Barnard, 1959: 235, fig. 52c.

Syntypes: SAM-A4608. Three shells, operculum, radula slide.

Locality: off Cape Point; 1 480–1 650 m; 14 July 1903.

Collected by: R.S. *Pieter Faure*.

Columbarium formosissimum Tomlin, 1928: 331, pl. 25 (fig. 1).

Holotype: SAM-A3501. Shell.

Locality: Cape St. Blaize; 'N by E $\frac{1}{4}$ E 65 miles'; 90 fm.; 22 December 1899.

Collected by: R.S. *Pieter Faure*.

Paratype: SAM-A3499; Shell.

Locality: Cape Seal; 'N by W $\frac{1}{2}$ W 55 miles'; 87 fm.; 19 February 1902.

Collected by: R.S. *Pieter Faure*.

Paratype: SAM-A3450; Shell.

Locality: Cape Seal; 'N by W $\frac{1}{2}$ W 55 miles'; 87 fm.; 19 February 1902.

Collected by: R. S. *Pieter Faure*.

Paratype: SAM-A3498; Shell.

Locality: Glendower Beacon; 'N $\frac{1}{2}$ W 6 miles'; 66 fm.; 10 September 1901.

Collected by: R.S. *Pieter Faure*.

Columbarium natalense Tomlin, 1928: 331, pl. 25 (fig. 2).

Holotype: SAM-A3497. Shell.

Locality: off Cape Natal; 153 m; 17 December 1900.

Collected by: R.S. *Pieter Faure*.

Columbarium rotundum Barnard, 1959: 236, fig. 52d.

Syntypes: SAM-A4592. Two shells, two opercula.

Locality: off Cape Point; 1 400 m; 27 August 1903.

Collected by: R.S. *Pieter Faure*.

Family **Colubrariidae**

Epidromus crebrilirata Sowerby, 1903: 220, pl. 4 (fig. 4)

= *Nivitrion fictilis* (Hinds): Kilburn, 1977: 194.

Holotype: SAM-A4974. Shell.

Locality: off Glendower Beacon, Port Alfred; 183 m; 10 September 1901.

Collected by: R.S. *Pieter Faure*.

Family **Muricidae**

Tritonalia juritzi Barnard, 1969: 639, fig. 18d.

Holotype: SAM-A30051. Shell, broken.

Locality: doubtful, probably Cape Peninsula.

Collected by: C. Juritz.

Trophon acceptans Barnard, 1959: 202, figs 40d-43b; 1963c; 435, fig. 7a; 1969: 638.

Holotype: SAM-A3473. Shell with operculum, radula slide.

Locality: off Cape Point, 'N 64° E 37 miles'; 1 270-1 460 m; 9 September 1903.

Paratype: SAM-A3449. Three shells.

Locality: off Cape Point, 'E ¾° N 38 miles'; 1 190 m; 9 September 1903.

Paratype: SAM-A3480. Shell.

Locality: off Cape Point, '64° NE 37 miles'; 1 270-1 460 m; 10 September 1903.

Collected by: R.S. Pieter Faure.

Trophon? incertus Barnard, 1959: 203, fig. 32a.

Syntypes: SAM-A8843. Two shells.

Locality: off Cape Natal; 800 m; 4 April 1901.

Collected by: R.S. Pieter Faure.

Trophon johanthielei Barnard, 1959: 206, fig. 44b.

Holotype: SAM-A8844. Shell, broken.

Locality: off East London; 730-820 m; 17 April 1901.

Collected by: R.S. Pieter Faure.

Trophon mioplectos Barnard, 1959: 206, fig. 44a.

Holotype: SAM-A8631. Shell.

Locality: 34°27'S 25°42'E; 466 m; 16 November 1898.

Collected by: R.S. Pieter Faure.

Trophon pistillum Barnard, 1959: 206, fig. 44f.

Holotype: SAM-A8842. Shell, broken; radula slide.

Locality: off Cape Natal; 802 m; 4 April 1901.

Collected by: R.S. Pieter Faure.

Typhus pentaphasios Barnard, 1959: 211, fig. 46h-i

= *Siphonochelus pentaphasios* (Barnard 1959): Radwin & D'Attilo 1976: 199, fig. 144.

Syntypes: SAM-A4949. Two shells.

Locality: off Cape Point; 1 204 m; 10 September 1903.

Collected by: R.S. Pieter Faure.

Family **Coralliophilidae**

Coralliophila isosceles Barnard, 1959: 191, fig. 39a.

Syntypes: SAM-A4951. Two shells.

Locality: off Glendower Beacon, Port Alfred; 121 m; 10 September 1901.

Collected by: R.S. Pieter Faure.

Coralliophila zuluensis Barnard, 1959: 192, fig. 39b.

Holotype: SAM-A8852. Shell.

Locality: off O'Neil Peak, Natal; 163 m; 28 February 1901.

Collected by: R.S. Pieter Faure.

Latiaxis capensis Tomlin, 1928: 332.

Holotype: SAM-A3522. Shell.

Locality: off Sandy Point, Transkei; 173 m; 14 August 1901.

Collected by: R.S. Pieter Faure.

Latiaxis? elstoni Barnard, 1962b: 148, fig. 1.

Holotype: SAM-A9346. Shell.

Locality: Natal coast; *ex pisce*; donated 1961.

Collector unknown.

Latiaxis kyllix Barnard, 1959: 188, fig. 27

= *Latiaxis mawae kyllix* Barnard: Kilburn, 1973: 565, fig. 9b.

Holotype: SAM-A8850. Shell, juvenile.

Locality: off Cape Natal; 98 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Family **Buccinidae**

Babylonia pintado Kilburn, 1971: 486, figs 3, 7c, e.

Paratypes: SAM-A4751. Shell.

Locality: off Port Shepstone, 'WNW 8 miles'; 27 fm.; 14 March 1901.

Collected by: R.S. Pieter Faure.

Paratype: SAM-A7706. Shell.

Locality: Natal; *ex pisce*; no depth or date.

Collected by: Mr Casey.

Paratype: SAM-A8239. Shell.

Locality: Natal; *ex pisce*; no depth or date.

Collected by: H. W. Bell-Marley.

Paratypes: SAM-A30956. Six shells.

Locality: Natal; *ex pisce*; no depth or date.

Collected by: R. Frames.

Glypteuthria solidissima Tomlin, 1932: 166, fig. 7

= *Afrocominella elongata* (Dunker): Barnard, 1959: 153, fig. 31f.

Holotype: SAM-A3543. Shell.

Locality: off Cape Point; 82 m; 6 June 1900.

Collected by: R.S. Pieter Faure.

Neptunea bonaespei Barnard, 1960: 440, fig. 3.

Syntypes: SAM-A9826. Three shells (one broken), operculum, radula slide.

Locality: off Cape Point, 33°52'S 16°51'E; 2 520–2 820 m; December 1959.

Collected by: R.S. *Africana II*.

Nux alabaster Barnard, 1960: 440, fig. 3.

Holotype: SAM-A9715. Shell with operculum, radula slide.

Locality: off Cape Point, 33°26'S 16°33'E; 2 270–2 380 m; December 1959.

Paratypes: SAM-A9827. Two shells with opercula.

Locality: off Cape Point; 35°52'S 16°51'E; 2 540–2 820 m; December 1959.

Collected by: R.S. *Africana II*.

Prosipho torquatus Barnard, 1963c: 433, fig. 6c–e.

Holotype: SAM-A9884. Shell with operculum, radula slide.

Locality: off Cape Point, 34°37'S 17°03'E; 2 890–2 960 m; December 1959.

Collected by: R.S. *Africana II*.

Family Columbellidae

Columbella beckeri Sowerby, 1900: 3, pl. 1 (fig. 7).

Syntype: SAM-A3322. Shell.

Locality: Port Alfred; intertidal; 1915.

Collected by: H. Becker.

Columbella confertilirata Barnard, 1959: 182, fig. 35d.

Syntypes: SAM-A8879. One adult, two juveniles, fifteen fragments.

Locality: off Umkomaas; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Columbella dibolos Barnard, 1964c: 17

= *Mitrolumna stepheni* (Melvill & Standen): Kilburn, 1977: 204.

Syntypes: SAM-A29636. Three worn juveniles, one broken.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Columbella lightfooti Smith, 1901; 112, pl. 1 (fig. 3).

Paratypes: SAM-A6936. Three shells.

Locality: Kalk Bay, False Bay; no depth or date.

Collected by: R. M. Lightfoot.

'*Columbella*' *polyarosus* Barnard, 1959: 182, fig. 35c.

Holotype: SAM-A8875. Shell, broken.

Locality: off Cape Natal; 99 m; 14 December 1900.

Paratype: SAM-A8876. Apex.

Locality: off O'Neil Peak; 165 m; 28 February 1901.

Paratypes: SAM-A8877. Shell, three fragments.

Locality: off Umhloti River; 73 m; 18 December 1900.

Paratype: SAM-A8878. Apex.

Locality: off Hood Point; 90 m; 15 July 1901.

Collected by: R.S. Pieter Faure.

'*Columbella*' *sigma* Barnard, 1959: 185, fig. 36b.

Holotype: SAM-A8890. Shell.

Locality: off Cove Rock, East London; 40 m; 6 August 1901.

Collected by: R.S. Pieter Faure.

'*Columbella*' *vitula* Barnard, 1959: 184, fig. 36a.

Holotype: SAM-A8887. Shell, juvenile.

Locality: off Cove Rock, East London; 80-130 fm.; 30 July 1901.

Collected by: R.S. Pieter Faure.

Pyrene parhelena Barnard, 1959: 177, fig. 36b.

Syntypes: SAM-A8870. Two shells (one broken), radula slide.

Locality: off Cape St. Blaize; 229 m; 21 December 1899.

Collected by: R.S. Pieter Faure.

Pyrene salmoneus Barnard, 1963b: 7.

Syntypes: SAM-A29920. One hundred and fifty-six shells, opercula, many fragments.

Locality: South of Madagascar, 36°48'S 52°08'E; 400 m; 9 July 1961.

Collected by: R.S. Africana II.

Family Nassariidae

Nassa muii Barnard, 1959: 105.

Syntypes: SAM-A29919. Eleven shells.

Locality: uncertain.

Collected by: University of Cape Town.

Nassa rhysonopia Barnard, 1969: 627, fig. 15a.

Holotype: SAM-A29990. Shell, juvenile.

Paratype: SAM-A30551. Shell, juvenile.

Locality: off Cove Rock, East London; 40 m; 6 August 1901.

Collected by: R.S. Pieter Faure.

Nassa scopularcus Barnard, 1959: 120, fig. 24a.

Holotype: SAM-A9230. Shell.

Locality: Late Tertiary marine beds, lagoon shore, south of Bogenfels, South West Africa; 1930.

Collected by: S. H. Haughton, University of Cape Town.

Nassa vidalensis Barnard, 1959: 118, fig. 24b.

Holotype: SAM-A8839. Shell.

Locality: off Cape Vidal; 146–183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Family Fascioliariidae

Fasciolaria agulhasensis Tomlin, 1932: 157, fig. 1

= *Fasciolaria (Pleuroploca) scholveni* Strebel: Kilburn, 1974: 204, fig. 13a.

Holotype: SAM-A6539. Shell.

Locality: Agulhas Bank; 28 fm.; 5 January 1904.

Collected by: R.S. Pieter Faure.

Fasciolaria? holcophorus Barnard, 1959: 98, fig. 21.

Holotype: SAM-A8819. Shell.

Locality: off Cape St. Blaize; 228 m; 21 December 1899.

Collected by: R.S. Pieter Faure.

Fusus africanae Barnard, 1959: 96, figs 19k–20d.

Holotype: SAM-A8610. Shell, juvenile with operculum, radula slide.

Locality: Brown's Bank; 146–183 m; 17 July 1906.

Paratype: SAM-A8826. Shell, juvenile, radula slide.

Locality: off western Cape Peninsula; 256–276 m; 28 March 1900.

Collected by: R.S. Pieter Faure.

Fusus bonaspei Barnard, 1959: 95, fig. 20c–f.

Holotype: SAM-A4632. Shell with operculum.

Locality: doubtful, wrong *Pieter Faure* station number recorded but probably off Cape Point, depth and date unknown.

Paratypes: SAM-A4629. Two shells with opercula.

Locality: off Cape Point, 'NE $\frac{1}{2}$ N 19 miles'; 266 m; 27 February 1902.

Paratype: SAM-A4630. Six shells, one operculum.

Locality: off Cape Hangklip 'NE $\frac{3}{4}$ N 28 miles'; 183 m; 27 August 1903.

Collected by: R.S. Pieter Faure.

Fusus faurei Barnard, 1959: 94, figs 19h–20e.

Syntypes: SAM-A4581. Nine shells, six opercula, radula slide.

Locality: off Cape Point, 'N 41° E 38 miles'; 578–730 m; 16 September 1903.

Syntype: SAM-A4582. Shell.

Locality: off Cape Point, 'NE $\frac{1}{2}$ N 39 miles'; 580–1 020 m; 17 September 1903.

Collected by: R.S. *Pieter Faure*.

Latirus mosselensis Tomlin, 1932: 158, fig. 1.

Syntype: SAM-A3504. Shell.

Locality: off Mossel Bay; 49 m; 14 June 1899.

Collected by: R.S. *Pieter Faure*.

Family *Volutidae*

Fulgoraria blaizei Barnard, 1959: 28, fig. 8b; 1969: 620, fig. 11

= *Fusivoluta blaizei* (Barnard, 1959): Weaver, 1963: 5.

Holotype: SAM-A3433. Shell with operculum.

Locality: off Cape St. Blaize, 'NE $\frac{3}{4}$ E 73 miles'; 192 m; 21 February 1902.

Paratypes: SAM-A3430. Shell, adult, 2 juveniles.

Locality: off Cape St. Blaize, 'N by E 73 miles'; 230 m; 21 December 1889.

Collected by: R.S. *Pieter Faure*.

Glypteuthria capensis Tomlin, 1932: 165; 1945: 135

= *Fusivoluta sculpturata* (Tomlin): Weaver & Dupont, 1970: 185.

Holotype: SAM-A3446. Shell with operculum.

Locality: off Cape Point, 'N 41° E 38 miles'; 593–730 m; 16 September 1903.

Paratype: SAM-A3448. Shell.

Locality: off Cape Point, 'NE by E $\frac{1}{4}$ S 28 miles'; 393–733 m; 28 September 1903.

Collected by: R.S. *Pieter Faure*.

Fusivoluta decussata Barnard, 1959: 31, fig. 8c.

Holotype: SAM-A3432. Shell.

Locality: off East London, Buffalo River, 'N 15 miles'; 566 m; 24 April 1901.

Collected by: R.S. *Pieter Faure*.

Fusivoluta elegans Barnard, 1959: 32, fig. 8a.

Holotype: SAM-A8803. Shell.

Locality: off East London, Buffalo River; 830 m; 17 April 1901.

Collected by: R.S. *Pieter Faure*.

Volutocorbis boswellae Rehder, 1969: 202, pl. 40 (fig. 5), pl. 41 (figs 16–19).

Paratype: SAM-A2010. Shell.

Locality: off Cape St. Blaize, 'N by E $\frac{1}{4}$ E 65 miles'; 155 m; 28 December 1899.

Paratype: SAM-A2011. Shell.

Locality: off Cape St. Blaize, 'N by E $\frac{1}{4}$ E 67 miles'; 164 m; 22 December 1899.

Paratype: SAM-A2009. Shell.

Locality: off Cape Seal, 'N by E $\frac{3}{4}$ E 37 miles'; 146 m; 20 February 1902.

Paratypes: SAM-A31976 (previously SAM-A3335). Six shells.

Locality: Brown's Bank, 36°40'S 21°26'E; 146–183 m; 17 July 1906.

Collected by: R.S. Pieter Faure.

Volutocorbis dispirilis Rehder, 1969: 203, pl. 40 (fig. 4), pl. 41.

Holotype: SAM-A31977 (previously SAM-A3335). Shell.

Paratype: SAM-A33687 (previously SAM-A3335). Shell.

Locality: Brown's Bank, 36°40'S 21°26'E; 146–183 m; 17 July 1906.

Collected by: R.S. Pieter Faure.

Volutilithes gilchristi Sowerby, 1902: 99, pl. 2 (fig. 5)

= *Volutocorbis gilchristi* (Sowerby): Barnard, 1959: 28.

Paratype: SAM-A1974. Shell.

Locality: off Cape Natal, 'W by N $\frac{3}{4}$ N 11 miles'; 189–366 m; 1 April 1901.

Collected by: R.S. Pieter Faure.

Family Marginellidae

Diliculum inopinatum Barnard, 1962a: 14, fig. 1.

Paratypes: SAM-A29917. Three shells, radula slide.

Locality: Saldanha Bay; 3–28 fm.; 5 May 1960.

Collected by: University of Cape Town.

Persicula alborubida Barnard, 1969: 620, fig. 10d.

Holotype: SAM-A30050. Shell.

Locality: Kommetjie; intertidal; no date.

Collected by: C. Connolly.

Paratype: SAM-A30550. Shell.

Locality: Kommetjie; intertidal; no date.

Collected by: C. Connolly.

Persicula nigrocrocea Barnard, 1969: 619, fig. 10b–c.

Holotype: SAM-A30049. Shell.

Locality: Simonstown; no depth or date.

Collected by: C. Connolly.

Paratype: SAM-A30549. Shell.

Locality: Simonstown; no depth or date.

Collected by: C. Connolly.

Marginella brocktoni Shackleford, 1914: 98, two figures.

Syntypes: SAM-A1956. Shell with animal, one shell in pieces.

Locality: off Cape Point, 'N 50° E 18 miles'; 329 m; 27 February 1902.
Collected by: R.S. Pieter Faure.

Marginella differens eugenes Barnard, 1959: 8; 1969: 619, fig. 10a.

Holotype: SAM-A8786. Shell.

Locality: off Umkomaas River; 73 m; 31 December 1900.

Collected by: R.S. Pieter Faure.

Marginella kerochuta Shackleford, 1914: 97, two figures.

Syntypes: SAM-A1954. Two shells.

Locality: off Cape Point, 'NE $\frac{1}{4}$ N 18 miles'; 244 m; 27 February 1902.

Collected by: R.S. Pieter Faure.

Marginella taylori Shackleford, 1916: 194, figs 3-4

= *Marginella differens* Smith: Barnard, 1959: 8.

Syntypes: SAM-A7191. Two shells, one broken.

Locality: off Cape St. Blaize, 'N by E $\frac{1}{2}$ E'; 193 m; no date.

Collected by: R.S. Pieter Faure.

Marginella tomlini Shackleford, 1916: 193, figs 1-2

= *Marginella bicatenata* Sowerby: Barnard, 1959: 6.

Holotype: SAM-A3704. Shell with animal.

Locality: off Cape St. Blaize, 'N by E $\frac{1}{2}$ E 68 miles'; 193 m; 21 February 1902.

Collected by: R.S. Pieter Faure.

Marginella walvisiana Tomlin, 1920: 88, fig. 3.

Syntypes: SAM-A30666. Three shells.

Locality: Walvis Bay; no depth or date.

Collected by: P. R. Frames.

Family Olividae

Ancilla errorum Tomlin, 1921: 216, pl. 8, fig. 2.

Holotype: SAM-A1811. Shell.

Locality: Walker Point, 'NE by N $\frac{1}{2}$ N 7 miles'; 47 fm.; 11 October 1900.

Paratype: SAM-A1816. Shell.

Locality: off Cape Point; 42 fm.; 18 December 1900.

Collected by: R.S. Pieter Faure.

Ancilla rouillardi Kilburn, 1981: 381, figs 6, 50, 87, 88, 99, 104-105.

Paratype: SAM-A1797. Shell.

Locality: ?Cape St. Blaize; 40 fm.; 13 December 1900.

Collected by: R.S. Pieter Faure.

Family **Mitridae**

Charitodoron aglaia Tomlin, 1932: 169, fig. 9

= *Charitodoron agulhasensis* (Thiele): Barnard, 1959: 146.

Holotype: SAM-A30719 (previously A3440). Shell.

Paratype: SAM-A3440. Shell.

Locality: uncertain, no *Pieter Faure* station number recorded.

Collected by: R.S. *Pieter Faure*.

Charitodoron euphrosyne Tomlin, 1932: 167, fig. 8.

Holotype: SAM-A3441. Shell, broken.

Locality: off Cape Point, N 77° E; 1 220–1 275 m; 28 March 1900.

Collected by: R.S. *Pieter Faure*.

Charitodoron thalia Tomlin, 1932: 169, fig. 10.

Holotype: SAM-A8602 (previously A1742). Shell, radula slide.

Locality: off Cape Point; 240 m; 28 March 1900.

Collected by: R.S. *Pieter Faure*.

Mitra (Dibaphus) bathybius Barnard, 1959: 51, figs 11a–13b.

Holotype: SAM-A8827. Shell, broken, radula slide.

Locality: off Cape Natal; 805 m; 4 April 1901.

Collected by: R.S. *Pieter Faure*.

Mitra (Mitra) boswellae Cate, 1964: 219, pl. 28 (fig. 1a–b)

= *Mitra guttata* Swainson: Cernohorsky, 1976: 326.

Holotype: SAM-A29799. Shell.

Locality: uncertain; no date.

Collected by: probably commercial trawler.

Mitra fidis Sowerby, 1916: 491, text figure

= *Pusia patula* (Reeve): Barnard, 1958: 58.

Syntypes: SAM-A29918. Two shells.

Locality: 'South Africa'; no date.

Donated by: A. E. Salisbury, 1957.

Family **Cancellariidae**

Admete decapensis Barnard, 1960: 439, fig. 1a.

Holotype: SAM-A9777. Shell, partly corroded.

Locality: off Cape Point, 34°37'S 17°03'E; 3 070–3 150 m; December 1959.

Collected by: R.S. *Africana II*.

Cancellaria euetrios Barnard, 1959: 14, fig. 3.

Holotype: SAM-A8747. Shell.

Locality: off Cape Recife, 34°26'S 25°42'E; 227 m; 14 November 1898.
Collected by: R.S. *Pieter Faure*.

Cancellaria euthymei Barnard, 1960: 438, fig. 16.

Holotype: SAM-A9888. Shell.

Locality: off Cape Point, 34°26'S 17°00'E; 2 750–3 260 m; December 1959.
Collected by: R.S. *Africana II*.

Cancellaria producta Sowerby, 1903: 220, pl. 4 (fig. 5).

Syntype: SAM-A339. Shell.

Locality: off Umhloti River; 73 m; 21 December 1900.
Collected by: R.S. *Pieter Faure*.

Family Conidae

Conus eucoronatus Sowerby, 1903: 217, pl. 3 (fig. 9).

Holotype: SAM-A1753. Shell.

Locality: off Cape St. Blaize, 'N 85° W 4,5 miles'; 27 fm.; 15 June 1899.
Collected by: R.S. *Pieter Faure*.

Conus gilchristi Sowerby 1903: 217, pl. 3 (fig. 8)

= *Conus natalis* Sowerby: Walls, 1979: 757.

Holotype: SAM-A1752. Shell.

Locality: Umhlangkulu River mouth, 'NW by N 7,5 miles'; 50 fm.; 14
March 1901.
Collected by: R.S. *Pieter Faure*.

Conus patens Sowerby, 1903: 218, pl. 3 (fig. 7).

Holotype: SAM-A1756. Shell.

Locality: Vasco de Gama Peak, 'N 10° E 13 miles'; 85 fm.; 3 May 1900.
Collected by: R.S. *Pieter Faure*.

Family Terebridae

Terebra (Abretia) lightfooti Smith, 1899: 247, pl. 6 (fig. 1).

Paratype: SAM-5519. Shell.

Locality: Table Bay; 10 fm.; no date.
Collected by: R. M. Lightfoot.

Terebra planecosta Barnard, 1958: 81, fig. 1a–b.

Holotype: SAM-A8659. Shell.

Locality: off Cove Rock, '4,5 miles'; 22 fm.; 6 August 1901.
Collected by: R.S. *Pieter Faure*.

Paratypes: SAM-A8658. Two shells.

Locality: off Cape St. Blaize, 'N by E 73 miles'; 125 fm.; 21 December 1899.
Collected by: R.S. *Pieter Faure*.

Terebra thielei Barnard, 1958: 80, fig. 1d.

Syntypes: SAM-A8657. Four shells.

Locality: Algoa Bay; 67 fm.; 10 November 1898.

Collected by: R.S. Pieter Faure.

Family Turridae

'*Acrobella*' *acus* Barnard, 1958: 149, fig. 21e.

Syntypes: SAM-A8748. Two shells, one fragment.

Locality: off Cape Recife, 34°27'S 25°42'E; 468 m; 16 November 1898.

Collected by: R.S. Pieter Faure.

'*Bela*' *bella* Barnard, 1958: 140, fig. 21c.

Syntypes: SAM-A8639. Three shells.

Locality: off Cape Agulhas; 146–183 m; 17 July 1903.

Collected by: R.S. Pieter Faure.

Clavatula lobatopsis Barnard, 1963c: 420, fig. 2a.

Syntypes: SAM-A9730. Three shells with opercula, radula slide.

Locality: 33°36'S 16°15'E; 2 780–2 880 m; August 1959.

Collected by: R.S. *Africana II*.

'*Cythara*' *dagama* Barnard 1963c: 423, fig. 2g–h.

Syntypes: SAM-A9731. Four shells, three with animals.

Locality: 33°36'S 16°15'E; 2 790–2 890 m; August 1959.

Collected by: R.S. *Africana II*.

'*Cythara*' *deliciosa* Barnard, 1958: 151, fig. 24

= *Eucithera deliciosa* (Barnard): Barnard, 1969: 610.

Syntypes: SAM-A8692. Six shells.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Cythara? *glaucocreas* Barnard, 1963c: 422, fig. 2d.

Holotype: SAM-A9821. Shell, radula slide.

Locality: 33°52'S 16°51'E; 2 430–2 790 m; December 1959.

Paratype: SAM-A9753. Shell.

Locality: 33°49'S 16°30'E; 2 750 m; August 1959.

Collected by: R.S. *Africana II*.

Daphnella? *bitrudis* Barnard, 1963c: 428, fig. 1b.

Syntypes: SAM-A9754. Two shells.

Locality: 33°49'S 16°30'E; 2 750 m; August 1959.

Collected by: R.S. *Africana II*.

Daphnella recifensis Barnard, 1958: 161, fig. 30a.

Holotype: SAM-A8757. Shell.

Locality: off Cape Recife, 34°27'S 25°42'E; 468 m; 14 November 1898.

Collected by: R.S. Pieter Faure.

Daphnella? verecunda Barnard, 1963c: 427, fig. 2e.

Syntypes: SAM-A9697. Three shells, one with animal.

Locality: 33°50'S 17°21'E; 1 100 m; August 1959.

Collected by: R.S. Africana II.

Drillia armilla Barnard, 1958: 137.

Holotype: SAM-A8714. Shell.

Locality: off Cove Rock; 146–239 m; 30 July 1901.

Collected by: R.S. Pieter Faure.

Drillia bruchia Barnard, 1958: 130, fig. 13b.

Holotype: SAM-A8717. Shell, apex missing.

Locality: off Cape Natal; 440 fm.; 4 April 1901.

Collected by: R.S. Pieter Faure.

Drillia collina Barnard, 1958: 129, fig. 13b.

Syntype: SAM-A8587. Shell.

Locality: off East London; 32 fm.; 1898.

Syntypes: SAM-A8710. Shell, two fragments.

Locality: off Hood Point; 49 fm.; 1901.

Collected by: R.S. Pieter Faure.

Drillia diasi Barnard, 1958: 137, fig. 19b.

Syntypes: SAM-A8566. Two shells.

Locality: 34°26'S 25°42'E; 124 fm.; 1898.

Collected by: R.S. Pieter Faure.

Drillia dovyalis Barnard, 1969: 606, fig. 6a.

Holotype: SAM-A29760. Shell.

Locality: off Sandy Point; 93 m; 14 August 1901.

Collected by: R.S. Pieter Faure.

Drillia erepta Barnard, 1969: 609, fig. b.

Syntype: SAM-A8734. Shell.

Locality: off Cape Morgan; 47 fm.; 25 July 1901.

Collected by: R.S. Pieter Faure.

Syntype: SAM-A29763. Shell.

Locality: 33°50'S 25°54'E (Algoa Bay); ?30 fm.; 11 November 1898.

Collected by: R.S. Pieter Faure.

Syntypes: SAM-A29764. Two shells.

Locality: off Cape St. Blaize; 125 fm.; 21 December 1899.
Collected by: R.S. Pieter Faure.

Drillia falcicosta Barnard, 1958: 132, fig. 15b.

Syntypes: SAM-A8724. Two shells, one apex.
Locality: off Umhloti River; 40 fm.; 1900.
Collected by: R.S. Pieter Faure.

Drillia laterculoides Barnard, 1958: 129, fig. 12c.

Syntypes: SAM-A8709. Shell, apex.
Locality: off Hood Point; 90 m; 15 July 1901.
Collected by: R.S. Pieter Faure.

Drillia latisulcus Barnard, 1958: 131, fig. 13c.

Syntypes: SAM-A8718. Five shells.
Locality: off Hood Point; 90 m; 15 July 1901.
Collected by: R.S. Pieter Faure.

Drillia morgana Barnard, 1958: 133, fig. 16.

Holotype: SAM-A8739. Shell.
Locality: off Cape Morgan; 47 fm.; 25 July 1901.
Collected by: R.S. Pieter Faure.

Drillia omia Barnard, 1958: 123, fig. 11a.

Syntypes: SAM-A8651. Ten shells.
Locality: ?Port Alfred, probably Table Bay-Saldanha Bay.
Collector unknown.

Drillia oneili Barnard, 1958: 133, fig. 15c.

Holotype: SAM-A8731. Shell, slightly worn.
Locality: off O'Neil Peak; 90 fm.; 1901.
Collected by: R.S. Pieter Faure.

Drillia pecus Barnard, 1969: 607, fig. 5b.

Holotype: SAM-A29761. Shell.
Locality: off East London; 400-450 fm.; 17 April 1901.
Collected by: R.S. Pieter Faure.

Drillia perfluans Barnard, 1958: 132, fig. 15a.

Holotype: SAM-A8716. Shell.
Locality: off Hood Point; 49 fm.; 15 July 1901.
Collected by: R.S. Pieter Faure.

Drillia pleonastica Barnard, 1958: 133, fig. 17a.

Holotype: SAM-A8565. Shell.
Locality: 34°26'S 25°42'E; 228 m; 14 November 1898.
Collected by: R.S. Pieter Faure.

Drillia pselia Barnard, 1958: 138.

Syntypes: SAM-A8715. Shell, two broken shells.
Locality: off Cape St. Blaize; 125 fm.; 1899.
Collected by: R.S. Pieter Faure.

Drillia simplicingula Barnard, 1958: 135, fig. 18b.

Holotype: SAM-A8666. Shell.
Locality: off Hood Point; 49 fm.; 15 July 1901.
Paratype: SAM-A3471. Shell.
Locality: off Cape Morgan; 104 m; 6 February 1901.
Collected by: R.S. Pieter Faure.

Drillia spiralis Barnard, 1958: 134, fig. 17b.

Holotype: SAM-A8583. Shell.
Locality: off Cape St. Blaize; 228 m; 21 December 1899.
Collected by: R.S. Pieter Faure.

Drillia tholos Barnard, 1958: 130, fig. 14.

Syntypes: SAM-A8735. Fourteen shells.
Locality: off Hood Point; 49 fm.; 15 July 1901.
Collected by: R.S. Pieter Faure.

Mangilia (Eucythara) africana Sowerby, 1903: 21, pl. 5 (fig. 9)

= *Cythara africana* (Sowerby): Barnard, 1958: 115.

Holotype: SAM-A345. Shell.
Paratype: SAM-A33954. Shell, broken, outer lip thin.
Locality: off Umhloti River; 46 m; 18 December 1900.
Collected by: R.S. Pieter Faure.

Mangilia extans Barnard, 1958: 156, fig. 27c.

Holotype: SAM-A8756. Shell.
Locality: off Cove Rock; 40 m; 6 August 1901.
Collected by: R.S. Pieter Faure.

Mangilia muiri Barnard, 1958: 153, fig. 26a.

Syntypes: SAM-A8647. Seven shells, in growth series.
Locality: Still Bay; intertidal; 1921.
Muir Collection.

Mangilia phoxos Barnard, 1958: 155, fig. 27b.

Holotype: SAM-A8730. Shell.
Locality: off Umhloti River; 73 m; 18 December 1900.
Collected by: R.S. Pieter Faure.

Mangilia sciola Barnard, 1958: 157, fig. 28c.

Syntype: SAM-A8642. Shell.

Locality: off Cape Recife, 34°27'S 25°42'E; 468 m; 14 November 1898.

Syntype: SAM-A8643. Shell.

Locality: near East London, 33°06'S 27°55'E; 78 m; 14 November 1898.

Collected by: R.S. Pieter Faure.

Mangilia serrula Barnard, 1964c: 15, fig. 1a-b.

Syntypes: SAM-A8728. Five shells.

Locality: off Illovo and Umkomaas; 30-40 fm.; 31 December 1900.

Collected by: R.S. Pieter Faure.

Mangilia tranquilla Barnard, 1958: 158, fig. 28b.

Syntypes: SAM-A8648. Five shells.

Locality: Still Bay; intertidal; no date.

Collected by: J. Muir.

Mangilia translucens Barnard, 1958: 155, fig. 27a.

Syntypes: SAM-A8586. Twelve shells.

Locality: off Umhloti River mouth; 40 fm.; 28 December 1898.

Collected by: R.S. Pieter Faure.

Mitramorpha veneris Barnard, 1964c: 16.

Holotype: SAM-A8750. Shell, broken.

Locality: off Cape Vidal; 146-183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Monilopsis psilarosis Barnard, 1963c: 421, fig. 4a.

Syntypes: SAM-A9789. Two shells, radula slide.

Locality: 34°42'S 16°54'E; 3 140-3 270 m; December 1959.

Collected by: R.S. *Africana II*.

Philbertia natalensis Barnard, 1958: 158, fig. 29a.

Syntype: SAM-A8654. Shell.

Locality: off Umhloti River mouth; 40 fm.; 18 December 1900.

Collected by: R.S. Pieter Faure.

Syntype: SAM-A8758. Shell.

Locality: off Cape Natal, 54 fm.; 14 December 1900.

Collected by: R.S. Pieter Faure.

Pleurotoma (Genotia) belaeformis Sowerby, 1903: 216, pl. 4 (fig. 8)

= '*Genotia*' *belaeformis* (Sowerby): Barnard, 1958: 112, figs 8b-9b.

Paratypes: SAM-A1687. Two shells.

Locality: off Cape Point; 230 fm.; 4 May 1900.

Collected by: R.S. Pieter Faure.

'*Pleurotoma*' *curricula* Barnard, 1969: 612, fig. 8.

Syntypes: SAM-A9859. Shell, two broken.

Locality: 34°36'S 17°00'E; 2 750-3 200 m; December 1959.

Collected by: R.S. *Africana II*.

Pleurotoma (*Drillia*) *fossata* Sowerby, 1903: 214, pl. 3 (fig. 5)

= *Drillia fossata* (Sowerby): Barnard, 1958: 135.

Holotype: SAM-A346. Shell.

Paratype: SAM-A346. Shell.

Locality: off Cape Vidal; 80-100 fm.; 27 February 1901.

Collected by: R.S. *Pieter Faure*.

Pleurotoma (*Clavus*) *lignaria* Sowerby, 1903: 215, pl. 3 (fig. 4)

= *Turris lignaria* (Sowerby): Barnard, 1958: 102.

Paratype: SAM-A357. Shell.

Locality: off Table Bay; 240 m; 28 March 1900.

Collected by: R.S. *Pieter Faure*.

Pleurotoma (*Surcula*) *lobata* Sowerby, 1903: 213, pl. 4 (fig. 9)

= *Turris lobata* (Sowerby): Barnard, 1958: 107, fig. 3i-j.

Syntypes: SAM-A1673. Five shells, radula slide.

Locality: off Cape Natal; 810 m; 4 April 1901.

Syntypes: SAM-A1674. Three shells, one with operculum.

Locality: off Buffalo River, East London; 560 m; 24 April 1901.

Collected by: R.S. *Pieter Faure*.

Pleurotoma (*Drillia*) *scitecostata* Sowerby, 1903: 214, pl. 4 (fig. 10)

= '*Drillia*' *scitecostata* (Sowerby): Barnard, 1958: 119, figs 8f, 20.

Syntypes: SAM-A347. Two shells.

Locality: off Glendower Beacon; 100 fm.; 10 September 1901.

Collected by: R.S. *Pieter Faure*.

Pleurotoma (*Clavatula*) *turriplana* Sowerby, 1903: 215, pl. 3 (fig. 6)

= *Clavatula turriplana* Sowerby: Barnard, 1958: 144.

Holotype: SAM-A1646. Shell.

Locality: off Cape St. Blaize, 'N by E $\frac{1}{4}$ E 65 miles'; 155 m; 22 December 1899.

Collected by: R.S. *Pieter Faure*.

Surcula aditus Barnard, 1969: 604, fig. 4a.

Holotype: SAM-A29759. Shell.

Locality: off Cove Rock; 22 fm.; 6 August 1901.

Collected by: R.S. *Pieter Faure*.

Surcula amplisulcus Barnard, 1958: 147, fig. 22a.

Syntypes: SAM-A1689. Five shells.

Locality: west coast of Cape Peninsula; 120 fm.; 4 April 1902.

Collected by: R.S. Pieter Faure.

Surcula faurei Barnard, 1958: 147, fig. 22b.

Holotype: SAM-A8611. Shell.

Locality: Brown's Bank, 36,5°S 21°E; 80–100 fm.; 17 July 1906.

Collected by: R.S. Pieter Faure.

Surcula scalaria Barnard, 1958: 146, fig. 22d.

Syntypes: SAM-A358. Seven shells.

Locality: off Cape Point; 480–800 fm.; 10 September 1903.

Collected by: R.S. Pieter Faure.

Surcula sulcancellata Barnard, 1958: 145, fig. 22c.

Syntypes: SAM-A361. Five shells.

Locality: off Cape Point; 130–300 fm.; 28 September 1903.

Collected by: R.S. Pieter Faure.

Turris ambages Barnard, 1958: 148, fig. 23b.

Syntypes: SAM-A8683. Two shells.

Locality: off Cape Natal; 54 fm.; 14 December 1900.

Collected by: R.S. Pieter Faure.

Syntype: SAM-A8684. Shell.

Locality: off Umkomaas River; 40 fm.; 31 December 1900.

Collected by: R.S. Pieter Faure.

Syntype: SAM-A8685. Shell.

Locality: off O'Neil Peak; 90 fm.; 28 February 1901.

Collected by: R.S. Pieter Faure.

Turris saldanhae Barnard, 1958: 109, figs 3f, 7.

Syntypes: SAM-A1738. Seventeen shells.

Locality: Baboon Point, Saldanha Bay; 31 fm.; 18 March 1902.

Collected by: R.S. Pieter Faure.

Typhlomangilia? polythele Barnard, 1963c: 422, fig. 3e–f.

Syntypes: SAM-A9802. Two shells.

Locality: 33°50'S 16°30'E; 1 480–1 660 fm.; December 1950.

Collected by: F. H. Talbot.

Typhlosyrinx chrysopelex Barnard, 1963c: 425, fig. 3g.

Holotype: SAM-A9857. Shell.

Locality: 34°36'S 17°00'E; 1 500–1 760 fm.; December 1959.

Collected by: F. H. Talbot.

Typhlosyrinx pyrropelex Barnard, 1963c: 423, fig. 2c.

Syntypes: SAM-A1643. Two shells.

Locality: off Cape Point, N 77° E; 650–700 fm.; 29 July 1903.

Collected by: R. S. Pieter Faure.

Syntypes: SAM-A9858. Three shells, juveniles with animals.

Locality: 34°36'S 17°00'E; 1 500–1 760 fm.; December 1959.

Collected by: F. H. Talbot.

Typhlosyrinx subrosea Barnard, 1963c: 425, fig. 3a–d.

Holotype: SAM-A9822. Shell with animal.

Locality: 33°52'S 16°51'E; 1 380–1 520 fm.; December 1959.

Collected by: F. H. Talbot.

Paratype: SAM-A9822. Shell.

Locality: 33°52'S 16°51'E; 1 380–1 520 fm.; December 1959.

Collected by: F. H. Talbot.

Subclass OPISTHOBRANCHIA

Family Acteonidae

Solidula niecaensis Barnard, 1963d: 317

= *Pupa niecaensis* (Barnard): **comb. nov.**

Holotype: SAM-A6553. Shell.

Locality: off Nieca River; 80 m; 7 August 1901.

Collected by: R.S. Pieter Faure.

Family Retusidae

Retusa natalensis Barnard, 1963d: 321, fig. 28a.

Syntypes: SAM-A9409. Two shells.

Locality: off Umkomaas River; 40 fm.; 1900.

Collected by: R.S. Pieter Faure.

Volvula mutabilis Barnard, 1963d: 322, fig. 28b.

Syntypes: SAM-A9410. Two shells.

Locality: off Umhloti River; 40 fm.; 1900.

Collected by: R.S. Pieter Faure.

Family Scaphandridae

Acteocina natalensis Barnard, 1963d: 324, fig. 28c.

Syntypes: SAM-A9388. Two shells.

Locality: off Illovo River; 27–30 fm.; 1900.

Collected by: R.S. Pieter Faure.

Family **Doridoxidae**

Doridoxa benthalis Barnard, 1963c: 443, fig. 10.

Holotype: SAM-A9796. Animal, preserved, jaws, radula slide.

Locality: 34°42'S 16°54'E; 1 725-1 780 fm.; December 1959.

Collected by: F. H. Talbot.

Family **Chromodorididae**

Glossodoris capensis Barnard, 1927: 181, pl. 19 (figs 3-4)

= *Hypselodoris capensis* (Barnard): **comb. nov.**

Syntypes: SAM-A6230. Two animals, preserved, two pairs jaws, two radula slides.

Locality: St. James, False Bay; intertidal; April 1912.

Collected by: K. H. Barnard.

Family **Polyceridae**

Polycera nigrocrocea Barnard, 1927: 191, pl. 19 (figs 7-8)

= *Polycera capensis* Quoy & Gaimard: Pruvot-Fol, 1934: 75.

Syntype: SAM-A6225. Two animals, preserved, radula.

Locality: St. James; intertidal; March 1912.

Collected by: K. H. Barnard.

Plocamopherus apheles Barnard, 1927: 195, fig. 1.

Holotype: SAM-A6232. Animal, preserved, jaws, radula slide.

Locality: Nahoon estuary, East London; no depth; 31 May 1901.

Collected by: J. D. F. Gilchrist.

Family **Goniodorididae**

Goniodoris ovata Barnard, 1934: 2, 2 text figures.

Holotype: SAM-A6270. Animal, preserved.

Paratype: SAM-A6270. Radula slide.

Locality: Simonstown; from boat hull; June 1933.

Collected by: K. H. Barnard.

Family **Janolidae**

Bonisa nakaza Gosliner, 1981: 19, figs 1d-f, 18-25.

Holotype: SAM-A34886. Animal, preserved.

Paratypes: SAM-A34887. Four animals, preserved.

Locality: off Llandudno, 34°01'S 18°20'E; 20 m; 23 December 1979.

Collected by: W. R. Liltved.

Janolus longidentatus Gosliner, 1981: 9, figs 1c, 10–17.

Holotype: SAM–A34883. Animal, preserved.

Locality: Miller's Point, 34°14'S 18°29'E; 3 m; 10 December 1980.

Collected by: T. M. Gosliner.

Paratypes: SAM–A34884. Two animals, preserved.

Locality: Castle Rocks, 34°18'S 18°29'E; 10 m; 1 October 1980.

Collected by: T. M. Gosliner.

Paratype: SAM–A34885. Animal, preserved.

Locality: Miller's Point, 34°14'S 18°29'E; 5 m; 11 July 1980.

Collected by: T. M. Gosliner.

Family **Flabellinidae**

Flabellina funeka Gosliner & Griffiths, 1981: 106, figs 1a, 2–4.

Holotype: SAM–A34317. Animal, preserved.

Locality: Castle Rocks, 34°14'S 18°29'E; 10 m; 17 January 1980.

Collected by: T. M. Gosliner.

Paratype: SAM–A34318. Animal, preserved.

Locality: Castle Rocks, 34°14'S 18°29'E; 10 m; 17 January 1980.

Collected by: T. M. Gosliner.

Paratype: SAM–A34319. Animal, preserved.

Locality: Venus Pool, 34°17'S 18°28'E; 10 m; 6 January 1980.

Collected by: T. M. Gosliner.

Paratype: SAM–A34320. Animal, preserved.

Locality: Hermanus, 34°17'S 19°15'E; 17 m; 11 October 1971.

Collected by: R. J. Griffiths.

Paratype: SAM–A34321. Animal, preserved.

Locality: Hermanus, 34°17'S 19°15'E; 17 m; 11 October 1971.

Collected by: R. J. Griffiths.

Family **Tergipedidae**

Catriona casha Gosliner & Griffiths, 1981: 130, figs 12–14.

Holotype: SAM–A34871. Animal, preserved.

Paratypes: SAM–A34872. Five animals, preserved.

Locality: Cape Town docks, 33°54'S 18°26'E; 1 m; 26 June 1972.

Collected by: R. J. Griffiths.

Family **Facelinidae**

Facelina faurei Barnard, 1927: 205, figs. 4–5

= *Pruvotfolia faurei* (Barnard): Tardy, 1969: 343.

Syntypes: SAM–A6249. Several animals, preserved, jaws, radula slide.

Locality: off Saldanha Bay; 33 fm.; 12 March 1902.

Collected by: R.S. Pieter Faure.

Favorinus horridus Macnae, 1954: 19, pl. 1 (fig. 4) figs 11–13

= *Phyllodesmium serratum* (Baba): Baba, 1955: 56.

Paratypes: SAM–A29578. Fifteen animals, preserved.

Locality: '½ mile S of Kalk Bay Harbour'; intertidal; 1949.

Collected by: W. Macnae.

Hervia quadricolor Barnard, 1927: 203, pl. 20 (figs 9–10)

= *Godiva quadricolor* (Barnard): Macnae, 1954: 23.

Holotype: SAM–A6248. Animal, preserved.

Locality: St. James (False Bay); intertidal; 20 June 1912.

Collected by: K. H. Barnard.

Family Cratenidae

Cratena capensis Barnard, 1927: 204, pl. 20 (fig. 8).

Syntype: SAM–A6247. Jaws, radula slide.

Locality: Sea Point; intertidal; 29 November 1913.

Collected by: K. H. Barnard.

Family Aeolidiidae

Aeolidiella saldanhensis Barnard, 1927: 201, figs 2–3

= *Aeolidiella indica* Bergh: Gosliner & Griffiths, 1981: 119.

Syntype: SAM–A6257. Jaws, radula slide.

Locality: Saldanha Bay; intertidal; 5 September 1912.

Collected by: R.S. Pieter Faure.

Subclass PULMONATA

Family Siphonariidae

Siphonaria (Patellopsis) anneae Tomlin, 1944: 92, text figure.

Syntypes: SAM–A2988. Two shells.

Locality: Umhlali; no depth or date.

Collected by: H. C. Burnup.

Siphonaria cyaneomaculata Sowerby, 1906: 37, text figure

= *Siphonaria (Patellopsis) deflexa* (Helbling): Allanson, 1958: 159.

Syntypes: SAM–A3330. Two shells.

Locality: Kowie, Port Alfred; intertidal; 1915.

Collected by: H. Becker.

Siphonaria (Patellopsis) dayi Allanson, 1958: 169, pl. 16 (figs 10–15), text figure.

Holotype: SAM–A32707. Shell.

Locality: Delagoa Bay; no depth or date.

Collected by: University of Cape Town.

Paratypes: SAM–A33403. Three shells.

Locality: Inhaca Island; no depth; 30 December 1958.

Collected by: University of Cape Town.

Siphonaria (Siphonaria) aspera pallida Allanson, 1958: 171, pl. 4, fig. 17.

Syntypes: SAM–A33402. Four shells.

Locality: Langebaan Lagoon; intertidal; 25 April 1949.

Collected by: University of Cape Town.

Class SCHAPHOPODA

Family Dentaliidae

Dentalium africanum Sowerby, 1903: 224, pl. 5 (fig. 10).

Paratypes: SAM–A5489. Six shells, radula slide.

Locality: off Umtwalumi River; 25 fm.; 22 March 1901.

Collected by: R.S. Pieter Faure.

Dentalium (Compressidens) capense Tomlin, 1931: 340.

Holotype: SAM–A6191. Shell.

Locality: off Cape Point; 900 fm.; 19 August 1903.

Collected by: R.S. Pieter Faure.

Dentalium engischistum Barnard, 1963d: 352, fig. 30f.

Syntypes: SAM–A5463. Six shells, two with animals, one broken, radula slide.

Locality: off Cape Natal; 62 fm.; 1900.

Collected by: R.S. Pieter Faure.

Dentalium eualdes Barnard, 1963c: 444.

Syntypes: SAM–A9736. Two shells, radula slide.

Locality: 33°36'S 16°15'E; 2 780–2 880 m; August 1959.

Collected by: R.S. Africana II.

Dentalium lardum Barnard, 1963c: 445.

Syntypes: SAM–A9768. Three shells.

Locality: 33°39'S 16°30'E; 1 500 fm.; August 1959.

Collected by: R.S. Africana II.

Dentalium natalense Barnard, 1963d: 350, fig. 30e.

Syntypes: SAM-A9364. Forty-nine shells.

Locality: off Cape Natal; 85 fm.; 17 December 1900.

Collected by: R.S. Pieter Faure.

Dentalium (Fissidentalium) platypleurum Tomlin, 1931: 339, text figure.

Holotype: SAM-A3631. Shell.

Locality: off Itongazi River; 25 fm.; 14 March 1901.

Collected by: R.S. Pieter Faure.

Dentalium salpinx Tomlin, 1931: 338, text figure.

Holotype: SAM-A5459. Shell.

Paratypes: SAM-A5459. Nine shells.

Locality: off Cape Point, 'NE $\frac{3}{4}$ E, 40 miles'; 700-800 fm.; 15 September 1903.

Collected by: R.S. Pieter Faure.

Dentalium subterlineatum Tomlin, 1931: 337.

Holotype: SAM-A6192. Shell.

Locality: off Cape Point; 900 fm.; 19 August 1903.

Collected by: R.S. Pieter Faure.

Family **Cadulidae**

Cadulus promontorii Barnard, 1963d: 353, fig. 30h-l.

Syntypes: SAM-A7460. Four shells, radula slide.

Locality: off Cape Point; 700 fm.; 20 August 1903.

Collected by: R.S. Pieter Faure.

Class BIVALVIA

Family **Nuculidae**

Nucula aequalitas Barnard, 1964a: 365.

Holotype: SAM-A9472. Two valves.

Locality: off East London; 732-915 m; 17 April 1901.

Collected by: R.S. Pieter Faure.

Nucula fragilis Boshoff, 1968: 95, pl. 8a, text fig. 1.

Syntypes: SAM-A30212. Two valves.

Locality: 29°34'S 31°39'E; 115-118 m; 9 September 1964.

Collected by: R.V. Anton Bruun.

Nucula irregularis Sowerby, 1904: 7, pl. 6 (fig. 12).

Paratypes: SAM-14843. Two valves.

Locality: off Struis Point; 28 m; 17 July 1902.

Collected by: R.S. *Pieter Faure*.

Nucula sculpturata Sowerby, 1904: 7, pl. 6 (fig. 11)

= *Nucula pulchra* Hinds: Barnard, 1964a: 362.

Paratypes: SAM-14830. Ten valves, three with dry animals.

Locality: 33°03'S 27°57'E; 62 m; 28 December 1898.

Collected by: R.S. *Pieter Faure*.

Family Malletiidae

Malletia estheriopsis Barnard, 1963c: 447, fig. 11b.

Syntypes: SAM-A9817. Four valves.

Locality: 33°50'S 16°30'E; 2 700-3 040 m; December 1959.

Collected by: F. H. Talbot on R.S. *Africana II*.

Family Nuculanidae

Leda lanceta Boshoff, 1968: 96, pl. 8b-c.

Holotype: SAM-A30213. Two valves.

Locality: 29°21'S 31°58'E; 370 m; no date.

Collected by: R.V. *Anton Bruun*.

Leda macella Barnard, 1963c: 448, fig. 11d

= *Nuculana vestita* (Locard): Knudsen, 1970: 28, fig. 11.

Syntypes: SAM-A9851. Sixty-six complete shells, nine valves.

Locality: 34°05'S 16°58'E; 2 690-2 720 m; December 1959.

Collected by: F. H. Talbot on R.S. *Africana II*.

Leda parceplicata Barnard, 1964b: 21

= *Portlandia (Portlandia) parceplicata* (Barnard): Kilburn, 1973b: 698.

Syntypes: SAM-A9465. Thirty-nine complete shells, 157 valves.

Locality: off Umhloti River, Natal; 73 m; 18 December 1900.

Collected by: R.S. *Pieter Faure*.

Leda parsimonia Barnard, 1963c: 448.

Holotype: SAM-A9818. Two valves.

Locality: 33°50'S 16°30'E; 2 700-3 040 m; August 1959.

Collected by: F. H. Talbot on R.S. *Africana II*.

Nuculana compta Sowerby, 1904: 6, pl. 6 (fig. 10)

= *Leda compta* (Sowerby): Barnard, 1964a: 367, fig. 1a.

Paratype: SAM-14818. Two valves.

Locality: off Cape Natal; 805 m; 4 April 1901.

Collected by: R.S. *Pieter Faure*.

Nuculana gemmulata Sowerby, 1904: 6, pl. 6 (fig. 9)

= *Leda gemmulata* (Sowerby): Barnard 1964a: 366.

Paratypes: SAM-14785. Four valves.

Locality: off Tugela River; 68 m; 29 January 1901.

Collected by: R.S. Pieter Faure.

Nuculana lamellata Sowerby, 1904: 5, pl. 6 (fig. 8)

= *Leda lamellata* (Sowerby): Barnard, 1964a: 366.

Paratypes: SAM-14787. Sixteen complete shells, thirteen valves.

Locality: off Cape Natal; 99 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Sarepta natalensis Barnard, 1964c: 22, fig. 4a.

Holotype: SAM-A9474. Valve.

Locality: off Cape Natal; 90 m; 14 December 1900.

Paratypes: SAM-A9470. Seven valves.

Locality: off Tugela River, Natal; 110-146 m; 11 January 1901.

Collected by: R.S. Pieter Faure.

Family Arcidae

Arca (Scapharca) africana Sowerby, 1904: 4, pl. 6 (fig. 4).

Paratypes: SAM-14831. Complete shell with animal, two valves.

Locality: off Tugela River; 84-100 m; 6 February 1901.

Collected by: R.S. Pieter Faure.

Deltaodon tugelae Barnard, 1962b: 249, figs 2a-e. Kilburn, 1973b: 699.

Lectotype: SAM-A31736. One valve.

Paralectotypes: SAM-A9477. Eighteen valves.

Locality: off Zululand; no depth or date.

Collected by: R.S. Pieter Faure.

Family Limopsidae

Limopsis natalis Barnard, 1964b: 23, figs.

Syntypes: SAM-A9479. Complete shell, two valves.

Locality: off O'Neil Peak, Natal; 103 m; 28 February 1901.

Collected by: R.S. Pieter Faure.

Family Mytilidae

Crenella striatissima Sowerby, 1904: 3, pl. 6 (fig. 1). Barnard 1964a: 403.

Holotype: SAM-14855. Two valves.

Locality: 37°07'S 25°40'E; 106 m; 14 November 1898.

Paratype: SAM-14856. Valve, broken.

Locality: off Umhloti River, Natal; 183 m; 19 December 1900.
Collected by: R.S. *Pieter Faure*.

Gregariella simplicifilis Barnard, 1964a: 402.

Syntypes: SAM-6878. Five complete shells, animals in three, five valves.
Locality: Gordon's Bay, False Bay; intertidal; no date.
Collected by: R. M. Lightfoot.

Musculus (Musculus) virgiliae Barnard, 1964a: 399, fig. 8d.

Syntypes: SAM-A7776. Six complete shells, two valves, one broken.
Locality: Keurbooms River, eastern Cape; intertidal; 1931.
Collected by: K. H. Barnard.

Septifer bisculpturata Barnard, 1964c: 23, fig. 4c-d.

Holotype: SAM-A9482. Valve.
Locality: off Tugela River, Natal; 86 m; 29 January 1901.
Collected by: R.S. *Pieter Faure*.

Family **Pectinidae**

Chlamys fultoni Sowerby, 1904: 2, pl. 6 (fig. 5).

Paratype: SAM-14970. Valve.
Locality: off Amatikulu River, Natal; 48 m; 1 February 1901.
Collected by: R.S. *Pieter Faure*.

Chlamys gilchristi Sowerby, 1904: 1, pl. 6 (fig. 6). Barnard 1964a: 427.

Holotype: SAM-14853. Shell, complete.
Locality: False Bay; 416 m; 4 May 1900.
Collected by: R.S. *Pieter Faure*.

Chlamys humilis Sowerby, 1904: 3, pl. 6 (fig. 3)

= *Chlamys tinctus* (Reeve): Barnard, 1964a: 425.

Paratype: SAM-14858. Shell, complete.
Locality: off Cape St. Blaize, Mossel Bay; 167-183 m; 20 December 1900.
Collected by: R.S. *Pieter Faure*.

Cyclopecten incubans Barnard, 1964a: 432.

Syntypes: SAM-A9493. Twelve valves.
Locality: off Cape St. Blaize; 230 m; 21 December 1899.
Collected by: R.S. *Pieter Faure*.

Cyclopecten vidalensis Barnard, 1964a: 433, fig. 14e-g.

Holotype: SAM-A9495. Valve.
Locality: off Cape Vidal, Zululand; 146-183 m; 27 February 1901.
Collected by: R.S. *Pieter Faure*.

Family **Limidae**

Lima abscisa Barnard, 1964a: 441, fig. 16f.

Syntypes: SAM-A9504. Three valves.

Locality: off Cape Morgan, near East London; 86 m; 25 July 1901.

Collected by: R.S. Pieter Faure.

Lima divericata Barnard, 1964a: 440, fig. 16e.

Syntypes: SAM-A9501. Two valves.

Locality: off O'Neil Peak, Zululand; 165 m; 28 February 1901.

Collected by: R.S. Pieter Faure.

Lima symmetrica Barnard, 1964a: 441.

Holotype: SAM-A9503. Valve.

Locality: off Cape Vidal; 146–183 m; 27 February 1901.

Collected by: R.S. Pieter Faure.

Family **Astartidae**

Astarte (Digitaria) lunulata Barnard, 1964a: 449, fig. 18b.

Syntypes: SAM-A9506. Three valves.

Locality: 34°26'S 25°42'E; 226 m; 14 November 1898.

Collected by: R.S. Pieter Faure.

Family **Crassatellidae**

Crassatella natalensis Barnard, 1964a: 457, fig. 19b.

Syntypes: SAM-A9509. Four valves, one juvenile.

Locality: off Cape Natal; 98 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Crassatella pilula Barnard, 1964a: 457, fig. 19c.

Syntypes: SAM-A3665. Three complete shells, five valves.

Locality: off Cape Morgan, N of East London; 144 m; 26 July 1901.

Collected by: R.S. Pieter Faure.

Family **Carditidae**

Cardita pulcherrima Sowerby, 1904: 7, pl. 6 (fig. 2). Barnard, 1964a: 459.

Paratypes: SAM-A9512. Nine valves.

Locality: off Cape Natal; 98 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Venericardia fortisculpta Barnard, 1964a: 462.

Syntypes: SAM-A9519. Four valves.

Locality: Algoa Bay; 95 m; 14 November 1898.
Collected by: R.S. Pieter Faure.

Venericardia nuculoides Barnard, 1964a: 462.

Syntypes: SAM-A29661. Twenty-two complete shells, eight valves.
Locality: 35°05'S 18°17'E; 27 m; 2 July 1961.
Collected by: University of Cape Town.

Family Lucinidae

Phacoides peritaphros Barnard, 1964a: 476, fig. 22.

Syntypes: SAM-A9524. Five valves.
Locality: off Nieca River, East London; 43 fm.; 7 August 1901.
Collected by: R.S. Pieter Faure.

Phacoides saldanhae Barnard, 1964a: 474, fig. 21c.

Syntypes: SAM-A4473. Four valves.
Locality: off Baboon Point, Saldanha Bay; 56 m; 18 March 1902.
Collected by: R.S. Pieter Faure.

Phacoides sepes Barnard, 1964c: 25.

Syntypes: SAM-A9529. Two valves.
Locality: off Morewood Cove, Natal; 49 m; 19 December 1900.
Collected by: R.S. Pieter Faure.

Phacoides sudes Barnard, 1964c: 25, fig. 6a-b

= *Gonimyrtea sudes* (Barnard): Kilburn, 1973b: 701.

Syntypes: SAM-A9531. Six valves.
Locality: off Cape Natal; 98 m; 14 December 1900.
Collected by: R.S. Pieter Faure.

Family Laternulidae

Periploma fractura Boshoff, 1968: 97, pl. 8d, text-fig. 2.

Holotype: SAM-A30211. Shell, complete.
Locality: 29°29'S 30°41'E; 86 m; 9 September 1969.
Collected by: R.V. Anton Bruun.

Family Thyasiridae

Thyasira unilateralis Barnard, 1964c: 24, fig. 5a.

Syntypes: SAM-A9520. Two valves.
Locality: off O'Neil Peak, Natal; 165 m; 28 February 1901.
Collected by: R.S. Pieter Faure.

Family **Erycinidae**

Tellimya biradialis Barnard, 1964a: 484, fig. 23a.

Syntypes: SAM-A9535. Two valves.

Locality: off Cape Natal; 155 m; 17 December 1900.

Collected by: R.S. Pieter Faure.

Tellimya trigona Barnard, 1964a: 484, fig. 23b.

Syntypes: SAM-A29741. Five valves.

Locality: Langebaan (Saldanha Bay); no depth; 26 April 1949.

Collected by: University of Cape Town.

Family **Montacutidae**

Conchentopyx granulosa Barnard, 1964b: 35, fig. 2.

?Holotype: SAM-A33071. Animal, preserved.

Locality: Langebaan (Saldanha Bay); no depth or date.

Collected by: University of Cape Town.

Montacula ornata Barnard, 1964b: 26, fig. 6c-d

= *Barrimysia (Callomysia) ornata* (Barnard): Kilburn, 1973b: 702.

Syntypes: SAM-A9538. Three valves.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Montacuta siliqua Barnard, 1964b: 26, fig. 6e

= *Nippon mysella* (Barnard): Kilburn, 1973b: 702.

Syntypes: SAM-A9539. Three valves.

Locality: off Umhloti River; 73 m; 18 December 1900.

Collected by: R.S. Pieter Faure.

Family **Veneridae**

Venus (Anaitis) intersculpta Sowerby, 1904: 11, pl. 7 (fig. 2)

= *Venus verrucosa* Linnaeus: Barnard, 1964a: 496.

Paratype: SAM-14841. Shell, complete.

Locality: Algoa Bay; 18-29 m; 15 March 1899.

Collected by: R.S. Pieter Faure.

Family **Mesodesmatidae**

Donacilla delagoae Barnard, 1964a: 515, fig. 28b.

Syntypes: SAM-A29742. Two complete shells, juvenile, ten valves.

Locality: Inhaca Island, Delagoa Bay; no depth or date.

Collected by: University of the Witwatersrand.

Family **Tellinidae**

Tellina acropisthus Barnard, 1964b: 26. fig. 5b

= *Tellina (Tellinella) staurella* Lamarck: Boss, 1969: 95, pl. 2 (fig. 2), pl. 3 (figs 1-2), pl. 4 (fig. 2).

Syntype: SAM-A9547. Valve.

Locality: off Cape Natal; 88 m; 17 December 1900.

Collected by: R.S. Pieter Faure.

Tellina europisthus Barnard, 1964b: 27, fig. c

= *Tellina (Cadella) semen* Hanley: Boss, 1969: 136.

Syntypes: SAM-A9549. Four valves.

Locality: off Cape Natal; 98 m; 14 December 1900.

Collected by: R.S. Pieter Faure.

Tellina gilchristi Sowerby, 1904: 12, pl. 7 (fig. 3). Barnard, 1964a: 540

= *Tellina (Moerella) gilchristi* Sowerby: Boss, 1969: 144.

Paratypes: SAM-14751. Six valves.

Locality: off Cape Point; 92 m; 6 June 1900.

Collected by: R.S. Pieter Faure.

Tellina (Macoma) inclinata Sowerby, 1904: 14, pl. 7 (fig. 9)

= *Macoma inclinata* (Sowerby): Barnard 1964a: 549, fig. 31i.

Syntypes: SAM-14835. Six valves.

Locality: off Tugela River; 84-92 m; 6 February 1901.

Collected by: R.S. Pieter Faure.

Tellina (Macoma) levior Sowerby, 1904: 13, pl. 7 (fig. 6)

= *Macoma levior* (Sowerby): Barnard, 1964a: 548.

Paratype: SAM-14797. Four complete shells, 8 valves.

Locality: Tugela River, 'N by W 4 miles'; 24 fm.; 21 January 1901.

Collected by: R.S. Pieter Faure.

Paratype: SAM-14798. Six complete shells, 2 valves.

Locality: Amatakulu River, NW by W $\frac{3}{4}$ W 12 miles; 26 fm.; 7 February 1901.

Collected by: R.S. Pieter Faure.

Tellina (Macoma) ordinaria Sowerby, 1904: 14, pl. 7 (fig. 7)

= *Macoma ordinaria* (Sowerby): Barnard, 1964a: 547, fig. 31e.

Paratypes: SAM-14824. Three valves.

Locality: off Saldanha Bay; 18-26 m; 19 March 1902.

Collected by: R.S. Pieter Faure.

Tellina vidalensis Sowerby, 1904: 13, pl. 7 (fig. 6). Barnard 1964a: 541

= *Tellina (Moerella) vidalensis* Sowerby: Boss, 1969: 141, pl. 16 (figs 2-5).

Holotype: SAM-14848. Shell, complete.
 Locality: off Cape Vidal; 23 m; no date.
 Collected by: R.S. Pieter Faure.

Family Pandoridae

Pandora dissimilis Sowerby, 1894: 374; 1897: 21, pl. 6 (fig. 33). Barnard, 1964a: 372.

Paratypes: SAM-5622. Two shells, complete.
 Locality: Table Bay, Green Point; intertidal; no date.
 Collected by: E. L. Layard.

Pandora similis Sowerby, 1897: 29. Barnard, 1964a: 572.

Paratypes: SAM-A29743. Two shells, complete.
 Locality: Bluff Channel, Durban; no depth or date.
 Donated by: Mr Ponsonby.

Family Cuspidariidae

Cuspidaria nasuta Sowerby, 1904: 18, pl. 7, fig. 14
 = *Cuspidaria capensis* (Smith): Barnard, 1964a: 580.

Holotype: SAM-14819. Shell, complete.
 Paratype: SAM-A4432. Shell, complete.
 Locality: off Cape Point Lighthouse; 155 m; 3 May 1900.
 Collected by: R.S. Pieter Faure.

Cuspidaria optima Sowerby, 1904: 17, pl. 11 (fig. 16). Barnard, 1964a: 580.

Paratype: SAM-14764. Shell, complete.
 Locality: off Umtwalumi River, Natal; 92 m; 11 March 1901.
 Collected by: R.S. Pieter Faure.

Family Myochamidae

Myodora rectangulata Barnard, 1964b: 28
 = *Myodora (Myodora) quadrata* E. A. Smith: Kilburn 1973: 709.

Syntypes: SAM-A9556. Twelve valves.
 Locality: off O'Neil Peak, Natal; 92 m; 28 February 1901.
 Collected by: R.S. Pieter Faure.

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

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Family Nuculanidae

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

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laecla bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula targillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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Holotype

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

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PRIMARY TYPE SPECIMENS OF MARINE
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(continued inside back cover)

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MORPHOLOGICAL AND BIOLOGICAL
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SOUTH AFRICAN ARTHROPODS ASSOCIATED
WITH DECAYING ORGANIC MATTER
PART 1
CHILOPODA, DIPLOPODA, ARACHNIDA,
CRUSTACEA, AND INSECTA

By
A. J. PRINS

Cape Town Kaapstad

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MORPHOLOGICAL AND BIOLOGICAL NOTES ON
SOME SOUTH AFRICAN ARTHROPODS
ASSOCIATED WITH DECAYING ORGANIC MATTER

PART 1

CHILOPODA, DIPLOPODA, ARACHNIDA, CRUSTACEA,
AND INSECTA

By

A. J. PRINS

South African Museum, Cape Town

(With 17 figures and 2 tables)

[MS accepted 5 May 1983]

ABSTRACT

Arthropods found in association with leaf litter and other decaying matter were collected for forensic purposes in a narrow strip along the south and west coasts. Twenty-one species in nine orders are discussed in some detail and information is given regarding their morphology, biology, and ecology. Most of these arthropods play an important role in the breakdown of organic matter, others are merely predators, which are mainly discussed here.

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GENERAL INTRODUCTION

Intensive studies have been conducted in the past in the field of medical and veterinary entomology; however, forensic research has been neglected by entomologists and our knowledge on this subject is therefore very limited. The few facts that are known are usually included as a chapter in occasional major works on forensic medicine. The most comprehensive data for South African entomologists are probably various paragraphs in *Medical Jurisprudence* (Gordon, Turner & Price 1953) and an article on flies on human faeces and carcasses (Zumpt & Patterson 1952).

Following requests by the police and State Health Department regarding cases of murder and cattle theft, the author undertook research to obtain a better knowledge of the arthropod successions related to decaying cadavers and thereby to provide additional evidence in cases presenting problems in judicial examinations.

In an investigation of this nature two aspects have to be considered, first, a survey of the various arthropod populations associated with decaying organic

matter in a certain area, most of which may be indirectly involved, and second, an assessment of those directly responsible for the destruction of cadavers and carcasses.

As part of a survey of insects that may be involved in forensic entomology, a preliminary study was conducted during 1976 to 1979 on the arthropods associated with organic matter. Large numbers of arthropods were collected along a narrow strip of the southern and western coastal regions of South Africa, on the beach, the dune system, and some 20–30 km inland. A small strip between Laingsburg and Beaufort West and another between Worcester and Tulbagh were also included.

As the immature stages of the vast majority of these arthropods are still unknown, an attempt was made to rear the various species either in their natural breeding media or in suitable substitutes in order to obtain information on their life cycles. The condition and colour of the specimens were noted before preservation in 80 per cent alcohol and drawings were made with the aid of a camera lucida. The average monthly temperature in the laboratory was recorded throughout the observation periods (Fig. 1A–D). The morphological terms used in this series of papers in the descriptions of the various instars are those of Greene (1922), Böving & Craighead (1931), and Hennig (1968), unless otherwise stated. Identification of the specimens was made by reference to material in the collection of the South African Museum or as verified by specialists in various other institutions.

The first part of this series includes centipedes, spiders, scorpions, ticks and mites, mantids, earwigs, flower-bugs and assassin-bugs, which are all predacious except for ticks and certain mites. It also includes millepedes, sow-bugs, beach-fleas, cockroaches, crickets, red-bugs, chinch-bugs and shield-bugs, which are mostly phytophagous or are in some or other way associated with decaying organic matter. These arthropods are really of minor importance to the forensic entomologist but may play a role either as predators or in breaking down organic material in the soil. Some species such as the chinch-bugs, red-bugs and shield-bugs are mainly phytophagous, but they were often found in leaf litter or accumulations of debris and have therefore been included.

The terrestrial arthropods of a particular region are dependent in most cases directly or indirectly on the floral elements of that region. The coast, with its marine, animal and plant detritus, and unique flora of its adjacent dunes in general, has a very different arthropod fauna from the inland areas.

The beaches along the south and west coasts that were surveyed are usually separated from the interior by a sand-dune biotope which is characterized by the presence of a fairly large variety of plants of which the 'kinkelbossies', *Tetragonium decumbens* and *T. fruticosum*, as well as *Arctotheca populifolia*, *Heteroptilis suffruticosa*, *Matricaria sabulosa*, *Mesembryanthemum crystallinum*, and *Limonium perigrinum* are mostly found on the small fore-dunes. Various other plants such as *Ruppia*, *Zostera*, *Phragmites* and *Spartina* spp. are to be found along the river-banks and in estuaries. Grasses including *Agropyron distichum*, *Sporo-*

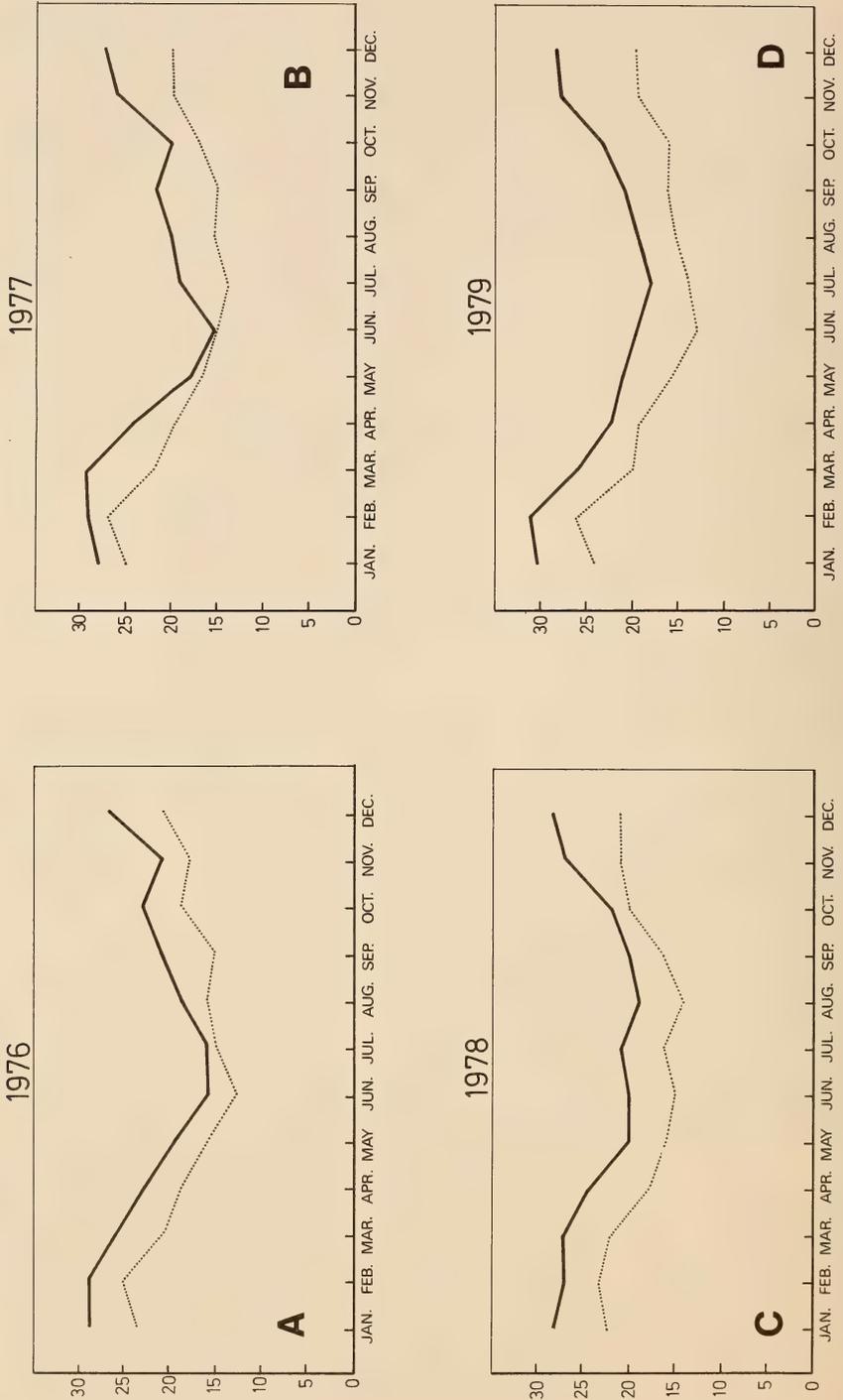


Fig. 1. A-D. Average monthly maximum and minimum temperatures (in degrees Celsius) in laboratory for 1976-9.

bolus virginicus, and *Eragrostis spinosa* frequently grow on the beaches, even reaching the intertidal zone in some areas, and along the Cape south coast *Osteospermum fruticosum* and *Polygala mystifolia* often reach the shingle-covered parts of the beach above the highwater mark.

On the beach itself there are mainly brown and green seaweeds such as *Ecklonia maxima* and *Laminaria pallida*, and very often also the dead bodies of marine animals and birds. In some areas along the south and south-east coast the large kelps are entirely absent and the beaches are usually completely barren and devoid of any seaweed, which results in a sparse arthropod fauna. Further west, however, the number of plants washed up by wave action increases and provides an excellent habitat for a large variety of arthropods.

Various factors will influence the properties of the wrack arthropod communities and man as an extra-biotope agent cannot be excluded, particularly in areas where commercial collection of kelp occurs as some eucoenic species can exist only in large banks of kelp (Backlund 1945). In certain parts along the west coast where kelp is collected for commercial purposes, some of the species normally present were not found during the surveys.

Three types of wrack are generally recognized, wrack strings, wrack flakes, and wrack banks (Backlund 1945; Egglisshaw 1960). The banks are the most important as they provide the main source of food for the various species of the shore fauna.

Continuous exposure of the marine rejectamenta to sprays and wind-borne moisture from the sea affects the composition of the arthropod communities and there is therefore a marked difference between the amnicolous and thinicolous associations and the fauna of the greater interior. Although the maritime species of arthropods exhibit a far greater tolerance to salt than those living further away from the sea, there is an overlap of the various species along the coast, especially among certain Coleoptera, Diptera and Lepidoptera. On the other hand, the vast interior with its variable ecosystems and very large floristic potential presents a wide range of biotopes supporting a comparatively large invertebrate fauna, and a greater number of arthropod species will therefore attack decaying and dry organic matter.

ECOLOGICAL AND BIOLOGICAL NOTES

CLASS CHILOPODA

Usually active, nocturnal predators with dorsoventrally flattened or depressed bodies. Only one pair of legs on each body segment; first pair modified into poison claws. Ocelli may be present.

Various centipedes were found to be associated with decaying matter, and these include the rather small species of the genus *Lamyctes* with only fifteen pairs of legs and the very elongate, worm-like species of *Eurytion* such as *E. dolichocephalus* Attems, which is pale reddish in colour, measures up to 60 mm in length and has nearly eighty pairs of legs. The latter species was collected in all

the areas surveyed and was often found deeply imbedded in semi-dry dung during the winter. Cast skins have often been found together with medium-sized specimens. From collection records it seems to be endemic to the Cape, having been found along the west and south coasts and inland as far as De Aar and Hanover. However, further collections may prove otherwise.

Of the Scolopendromorpha, at least two species appeared to be fairly common under semi-fresh to almost dry cow-pats wherever collections were made. The one, a bluish-coloured *Cormocephalus* species (about 50 mm long, and its larvae), occurred at Hermanus and Stilbaai during the winter; it is apparently the same species that was collected near Philadelphia during the same period. In the western and north-western parts, particularly in the coastal areas of Namaqualand, a large proportion of the pats contained the bluish-green *Arthrorhabdus formosus* Pocock, most of which were about 45 mm long with a broad, brownish-red, longitudinal stripe over the dorsum. Specimens from Saldanha, on the other hand, were more reddish in colour and the mid-dorsal stripe was greenish. This centipede is very similar to *Cormocephalus* species, but is easily distinguished by the spines on the tarsi (absent in *Cormocephalus* species) and by the posterior margin of the head plate, which is free (covered by the first body segment in *Cormocephalus* species). Prey of both species included spiders, cockroaches, and silver-fish.

The introduced house centipede, *Scutigera coleoptrata* (Linnaeus), with its long slender legs, often appeared at carcasses in various parts of the Cape Peninsula during the later post-mortem stage of decay where it mainly devoured some of the members of the fly population. It is widely distributed in the western, southern, and eastern Cape and in Natal.

ORDER LITHOBIOMORPHA

Family **Henicopidae**

Lamyctes castanea Attems

Adult centipede small, brownish red to reddish, 10–12 mm long. Head somewhat darker in colour with one ocellus on each side. Fifteen pairs of legs, tibia of twelfth pair not toothed. Posterior angles of all tergites rounded, not dentate (Fig. 2A–B).

The species seems to be endemic to the Cape Province and is commonly found under semi-fresh to almost dry cow-pats both inland and on the beach, often in association with *L. africana* Porat; it regularly visits carcasses and corpses to feed on the small soft-bodied insects attracted to the decaying material. Both *L. castanea* and *L. africana* are more or less of the same length and colour, but *L. africana* may be recognized by the toothed tibiae of the twelfth pair of legs (Fig. 2C). The first-mentioned centipede was found almost throughout the areas visited, but *L. africana* occurred mostly in the north-western parts. A large red species, *Lamyctes denticulata* Attems, about 13,8 mm long, appeared in fairly fresh dung at Mamre and fed in captivity on soft-bodied insects.

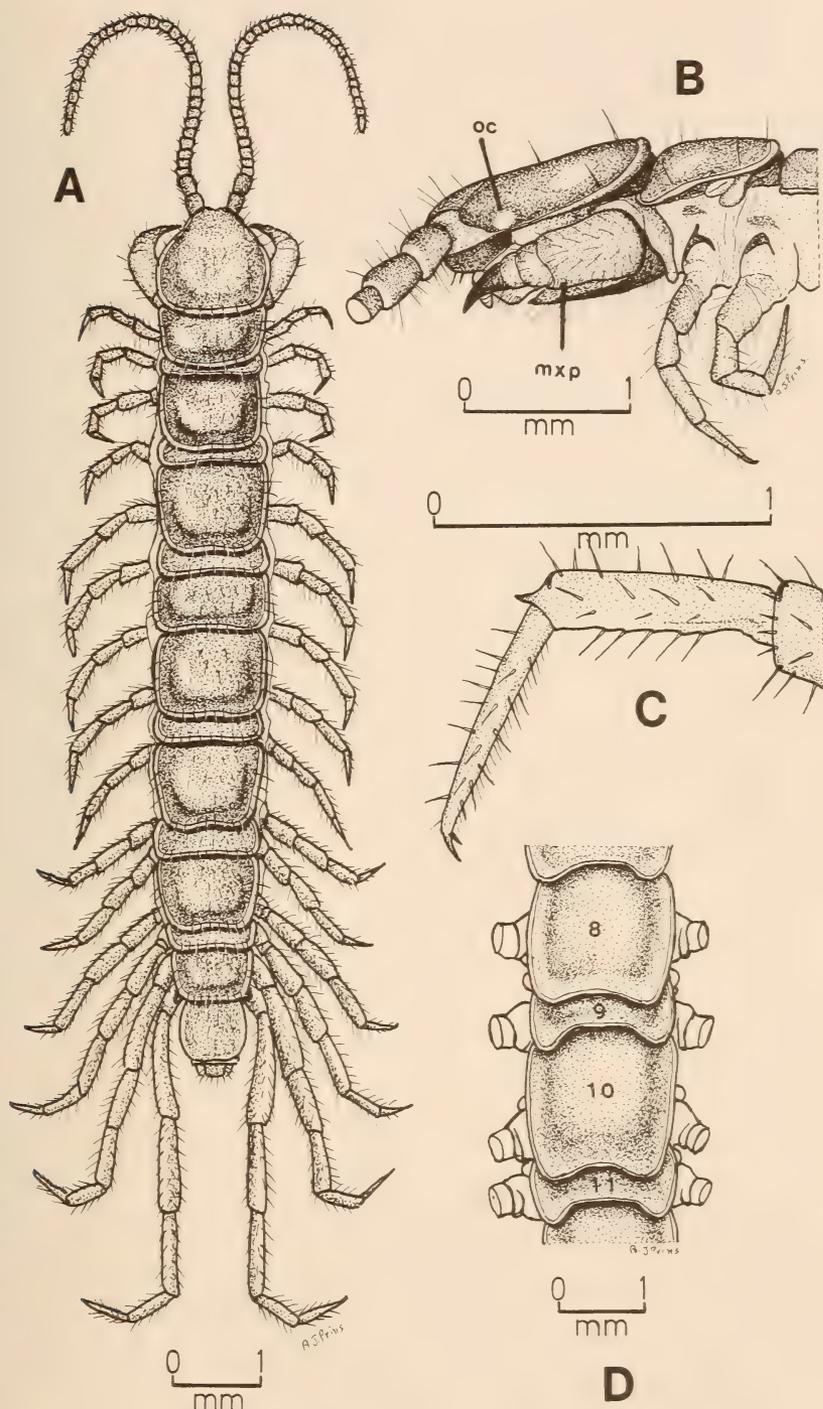


Fig. 2. A-B. *Lamyctes castanea*. A. Adult. B. Head of adult showing first and second pairs of legs, ocellus (oc) and maxillipeds (mxp). (Left lateral view.) C. *Lamyctes africanus*. Tibia and tarsus of twelfth pair of legs to show tibial tooth. D. *Lamyctes denticulatus*. Segments 8-11 to show denticulate posterior border of segments 9 and 11.

It differs from both *L. castanea* and *L. africana* by the toothed posterior angles of segments 9, 11, and 13 (Fig. 2D).

As these centipedes are long lived, both larvae and adults are usually found together. According to Cloudsley-Thompson (1957) the Lithobiomorpha (which includes *Lamyctes*) hatch with seven pairs of legs, including the poison claws, but this stage apparently lasts only for a few hours. Almost pure white, anamorphic larval forms of *L. castanea* with seven pairs of legs, excluding the maxillipeds (Fig. 3D) and measuring 1,3–1,5 mm in length, were observed in the soil around Cape Town during August. They are further characterized by the presence of an eighth pair of legs visible posteriorly through the integument. Eyes are apparently absent and the antennae consist of only six segments.

Anamorphic larvae with eight and ten pairs of legs (maxillipeds excluded) appeared in large numbers during August and September and in both cases two pairs of legs are visible posteriorly through the integument (Fig. 3A–C). The antennae are fourteen-segmented. The specimens with ten pairs of legs are somewhat larger, measuring 2,6–2,8 mm. In both forms the head and antennae are already pale yellowish red and the tergites, including the intercalary tergites, are fairly well defined; indications of eyes are present.

The final anamorphic stage larvae with twelve pairs of legs are very similar to those with ten pairs; however, in specimens collected during October, the antennae consist of sixteen segments and three pairs of posterior legs are visible through the integument. These larvae measure 2,6–3,5 mm in length.

Various groups of the second or final epimorphic stage individuals were observed during the late spring and almost throughout the summer and autumn. These specimens, with fifteen pairs of legs, measure 3,8–11 mm in length and their antennae consist of twenty segments in the 3,8 mm specimens, and thirty-one segments in the 11 mm specimens.

CLASS DIPLOPODA

Slow-moving herbivorous animals with cylindrical bodies characterized by presence of diplosegments, each bearing two pairs of legs. Ocelli present or absent. Defence is effected either by rolling up into a ball or by secretion of protective chemicals in segmentally arranged glands.

Millepedes are usually present wherever leaf litter or decaying dung is found, particularly the garden millepede, *Ommatoiulus moreleti* (Lucas), the large black *Harpagophora nigra* Attems, the black and reddish striped *Chersasus digrammus* (Pocock), a brownish species of the genus *Julomorpha*, the pale-brownish *Gnomeskelus repandus* Attems, and the hothouse millepede, *Orthomorpha gracilis* (Koch).

The last-mentioned millepede is widely distributed in the Republic of South Africa and, according to Causey (1943), its eggs hatch within 5–10 days (in the USA). He gives the size of the eggs as 0,35–0,41 mm. It is a polydesmid like *Gnomeskelus repandus*, and therefore has a fixed number of instars of which the eighth, with thirty to thirty-one pairs of legs, is the final or adult form (compare

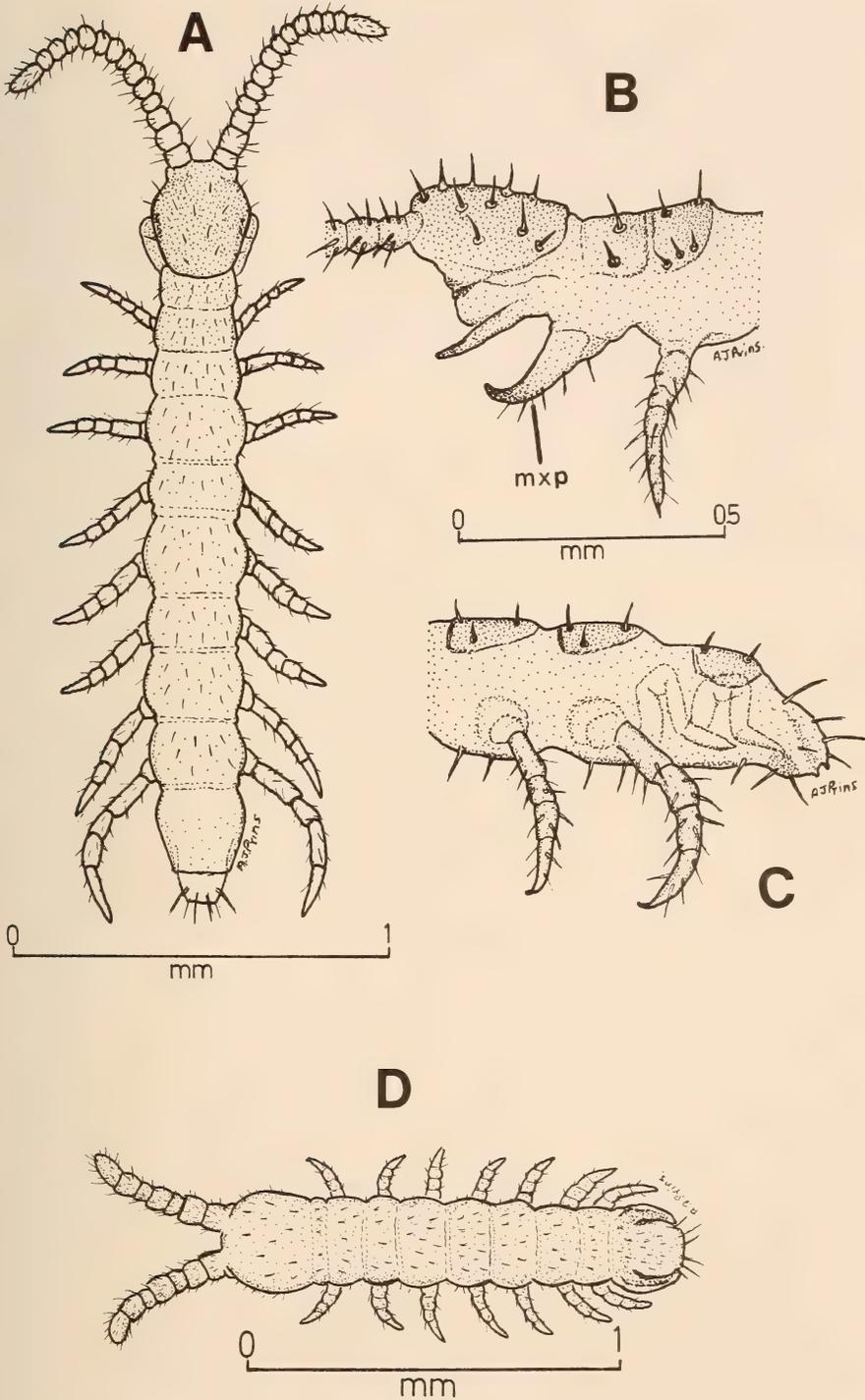


Fig. 3. *Lamyctes castanea*. A. Anamorphic larva with eight pairs of legs (dorsal view). B. Poison fangs (mxp) and first pair of walking legs of anamorphic larva (left lateral view). C. Last two pairs of legs of anamorphic larva (left lateral view). D. Anamorphic larva with seven pairs of legs (dorsal view).

with the juliformids, *Ommatoiulus moreleti* and *Chersastus digrammus* where a large number of instars occur).

A tiny unidentified dermestid-like pincushion millepede (Penicillata or Pselaphognatha) (Fig. 11H) was found together with *Ommatoiulus moreleti* under cow-pats near Jacob's Bay on the west coast. It is about 2,9 mm long, has twelve pairs of legs and is brownish red in colour with tufts of dark-brown, thick hairs on each segment including the head. It was seen to nibble on certain parts of the dung and its remains were often found in the shelters of reduviids of the genus *Coranus*.

Another unidentified species (the specimen collected is about 1,8 mm long with eight pairs of legs), which is pale yellowish white in colour, is often observed in leaf litter in the Cape Peninsula. It differs from the latter species by the longer hairs and antennae in relation to body size and by the almost glabrous dorsum, devoid of any hairs except for some long scale-like setae placed dorso-laterally. Its habits are unknown. The specimens of both the species collected are apparently immature, as adult forms usually have at least thirteen pairs of legs. Lawrence (1981) gives some idea of the life history of these millepedes.

ORDER JULIFORMIA

Family **Julidae**

Ommatoiulus moreleti (Lucas)

Adults small to medium sized, dark slate-grey to blackish in colour and 20–45 mm long when full grown. Characterized by longitudinal striae on each body segment and presence of a mid-dorsal posterior extension or tail. After the adult stage is reached, several further moults occur with an increase in the body length and the number of legs and ocelli, as is shown in Table 1 for adults collected around Cape Town and Philadelphia during January and February 1979.

This introduced millepede is almost cosmopolitan and is very widely distributed in the southern and western Cape. It was collected along the coast as far north as Citrusdal and as far east as Stilbaai. It sometimes occurs in very large numbers, particularly in soils rich in organic material, and may cause damage to young plants and even plant bulbs. It is often found in thatched roofs of houses together with scarabaeid larvae and it is quite possible that their way of feeding provides the correct stratum for these scarabs. Schubert (1966) gives a good description of the species and an almost complete distribution in the Cape.

It is commonly found in leaf litter as well as in soil rich in compost and other organic materials used as manure such as fishmeal, and is also attracted to decaying carcasses and human cadavers; on the beach it was often seen feeding on the dry remains of bird and seal carcasses and further inland even appeared at carcasses during the early part of the dermatophagous stage of decay. It was the only millepede found at wrack strings in the Cape Peninsula during the surveys. Together with *Chersastus digrammus* it usually appears in large numbers

TABLE 1
Body length of adults of *Ommatoiulus moreleti* in relation to
number of legs and ocelli.

<i>Number of leg pairs</i>	<i>Number of ocelli on each side</i>	<i>Body length in mm</i>
73	27	19.1
74	27	18.0
74	32	18.0
75	27	22.0
75	27	19.0
77	33	20.0
77	27	20.0
80	35	26.0
80	33	17.0
80	41	24.0
80	27	28.0
82	40	30.0
83	41	32.0
85	45	31.0
86	40	40.0
87	39	27.0
87	40	28.0
87	46	34.0
90	50	31.0

TABLE 2
Body length of *Ommatoiulus moreleti* in relation to number
of legs and ocelli.

<i>Number of leg pairs</i>	<i>Number of ocelli on each side</i>	<i>Body length in mm</i>
43	10	6.6
51	15	12.0
51	15	13.0
53	15	13.0
61	21	16.0
63	20	13.0
63	20	14.9
63	21	15.0
64	21	15.0
65	21	16.0
65	21	17.0
66	21	17.0
67	20	18.0
69	21	17.0

during April and May under semi-fresh cow-pats in sandy areas, feeding on the wet parts of the dung. It is also common under dry cow-pats.

Copulation between males (19,9 mm long with seventy-three pairs of legs), and females (32 mm long with eighty-three pairs of legs) of *O. moreleti* was observed near Philadelphia during May. In most cases this lasted for about 10 minutes and after a few days each female laid some 200 eggs in a small hollowed-out chamber in the topsoil. The eggs are somewhat oblong, slightly shiny and dirty, yellowish white, measuring from $0,76 \times 0,64$ mm to $0,80 \times 0,60$ mm. The incubation period in the laboratory was about 16 days at 22 °C. The first sign of the so-called preliminary hatching is a rupture in the chorion of the egg, after which the immobile, legless embryonic pupoid stage (Fig. 4A), which is still enclosed in an embryonic cuticle and is almost pure white, appears. About 4 days later the legs become visible through the membrane and anteriorly a tiny eye-spot appears on each side, and a pair of larger, darkish-orange spots also becomes visible at the posterior third of the body. This pupoid stage is about 1,0 mm long.

After about 6 days the embryonic cuticle is shed and the active first instar with three pairs of legs appears (Fig. 4B). It is about 1,6 mm long, still pure white and with about eight visible body segments. The darkish orange spot is then situated on about the fifth segment. After 5–6 days it moults again and then has seven pairs of legs (Fig. 4C) and one pair of eye-spots and the large lateral orange spot is then situated near the middle of the body. The first five trunk segments are more yellowish in colour and the body-length remains about 1,6 mm long.

In the case of *Chersastus digrammus* (Trigoniulidae) the second larval instar is slightly darker and three distinct black ocelli are visible on the head, but the dark posterior spot is much less conspicuous. Young specimens of the latter species were observed along the west coast during December, the smallest found being 5,3 mm long with a brownish, longitudinal median line on the dorsum, as in *O. moreleti*.

After 16–17 days the young larva moults again and is now about 2,8 mm long with seventeen pairs of legs and three clearly demarcated ocelli on each side of the head (Fig. 4D). This third instar is characterized by a pair of large, dark, reddish spots on the fifth body segment as well as five pairs of smaller, reddish, oval spots posterior to it (these are the openings of the repugnatorial glands). The posterior extension or tail and the antennae, which are very conspicuous at this stage, are already visible from the first instar. The body colour usually becomes darker and after about a month it moults for the third time, producing an individual with twenty-nine pairs of legs and six black ocelli on each side (Fig. 4E). It is then about 4,9 mm long and laterally bears eleven small reddish spots of which five are very conspicuous, in addition to the large spot.

This fourth stage lasts for about 25 days before it moults again and then reaches a length of about 6,2 mm. There are thirty-nine pairs of legs, ten ocelli and laterally eleven small, clearly defined, reddish spots and five inconspicuous spots in addition to the larger one on the fifth segment (Fig. 4F). The colour of

the body is pale brownish white, with a fairly broad, longitudinal, brown median line along the dorsum. This fifth instar lasts for about 32 days and again moults near the end of September. The sixth instar has about fifty-one pairs of legs and fifteen ocelli on each side of the head.

The number of legs varies apparently according to the sex of the animal and therefore fifth-instar specimens with forty-three pairs of legs and ten ocelli were often collected. As the animal increases in size, the number of legs and ocelli corresponds with the size of the millepede, as is shown in Table 2 (see also Table 1).

Baker (1978) described the post-embryonic development and life-history of this species in Australia and stated that after 1 year *O. moreleti* was in the seventh, eighth or ninth stage. After 2 years the tenth or eleventh stage was reached and after 3 years the twelfth or thirteenth.

CLASS ARACHNIDA

Arthropods with the prosoma (or cephalothorax) or both the prosoma and opisthosoma unsegmented; sometimes all the segments fused. Mostly terrestrial except for a few aquatic mites and spiders. No antennae, compound eyes or wings present. Respiration by means of tracheae, or book-lungs or both. Generally carnivorous and cryptozoic.

ORDER ACARINA

Mostly small arthropods, with the prosoma and opisthosoma completely fused. Larvae with three pairs of legs, nymphs exactly as adults with four pairs of legs but lacking the genital opening. In certain groups such as the Tetrapodili adults have only two pairs of legs.

Ticks (Ixodides) have the hypostome barbed and are usually parasitic on vertebrates. Only two species were found to shelter under semi-dry to almost dry cow-pats, namely the bont-legged tick, *Hyalomma truncatum* Koch and the red tick, *Rhipicephalus evertsi* Neumann. Both males and engorged females of the two species were recovered during March, *H. truncatum* in the Philadelphia district and near Saldanha and *R. evertsi* in the Stilbaai area. Males of *H. truncatum* measured 4,8 mm from the tip of rostrum to the posterior border of the body and were dark brown to blackish brown in colour. Engorged females were red and measured about 13 mm. Females of *R. evertsi* were somewhat under-developed, with light-red shields; their bodies were yellowish white and the legs pale reddish. The females of both species were embedded in the cake of the pats and, in the case of the red tick, large numbers of eggs were found with them. The eggs are roundly oval, dark reddish brown to wine coloured and shiny, and measure 0,52 mm in length and 0,38 mm in width. They hatched in about 50 days, producing transparent six-legged larvae measuring 0,60 mm shortly after hatching.

Mites (Acari), on the other hand, are usually small to minute with the hypostome smooth and without barbs, and are generally found in almost every

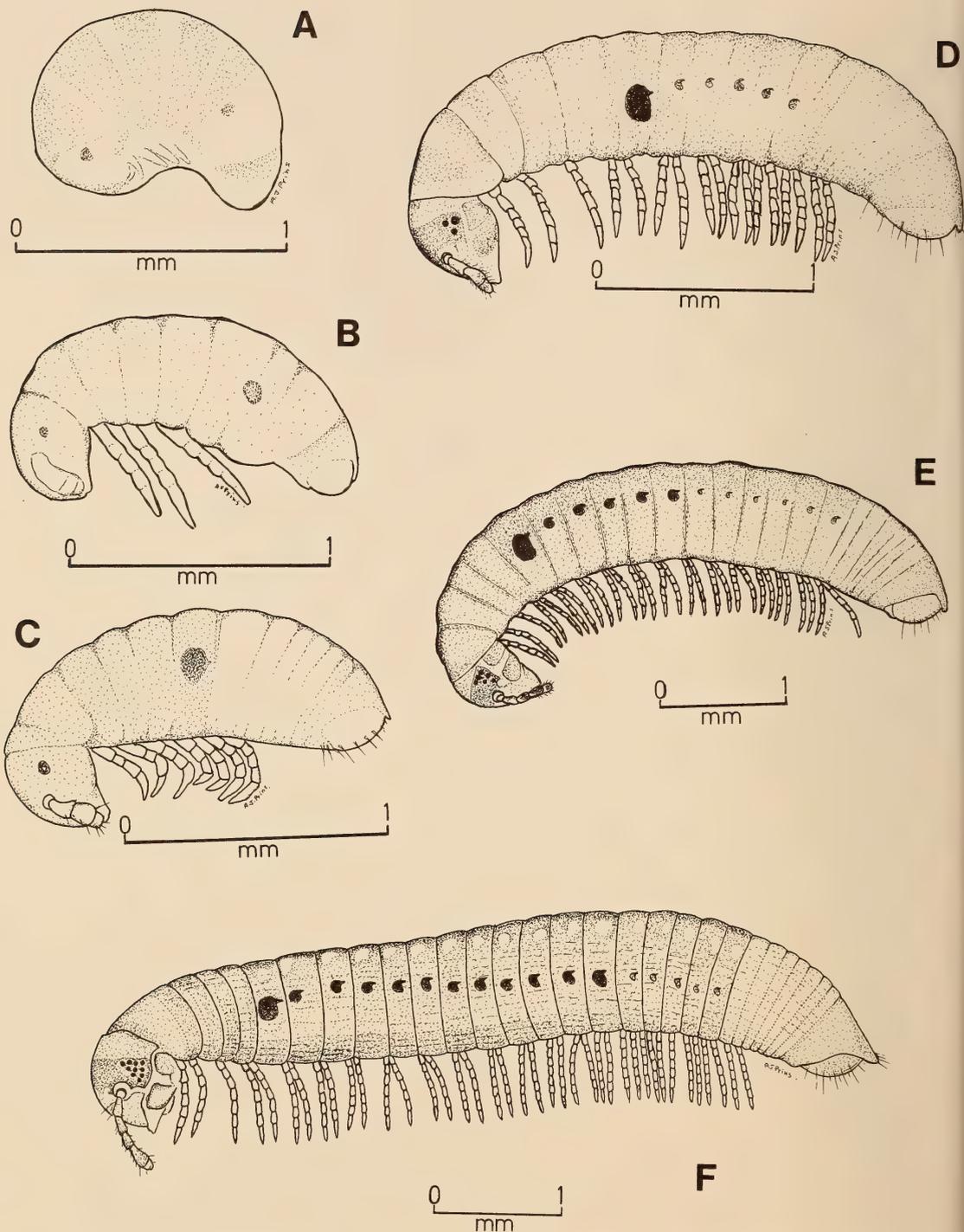


Fig. 4. *Ommatoiulus moreleti*. A. Pupoid stage. B. First stage. C. Second stage. D. Third stage. E. Fourth stage. F. Fifth stage.

habitat available to animal life. Some species are phytophagous, causing severe losses to crops, others again are parasitic and have developed a close relationship to man, such as the asthma epidermoptid, *Dermatophagoides pteronyssinus* (Trouessart), also known as the house-dust mite, which is associated with the scales of the human skin; it allergizes the bronchi by inhalation (Glass 1971) and contributes to allergic rhinitis and asthma.

Free-living mites are abundant in debris on the ground or in litter-like accumulations and particularly in soil rich in compost or other decaying organic matter. The most common species in the Cape Peninsula in soils containing decaying fish-meal was the Sarcoptiform, *Lardoglyphus zacheri* Oudemans (Fig. 5I), a minute whitish species only 0.2–0.24 mm long. This mite was also found to infest certain carcasses and when large numbers were present even the larvae of the skin beetle, *Dermestes maculatus* de Geer, were covered with numerous specimens. They apparently did not harm the insects at first, although their movements were slowed down. Later, however, after prolonged exposure to large numbers of this mite, growth was retarded and mortality increased.

In the oribatid mites (Fig. 5F) the bodies are usually strongly sclerotized and darkly coloured and some have large lateral shields or pteromorphs. They are fairly numerous in rich soils and may play an important role in digesting the organic matter (see also results by Fujikawa (1979) in Japan). They are found to be common around carcasses and one species of *Baloghobates* of the family Ceratozetidae, which has small pteromorphs, was found to accumulate in large numbers on the decaying leaves of *Arctotheca populifolia* along the Strandfontein sand-dune system during the summer and early autumn, in some areas actually feeding on the growing plants.

The variable Trombidiformes include a large number of phytophagous species as well as several parasitic mites, particularly of the family Tarsonemidae of which one species of *Tarsonemus* (Fig. 5D) was very common on a large variety of arthropods. It is small, about 0.24 mm long, whitish, and with long setae on the hind legs. In the Karoo it occurred in exceptionally large numbers on the larvae of the skin beetle, *Dermestes maculatus* de Geer, feeding on the droppings of the Cape grey mongoose, *Myonax pulverulentus* (Wagner). Heavy infestations of this species on insects in breeding jars in the laboratory usually resulted in the death of the hosts. This mite, together with one species of pyemotid (Fig. 5E), was found to be common around Cape Town in the soil surrounding half-buried carcasses. The latter is also very small, about 0.5 mm in length, almost globular, and pure white in colour. Specimens observed during the dermatophagous stage of decay of various carcasses were found to feed on the eggs of skin-and-hide beetles. The grain itch-mite, *Pyemotes ventricosus* (Newport), another member of the family Pyemotidae and normally beneficial as it is parasitic on the larvae of grain-infesting insects, may cause skin irritations or eruptions in humans handling infested material. (This mite is not to be confused with the human itch-mite, *Sarcoptes scabiei* (de Geer) (Sarcoptiformes) which is transmitted by direct contact with infested persons or domestic animals.)

Prostigmatid mites of the genus *Pimeliaphilus*, also belonging to the sub-order Trombidiformes, have been found in association with various reptiles and arthropods in different parts of the world. Olivier (1977) described four species from South West Africa of which three were found on insects, viz. *P. penrithi* Olivier on cockroaches of the genus *Derocalymma*, *P. buysi* Olivier on the tenebrionid beetle, *Stips dohrni* (Haag) and *P. desertus* Olivier on the carabid *Anthia thoracica* (Fabricius) (see also discussion on Scorpionida). Most of these species also seem to be free-living under stones and debris.

In completely dry cow-pats only two undescribed species of prostigmatic caeculid or rake-legged mites were found. The one species, observed along the west coast, is about 2,5 mm long, its body trapeziform and broad. Its colour is brownish to greyish marked with black; the front and sides of the shield are whitish and the legs are black marked with white. Body-hairs are sparse and spatulate. The front legs are strongly developed, with long golden-brown spines on the inner surface.

The other xerophilous species collected in the Karoo is much smaller, about 1,6 mm long, piceous brown, and covered with longer hairs. It lacks the white marks of the former species. The colour of these mites blends with that of the dry dung to bring about a perfect camouflage. In the laboratory they were seen to stalk other mites, but otherwise their habits are unknown. Lawrence (1939) maintains that they are probably scavengers, feeding on decaying animal remains.

A large variety of mostly unidentified mesostigmatid mites were very common in both fresh and semi-fresh cow-dung. These included various *Macrocheles* species such as *M. distanti* Evans & Hyatt (Fig. 5A), *M. peniculatus* Berlese, and *Parasitus* species (Fig. 5B). An unidentified crimson, prostigmatid spouted mite of the genus *Bdella* (Fig. 5G), about 1,6 mm long, appeared regularly but was not abundant in semi-fresh pats. One of the most numerous species in decaying dung was a small, whitish mite about 0,32 mm long and very similar to *Parasitus* sp.; it is probably also a member of the Parasitidae. These species are all predacious, the snouted mite feeding on the Collembola present.

Specimens of *M. distanti* that were collected measured only 1,1–1,2 mm long, with the holodorsal shield yellowish brown in colour; specimens of *M. peniculatus*, on the other hand, were somewhat bigger, 1,2–1,4 mm long, and darker in colour. *Macrocheles distanti* is commonly found on various scarab beetles such as *Onitis*, *Scarabaeus* and *Circellium* species (Evans & Hyatt 1963). *Parasitus* species are more or less oblong mites and, although of the same colour as the above-mentioned species, they are easily distinguished by the divided dorsal plate; their legs are also more slender and more or less of the same size, whereas in the macrochelids the first pair is elongate and much thinner than the others. All these mesostigmatid species also occurred in decaying animal carcasses and human cadavers.

Some of the *Macrocheles* species are ectoparasites of flies, as they are often found attached to their hosts, their mouth-parts deeply embedded in the tissues

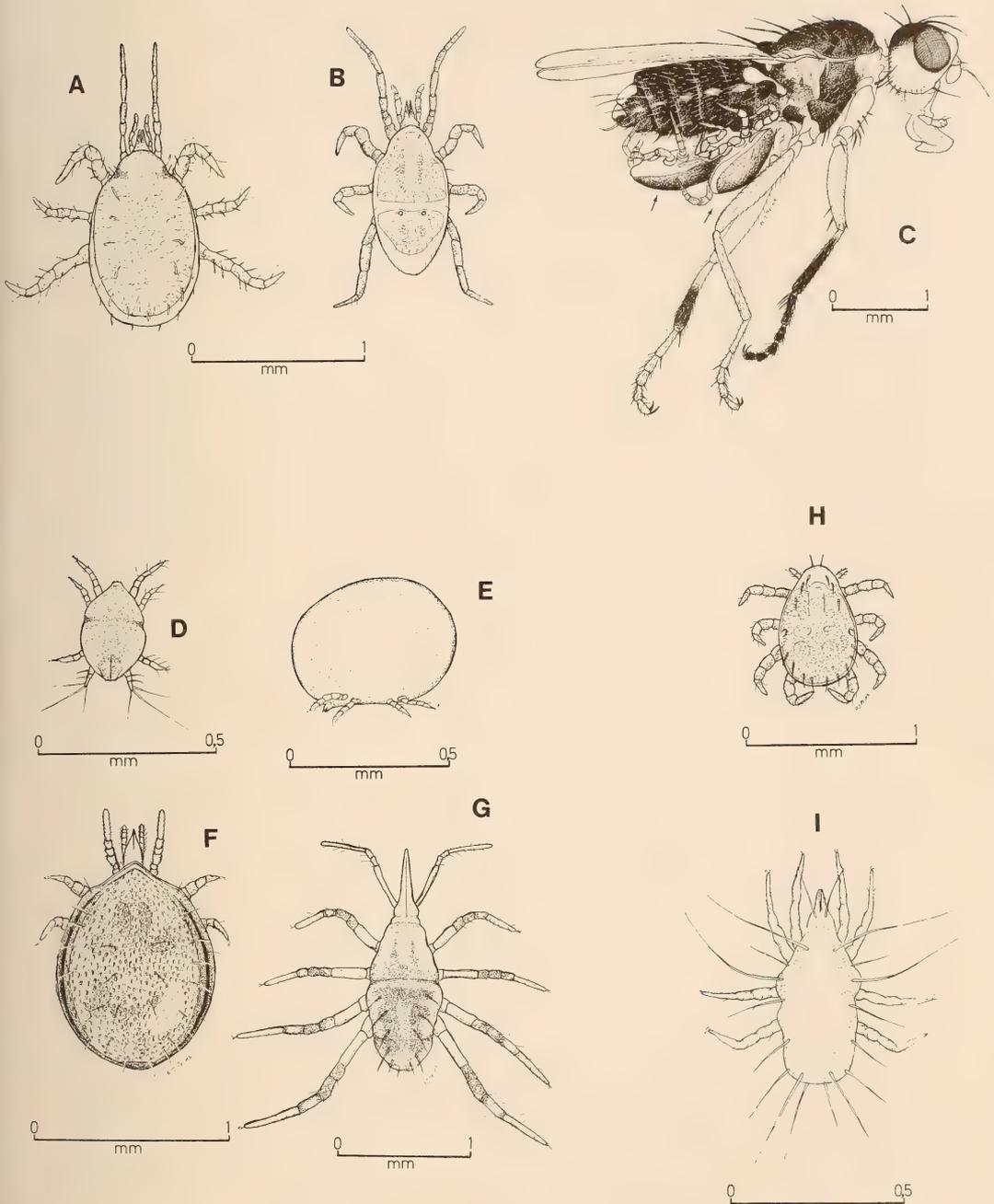


Fig. 5. A. *Macrocheles distanti*. B. *Parasitus* sp. C. Cheese skipper, *Piophila megastigmata* McAlpine, with two mites, *M. distanti* attached to abdomen. D. *Tarsonemus* sp. E. Pyemotid mite. F. Oribatei mite. G. *Bdella* sp. H. *Aleuroglyphus* sp. I. *Lardoglyphus zacheri*.

between the segments (Fig. 5C). Phoresy, therefore, seems to be one of the main factors influencing the presence and abundance of these mites in cow-pats and carcasses. According to Axtell (1963) several species of the family Macrochelidae are predacious on house-fly eggs and first instar larvae.

The mesostigmatic poultry mite, *Dermanyssus gallinae* (de Geer), is often found to shelter in roosting sites of birds in human dwellings, particularly in air-vents, and may cause minor infestations. In some respects it resembles the larger *Parasitus* species, but may be distinguished by the absence of a clearly divided dorsal plate.

Decaying kelp yielded numerous mites, mainly Mesostigmata and Sarcoptiformes, especially of the families Laelaptidae and Acaridae. Various species of a brownish *Peletiphis* have been seen, while the acarids were represented by a pale-brown, parasitic *Aleuroglyphus* sp. (Fig. 5H). Often kelp-flies were so heavily infested with them, particularly on their legs, that their movements became sluggish. Most of the mites are about 0.68 mm long. A *Parasitus* sp. (Fig. 5B) also occurred and was found to feed on the eggs of flies laid on the kelp. It was noticed that when disturbed each mite snatched an egg and disappeared with it among the kelp leaves. When fly maggots or beetle grubs were preyed upon by predacious beetles and their larvae, these mites were seen to approach the prey and imbibe some of the available body fluids.

ORDER ARANEIDA

In the spiders the abdomen is usually unsegmented except in the Liphistiomorphae; in this suborder as well as in the Mygalomorphae, which includes the baboon-spiders, the fangs move up and down. In the rest of the spiders the fangs move from side to side (or in and out).

Most spiders are poisonous and, although necrotic ulceration or loxoscelism is caused by the cytotoxic venom of the violin spiders, most of them, such as the baboon-spiders and the button-spiders, have a neurotoxic poison.

At least four species have been observed in debris in the sand, on dunes, and on the supratidal zone of the beach. These are mostly burrowing spiders and they disappear very quickly under the sand when left on the surface. The most common of these were the armoured spiders (family Zodariidae) (Fig. 6C), and a small theraphosid. Occasionally a species of *Clubiona* (family Clubionidae), found on the dunes, occurred under semi-dry crow-dung both along the south and west coasts, while one species of the family Ctenidae also frequently appeared under the stranded kelp and debris in the western parts.

These are all small spiders of which the feeding habits are unknown. However, there is evidence to believe that some of the zodariids prey on the small fly larvae in the sand, particularly those of the horse-flies belonging to the genus *Limata*, which occur in this stratum.

Spiders were common in both semi-fresh and semi-dry cow-pats; the most widespread appearing to be the wolf-spiders (family Lycosidae). A small *Pardosa* sp., easily recognized by the broad, brown longitudinal band on each side

of the pale carapace, the arrow-like pale line down the middle of the abdomen, and the mottled legs, occurred throughout the region surveyed, most often together with a larger unidentified species. The latter, about 15 mm long, has a similarly marked carapace, but its pale-brown abdomen is mottled with dark brown.

Wolf-spiders were also found to be the most common arachnids under stranded kelp, and a small species of *Lycosa* (pale reddish-brown with a broad, brown longitudinal stripe along each side of the body, the middle of the abdomen whitish) was very numerous, particularly along the west coast; it was sometimes in association with members of the family Ctenidae, which in some respects resemble the wolf-spiders. A larger species, about 10,5 mm long and rather similar to the *Lycosa*, its abdomen marked with dark brown, seemed to be just as common along the south coast. Most of them feed on the smaller insects, particularly the flies that are attracted.

The large, brown hairy baboon-spiders, *Harpactira* spp. and the lesser baboon-spiders, *Harpactirella* spp. (family Theraphosidae), particularly *H. lightfooti* Purcell, have all been collected under semi-dry to almost dry cow-pats along the west coast as far north as Port Nolloth. In some cases the nests were hollowed out in the pats, while in others they were just below the surface of the soil, their tunnels leading into the pats. *Harpactirella* spp. are very similar to those belonging to *Harpactira*, but differ from them by the absence of a brush of short stiff hairs on the external side of each chelicera. The bite of *H. lightfooti* is of medical importance (Newlands 1972). Specimens of *Harpactira* when in a state of moulting are very susceptible to the attacks by pentatomids of the genus *Halyomorpha*. An unidentified dark-grey species, very near *H. viridescens* Walker and about 13 mm long, was found in the vicinity of Saldanha feeding gregariously on fairly large specimens of the brown baboon-spider.

Small (1,9 mm long) blattid-like nymphs, found in the same area, probably belong to this shield-bug. They are pale greyish yellow on the thorax and connexivum, with greyish-yellow legs and antennae and crimson abdomen.

The family Drassidae were also well represented. In the Saldanha and Veld-drif areas *Amusia cataracta* Tucker (Fig. 7B), *Zelotes* sp., and an unidentified species very near *A. cataracta* were mostly present. They are all small, sombre-coloured, brownish to pale bluish-brown spiders. A similar but much paler species of *Anagraphis* was common almost throughout the region, and in the vicinity of the Gouritz River mouth an unidentified *Drassodes* sp. appeared in pats containing large numbers of dipterous and scarab larvae. Its colour is pale brownish red, the abdomen lighter with brownish spots on the posterior half, and it is easily separated from the other drassids by its long chelicerae carried almost horizontally.

The erigonids resemble in some ways small theridiids (button-spiders), but the males and females are about equal in size. However, in the males there is a raised area or knob on the front part of the carapace on which their eyes are situated. Most of them are very small and sombre coloured and five to six

species were well represented under semi-dry pats, the most common being a species of *Araeoncus*. Other small spiders observed in dry dung were species of *Heriaeus*, *Clubiona* and the lungless spiders, *Caponia*, which resemble baboon-spiders.

One of the most beautiful spiders that shelters under semi-dry cow-pats is the tiny spitting spider, *Scytodes* sp. (Fig. 6A) (family Sicariidae), which is yellowish white with dark-brown stripes and spots on the body. It is easily recognized by its strongly convex and bulbous carapace. Specimens collected near Saldanha measured only 3–4 mm in length. Prey consisted mostly of small flies, silver-fish, and other small insects, which are usually immobilized by a sticky saliva.

Nests of the brown or house button-spider, *Latrodectus geometricus* Koch (family Theridiidae), were not uncommon under pats and it was observed to feed on various beetles and other soft-bodied insects such as cockroaches. The black widow, *L. mactans* Linnaeus, on the other hand, was much scarcer and only two nests were observed in the vicinity of Leipoldtville during April, both under large dry pats, each nest with one or two smooth, oval, white egg cocoons containing the exuviae of newly hatched spiders. The prey included tenebrionid beetles, the most abundant victims being the elongate, brownish *Oxura setosa* Kirby (16,5–19 mm long) that shelters under dry cow-pats during the summer and is characterized by the two acute posterior prolongations of the elytra. Hesse (1942) gives an almost complete list of insect victims of this spider, including this tenebrionid. Skeletons of an almost equal number of a black *Onymacris* sp. (about 14 mm long), and a few shiny brown *Ograbies subdentatus* Koch (7,5–8,3 mm long), were among the remains of the one nest, together with almost intact specimens of a small black *Psammodes* sp. and a *Zophosis* sp., both varying in length from 9,9 to 13,0 mm.

It is interesting to note that the sphecid *Chalybion spinolae* (Lepeletier) provisions its nest with both species of button-spiders. According to observations, this wasp accounts for the destruction of a large number of the black widow in certain areas (J. E. Nel, Durbanville, 1983 pers. comm.).

At least eight spiders were found in the Cape Peninsula in soil surrounding carcasses, of which a dark crimson species of *Dysdera* (family Dysderidae) was the largest (approximately 14 mm). It has a pale-reddish abdomen and exceptionally long chelicerae and was particularly abundant during the summer and autumn. Young individuals collected during the summer varied from 3 to 5 mm long and were almost pure white. The comb-footed spiders (family Theridiidae) included a small brownish *Enoplognatha* sp., its abdomen marked with white stripes and patches, and an even smaller *Anelosimus* sp. (Fig. 7A), which is pale brown with darker brown on its abdomen.

An unidentified *Erigone* sp. (Fig. 6B) (family Erigonidae), probably the same species that was found under cow-pats near Hermanus and Darling, has the spinners surrounded with black. It occurred together with a related button-spider-like linyphiid and some larger dictynids (mesh-web spiders) under fairly decayed carcasses. *Hahnia* sp. (family Agelenidae), about 4 mm long, with

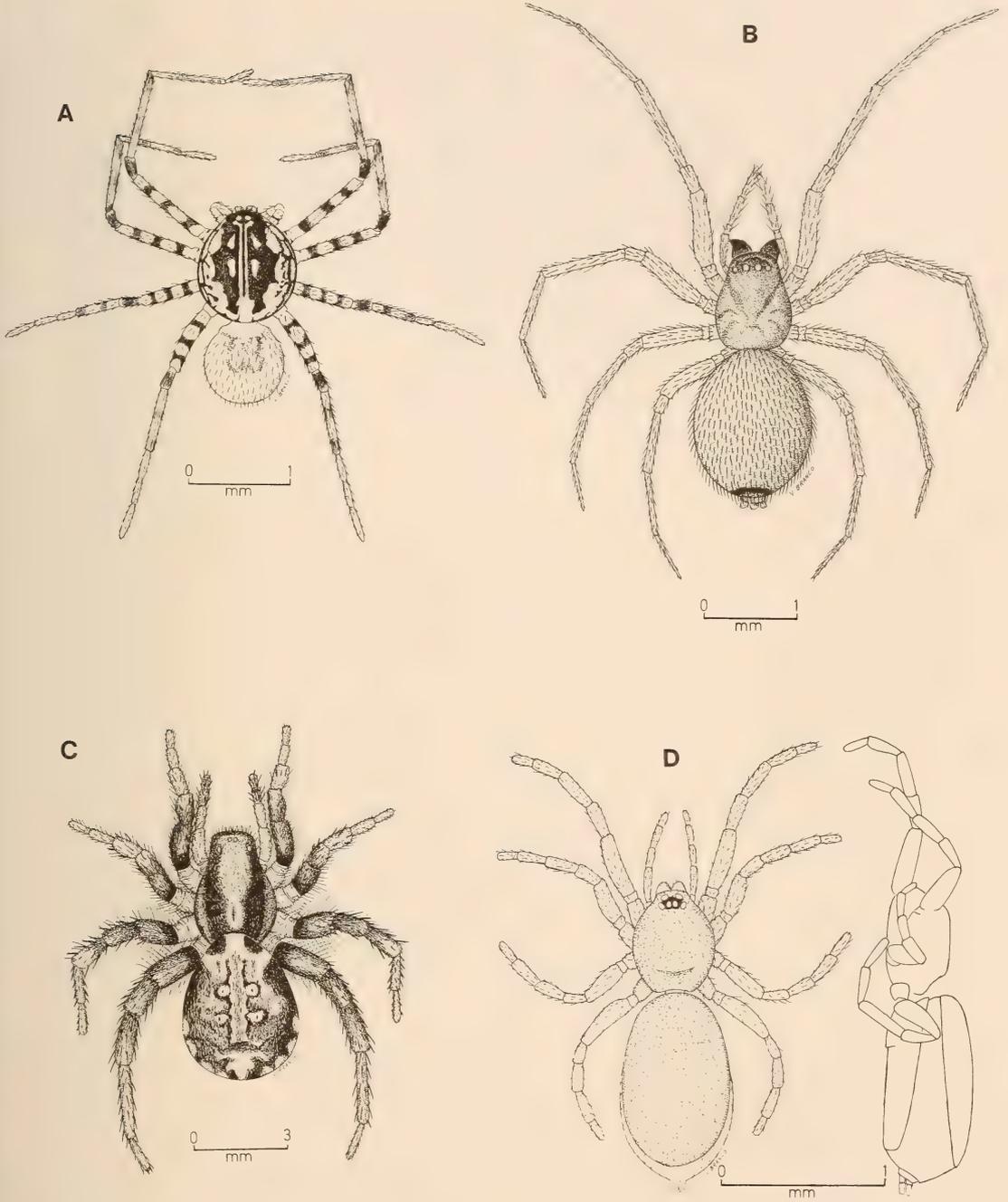


Fig. 6. A. *Scytodes* sp. B. *Erigone* sp. C. Zodariid spider. D. *Gamasomorpha australis* (dorsal and left lateral view).

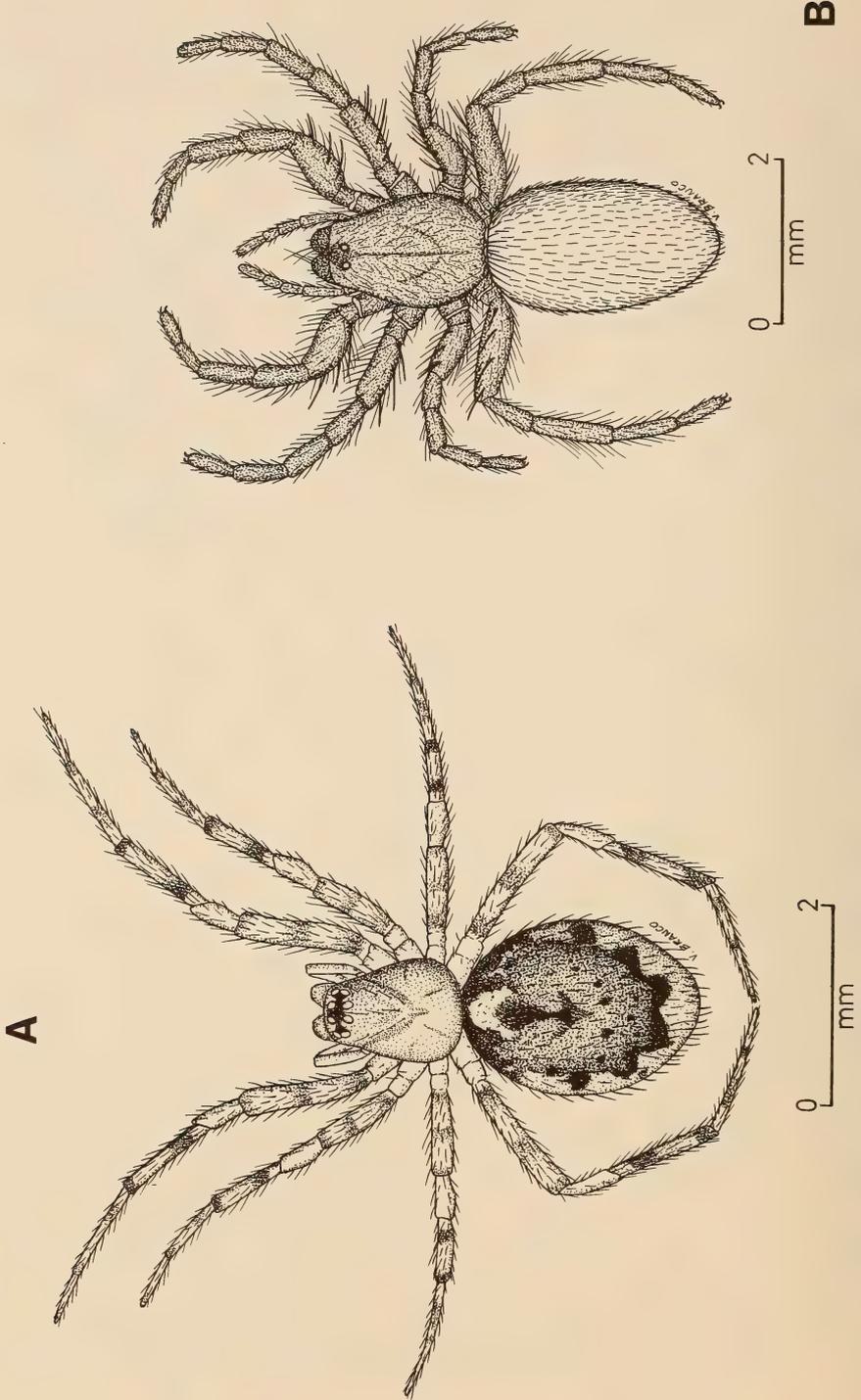


Fig. 7. A. *Anelosinus* sp. B. *Amusia cataracta*.

brownish, speckled abdomen, appeared in places where the soil was fairly damp. Its long spinners are placed in a line along the posterior border of its abdomen; young individuals collected were almost white.

One of the smallest spiders collected in the soil partly covering carcasses was the bright brownish-red *Gamasomorpha australis* Hewitt (family Oonopidae) (Fig. 6D), which is only 1.8 mm long and easily recognized by the two oval shields covering the abdomen.

Apart from the true spiders, only one brownish harvest spider of the genus *Opiliones* (order Phalangida), which is generally found under stones along the west coast, was collected under dry cow-pats. It feeds on other spiders, flies, and snails. Near Saldanha Bay a young specimen (37 mm long) of an unidentified *Solpuga* sp. (order Solpugida) appeared during midsummer under a large dry pat and, judging by the remains found near it, this animal must have been feeding on the scorpions *Uroplectes variegatus* (Koch) and a *Parabuthus* species.

ORDER SCORPIONIDA

Fairly large nocturnal carnivores with segmented opisthosoma divided into pre-abdomen or mesosoma, bearing ventrally openings of book lungs and paired comb-like pectines, and with the tail or metasoma with apical sting. Usually one pair of dorsal eyes present on cephalothorax and groups of two to five lateral eyes.

These animals, which include burrowing, arboreal, and rupicolous members, are usually characteristic of arid environments; however, habitat selection as in the other arthropods is governed by ecological factors such as vegetation, geology, and climate.

Their venom apparently consists of two types in which the one produces only local reaction without systemic effects except in cases of hypersensitivity. This is usually found in species with a thin metasoma and large flat hands on the pedipalpi such as the yellow Cape scorpion, *Opisthophthalmus capensis* Herbst (family Scorpionidae), a species that was periodically observed under large cow-pats.

In the family Buthidae, however, the venom is a neurotoxin, comparable to that of the colubrine snakes, and may be lethal. In this family the scorpions have a thick metasoma and the hands of the pedipalpi are ovoid, slender, and rather small. Only one large species, *Parabuthus capensis* Hemprich & Ehrenberg, rarely occurred under dry cow-pats during the surveys and was found to prey on the smaller and more common *Uroplectes variegatus*. The latter and *Parabuthus brevimanus* (Thorell), the smallest species in the genus, are fairly common under dry cow-pats all along the west coast where surveys were made.

Family **Buthidae**

Uroplectes variegatus (Koch)

Full-grown females (32–45 mm long) (Fig. 8G) vary from pale cadmium yellow to yellowish brown; some are mottled with brown, with three rather indistinct longitudinal stripes over middle of dorsum; most of them, however,

have only a single broken, median line and body segments are marked with light brown. In all the specimens examined, the largest part of the fifth metasomal segment is darker in colour than the rest; in some specimens it is piceous brown, in others very slightly darker. It is rather similar to *Parabuthus brevimanus* both in shape and size, but differs from it by the longitudinal body stripes, *P. brevimanus* being of a more uniform coloration.

This species was found inland along the west coast throughout the year, usually only one specimen per dry cow-pat. Sometimes six out of every ten pats examined harboured at least one specimen during the summer months; these scorpions varied from very young (about 12 mm total length) to full-grown females. In the case of the full-grown specimens, the under surface of the cow-pats was hollowed out in the form of a chamber in which the animals sheltered.

In the Karoo near Laingsburg, where collections were made during the autumn, *U. variegatus* was replaced by pale yellowish-brown immature specimens of *U. schlechteri* Purcell, which also has a dark fifth metasomal segment; the tail segments, however, are more slender and longer than in *U. variegatus*.

Adults of *U. variegatus* living in association with the pugnacious ant, *Anoplolepis custodiens* (Smith), in the Citrusdal district were found by Eastwood (1978) to be parasitized by the trombidiform mite *Pimeliaphilus isometri* Cunliffe, which is also found on scorpions in the Philippine Islands (Baker & Wharton 1952). Eastwood regarded this South African scorpion as *U. carinatus* but, according to Lamoral (1979), this species occurs only in the northern regions of the Cape; *U. variegatus*, on the other hand, is confined to the north-western and south-western Cape. It is interesting to note that a similar mite *Pimeliaphilus cunliffei* Jack, in the U.S.A., uses the cockroach *Periplaneta americana* (Linnaeus) as its natural host (Cunliffe 1952; Jack 1961).

Pregnant females of this species and of *Parabuthus brevimanus* were observed during September to December, and newborn young were actually found during the middle of December to the middle of February. Pregnant dissected specimens of *U. variegatus* yielded fourteen to twenty embryos of which most were situated on the sides of the mesosoma. The fully-developed bean-shaped embryo (Fig. 8C) is enveloped in a transparent membrane and has the metasoma folded in under the body. According to observations made, the gestation period is fairly long, probably lasting a year. Newly emerged young are pure white with black eyes (Fig. 8B) and an inconspicuous, longitudinal median line on the dorsum of the mesosoma; the body is devoid of setae except for a few setae on the pedipalpi (particularly on the fingers) and two or three setae on the last two apical segments of the legs.

After birth the young immediately climb on to the mother's back and after a few days the penultimate metasomal segment becomes pale purplish. Two days after birth they measure 7.2 mm from the tip of mouth-parts to the tip of the sting. The developing mouth-parts, claws and sting are still enveloped in the membranous covering during this stage and are freed only at the first moult, which occurs 10 days after birth. At this stage the larvae are almost 10 mm long

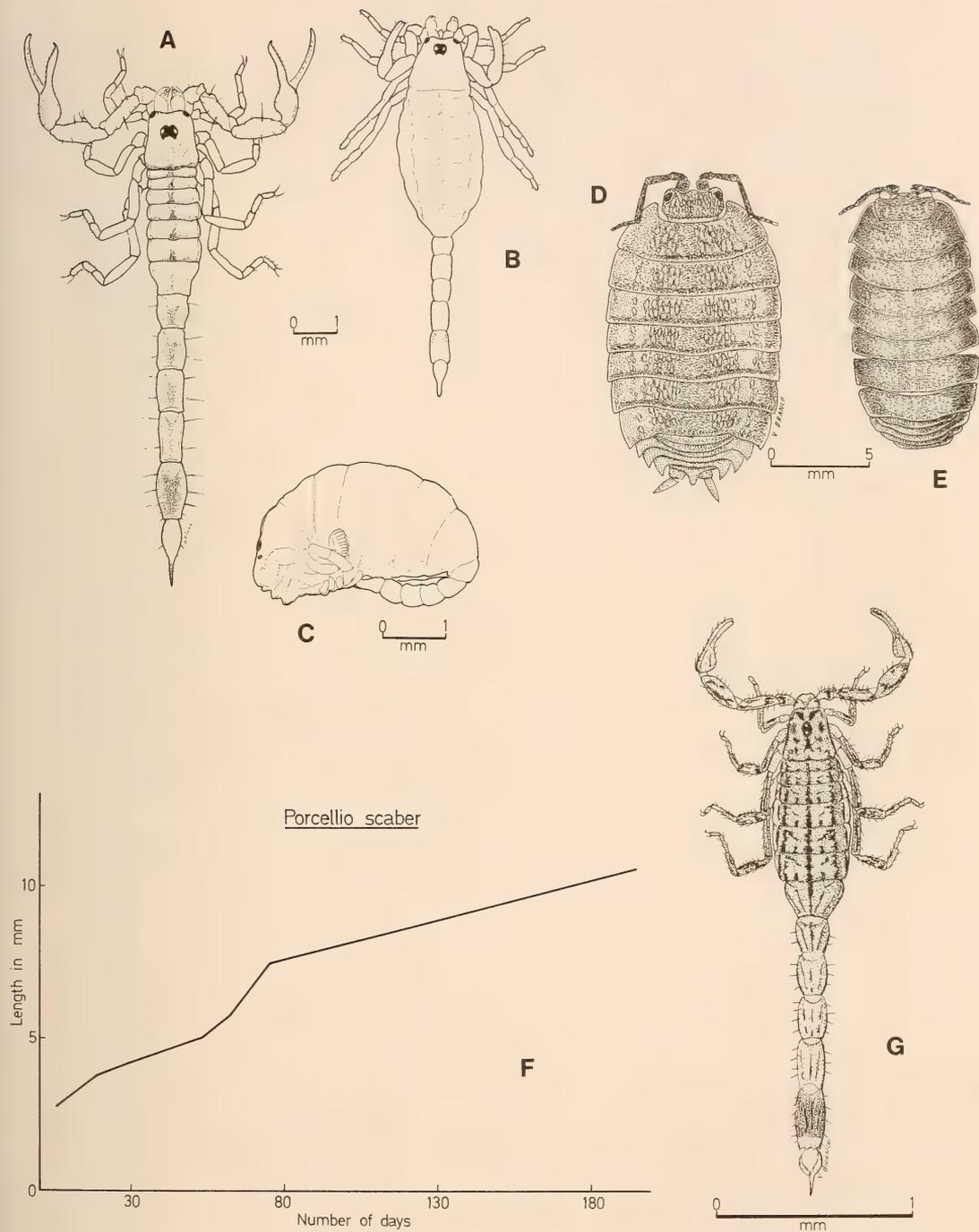


Fig. 8. A-C, G. *Uroplectes variegatus*. A. Eleven days after birth. B. Two days after birth. C. Fully developed embryo in adult female. G. Young female. D, F. *Porcellio scaber*. D. Adult. F. Increase in body length of the larvae of *P. scaber* as observed in the laboratory. E. *Armadillidium vulgare* (adult).

(Fig. 8A) and, although still very pale, the penultimate metasomal segment is clearly darker than the rest and the longitudinal median line on the mesosoma is much more conspicuous. The apical metasomal segment is pure white and the apical half of the sting brown. The legs are almost white and at this stage some of the young already begin to leave the mother, although they still cluster together on the ground. Body hairs are much more abundant, particularly on the pedipalpi and metasoma; they now clearly resemble the adult, except for the much narrower mesosoma.

CLASS CRUSTACEA

Mostly aquatic arthropods with calcareous exoskeletons in contrast to the chitinous covering of insects; with two pairs of antennae and usually five pairs of legs.

The majority are free-living. They may be vegetarians, predators, or scavengers.

Destruction of stranded kelp by arthropods is mainly brought about by the large numbers of halophilous crustaceans, both Isopoda and Amphipoda. Their presence on the beach is indicated by numerous tunnels in the stems of decaying plants; the crustaceans and large kelp-flies undoubtedly form the most important part of the wrack fauna that was examined.

ORDER AMPHIPODA

Body usually compressed, thoracic limbs without exopodites and with first pair modified as maxillipeds.

Apart from *Orchestia gammarella* Pallas, very few species seem to be euecoenic and some of the *Talorchestia* species observed were even found to breed in semi-fresh cow-dung in the laboratory. At least four species of the more common amphipods were collected during the surveys, namely the Atlantic species *T. capensis* Dana (Fig. 9I), the above-mentioned widespread *O. gammarella* (Fig. 9F), which is also found in North America, and the endemic *T. quadrispinosa* Barnard, which is known to prey on other beach-hoppers, including *T. capensis* (Branch & Branch 1981) and *T. australis* Barnard (Fig. 9G). All the species of these light grey to whitish beach-hoppers or sand-fleas are very similar and mostly scavenge between and just above the intertidal zone, although some have been found rather far above the supratidal zone on the small dunes. From the available data it seems as if *T. australis* and *O. gammarella* are more restricted to the southern parts of the Cape, while *T. capensis* and *T. quadrispinosa* are more widely distributed along the west coast.

The indigenous *Talitrus eastwoodae* (Methuen) (Fig. 9H), which is very similar to the beach-fleas but has reddish transverse bands over its body, is a scavenger confined to forests (Lawrence 1952). It was found in rather large numbers around Cape Town in the vicinity of Table Mountain at carcasses lying in shady surroundings. In the Cape Peninsula it is often found under carpets in houses during the warmer parts of the year.

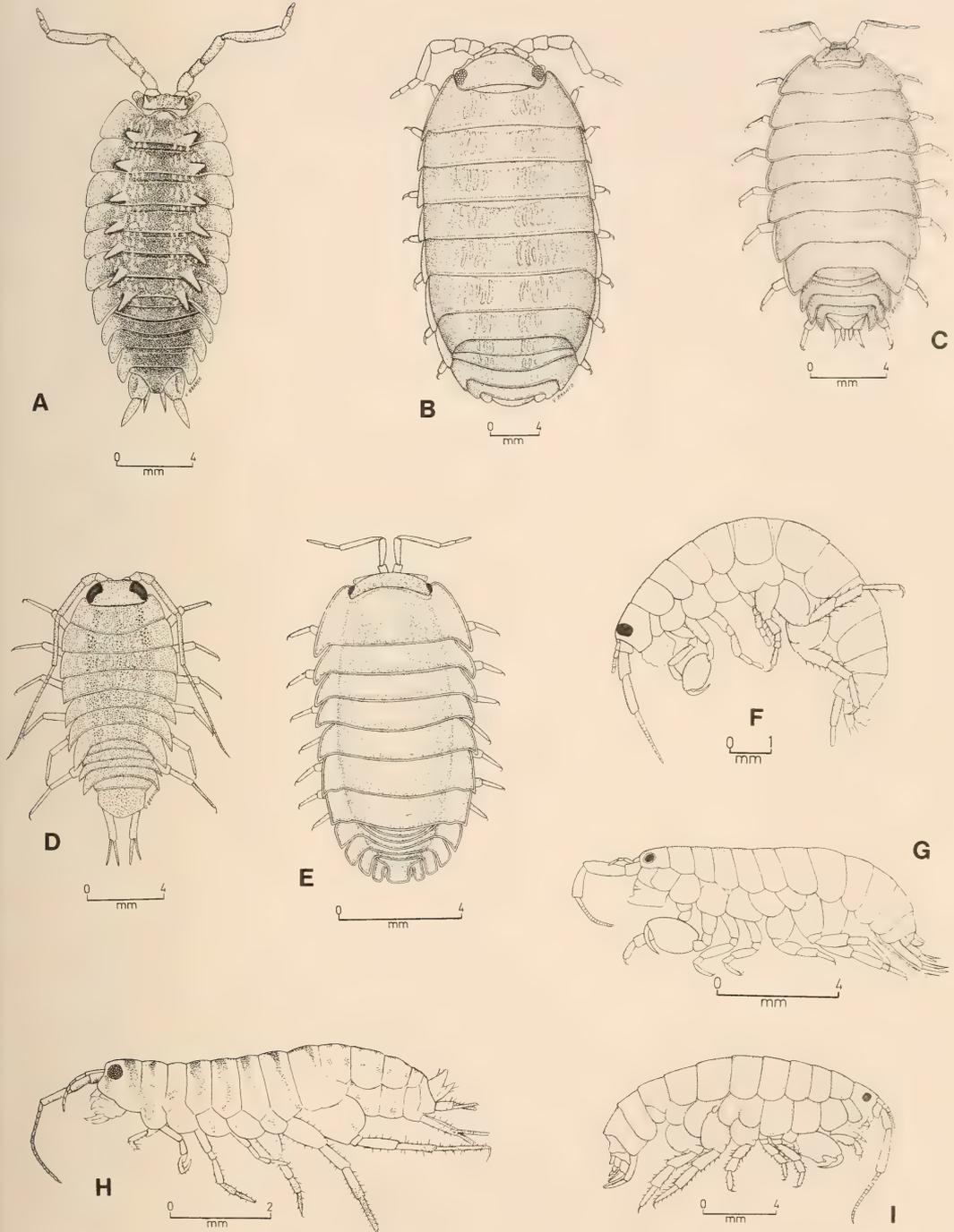


Fig. 9. A. *Deto echinata*. B. *Tylos capensis*. C. *Marioniscus spatulifrons*. D. *Ligia dilatata*. E. *Bethalus* sp. F. *Orchestia gammarella*. G. *Talorchestia australis*. H. *Talitrus eastwoodae*. I. *Talorchestia capensis*.

ORDER ISOPODA

A large, variable group with depressed bodies. Thoracic limbs also without exopodites and first pair always modified as maxillipeds.

The majority are aquatic, but the oniscoid group has adapted to terrestrial or semi-terrestrial life.

The largest species present under kelp is *Tylos* (length up to 50 mm), of which there are two species, *T. capensis* Krauss (Fig. 9B), occurring from the Cape Peninsula eastwards along the coast, and *T. granulatus* Krauss with a westerly distribution. The biggest difference between the two seems to be the texture of the integument, which is granulate in the case of *T. granulatus* and minutely granulose in *T. capensis* (Barnard 1932); their distribution and morphological similarity, however, seem to indicate that one may rank as a subspecies. According to Kensley (1974), both species are omnivorous but with a bias towards a herbivorous diet.

Most of the isopods are rather slow-moving, except *Ligia* species, which are also characterized by the long antennae and uropods. The common greenish-brown to olive-grey sea cockroach or shoreslater, *L. dilatata* Brandt (Fig. 9D), is widely distributed along the south and west coasts. When collections were made in wrack during the winter months, large numbers of this isopod were found to carry small, round, yellowish eggs (0,92–0,76 mm diameter) in their marsupia.

Deto echinata Guerin (Fig. 9A), slate to greyish green with lighter specks, is also widely distributed from the Namaqualand coast to Cape Agulhas. Large numbers (some with eggs) were usually present under the kelp during the winter, and very often they were found in seal carcasses in the intertidal zone. They were often found to prey on other arthropods. The slightly smaller *Marioniscus spatulifrons* Barnard (Fig. 9C), of similar coloration, has more or less the same distribution as *Deto echinata*, and was usually in association with the latter. *Bethalus* species (Fig. 9E) are darker orange in colour and were mostly found during the winter under semi-dry wrack strings along the south coast.

Family Oniscidae

Porcellio scaber (Latreille)

Full-grown females (Fig. 8D) are 15–16 mm long, with a brownish-grey colour, mottled with pale or creamy white; colour variation, however, is considerable. It cannot roll up into a ball and its uropods are much longer than those of *Armadillidium vulgare* (Latreille) (family Armadillidiidae, see below). Males somewhat more slender with longer uropods.

This species is widely distributed in South Africa and is found in many places in the world (Barnard 1932).

Adult sow-bugs collected during the first week in September from soil containing decaying carcasses moulted about 10 days later, and after a month produced about 50 larvae. The latter were kept under observation in the laboratory and were found to produce larvae 194–200 days after birth. The increase in size

of the larvae with age is shown graphically in Figure 8F. The average monthly temperature during the day during the period of observation varied from 21° to 29 °C in September to March and from 18° to 24 °C in April and May.

Young larvae of about 2 mm in length are nearly white with blackish eye-spots. As their size increases, the colour becomes darker and after about 20 days they are already pale brownish grey and inconspicuously mottled with dirty white. After about 80 days they look exactly like their parents and are fairly dark brownish grey, mottled with creamy white. According to Heeley (1941), who gives a good account of their biology in England, the development of the young may be regarded as complete by about the fifth moult.

This eurytopic sow-bug is omnivorous and was found to feed on various materials, including decaying kelp. It is very common under loose bark (Heeley 1941, Cloudsley-Thompson 1957). It is often found in large numbers under fresh and semi-fresh cow-pats and plays a vital part in the destruction of the remaining parts of the dung, especially when the number of fly maggots begins to decrease. It is sometimes attracted to rotting carcasses and may remain throughout the decaying process.

Family Armadillidiidae

Armadillidium vulgare (Latreille)

Adult females (Fig. 8E) about 14,6 mm long and dark slate grey in colour, mottled with paler spots similar to those of *Porcellio scaber*, but forming a definite, inconspicuous, pale longitudinal band over the middle of the dorsum.

This species is very widely distributed in South Africa as well as other parts of the world (Barnard 1932).

Its biology is very similar to that of *P. scaber*, but *A. vulgare* seems to produce more young than the latter. However, in specimens observed during the surveys the survival rate of the very young larvae was much lower than in the case of *P. scaber*. Young larvae about 1,7 mm long, collected during January near a turtle carcass, were (as in the latter species) almost pure white with black eyes. After about a month the body already showed four brownish, longitudinal lines and the colour gradually darkened until maturity was reached. The growth of specimens kept under conditions similar to those of *P. scaber* was, however, much slower and 200 days after birth some larvae were still only 5 mm long.

This pill bug is mainly omnivorous and is common around houses; it was abundantly collected in leaf litter and compost heaps all over the Cape Peninsula. Both Heeley (1941) and Paris (1963) give valuable information on the life cycle of this species, which is considered by Brereton (1957) to prefer the shade of stones both in open land and in woodlands. It often occurs in very large numbers together with *P. scaber* under semi-fresh to fresh cow-pats, and is also attracted to decaying carcasses. Albino forms, which are often present among individuals of this species, point to a calcium deficiency in the soil. They are highly dependent on humidity and are, therefore, always found in locations that are fairly damp.

CLASS INSECTA

ORDER BLATTODEA

Family **Blattidae**

Dorsoventrally compressed exopterygote hexapods with cursorial legs, well-developed cerci and multi-segmented antennae. Wings usually well developed, but some are apterous. A few species are sub-social, some are gregarious, and they may be oviparous, ovoviviparous, or viviparous; an ootheca of a tough leathery substance is produced during oviposition.

Although they are usually omnivorous, there is evidence that the Table Mountain cockroach, *Aptera fusca* (Thunberg), is a plant-feeding species as it was observed to feed on the berries of a *Cuscuta* sp. (Skaife 1979). In the Cape Peninsula it was sometimes observed under stranded kelp on the intertidal zone, but repeated efforts to feed the cockroach on this medium were in vain. It often congregates in familial groups under stones and dry cow-pats as is the case with other veld species such as *Deropeltis erythrocephala* (Fabricius) (Fig. 10J).

Of the oviparous species, the American cockroach *Periplaneta americana* (Linnaeus) drops the ootheca long before the eggs hatch. This is also the case with the indigenous *Pseudoderopeltis foveolata* (Walker), whereas the female of the German cockroach *Blatella germanica* (Linnaeus), on the other hand, carries the ootheca externally until shortly before the eggs hatch. This was also observed in some specimens of the short-winged mountain cockroach, *Temnopteryx phalerata* (Saussure), although evidence seems to indicate that this species behave rather like *Periplaneta americana*. The Madeira cockroach *Leucophaea maderae* (Fabricius), which occurs in many parts of the world and is widespread in the Subsaharan region (Cornwell 1968), including Natal and probably also Transvaal, is ovoviviparous. Like *D. erythrocephala*, it is gregarious and may form large colonies outdoors and, according to Scharrer (1951), in Brazil twenty-five to thirty-two young are produced at one time during the warm weather. It has been found in sugar-cane on certain North Atlantic islands.

For many years it has been suspected that cockroaches carry pathogens such as *Mycobacterium tuberculosis* (Schroeter) (observed in the faeces of *Blatella germanica*), *Salmonella typhimurium* (Loeffler) (gastro-enteritis), and *Chlostridium perfringens* (Veillon & Zuber) (gaseous gangrene and one of the causative organisms of normal decay in carcasses and cadavers), as well as various other organisms including viruses (Roth & Willis 1957, 1960). Even the organism that causes bubonic plague, *Yersinia pestis* (Lehmann & Neumann), has been found in specimens of the oriental cockroach or black-beetle, *Blatta orientalis* Linnaeus, collected in infected areas (Roth & Willis 1957). The natural vectors of plague are fleas (Siphonaptera). Cockroaches are also capable of causing allergic dermatitis (Smith 1973).

Parasitoids include wasps of the genus *Tetrastichus*, reared from the oothecae and sphechids of the genera *Ampulex* and *Dolichurus*, which provision their

young with cockroaches (Arnold 1928; Roth & Willis 1960). Mites have already been mentioned (see discussion on Arachnida).

Pseudoderopeltis foveolata (Walker)

Princis (1963) has described the adults (Fig. 10A). Females black and fairly shiny, with vestigial mesothoracic wings. Depressed sixth and seventh tergites are characteristic of this genus. Cerci ten- to twelve-segmented in all females collected and fairly broad and compressed dorsoventrally; penultimate segment in most cases the longest. Antennae multisegmented (at least sixty to seventy segments).

This species is widely distributed in South Africa, Zimbabwe and Lesotho (Princis 1963). It was collected in the interior under semi-dry cow-pats together with other *Pseudoderopeltis* spp. (Fig. 11E) and *Perisphaeria* spp. (Fig. 11F-G), whereas cow-pats on the beach or on the sand-dune biotope produced mainly the psammophylic cockroaches *Blepharodera discoidalis* (Brunner) (Fig. 11D) and *B. ciliata* Burmeister (Fig. 10F). *B. discoidalis* is a blackish species whose body is surrounded by a pale yellowish white margin; *B. ciliata* is mottled with brown; the adult females of the latter measure up to 30 mm in length and males up to 25 mm with a wing-span of 65 mm; nymphs are mottled with grey and resemble the apterous females, except for size. Both species are usually found under the sand near the stems of plants and both adults and nymphs have been collected on the beach under the stems of *Tetragonia decumbens* and *Arctotheca populifolia* during October to December. The *Perisphaeria* spp. vary from pale light brown, mottled with darker brown, to almost black.

Oothecae of *P. foveolata* (Fig. 10D), produced from December to January by adults collected along the west coast, are 7,9–8,8 mm long and are all about 4,9 mm broad. Initially the ootheca is reddish white, but soon darkens to a pale brownish red and eventually to a red-brown, with the keel somewhat paler. The dorsal serrations are rounded, not acute. In this species the ootheca is held upright while the eggs are being deposited, with the keel fitting in the V-shaped groove in the tenth tergum (Fig. 10B). The ootheca is dropped as soon as all the eggs have been laid and buried about 5 mm deep in the soil. The incubation period varies from 47 to 56 days.

The newly hatched young (Fig. 10C) are pale piceous to yellowish brown in colour, 3,3–3,7 mm long, and smooth and shiny. In all the specimens examined the cerci are three-segmented as in *Periplaneta americana* (Guthrie & Tindall 1968) and the antennae twenty-two-segmented. The sixth and seventh tergites are already depressed in the first instar. The young nymphs remain clustered together on the ootheca for at least 4–5 days, during which time they turn almost black.

The first moult was observed 17 days after hatching and by this time they were about 5,5 mm long. After moulting they are pale whitish brown with almost black eyes. In all the second instar nymphs the cerci are six-segmented,

with the penultimate segment the longest. The antennae are twenty-five- to twenty-six-segmented. In the laboratory development was slow and after about a month the nymphs were only about 6 mm long, the antennae consisted of twenty-seven to thirty segments and the cerci were still six-segmented. After about 120 days their length had increased to 10 mm, the cerci were now seven- to eight-segmented and the antennae thirty-five-segmented. Nymphal growth over a period of about 130 days is shown graphically in Figure 10E. Some specimens reached maturity only 3–6 months later.

Temnopteryx phalerata (Saussure)

Princis (1963) has given a detailed description of this species. General body colour of adult (Fig. 10G) light yellowish brown, abdominal segments darker brown, posterior borders of pronotum and abdominal segments pale yellow. Legs and antennae yellowish brown, latter multisegmented (more than seventy segments). Cerci twelve-segmented, measuring about 3,7 mm in adult females. Total length of body 18–25 mm. A peculiarity of this species is the uneven number of tarsal segments on the hind legs; out of twenty-five specimens examined, with only one exception, the hind tarsi on the right side had four segments while those on the left had five.

According to available collecting data it is endemic to the Cape where it is widespread along the west and south coasts. This cockroach, which is often observed in leaf litter both on the coastal sand-dune area and in the interior, has on several occasions been found to feed on certain types of carpets in the Cape Peninsula; damage reported so far, however, was apparently only very slight.

Whereas in *Pseudoderopeltis foveolata* the ootheca is always held upright during oviposition, in this species it is held flat (Fig. 10G) as in the case of the German cockroach, with the keel in all the specimens examined pointing to the right side. The oothecae (Fig. 10I) are 10,8–15,4 mm long and 3,5–3,7 mm wide and most of them are dark brown to dark reddish brown in colour, including the keel of which the serrations are clearly dentate and close together. Oothecae of this species are very similar to those of *Deropeltis erythrocephala* (Fig. 10K), common under cow-pats, but in *Deropeltis* spp. the serrations resemble those of *Pseudoderopeltis foveolata* and are lighter in colour. In *Temnopteryx phalerata* the ootheca in most specimens examined was retained by the female for a day before being buried under 1–2 mm of sand. The incubation period varied from 32 to 39 days during February at a temperature of 30–31 °C. In a few specimens the ootheca was carried for a longer period before being dropped.

Newly hatched nymphs measure 3–3,2 mm in length and are pale yellowish brown with two white oval spots on the metanotum; the eyes are reddish. The nymphs soon turn almost black (Fig. 10H) but the posterior borders of the thoracic segments and the first three abdominal segments, as well as the two metanotal spots, remain white. A thin white line also runs over the head and thorax. The legs are piceous with the apical third of the middle and hind femora, as well

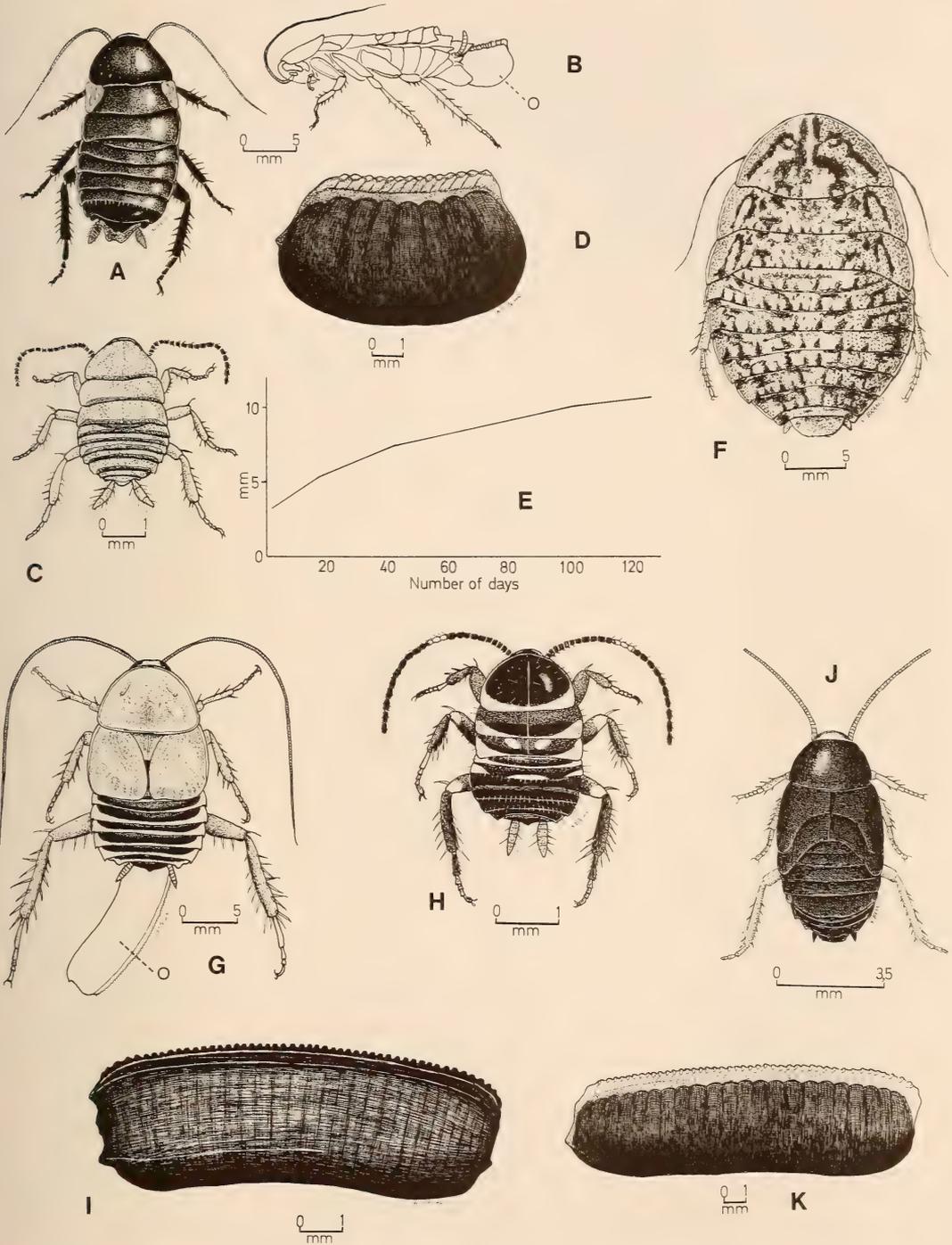


Fig. 10. A-E. *Pseudoderopeltis foveolata*. A. Female (adult). B. Female (left lateral view) to show oviposition and ootheca (o). C. Newly emerged larva. D. Ootheca. E. Body increase of larvae as observed in the laboratory. F. *Blepharodera ciliata* (adult). G-I. *Temnopteryx phalerata*. G. Female with ootheca (o). H. Larva at about 30 days. I. Ootheca. J-K. *Deropeltis erythrocephala*. J. Female (adult). K. Ootheca.

as the tarsi and the apical half of all the coxae, white. The antennae are twenty-two-segmented, with the second to fourth, the thirteenth and about one-third of the twelfth and fourteenth segments white in some specimens. In many specimens the thirteenth to the fifteenth segments, as well as the second to fourth, are also white, the remainder black. The cerci are piceous and three-segmented as in the other species. In the first instar the tarsi are five-segmented in all the legs.

Development was very slow and after about 161 days the nymphs were only about 5 mm long and coloured as shown in Figure 10H. The antennae had thirty-three to thirty-four segments, with the twenty-first and twenty-second segments white; the cerci were six-segmented.

Unfortunately, due to an invasion of mites and the excessive use of the insecticide Carbaryl to combat ants, most of the specimens died before maturity was reached.

ORDER MANTODEA

Family Mantidae

Elongate predacious exopterygote hexapods, usually with well-developed cerci, large eyes and raptorial forelegs. Antennae multi-segmented and pronotum long; wings usually well developed, absent in some females. Solitary insects producing oothecae of a tough material. Subsociality is known to occur in some species.

Oxypilus nasutus (Fabricius)

Full-grown females (Fig. 11B) 17–20 mm long, apterous and mottled with dark brown or dark grey and yellowish white. Very striking light coloration on ventral side of the abdomen and on front femora. As in most mantids, front femora spined on ventral side, with five spines on exterior margin, of which basal ones are largest. The three discoidal spines (Fig. 11B) large and agree with those described by Loxton & Nicholls (1979) for *Hierodula membranacea* (Burmeister), suggesting that this is a generalized predator. Front coxae also have six to seven spines on anterior margin. Males similar to females, but more slender, with a wing-span of 45–50 mm.

This species is widely distributed in South Africa and South West Africa, and is fairly common along the west coast, particularly in Namaqualand. It appeared occasionally in the vicinity of Saldanha Bay under plants growing on the edge of the fore-dune system adjoining the beach. It is very well camouflaged against the debris and remains of plant seeds that are found under plants such as *Arctotheca populifolia* and is therefore very rarely seen. Prey included small mantids, blow-flies and other soft-bodied insects.

Oothecae (Fig. 11C) collected during December varied from 8 to 16 mm in length and were glued to the seeds and to leaf litter under the plants. They are whitish when freshly produced, but after about a day become reddish brown to

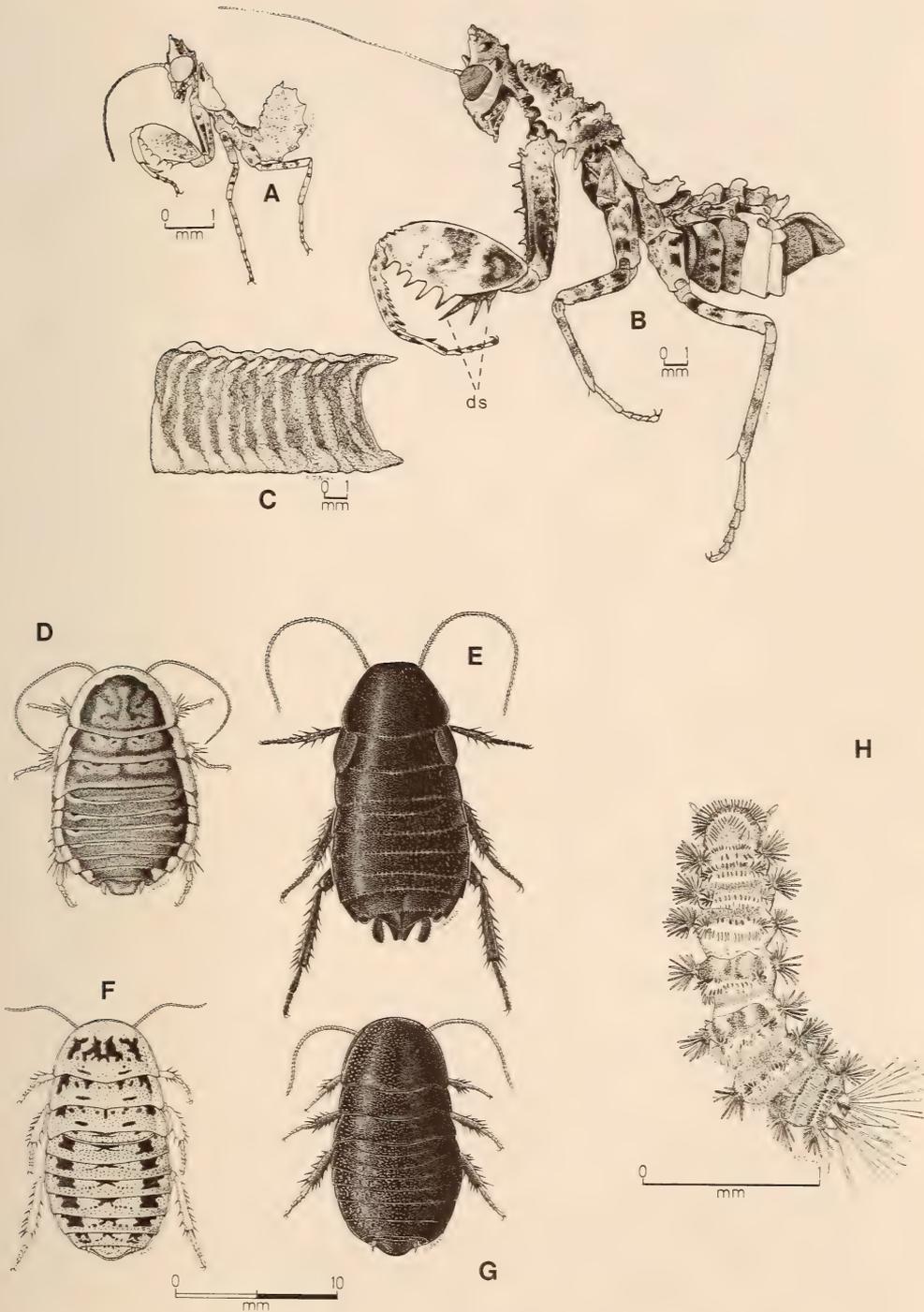


Fig. 11. A-C. *Oxyphilus nasutus*. A. Newly hatched young. B. Adult showing discoidal spines (ds). C. Egg packet (lateral view). D. *Blepharodera discoidalis*. E. *Pseudoderopeltis* sp. F. *Perisphaeria* sp. G. *Perisphaeria* sp. H. *Penicillata*, sp. indet.

dark brown with the dorsal edge yellowish white. The incubation period of the eggs was about 45 days.

The newly hatched mantids (Fig. 11A) are approximately 4,2 mm long, mottled with brown and pale yellowish white, except the last four or five abdominal segments, which are pale, almost white in colour. The eyes are large and pale brown. Almost the whole of the pronotum and the tibiae as well as the apical third of the front femora are white. As in the case of the adults, there are five spines on the exteroventral margin of the front femora, but the anterior margins of the front coxae are devoid of any spines. Exteroventral margin of front tibiae has only one strong spine.

In larger nymphs (8,5 mm long) taken during January and which exhibit the coloration of the adult, the anterior margins of the front coxae possess six to seven spines and the exteroventral margin of the front tibiae at least two developed spines and smaller dentations indicating the position of five more spines present in the adult form.

ORDER DERMAPTERA

Elongate exopterygote hexapods, cerci modified into forceps. Legs cursorial, antennae fairly long with variable number of segments. Forewings reduced to tegmina, hind wings membraneous, sometimes lacking. Mostly omnivorous; however, species of the family Hemimeridae are parasitic, such as *Hemimerus talpoides* Walker, living in the soft fur of the large African pouched rat, *Cricetomys gambianus* Waterhouse, and feeding on parts of the skin, fungus spores and other debris (Rehn & Rehn 1935, Walker 1964). Subsociality and viviparity are known to occur in some earwigs.

Only a few species were collected during the surveys, mainly under cowpats, of which *Labidura riparia* (Pallas) and an unidentified species were the most abundant. The latter, a brown earwig with pale yellowish stripes and markings giving it a mottled appearance, was found to be very common in dry pats near Saldanha Bay. Only wingless specimens, 11–16 mm in length (forceps included), with dark-brown heads and usually with two small, oval, lighter yellow marks on the front, were collected throughout the year. They were found to shelter in the crust and cake of the pat, their colour blending well with the surroundings, making them difficult to find. Their legs are pale, marked with brownish patches and the antennae dark brown with the apical borders of segments 15 to 16 white.

Young larvae of this earwig measuring 5,2–7,8 mm in length had the same colour as the adults, but were pale, sometimes pale yellowish and with the posterior part of the body darker as in the adults. The number of antennal segments varied in the immature stages from eleven (5 mm specimens) to fourteen (7 mm specimens) and the yellowish patches seemed to be absent on the head. These nymphs and their exuviae were observed in the pats during both summer and winter.

One light-brown specimen of the genus *Esphalmenus* was collected under an almost dry cow-pat in open sandveld, near the sand-dune system in the vicinity of Elands Bay during April. It is about 15 mm long (including the forceps) and differs from *E. peringueyi* (Bormans), *E. capensis* Brindle and *E. ecarinatus* Brindle, the only three other species of this genus described from South Africa, by having a strong tooth on the last tergite, just in front of the base of each branch of the forceps; the latter also carries a large tooth. Nymphs of the pyrrhocorid *Scantius forsteri* (Linnaeus), sheltered under the same pat.

Family Carcinophoridae

Euborellia annulipes (Lucas)

This earwig is always apterous (Fig. 12A). Females collected are dark reddish brown to piceous brown, but the pronotum (and in some specimens also the meso- and metanotum) is usually paler in colour. Antennae have sixteen to eighteen segments in most females examined, with fourteenth or thirteenth to fifteenth white. Forceps more or less straight. Males similar to females, except that forceps are more curved, particularly on right side (Fig. 12C). Antennae consist of fourteen to sixteen segments, with twelfth or twelfth to fourteenth white. Hincks (1947) and Brindle (1978) give good descriptions of males and females.

This species is cosmopolitan and widely distributed in Africa and is the most widely distributed earwig (Brindle 1978). It is very common in the Cape Peninsula and is often attracted to decaying carcasses, feeding on the organic material and on insects and other arthropods present under such conditions. It is a nocturnal species, attracted to houses by lights and, according to observations, it is thigmotactic as in the case of *Labidura riparia*. It was never encountered on the beach or on the dune system during the surveys.

Although this species appeared during the last post-mortem stage of decay when the surveys were made, it may, depending on various factors such as weather conditions, location of the carcass and the species of arthropods present, be attracted at a very early stage, as is the case with ants, certain beetles, arachnids, and chilopods.

Males and females were found to copulate during October. When mating the male and female face away from each other and the male's abdomen is twisted so that the genitalia on the ventral side are brought into contact with those of the female. Copulation in most cases lasted for about 2 minutes and most females produced a batch of 44–50 eggs about 18 days afterwards. Eggs were also found during the late summer and early autumn.

The eggs (Fig. 12B) are spherical, shiny white and almost without any sculpturing. They vary in size from $0,88 \times 0,76$ mm to $1,06 \times 0,90$ mm and are laid in a ground cell excavated by the female, who remains in the cell with the eggs. When disturbed the female carries the eggs away to a new excavation, or else devours them. The incubation period is at least 16 days.

The newly hatched nymph is pure white with brown eyes and about 3,4 mm long including the forceps, which measure 0,68 mm in the specimens examined. The antennae at this stage consist of eight segments. In about 3 days' time they turn to a pale yellowish brown, the head and posterior three or four abdominal segments becoming somewhat darker. The legs remain whitish, with a darker transverse band at about the middle of the femora. The penultimate antennal segment is also white (Fig. 12D).

At the age of 19 days the number of antennal segments have increased to eleven (after which stage the first moult apparently occurs) with the penultimate or, in some cases, the ninth segment remaining white. The general body colour is yellowish brown, with the head somewhat darker and the legs paler. About 44 days after hatching another moult takes place and the antennae consist of thirteen to fourteen segments, with the eleventh segment white. The body length is then 6,5–7,0 mm. The nymphs were observed to moult again after about 64 days from the time of hatching and the antennae were then found to consist of fifteen to seventeen segments in most cases. In the laboratory the developing nymphs required about five moults to reach maturity, but some specimens moulted only four times. The size increase over a period of about 150 days is shown graphically in Figure 12E. According to Hincks (1947) there are five instars and the third instar has thirteen-segmented and the fourth instar fourteen-segmented antennae.

Family Forficulidae

Forficula peringueyi (Burr)

Females (Fig. 12F) measure about 10 mm, forceps included; reddish brown in colour, with the posterior five segments almost black. Males fairly similar to females and measure 11–11,6 mm, forceps excluded; latter long, in most cases measuring about 7,5 mm (Fig. 12G). In both sexes antennae are eleven-segmented. Characteristic of both males and females are the lateral tubercles on third and fourth abdominal tergites, those on fourth being the largest. Brindle (1973) gives a description of the sexes.

This species is endemic to the Cape and, according to Brindle (1973), restricted to the western parts where it is common under debris and stones; it has been found to nest in cow-pats during the winter. The immature stages of this species look very much like those of *F. promontorii* (Burr), which was mainly observed along the south coast, but they seem to be more shiny.

Eggs (Fig. 12K) were found in hollowed-out chambers in fairly dry cow-pats during July. They are oval and measure $1,2 \times 0,72$ mm; most of them are shiny, creamy white to whitish yellow and without any form of sculpture. As in the case of *Euborellia annulipes*, the females usually tend the eggs.

Newly emerged nymphs (Fig. 12L) measure about 3,7 mm including the forceps, and are pure white but soon turn to a pale brown, the head and posterior two to three segments being somewhat darker. The antennae are eight-segmented and of the same colour as the body; the forceps are fairly long and

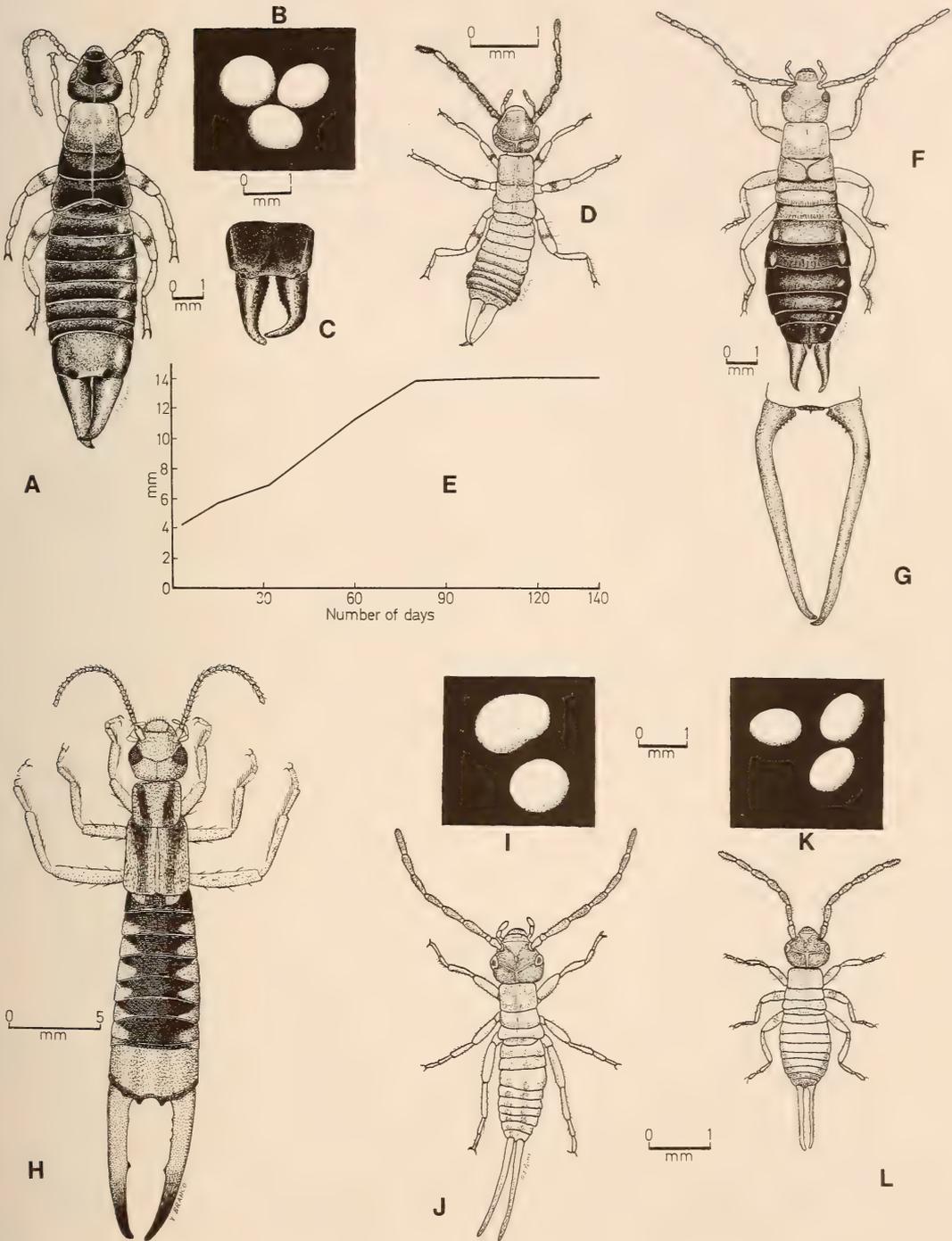


Fig. 12. A-E. *Euborellia annulipes*. A. Adult. B. Eggs. C. Forceps of male. D. Nymph at 3 days. E. Increase in body length of nymphs as observed in the laboratory. F-G, K-L. *Forficula peringueyi*. F. Adult female. G. Forceps of male. K. Eggs. L. Newly hatched nymph. H-J. *Labidura riparia*. H. Adult. I. Eggs. J. Newly hatched nymph.

measure 1,1 mm. Observations show that the nymphs require 4-5 months to reach maturity.

Family **Labiduridae**

Labidura riparia (Pallas)

This is a large species (Fig. 12H), specimens examined measuring 20-26 mm in length, including the forceps. Usually dark reddish brown, with central area of abdomen darker, in the shape of two longitudinal, median bands; pro- and mesonotum also with two darker stripes. Antennae and legs yellowish. Antennae consist of more than twenty segments, with fourth to about seventh shorter than the others. Brindle (1973) described both sexes.

This earwig is cosmopolitan and common in Africa, particularly along the shore (Brindle 1973). It is mainly a predator and generally feeds on the smaller staphylinids and scarabs and their larvae as well as on other beetles such as *Gonocephalum* spp. It is attracted to light and is therefore often seen in houses during the night. It is sometimes also attracted to semi-fresh cow-dung on the beach. According to Callan (1964) the pale sand-coloured ecotype is a maritime form restricted to sandy habitats of the coast. During this survey, however, only the dark ecotype was found both on the beach and inland. Moderately pale forms occurred only in the young nymphal stages.

In certain areas along the west coast it was seen to visit dried-out sea-birds on the high-water mark and was found to feed on other arthropods, particularly fly larvae, and on bits and pieces of the flesh still left on the skeletons. Near Elands Bay it was observed in large numbers together with the cicindelid *Platychila pallida* Fabricius in the top few millimetres of sand under the plant *Arctotheca populifolia* in the supratidal zone; they were associated with the larvae of the beetle *Melyris viridis* Fabricius, on which both predators fed. This earwig is very common under dry cow-pats in sandy areas.

The yellowish-white, shiny eggs (Fig. 12I) were collected under semi-fresh cow-pats during March. They measure $1,1 \times 0,96-1,8 \times 1,2$ mm, vary from nearly round to oval, and are without any significant sculpture.

The newly hatched nymphs (Fig. 12J) are 3,4 mm long (excluding the forceps) and almost white with pale brownish blotches, particularly on the abdomen. As in the two previously mentioned species, a white, longitudinal median line, representing the posterior part of the ecdysial suture, traverses the thorax. It is connected anteriorly to the so-called 'epicranial suture' of the head. The antennae are brownish and eight-segmented and the eyes brown. Most nymphs reached a length of 6 mm about 70 days after hatching.

Nymphs 8,7-10 mm long (including the forceps) collected during March, are darker in colour than newly hatched specimens. The antennae are fifteen-segmented, with the five apical segments much longer than the others, except the first and third segments. The eyes are almost black and the forceps measure about 2,3 mm.

In larger nymphs (16.6–17 mm long including the forceps) the colour remains the same, but the stripes on the abdomen are darker. The antennae are then twenty-segmented, the last ten segments being somewhat longer than the others, except the first and third segments, which are the longest. Wings are already partially developed and partly cover the first abdominal segment.

As in the other species, the forceps are used to crush the prey, which is then lifted over the body and devoured. The nymphs were found to feed on small scarabaeid larvae and for this purpose they often dug holes in the soil with their mandibles.

ORDER ORTHOPTERA

Family Gryllidae

Exopterygote hexapods with well-developed cerci, and short antennae with few segments to long and multi-segmented. Hind legs usually saltatorial, fore-legs often fossorial and in certain species with tympani. Wings well developed or absent. Usually omnivorous, but a few species are phytophagous, causing damage to crops and lawns; under certain circumstances they may even become predacious or cannibalistic. Some species of the genera *Tachysphex*, *Liris*, *Chlorion*, and *Isodontia*, and probably also *Gasteroceriscus*, prey on crickets (Arnold 1922, 1923, 1928; Bohart & Menke 1976).

Of the somewhat thirty-five species of true crickets (family Gryllidae) that have been collected in southern Africa, only three were observed in decaying matter during the surveys, of which the common field cricket, *Gryllus bimaculatus* de Geer, was the most abundant and most widespread. It often shelters under stranded kelp on the intertidal zone and when reared in the laboratory occasionally accepted pieces of wrack, though it preferred fish-meal and grass cuttings. According to Smit (1964) it can be a pest of the vegetable and flower garden.

Cophogryllus delalandi Saussure

A wingless species (Fig. 13C–D). Ground colour pale creamy white to pale whitish yellow, with dark-brown marks on dorsal side of body. Cerci, antennae and ovipositor brownish; the ovipositor being 11–11.6 mm long in mature females (Fig. 13E). Body length of adult females collected along the west coast vary from 14.9 to 18.3 mm; males measure about 13.7 mm.

According to Chopard (1955) *C. delalandi* is widely distributed in the western and southern Cape Province and has been collected as far east as Mossel Bay. It was found to be a common prey of the baboon-spider (*Harpactira* sp.).

Adults were collected almost throughout the year along the west coast under stones and dry to semi-fresh cow-pats. During the summer and early winter large numbers were often observed, in some cases up to six gravid females under a single small pat. Eggs (Fig. 13F) were found under the sand under semi-dry pats during November. These measure from 2.50×0.74 mm

to $2,7 \times 0,91$ mm and are fairly dull (only slightly shiny), with a fine superficial reticulation and varying in colour from creamy white to a dirty brownish white. Females with eggs were also noticed during April. It was impossible to determine the incubation period of the eggs, but in a few cases eggs laid during July hatched only in November. Just before the young cricket emerges the two reddish eyes, the mandibles, and the segmentation of the body become visible through the chorion.

Nymphs that hatched during November (Fig. 13A) measured about 2,5 mm long and were almost pure white with dark brownish eyes. After about 4 hours they usually turned to a pale grey colour (Fig. 13B) and after about 11 days the colour became quite dark. A thin pale longitudinal line over the thorax represents the ecdysial suture and anteriorly joins the epicranial suture. The legs are pale except for a dark transverse band near the apices of the femora. As the nymph increases in size, its body becomes mottled with brown. The size increase in the laboratory over a period of about 140 days is shown graphically in Figure 13G. Although growth was fairly fast during the first 100 days (the nymphs reaching a length of about 10 mm in March) some specimens matured only during midwinter.

In the females examined, rudiments of the ovipositor appeared about 103 days after hatching and within 50 days had reached a length of nearly 4,6 mm. At this stage the nymphs are all found in small burrows in the loose sand and in the laboratory they have to be kept in separate jars to prevent predation. In field collections made during February large numbers of young females, 11–11,6 mm in length, were found, their ovipositors being only 1,8 mm long; in specimens collected during June the ovipositors had already reached a length of 5,5–6,1 mm.

Cophogryllus sp.

This species is also wingless and somewhat larger than *C. delalandi*, females (Fig. 14A) measuring from 16,6 to 20 mm in length are somewhat more robust. The body marked with dark-brown stripes instead of the mottled coloration of *C. delalandi* and ovipositor much longer, measuring 16,6–25,0 mm. Femora of hind legs pale yellowish to creamish and not marked with dark coloration.

This species is widespread in the Cape and has been observed even in the Great Karoo near Beaufort West. In the western Cape adults of this species were collected under dry cow-pats in sandy areas during the late summer to early winter, and eggs were collected in the sand under the pats during the latter part of January.

The eggs (Fig. 14C) are somewhat larger than those of *C. delalandi* and vary in size from $2,8 \times 0,64$ to $3,2 \times 0,96$ mm. They are yellowish to yellowish white in colour, shiny and without any form of sculpture. The incubation period is about 28 days and the newly emerged nymphs (Fig. 14B) are dirty white, almost transparent, with the last two abdominal segments and distal half of the cerci somewhat orange. The head in all the specimens examined is of a pale

golden yellow, the eyes reddish. Most first-stage nymphs measure from 3 to 3,2 mm. About 4 hours after hatching they become piceous, but have reddish eyes surrounded by a whitish margin; even the thirty-four-segmented antennae and the cerci are piceous except for the hair bases, which are white. The borders of the apical antennal segments also have an orange coloration. As in the previous species, the ecdysial suture forms a pale, longitudinal median line over the body and is anteriorly continuous with the epicranial stem. The hind femora are pale piceous, lacking a dark transverse band.

Characteristic of the nymphs of both this species and those of *C. delalandi*, are the long, blackish median hairs on the thorax and posterior borders of the abdominal segments. Nymphs of this species differ from those of *C. delalandi* in that they construct a little burrow soon after hatching, into which they then retreat. The burrow was in most cases extended for several millimetres along the surface, in a similar way to those made by golden moles.

The nymphs are usually very pale after each moult. In the specimens examined, the first moult occurred 9–10 days after the nymphs had hatched and most of them at this stage measured about 3,3 mm, with the antennae in almost all the specimens consisting of about forty-nine segments. After the first moult the nymph already resembles the adult fairly closely in colour. Further moults were observed at 44 and 45 days and again at 100 to 102 days after hatching. The first rudiments of the developing ovipositor appeared after 202 to 207 days. In larger nymphs (about 14 mm long) collected during November, the ovipositor was only about 3,3 mm in length. In specimens kept under observation in the laboratory, the ovipositor reached a length of 4,3 mm about 300 days after hatching. The increase in size of the nymphs over a period of 280 days, as observed in the laboratory, is shown graphically in Figure 13G.

Gryllus bimaculatus de Geer

In the common black field cricket the wings are well developed, with the hind wings pointed in both sexes and extending beyond apex of abdomen (Fig. 14E). Males are easily recognized by the venation of the front wings (Fig. 14F) and absence of an ovipositor; front wings pale fulvous in most specimens examined. The species differs from *Cophogryllus* spp. by the presence of a distinct tympanum (Fig. 14J) on both sides of the front tibiae (absent on both sides in *Cophogryllus* spp.—Fig. 14D). Wing bases pale yellow and broadly so in males, but narrower in the case of females. Three distinct ocelli, reddish in colour, are present.

Very often crickets with reduced hind legs are found. Crickets are aggressive and when nymphs lose a leg in a skirmish, it is replaced at the following moult by one that is smaller than usual.

This species is widely distributed in Asia and Europe and has been collected all over South Africa and Zimbabwe, including some of the islands along the west coast such as Bird Island near Lambert's Bay.

In the western Cape adults were observed under decaying kelp on the beach and under semi-fresh to dry cow-pats, both in the winter and summer, and eggs (Fig. 14I) were collected under semi-dry pats throughout the summer and autumn. In some cases batches of twenty eggs were laid in cracks in the pats, in others eggs were deposited in the top 4 or 5 mm of soil in batches of fifteen or more; in a few instances, however, eggs were laid singly in the sand. Those found near Philadelphia measure $2,5 \times 0,56$ – $2,8 \times 0,76$ mm and are almost banana-shaped. The colour varies from a whitish yellow to almost golden yellow, the eggs being fairly shiny and without any form of sculpture.

As the embryo develops the egg becomes slightly darker and after a few days the body segmentation, the two black eyes, the apices of the mandibles, and the cerci become visible through the chorion; some eggs develop a dark ring at the anterior pole.

In the laboratory the incubation period was 8–15 days during January. Rivnay & Ziv (1963) gave the mean incubation period in Israel as 7,5 days (34°C) to 75 days (16°C).

The newly hatched nymphs are about 2,7 mm long and pale whitish, translucent, with blackish eyes; three ocelli are indicated by three black marks. They remain quiescent for 3–4 hours, after which they become piceous (Fig. 14G) with reddish eyes; they can then easily be distinguished from second instar nymphs and nymphs of the other two species by the white mesonotum and pale, almost white posterior half of the pronotum. The pale cerci are white at their bases, with piceous apices. As in the other species, there is a white, longitudinal median line over the back and the legs are also piceous. In the few specimens examined, the antennae consisted of thirty-four segments.

The first moult occurred 7–22 days after hatching in specimens that hatched during January–February and by this time they were about 4,9 mm long and black all over (including the pro- and mesonotum), except for the pale, median dorsal line, the brown eyes, pale brownish cerci, and the small whitish areas on the sides of the pro- and mesonotum. The antennae consisted of about forty-nine segments (Fig. 14H). A second moult occurred 40–48 days after hatching, the nymphs remaining more or less of the same colour as in the second instar. After each moult the colour is pale brownish white mottled with brownish, but they assume their normal black colour in 2,5–4 hours.

Development was fairly rapid in the laboratory during the first 100 days or so and most of the nymphs reached a length of 12,5–14 mm after 94–120 days, depending on the amount of food available. The size increase during the first 120 days is shown graphically in Figure 13G. The ovipositor appeared 37–52 days after hatching.

As already stated, adults were found throughout the year and large numbers of nymphs collected during September at Elands Bay reached maturity during that month. According to collection data it seems as if there was only one generation annually during the surveys with overlapping of the different stages.

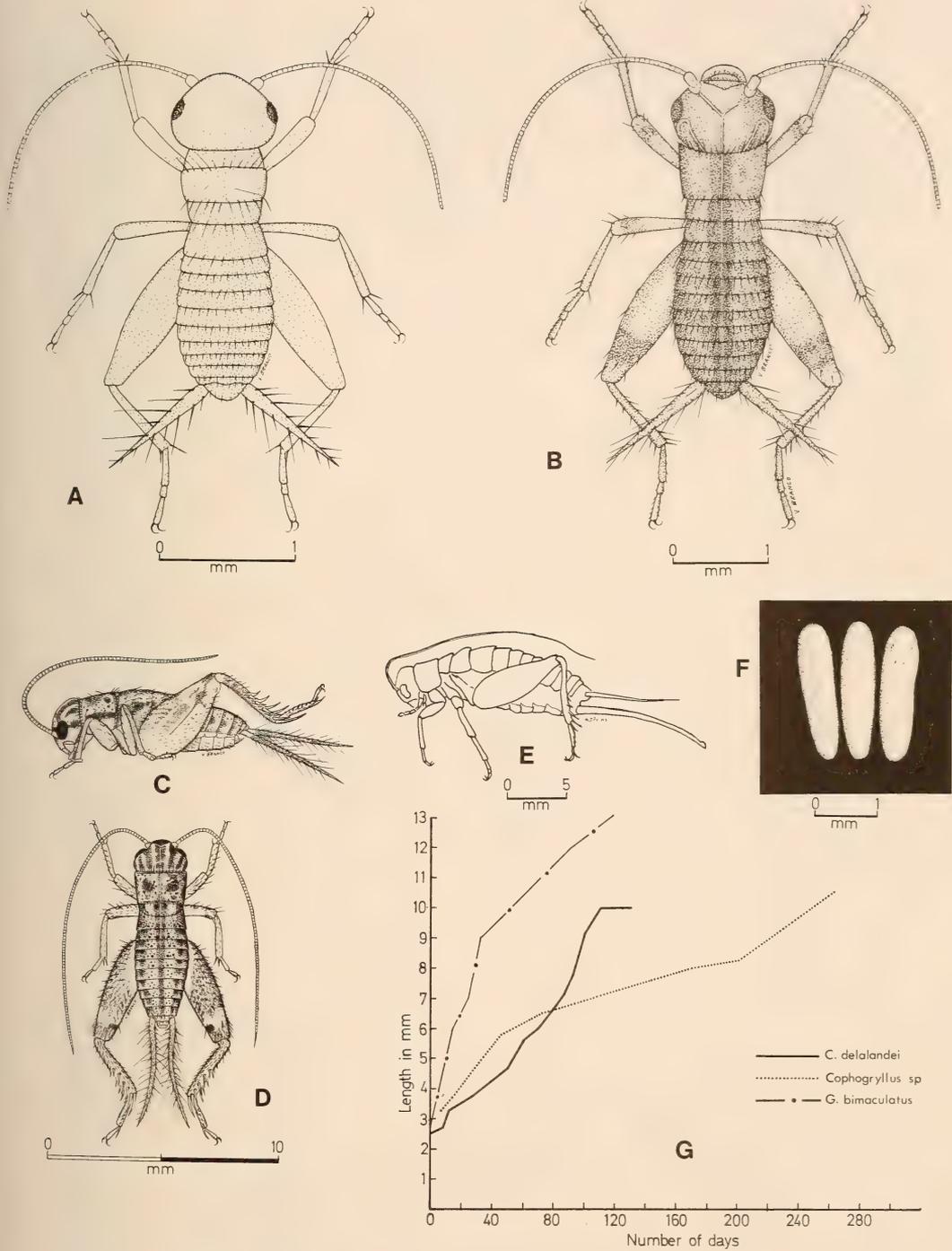


Fig. 13. A-F. *Cophogryllus delalandi*. A. Newly hatched nymph. B. Eleven-day-old nymph. C. Adult male (left lateral view). D. Adult male (dorsal view). E. Outline of adult female. F. Eggs. G. Size increase of *C. delalandei*, *Cophogryllus* sp., and *G. bimaculatus* as observed in the laboratory over a period of 140 to 300 days.

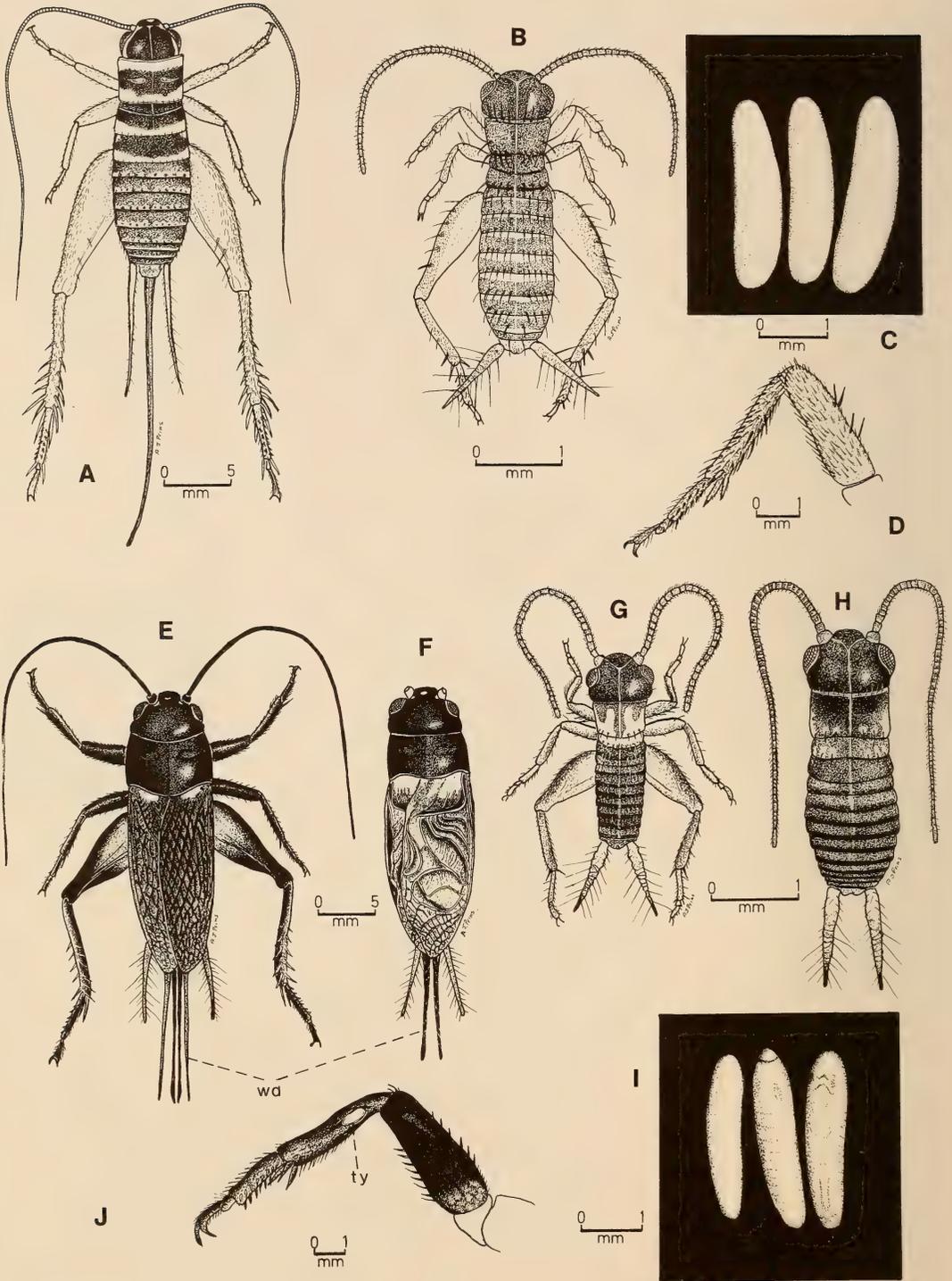


Fig. 14. A-D. *Cophogryllus* sp. A. Adult female. B. Newly hatched nymph. C. Eggs. D. Left foreleg (posterior view). E-J. *Gryllus bimaculatus*. E. Adult female showing pointed wing apices (wa). F. Adult male showing pointed wing apices. G. Newly hatched nymph. H. Second instar nymph. I. Eggs. Middle one showing black ring and body segmentation. Right one with developed embryo, showing cerci in lower pole. J. Left foreleg (posterior view showing tympanum (ty)).

A peak emergence of adults occurred during the spring and early summer months with an apparent second peak during the winter.

They were observed to feed on various substances including fish-meal, grass, and bran, and when they were confined to a small space they devoured each other; this was also found by Rivnay & Ziv (1963).

ORDER HEMIPTERA

Family **Anthocoridae**

Small, somewhat flattened, mostly predacious exopterygote hexapods with three-segmented rostrum and antennae with only a few segments. Cerci absent. Legs cursorial. Ocelli present.

Sp. indet.

The adults (Fig. 15K) vary from 2,8 mm to 4,2 mm and are dark brown with a lighter yellowish coloration on the hemelytra. Eyes scarlet and ocelli clearly visible. Legs with three-segmented tarsi, and antennae pale yellow.

This species was very common in the early dermatophagous stage of decay of certain animal carcasses around Cape Town and both adults and nymphs were found to feed on small fly larvae that were present, especially those of the blue-black carrion-fly *Ophyra capensis* (Wiedemann). It was also found in the Constantia area in poultry manure in which house-flies, false stable-flies, and the lesser house-fly were breeding.

Nymphs of all stages were collected during the period January to April. Those about 1,0 mm long (Fig. 15I) are pale brownish with scarlet eyes, cream-coloured abdomen and pale, almost translucent legs and antennae. Also three small, oval, reddish spots present on middle of abdomen, marking the openings of repugnatorial glands. Characteristic of these nymphs are two long setae on the apex of the abdomen; these are absent in the 1,4 mm long nymphs. Larger nymphs, about 2,1 mm long, are very similar to the smaller ones, but the colour is somewhat darker, especially on the abdomen, and the first two abdominal tergites are whitish in the middle.

In the 3,4 mm specimens (Fig. 15J) there is a clear, whitish-yellow, longitudinal, median line over the head and thorax, and wing rudiments are present. The six small, semicircular patches dorsally on the abdomen mark the openings of repugnatorial glands. The colour of these nymphs is yellowish with brownish patches.

All the immature stages have two-segmented tarsi and ocelli are indicated by two small scarlet patches in nymphs about 2,0 mm long and larger.

Family **Coreidae**

Rather similar to the Lygaeidae and also with four-segmented rostrum, but membrane of front wings with numerous branched veins. Ocelli present. All the species are phytophagous.

Very few squash bugs were associated with decaying organic matter when the surveys were made and, apart from the species discussed here, only the dull, greyish-brown *Stenocephalus testaceus* Stål, about 9,5 mm long, was found to shelter under dry cow-pats along the west coast. However, Payne *et al.* (1968) found three species in America, belonging to the genera *Megalotomus* and *Alydus*, actually feeding on pig carrion.

Leptocoris hexophthalma (Thunberg)

This species is pale crimson to crimson with brownish wings and measures 10–11,5 mm in length (Fig. 15H). It is widely distributed in the Cape, Natal, and the Transvaal and was also collected in east Africa. It is common in the Karoo and sometimes congregates in very large numbers on the debris beneath the bergvygie, *Drosanthemum* sp., and the skaapbossie, *Justicia orchioides*. Both newly hatched and mature nymphs have been collected on these plants during March, when they cause extensive damage to the foliage.

The nymphs of this species are quite different from those of the other Hemiptera inhabiting the same habitat, viz. *Melanostethus marginatus* (Thunberg), *Scantius forsteri* (Fabricius), and *Cenaeus carnifex* (Fabricius), as they are fairly hairy and the repugnatorial gland openings are small and inconspicuous. In small (2,0 mm) nymphs (Fig. 15F) the hairs are long, but in larger nymphs the hairs are short and almost spine-like. All stages of the nymphs are very similar except for the presence of wing rudiments in the later instars (Fig. 15G). Ocelli become visible subcutaneously only in nymphs larger than 7,0 mm; in adult forms the tarsi are three-segmented, as in most other Heteroptera.

Family Lygaeidae

Similar to Anthocoridae, but with four-segmented rostrum and membrane of front wings with only a few veins. Ocelli present. Apparently predominantly seed-feeding; however, a few species are predacious.

Masses of dying and dead stink-bugs, particularly the chinch-bugs *Microspilus proximus* (Dallas), *Geocoris scutellaris* Puton, and *Nysius binotatus* (Germar) (one of the crop pests, particularly crucifers), and the damsel-bug, *Nabis capsiformis* Germar (Nabidae), together with various other beetles such as coccinellids, tenebrionids and carabids, are often found in the intertidal zone along the west coast. This happens when these insects are blown out to sea by strong winds and are then washed on the beaches.

Melanostethus marginatus (Thunberg)

This species is 5,8–5,9 mm long, rather dull black, with two large reddish triangles on wings and clear circular spot on wing membrane (Fig. 16L). Heme-lytra covered with short silvery hairs, which are absent on disc of each clavus, thus forming an oval black spot. Pronotum deeply and abundantly pitted.

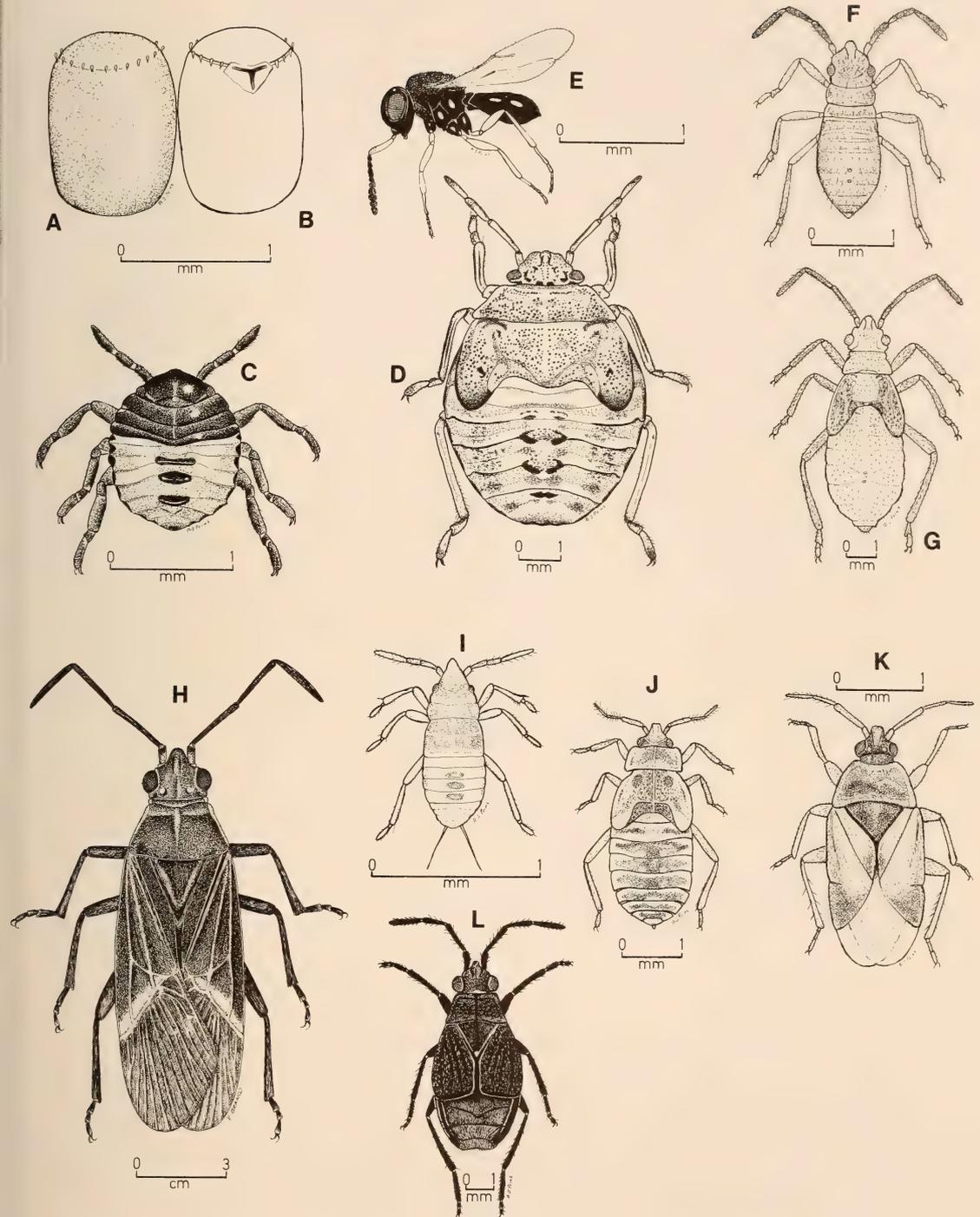


Fig. 15. A-D. *Antestiopsis orbitalis*. A. Egg. B. Egg from which nymph was hatched. C. Newly hatched nymph. D. Nearly mature nymph. E. *Telenomus* sp. (egg parasite of *A. orbitalis*). F-H. *Leptocoris hexophthalma*. F. Nymph measuring 2,0 mm. G. Nymph measuring 7,5 mm. H. Adult. I-K. Anthocoridae. I. Nymph measuring 1,0 mm. J. Nymph measuring 3,4 mm. K. Adult. L. *Aderrhis tartareus* (adult).

It is widely distributed in the Cape Province (Slater 1964) and the southern Orange Free State, and is a common feeder on *Arctotheca populifolia*, *Senecio elegans* (wild cineraria) and other plants, including *Clutia daphnoides*. It has also been found to feed on female Cantharidae. Nymphs are very often found among debris on the sand-dunes and large numbers of adult bugs have been collected under dry kelp strings on the beach.

As in the case of all other members of the family Lygaeidae, there are two ocelli in the adults and the tarsi are three-segmented (Fig. 16O). In the small nymphs (2,8 mm) (Fig. 16M), collected during April, the presence of the ocelli is indicated only by two dark brownish marks. In this stage the body is scarlet and the posterior corners and sides of the pronotum as well as the metanotum are pure white. There is a thin, yellowish, longitudinal line over the middle of the thorax; the eyes are brown. The two ostioles of the repugnatorial glands are indicated by two brown patches and the connexivum is marked with white on each segment. The femora are reddish marked with white on the bases and apices. The tibiae and tarsi are pale brownish. The first and last antennal segments are reddish, but the second is pale brownish, and the third whitish.

Larger nymphs (4,0 mm) (Fig. 16N), collected during December, are dark brownish red on the head and thorax, and the ecdysial suture is yellowish. The posterior margin of the pronotum is bordered by a white band, which is continued along the lateral margins; the white coloration of the metanotum is visible between the two wing rudiments. The antennae and the legs are the same colour as the body, except for the white apices of the femora and the terminal antennal segment, which is darker than the others. The two ostioles and extreme apex of abdomen are dark brown and the connexivum is almost the same colour as in the 2,8 mm long nymphs.

Family Pentatomidae

Easily recognized by the large scutellar area, rostrum also four-segmented. Most species are phytophagous such as the bagrada bug, green stink-bug, and the well-known antestia bug, which is a pest of coffee in the northern parts and a fruit pest in South Africa, and which will be very briefly discussed here. However, a few species are predacious, feeding mostly on the caterpillars of Lepidoptera.

Antestiopsis orbitalis (Westwood)

Specimens collected on the fore-dunes along the south and west coasts are pale cream to almost dirty white; some have orangy patches on the head, front margin of pronotum, scutellum, and along wing embolium. Eyes are brown. In some specimens there is an orange spot anterior to each eye, as well as two spots on the anterior part of the scutellum; in others these orange spots are completely absent. These bugs measure 6,9–7,5 mm in length. Greathead (1966) has given a good account of the different colour variations and the distribution.

They are widely distributed from the Cape to Kenya but, according to collecting data, they are absent from the Karoo. Eggs, nymphs, and full-grown specimens of this shield-bug were collected during the summer (December–February) on the foliage of *Arctotheca populifolia* along the coast. Brown patches on the leaves resulted where large numbers of the feeding stages were concentrated. They often congregate in large numbers on leaf litter under the above-mentioned plant.

The eggs of this species (Fig. 15A–B) are about 1,1 mm long and 0,9 mm wide, creamy white in colour, and the operculum is surrounded by a row of short micropylar processes; about twenty-seven were counted in most of the eggs collected. All the eggs found were laid in batches of twelve on the surface of leaves. After hatching, the black, T-shaped egg-burster can be seen on one side of the empty eggshell. The newly hatched, chocolate-brown nymphs (Fig. 15C), about 1.2 mm long, with two pale yellowish white patches on the pale abdomen, are apparently gregarious, at least up to the first moult, and were often seen clustered around the eggs during February. As the nymphs increase in size, they assume the coloration of the adult forms (Fig. 15D).

Skaife (1953) has given a short account of the life-history of this bug and Greathead (1966) has listed its food plants. According to Annecke & Moran (1982) it also damages the growth tips of *Protea* and *Leucadendron* species. An egg parasite, *Telenomus* sp. (Fig. 15E), has been recovered from the Strandfontein area near Muizenberg, Cape Province.

Family **Pyrhcoridae**

Similar to Lygaeidae, with membrane of front wings also with only a few veins, but ocelli absent. Usually brightly coloured with red, orange and black. Most of them are phytophagous and include the well-known cotton-stainers; however, a few are predacious.

Scantius forsteri (Fabricius)

The colour of this red bug (Fig. 16A) is dark chocolate-brown, but front of head, thorax, apex of scutellum, hemelytra, and connexivum are all marked with crimson. It is very variable in colour and in some specimens the hemelytra are uniformly chocolate-brown. The antennae and legs are dark chocolate-brown, almost black in some specimens. Brachyptery is common. Specimens collected vary from 7,5 to 10 mm in length.

It is widely distributed in Africa and very common along the western parts of the Cape Province where the surveys were made. Adults and nymphs often occur in large numbers during the summer and autumn under semi-fresh to dry cow-pats on the open beach and inland. It is also present on Dassen and Marcus islands.

The newly emerged, elongate nymphs (Fig. 16B) are pale piceous on the thorax and the head is pale brownish yellow with posterior border piceous. Eyes

scarlet, basal half of abdomen whitish flanked with scarlet and apical half yellowish white behind and scarlet in front; connexivum reddish; position of the repugnatorial glands indicated by three thin, transverse lines dorsally on apical half of abdomen. Legs pale piceous, first of the two tarsal segments and articulation points white. First two antennal segments pale brownish yellow, third and fourth pale piceous, with apical third of last segment white. Most of the specimens examined were about 1,6 mm long and in all of them minute denticles or spinules occur on the ventral side of the apices of the front femora.

As the nymphs increase in size (Fig. 16C), the ecdysial suture lengthens posteriorly over the first two to three abdominal terga and the wing rudiments enlarge (Fig. 16D). In the 10 mm newly moulted nymphs, the wings cover the greatest part of the abdomen and the tarsi are three-segmented. The whole insect is scarlet, except the wings and the largest part of the second antennal segment, which are almost white. Eyes are piceous. In older adults the colour is darker and the teeth on the apices of the femora are more strongly developed (Fig. 16E-G).

Along the south coast a dull, brownish-black brachypterous pyrrhocorid *Aderrhis tartareus* (Stål) (Fig. 15L) was fairly generally collected under dry cow-pats together with *Scantius*. It is 8-8,5 mm long, with a short, thin, orange-red, transverse band on the posterior border of the head and an orange-red spot on the apex of the scutellum. According to Stehlik (1965) it is found only in South Africa and seems to have predacious habits. A macropterous female, collected by R. W. Tucker in the Transvaal in December 1913, measured only 7,1 mm in length.

Cenaeus carnifex (Fabricius)

This species (Fig. 16H) is yellowish red, fairly dull or only slightly shiny; scutellum, frons and posterior border of head blackish. Antennae, proboscis and legs blackish, except for basal third of femora, which is reddish. The specimens examined measure 8,3-10,0 mm in length. Brachyptery is common. The genus is characterized by the crossed parameres (Stehlik 1965).

It is widely distributed in the Cape and Natal.

Nymphs and adults of *C. carnifex* were collected under dry cow-pats during midwinter. Adults are often seen on garden plants during the summer months. As in *Scantius*, all the immature stages have two-segmented tarsi, but the nymphs are quite different in other respects as they are more cicicoid in outline, paler in colour and the ostioles of the repugnatorial glands are represented by three larger blackish patches. In all the immature stages, as well as adults examined, spines are present only on the apices of the front femora (Fig. 16K).

In the 4,5-5 mm nymphs (Fig. 16I), the legs and antennae are piceous, the articulation points reddish. The head, except the median area, is yellowish and the thorax brown with yellowish ecdysial suture. The abdomen is pale yellowish red with a blackish apex.

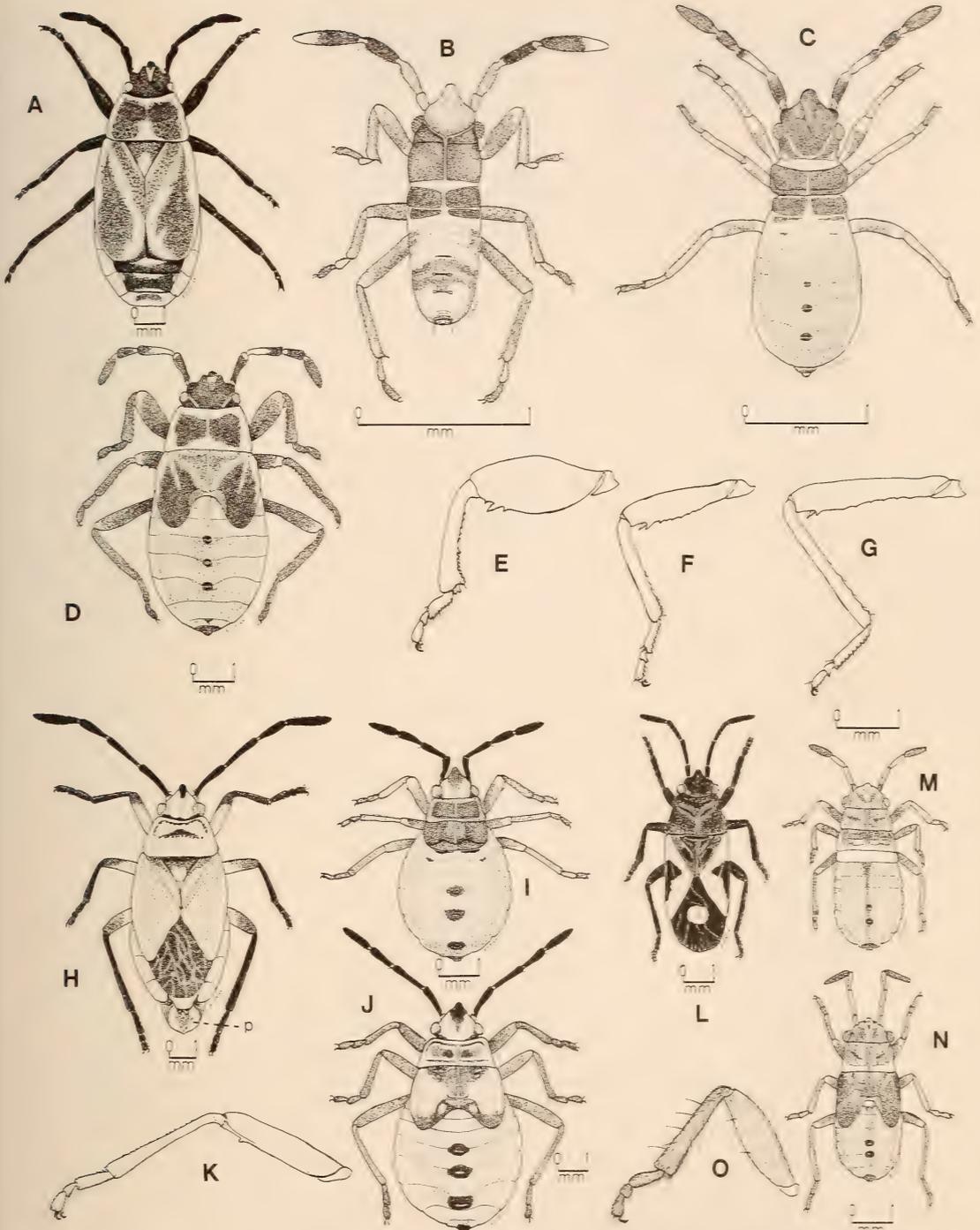


Fig. 16. A-G. *Scantius forsteri*. A. Adult. B. Newly hatched nymph. C. Nymph measuring 2.3 mm. D. Nymph measuring 6.4 mm. E. Prothoracic leg of male (posterior view). F. Mesothoracic leg of male (posterior view). G. Metathoracic leg of male (posterior view). H-K. *Cenaeus carnifex*. H. Adult showing crossed parameres (p). I. Nymph measuring 4.7 mm. J. Nymph measuring 7.8 mm. K. front leg (posterior view) showing spine on anterior ventral side. Enlarged to same scale as E-G. L-M. *Melanostethus marginatus*. L. Adult. M. Nymph measuring 2.8 mm. N. Nymph measuring 4.2 mm. O. Foreleg (posterior view).

Larger nymphs (6,5–8 mm) (Fig. 16J) are similar to the smaller ones, but rudiments of wings are present and most of the pronotum, except two darker areas on each side of the middle, is yellowish.

Family Reduviidae

Easily recognized by the strongly developed, curved, three-segmented rostrum. Wings usually well developed, though some species are apterous. Many species have raptorial front legs and many stridulate when handled, the stridulation being prolonged under certain conditions. Predacious, mainly feeding on arthropods. Most species inject a saliva containing a paralyzing agent, which also helps to digest the tissues. In man the bite causes severe pain; the tissues surrounding the puncture become inflamed and harden and the irritation can persist for several days. The subfamily Triatominae includes species that suck the blood of vertebrates and transmit disease-causing trypanosomes; however, none of these are known to occur in South Africa.

Certain assassin-bugs, particularly of the genus *Pirates*, are attracted to lights and are often found in houses. An unidentified black species (about 11 mm long) belonging to this genus as well as one shiny, metallic bluish-black, apterous *Glymmatophora* sp. (12–15 mm long) have on several occasions been reported to have bitten people in the western Cape, causing severe pain and swelling. Some assassin-bugs, including these two widely distributed species that have both been collected under cow-pats, bite without hesitation when carelessly handled or when pressed against the skin, and may cause severe symptoms in hypersensitive people.

Several assassin-bugs were found to shelter under semi-dry cow-pats, feeding on the smaller arthropods present. The most common of these is the hairy, black *Coranus carbonarius* (Stål) (Fig. 17H), which is 11–12,5 mm long. Blackish nymphs, with blackish-grey abdomen, found in the vicinity, probably belonged to this species. *Coranus pallescens* (Germar), a smaller, greyish bug (about 8 mm long) was found under similar conditions together with *C. papillosus* (Thunberg) (Fig. 17I), which is known to be a predator of codling moth larvae (Myburgh *et al.* 1973). *Coranus papillosus* is about 9,8 mm long, dark brownish grey in colour and very similar to *C. pallescens* (which was also found to be a victim of the black widow *Latrodectus mactans* (Hesse 1942)). It is well established on some of the islands along the south coast, e.g. Dyer Island.

A rather small, brownish *Didymocephalus braunsi* Bergroth (about 7,5 mm long), covered with fine velvety hairs as in the case of *Coranus* spp., was fairly numerous near Hermanus during winter, whereas a species of *Harpactor*, of about the same length as *C. papillosus* but almost black, the connexivum coloured black and yellowish white, was more common along the north-western parts of the coast. Specimens observed were found to feed on coleopterous larvae.

In the subfamily Holoptilinae the members attract their prey, which consists mainly of ants, by means of a special scent gland or trichome present on the

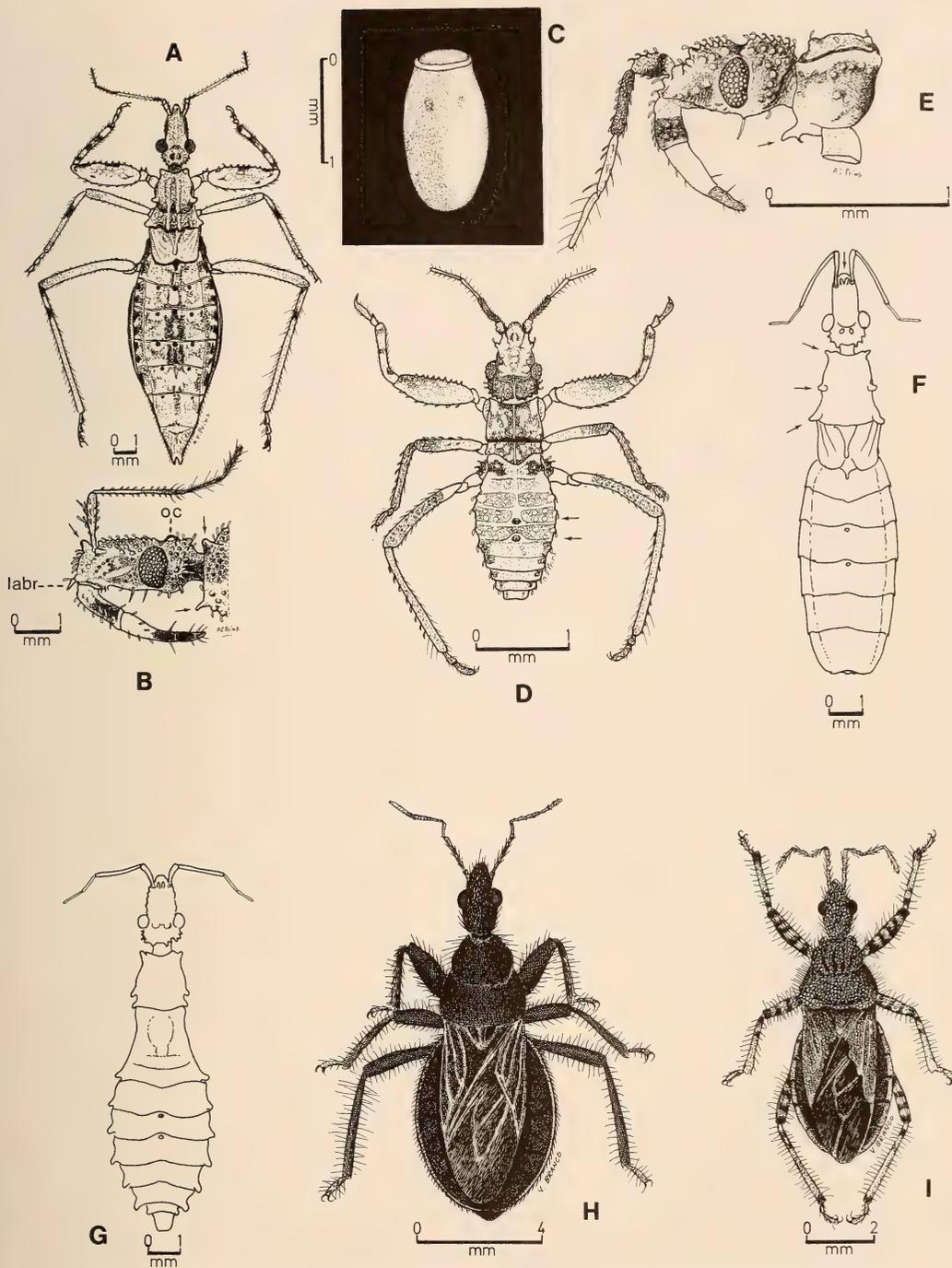


Fig. 17. A-G. *Oncocephalus* sp. A. Female (adult). B. Head of female showing labrum (labr) and ocelli (oc). C. Egg showing developing eyes of nymph. D. Newly hatched nymph. E. Head of newly hatched nymph. F. Outline of male. G. Nymph 11.6 mm long (outline of body), probably belonging to the second species. H. *Coranus carbonarius* (adult). I. *Coranus papillosus* (adult).

ventral surface of the abdomen. These bugs are sluggish and usually covered with long hairs. An unidentified species of *Holoptilus* was discovered in the nest galleries of the ant *Melissotarsus beccarii* Emery in the trunks of the pincushion *Leucospermum praemorsum* in the vicinity of Clanwilliam (Prins *et al.* 1975), the bugs living a 'double life' as symphile and predator. *Holoptilus ursus* le Peletier & Serville, a small brownish assassin-bug with a brown patch on the proximal half of the whitish hemelytra, is common on debris in sandy areas along the Cape south coast where it feeds on the smaller ants, particularly the minor workers of the pugnacious ant, *Anoplolepis steingroeveri* (Forel).

Oncocephalus sp.

The full-grown females (Fig. 17A) measure 18 mm in length and are cream coloured or greyish marked with piceous brown. Largest part of first segment of beak, apical half of second and whole of its third segment is piceous. Body, including legs, covered with fine tubercles, those on head and thorax being larger and tooth-like and each bearing a spatulate seta. Also present are some thickened hairs and fine whitish scale-like hairs that have the look of a pruinescence. Characteristic of most of the specimens examined are the two black dots on the median area of most of the abdominal segments and the tiny blackish ostioles of the repugnatorial glands on the anterior borders of the third and fourth visible terga.

Head (Fig. 17B) bears two rounded teeth between four-segmented antennae. Second antennal segment very long, about twice as long as first; apical and praepical segments of about equal length and together slightly more than half the length of the second. Labrum small and triangular. Pronotum with six teeth, four on anterior and two on posterior lobe. Also a fairly acute tooth present on each anteroventral corner of pronotum. Anterior lobe of pronotum fairly convex transversely and longitudinally.

Front femur swollen, its anteroventral margin bearing about twelve small teeth; front and middle tibiae clearly marked with two or three dark transverse bands. Wings atrophied in both females and males; latter similar to females but easily distinguished by rounded apex of abdomen (Fig. 17F); in females abdominal apex is pointed.

The specimens studied came from the Saldanha and Elands Bay areas along the west coast.

This is a rather slow-moving insect that feigns death when disturbed by extending its front and middle legs forward and its hind legs backward. The specimens were all collected under almost dry cow-pats during autumn and early winter. The eggs (Fig. 17C) are elongate with a convex operculum and have an almost matt, dirty yellowish-white colour and a very fine and superficial reticulation; they measure $1,60 \times 0,96$ mm to $1,80 \times 1,20$ mm. Eggs were laid under the sand under dry pats during July and August and the incubation period was at least 28 days in the laboratory (at 19 °C).

Newly hatched nymphs (Fig. 17D) measure about 2,55 mm in length and are pale brownish white, posterior half of head, pronotum and meso- and metanotum being darker. Eyes crimson. First two abdominal segments dark. Abdomen pale piceous or greyish and the two ostioles of repugnatorial glands already visible. A thin, white, longitudinal median line over the thorax represents the acdysial suture. Tubercles on body pale and each bears a spatulate seta. Legs pale and front femora already have teeth; hind femora somewhat darker.

These nymphs differ from the mature insects by the absence of both ocelli and rounded teeth between the antennae. Whole of second segment of beak is white (Fig. 17E). First and second antennal segments short; first only about half as long as second, latter about as long as third; apical and penultimate segments about equal in length. Head and pronotum much larger in relation to body than in adult, and dorsal teeth absent from thorax but anteroventral teeth fairly long. As in other Heteroptera the tarsi are two-segmented.

Development was very slow in the laboratory and after about 100 days they were only 3,6–4 mm long. Larger nymphs (about 5,1 mm long), collected during November, show the same characteristics as the newly hatched ones, but the thoracic teeth are more pronounced and each abdominal segment, except the first visible segment, has two pairs of small, oval, dark spots, the outer ones smaller; the connexivum also bears six dark spots on each side.

Fairly large nymphs, 11,6 mm long, collected during February, resemble the adults (including the presence of teeth between the antennae) but still possess abdominal spots (as in the 5 mm long nymphs).

The young nymphs unfortunately died of starvation in the laboratory, as they did not accept any prey offered to them.

From the specimens collected this is either a polymorphic species or possibly two species of similar coloration present in the same area, as some of the males have much longer wing stumps, the ocelli are absent, the scutellar tooth is much smaller and the abdomen is more pointed. Nymphs (probably belonging to males of this second form) measuring 11–12 mm long (Fig. 17G), found during February, have the connexivum sexdentate on each side and the abdomen more pointed than in the other form.

Nymphs of another unidentified species collected at Elands Bay during the late summer, more cimicoid in outline, with slightly darker coloration and measuring about 9,0 mm long, have longer developed wing-covers. In this case the body is covered with slightly longer hairs, which are simple on the abdomen and more rod-shaped on the head and thorax. Almost the whole of the rostrum is dark brown in colour, apical half being almost black; the third segment is much smaller in relation to the second than in the previously mentioned species. In younger nymphs (7,3 mm long and also with longer wing-covers) the pilosity, particularly of the head and thorax, consists of hamate setae. In all the specimens examined, ocelli and the rounded teeth between the antennae so characteristic of the adults and larger nymphs of the first mentioned species, are absent.

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

Family *Nuculanidae*

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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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.

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A. J. PRINS

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WITH DECAYING ORGANIC MATTER
PART 1
CHILOPODA, DIPLOPODA, ARACHNIDA,
CRUSTACEA, AND INSECTA

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CRETACEOUS FAUNAS FROM
ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE SUBFAMILY
PERONICERATINAE HYATT, 1900

By
HERBERT CHRISTIAN KLINGER
&
WILLIAM JAMES KENNEDY

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SOUTH AFRICA
THE AMMONITE SUBFAMILY PERONICERATINAE HYATT, 1900

By

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South African Museum, Cape Town

&

WILLIAM JAMES KENNEDY

Geological Collections, University Museum, Oxford

(With 135 figures and 1 table)

[MS accepted 10 May 1983]

ABSTRACT

The systematics of the South African representatives of the subfamily Peroniceratinae are critically reviewed, with special attention to the almost simultaneously published monographs of Van Hoepen (27 July 1965) and Matsumoto (20 November 1965) who, although working independently, reached a number of similar conclusions and erected a series of genera that are shown to be synonyms. The genera and subgenera *Peroniceras* (*Peroniceras*) de Grossouvre, 1894, *P. (Zuluiceras)* van Hoepen, 1965, and *Gauthierceras* de Grossouvre, 1894, include all the Zululand peroniceratids.

The present material is the richest assemblage of Peroniceratinae yet described, and it permits clarification of the limits of both inter- and intra-specific variability in the group as well as their evolution and stratigraphic distribution. Two new species are described: *Peroniceras (Zuluiceras) matsumotoi* and *Gauthierceras albiforme*.

Subdivision and zonation of the Coniacian stage is critically reviewed as this has bearing on the systematics of the subfamily.

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INTRODUCTION

Ammonites referable to the subfamily Peroniceratinae Hyatt, 1900, occur abundantly in two main areas in Zululand, the lower Hluhluwe and the lower Mzinene rivers, while isolated specimens are known from the environs of Mtu-batuba (Umkwelane Hill of earlier workers) and recent excavations for the construction of the new north-south highway that transects the region.

Peroniceratids were described by several early workers in the area, including Crick (1907), Spath (1921), Besairie (1930), Venzo (1936), and Van Hoepen (1955). In 1965 there appeared Van Hoepen's monographical study *The Peroniceratinae and allied forms of Zululand*. Unfortunately most of Van Hoepen's new species were based on single specimens, especially large individuals lacking the inner whorls. This led him to erect 1 new subfamily, 5 new genera, 2 new subgenera and 26 new species for his material. Only one previously established species was described, *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867).

In the same year as that of Van Hoepen's monograph, Matsumoto published his account of the Peroniceratinae from Hokkaido, Japan, in which he erected four new genera. Van Hoepen and Matsumoto, working independently, arrived at very similar conclusions in certain respects. Several of their taxa are synonyms, as will be shown below. Van Hoepen's work was published posthumously on 27 July 1965, four months before Matsumoto's on 20 November 1965. All these new taxa are reviewed in the present paper in order to stabilize nomenclature. In the process Van Hoepen's work is revised in the light of current systematic concepts and stratigraphic data. Species not described by Van Hoepen are also included in this review. The material at the present authors' disposal sheds some new light on the phylogeny and classification of the subfamily Peroniceratinae.

The following species from Zululand are described:

Peroniceras (*Peroniceras*) *lepeei* (Fallot, 1885)

P. (*P.*) *tridorsatum* (Schlüter, 1867)

P. (*P.*) *subtricarinatum* (d'Orbigny, 1850)

P. (*P.*) *westphalicum* (von Strombeck, 1859)

P. (*P.*) *dravidicum* Kossmat, 1895

P. (*Zuluiceras*) *zulu* van Hoepen, 1965

P. (*Z.*) *rarum* van Hoepen, 1965

- P. (Z.) henniei* van Hoepen, 1965
P. (Z.) undulato-carinatum van Hoepen, 1955
P. (Z.) modestum van Hoepen, 1965
P. (Z.) matsumotoi sp. nov.
P. (Z.) cf. *aberlei* (Redtenbacher, 1873)
P. (Z.) bajuvaricum (Redtenbacher, 1873)
Gauthiericeras obesum van Hoepen, 1955
G. listeri (van Hoepen, 1965)
G. album (van Hoepen, 1965)
G. albiforme sp. nov.
G. libertae van Hoepen, 1955

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

- BMNH British Museum (Natural History), London.
 EMP École des Mines, Paris, now in the Université Claude Bernard, Lyon
 GG Laboratoire de Géologie, Grenoble
 GPIB Geologisches und Paläontologisches Institut der Universität, Bonn
 LL Oberösterreichisches Landesmuseum, Linz
 MNHP Muséum d'Histoire Naturelle, Paris
 NMB National Museum, Bloemfontein (presently in the collections of the South African Museum)
 OUM Oxford University Museum
 SAM South African Museum, Cape Town
 SAS South African Geological Survey, Pretoria
 SP Collections of the Sorbonne, Paris, now in the Université Pierre et Marie Curie

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); fuller descriptions of these localities are deposited in the Department of Palaeontology, British Museum (National History), London; South African Geological Survey, Pretoria; and South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions are given in millimetres:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. R indicates ratio of umbilical to ventrolateral tubercles.

Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916) reviewed and discussed by Kullman & Wiedmann (1970) is followed here:

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

CONIACIAN STRATIGRAPHY AND CORRELATION

Introduction

The subfamily Peroniceratinae is predominantly Coniacian and members of the group provide a basis for subdivision and correlation of the stage. Present subdivision of the stage is in a state of chaos as was made painfully apparent by Matsumoto's (1981) recent review of Coniacian biostratigraphy. Some workers use only Lower and Upper Coniacian substages, others Lower, Middle and Upper, with no clear indication as to how these two schemes are related. The same species are recorded from the 'Lower' Coniacian of one region and the 'Upper' Coniacian of another so that the ranges of taxa appear to be anomalous. Zonal nomenclature is similarly confused.

Kennedy (in press) has reviewed the early history of subdivision of the Coniacian in France, and proposed a revised zonation and subdivision into substages as summarized below.

Zonation in the type region

The Coniacian stage was introduced by Henri Coquand in 1857 as the lowest division of D'Orbigny's Senonian stage, introduced in 1842-3. It has passed into the literature as a universally applied division of the Upper Cretaceous. The standard zonation of the stage is based on ammonites and is the twofold division of De Grossouvre (1889, 1901) who recognized a lower *Barroisiceras* ['*Barroisia*'] *haberfellneri* Zone and an upper *Paratexanites* ['*Mortoniceras*'] *emscheris* Zone on the evidence of sequences in Aquitaine and Touraine in France. These zones have been universally accepted as standard zones for the Coniacian and were adopted by the 1959 *Colloque sur le Crétacé supérieur français* (Dalbiez 1960), in the *Treatise* (Wright 1957), and by Séronie-Vivien (1972) in her definitive revision of the stratotype, among many others. Yet already in 1947 Basse has pointed out that the *Barroisiceras haberfellneri* of De Grossouvre was based on a misinterpretation of Von Hauer's species, and that the French material all belonged to a distinctive form which she named *Reesideoceras gallicum* Basse, 1947 (a synonym of *Ammonites petrocoriensis* Coquand, 1859), although nevertheless referring to a '*haberfellneri*' Zone in some of her later works. True *Barroisiceras* does not occur in France, indeed, there is no good evidence that the species *B. haberfellneri* actually occurs in the Coniacian. Similarly with the *Paratexanites emscheris* Zone, the index species does not occur in France.

Confusion is not limited to nomenclature. Collignon (e.g. 1960) used the *haberfellneri-emscheris* standard in his early works, and developed a threefold

zonation in Madagascar, with zones of *Peroniceras dravidicum* (oldest), *Kossmaticeras theobaldianum* and *Barroisiceras onilahyense*, and *Prionocycloceras guyabanum* and *Gauthiericeras margae* (youngest). In 1979 Collignon *et al.* recognized a sequence of three zones in the Coniacian of the Beausset Basin (Var, France): *Peroniceras tricarinatum* (oldest), *Barroisiceras haberfellneri*, and *Gauthiericeras margae* (youngest), although the middle zone was not proven by ammonites. Robaszynski *et al.* (1980) recognized a *Peroniceras tridorsatum* Zone at the base of the Coniacian in the Boulonnais, France (with, however, only eight specimens of the genus *Peroniceras* from the area), and French textbooks now cite a standard sequence of *tricarinatum*–*haberfellneri*–*margae* Zones despite the fact that *haberfellneri* does not occur in France.

In those areas where a faunal sequence can be determined, *Forresteria* (*Harleites*) *petrocoriensis* (Coquand, 1859)—the *Barroisiceras haberfellneri* of authors—always precedes *Peroniceras* species and marks the base of the Coniacian in the type area (Kennedy, Wright & Hancock 1983; Kennedy in press). Yet more recently, Matsumoto (in Matsumoto *et al.* 1981) proposed as standard zones for the European Coniacian a sequence of *Peroniceras tricarinatum* Zone (below) and *Protexanites bourgeoi* Zone (above) on the basis of what could be gleaned from the literature.

Ammonites are generally very rare in the Coniacian of France (and indeed most of north-western Europe), and only five areas, the Aquitaine Basin, a small area in Touraine in the southern Paris Basin, a few square kilometres of outcrop around Dieulefit (Drôme), the Beausset Basin (Var), and the environs of Rennes-les-Bains in the Corbières (Aude), have yielded ammonites in any numbers. In their revision of the Craie de Villedieu, Jarvis *et al.* (1983) do not mention new records of Coniacian ammonites around Villedieu-le-Château, the most famous Coniacian ammonite locality in France. In spite of these difficulties, the French succession provided Kennedy with the basis for the following subdivision of the Coniacian:

Lower Santonian	<i>Texanites gallicus</i> Zone (provisional)
Upper Coniacian	{ <i>Paratexanites serratmarginatus</i> Zone <i>Gauthiericeras margae</i> Zone
Middle Coniacian	
Lower Coniacian	<i>Peroniceras</i> (<i>Peroniceras</i>) <i>tridorsatum</i> Zone
Upper Turonian	<i>Forresteria</i> (<i>Harleites</i>) <i>petrocoriensis</i> Zone
	<i>Subprionocycclus neptuni</i> Zone

Details are as follows:

1. *Forresteria* (*Harleites*) *petrocoriensis* Zone

The base of the zone and the Coniacian stage are marked by the appearance of the index species, specimens of which occur only centimetres above the regional hardground or discontinuity surface that separates basal Coniacian sands and marls and underlying Turonian rudistid limestones in Aquitaine. Other ammonites are rare, with only single specimens of *Scaphites* (*Scaphites*) cf. *meslei* de Grossouvre, 1894, *Metatissotia desmoulinsi* (de Grossouvre, 1894),

and *M. nanclasi* (de Grossouvre, 1894). This is the fauna of Arnaud's (1877) Assize K of the Aquitaine sequence.

2. *Peroniceras (Peroniceras) tridorsatum* Zone

The base of the zone is marked by the appearance of diverse *Peroniceras (Peroniceras)* species. The fauna of this zone is widely recorded in Arnaud's Assize L¹ in Aquitaine and is marked by *P. (P.) tridorsatum* (Schlüter, 1867) and other *Peroniceras (Peroniceras)* species with rarer *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). Other ammonites are *Onitshoceras? ponsianum* (de Grossouvre, 1894), *Tongoboryceras* sp. nov., *Placenticeras fritschi* de Grossouvre, 1894, *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894), *Gauthiericeras? boreau*i (de Grossouvre, 1894), *Tissotia redtenbacheri* (de Grossouvre, 1894), *Metatissotia slizewiczi* (de Grossouvre, 1894), *Metatissotia ewaldi* (von Buch, 1847), *Metatissotia nodosa* (Hyatt, 1904), *Tissotioides haplophyllus* (Redtenbacher, 1873), *Scaphites meslei* (de Grossouvre, 1894), *Otoscaphtes arnaudi* (de Grossouvre, 1894), and nodose *Baculites*.

Sufficient of these ammonites occur together at single localities to indicate that a single fauna is present, but the evidence from the old collections is not unequivocal. More recent collecting showed *Peroniceras (Zuluiceras) bajuvaricum*, *Metatissotia ewaldi*, and *Scaphites (Scaphites) meslei* occurring together at Antignac (Charente-Maritime), but suitable outcrops are now rare in Aquitaine.

Further evidence for the composition of the *P. (P.) tridorsatum* Zone fauna in France comes from Dieulefit in Drôme, where the ammonite fauna includes many forms known only from L¹ in Aquitaine. Species in common are *P. (P.) tridorsatum*, *P. (Zuluiceras) bajuvaricum*, *Metatissotia robini*, *Tissotioides haplophyllus*, and *S. (Scaphites) meslei*, with as additional elements *Peroniceras (P.) lepeei* (Fallot, 1885), *P. (P.) westphalicum* (von Strombeck, 1859), *P. (Zuluiceras) isamberti* (Fallot, 1885), and *Scalarites* sp.

The association from the Marnes de Ceyreste in the Beausset Basin, Var, also suggests that the assemblage represents a single zonal fauna with the co-occurrence of *Peroniceras (P.) subtricarinum*, *Parapuzosia (Parapuzosia)* sp., *Placenticeras* sp., *Forresteria (Forresteria) alluaudi* (Boule, Lemoine and Thévenin, 1907) *Scaphites (Scaphites) meslei* and *Otoscaphtes arnaudi*.

3. *Gauthiericeras margae* Zone

The base of the zone is marked by the appearance of *Gauthiericeras margae* (Schlüter, 1867) and *G. nouelianum* (d'Orbigny, 1850). Also present are *G. ?boreau*i (de Grossouvre, 1894), which ranges from below, *Tridenticeras* sp., and nodose *Baculites*.

The position of the zone is unequivocally demonstrated by specimens of *G. margae* from Arnaud's (1877) Assize L² in Aquitaine, and the record from the middle part of the Grès de Baguier of the Beausset Basin (Collignon *et al.* 1979).

4. *Paratexanites serratomarginatus* Zone

The base of the zone is marked by the appearance of the index species. Other elements of the assemblage that are restricted to the zone in France are *Protexanites (Protexanites) bontanti* (de Grossouvre, 1894), *Placenticerias semior-natum* (d'Orbigny, 1850), *Phlycticrioceras trinodosus* (Geinitz, 1850), and no-dose *Baculites*. *Protexanites (P.) bourgeoisi* (d'Orbigny, 1850) ranges from below.

This is the fauna of Bed 4 of the Craie de Villedieu in Touraine (Kennedy in press). Its position is indicated by its occurrence above the condensed Cal-caires Durs, which contains *Gauthiericeras margae* there, by the index species and *Protexanites (Protexanites) bourgeoisi* occurring very high in the Coniacian of northern Aquitaine, and by the index occurring above *G. margae* in the Beausset Basin in Var.

5. *The Coniacian–Santonian boundary in France*

At Javrezac (Charente), a locality mentioned by Coquand as a type section for both Coniacian and Santonian stages, the boundary is easily drawn at a hard-ground between glauconitic limestones of the Coniacian below and marls of the Santonian above. Defining this boundary by using ammonites is much more difficult. The precise position of ammonites within the lower part of the Santonian—Arnaud's assize M¹—is poorly documented, and ammonites are very rare indeed. De Grossouvre (1894) recorded *Paratexanites* [*'Mortoniceras'*] *serratomarginatus* (Redtenbacher, 1873) from both the Coniacian and Lower Santonian; in 1901 he decided that the Coniacian specimens all belonged to *P.* [*'Mortoniceras'*] *emscheris* (Schlüter, 1876) and that *P. serratomarginatus* was exclusively Santonian. He never illustrated Santonian *serratomarginatus*, and none survive in museum collections that can be attributed to Arnaud's M¹. Indeed, later work has shown that *P. serratomarginatus* and *P. emscheris* are not synonyms and are both from high in the Coniacian (Wiedmann 1979; Kennedy, Klinger & Summesberger 1981). De Grossouvre (1901) also indicated in a table that *Protexanites* [*'Mortoniceras'*] *bourgeoisi* (d'Orbigny, 1850) also extended into the lower part of the Santonian, but made no mention of this in the text and no specimens from M¹ survive.

Far more widely recorded is *Texanites texanus* (Römer, 1852), and this was taken as the index of the lower zone of the Santonian by De Grossouvre. Collignon (1948) correctly interpreted Römer's species (excluding all European records), which he referred to two distinct varieties, regarded by subsequent workers as either subspecies or separate species. Material from M¹ in Aquitaine (De Grossouvre 1894: 80, pl. 16 (figs 2, 4)) was referred to the variety *gallica* Collignon, 1948; the two figured syntypes are actually from M² at Niel-le-Virouil (Charente-Maritime). The only other specimens seen from Aquitaine are two specimens labelled *Ammonites coniaciensis* Coquand, 1857, in the École des Mines Collection ex Boucheron Collection (now in the collections of the Université Claude-Bernard, Lyons) from La Valette (Charente), a locality referred to

Assize L² by Arnaud, and a specimen in the Sorbonne Collections ex Toucas Collection (now in the Université Pierre et Marie Curie, Paris) from M¹, at Rentes, Cognac. This specimen is a crushed *Texanites* (*Texanites*) sp.

Apart from texanitids, there are poorly preserved *Placenticeras* from L¹ in the Arnaud Collection and records of *Baculites incurvatus* (Dujardin, 1837) (e.g. De Grossouvre 1901).

The conclusion is that it is not possible to define the base of the Santonian in ammonite terms in Aquitaine with any great confidence. Only from occurrences elsewhere in France e.g. Provence (Fabre-Taxy 1963) and the Corbières (Collignon & Bilotte 1983) is it possible to suggest that the appearance of *Texanites sensu stricto* is the best marker for the base of the stage, and even then the name of the zone is uncertain—the fauna may be that of De Grossouvre's *T. texanus* Zone, but the correct name for the European 'texanus' is unresolved.

The Zululand succession

Kennedy & Klinger (1975) presented a series of working subdivisions of the Zululand Coniacian. These were not intended to be taken as zonal divisions but as a working framework only until such time as the taxonomic revisions needed to formulate a proper zonation were complete. The position has still not been achieved, but fuller faunal lists can now be given (see below). These lists included only those species known to be definitely from particular divisions. In the Upper Coniacian in particular, there are many specimens (especially in Van Hoepen's collection) collected loose from fields and hillslopes along the Hluhluwe and Mzinene rivers that may be from Coniacian IV or V (previously recorded as 'Coniacian IV-V', e.g. by Klinger & Kennedy (1980), which misleadingly suggested that the species ranged through these divisions).

Coniacian I

Gaudryceras cf. *varagurense* Kossmat, 1895, *Pachydesmoceras denisonianum* (Stoliczka, 1865), *Pachydesmoceras* sp., *Kossmaticeras* (*Kossmaticeras*) *theobaldianum theobaldianum* (Stoliczka, 1865), *K. (K.)* aff. *theobaldianum crassicostatum* Collignon, 1954, *Placenticeras kaffrarium* Etheridge, 1904, and *Didymoceras (Didymoceras) indicum* (Stoliczka, 1865). Of this assemblage, only *Kossmaticeras (K.) theobaldianum* provides indisputable ammonite evidence for a Coniacian date.

Coniacian II

Gaudryceras varicostatum van Hoepen, 1921, *Parapuzosia(?) donlisteri* (van Hoepen, 1968), *Kossmaticeras (Kossmaticeras) theobaldianum crassicostatum* Collignon, 1954, *K. (K.) jonesi* Collignon, 1965, *Placenticeras kaffrarium* Etheridge, 1904, *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867), *P. (P.) lepeei* (Fallot, 1885), *P. (P.) westphalicum* (von Strombeck, 1859), *P. (P.) dravidicum* Kossmat, 1895, *P. (Zuluiceras) cf. aberlei* (Redtenbacher, 1875), *P. (Z.) bajuvaricum* (Redtenbacher, 1873), *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), *F. (F.) cf. hobsoni* (Reeside, 1932), *F. (F.) madagascariensis* (Collignon, 1965), *Yabeiceras orientale* Tokunaga & Shimizu,

1926, *Y. cf. orientale*, *Y. transiens* Kennedy, Wright & Klinger, 1983, *Y. ank-natsyense* Collignon, 1965, *Y. costatum*, Collignon, 1965, *Y. manasoense* Collignon, 1965, *Y. aff. manasoense*, *Y. crassiornatum* Kennedy, Wright & Klinger, 1983, nodose *Baculites*, *Scaphites* (*Scaphites*) *meslei* de Grossouvre, 1894, and *Otoscaphtes arnaudi* (de Grossouvre, 1894).

Coniacian III

Placenticerias kaffrarium Etheridge, 1904, *Peroniceras* (*Peroniceras*) *lepeei* (Fallot, 1885), *P. (P.) tridorsatum* (Schlüter, 1867), *P. (P.) dravidicum* Kossmat, 1895, *P. (Zuluiceras) cf. aberlei*, *P. (Z.) bajuvaricum*, nodose *Baculites*, *Scaphites* (*Scaphites*) *meslei* de Grossouvre, 1894, and *Otoscaphtes arnaudi* (de Grossouvre, 1894).

Coniacian IV

Peroniceras (*Zuluiceras*) *zulu* van Hoepen, 1965, *P. (Z.) rarum* van Hoepen, 1965, *P. (Z.) modestum* van Hoepen, 1965, *P. (Z.) matsumotoi* sp. nov., *P. (Z.) henniei* van Hoepen, 1965, *P. (Z.) undulato-carinatum* (van Hoepen, 1955), *Gauthiericeras obesum* van Hoepen, 1955, *G. listeri* (van Hoepen, 1965), *G. albiforme* sp. nov., *G. planulatum* van Hoepen, 1955, *G. libertae* van Hoepen, 1955, *G. album* (van Hoepen, 1955), *Protexanites* (*Protexanites*) *cyn-ci* (van Hoepen, 1968), *Paratexanites australis* Klinger & Kennedy, 1980, *P. aff. P. emscheris* (Schlüter, 1876) (*Protexanites* and *Paratexanites* are very rare *in situ* in Coniacian IV), and nodose *Baculites*.

Coniacian V

Protexanites (*Protexanites*) *cyn-ci* (van Hoepen, 1968), *Paratexanites australis* Klinger & Kennedy, 1980 (many loose *Protexanites* and *Paratexanites* are probably from Coniacian V, outcrops of which are poor), *Pseudoschloenbachia* aff. *primitiva* Collignon, 1965, and feebly nodate and non-nodate *Baculites*.

Santonian I

The base of the Santonian is taken at the appearance of diverse *Texanites* species.

Correlation of the Zululand succession with that recognized by Kennedy in France is rendered difficult by the low diversity of the ammonite faunas of the European Lower Coniacian *Forresteria* (*Harleites*) *petrocoriensis* Zone and Coniacian I in Zululand, plus the difficulty of finding *in situ* faunas in Coniacian V.

Coniacian II and III correlate with the Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone, having many elements in common. Coniacian I may be equivalent to the Lower Coniacian *F. (H.) petrocoriensis* Zone. It is equally possible (at least on the ammonite evidence) that this is absent, with early Coniacian time represented in the sub-Coniacian unconformity. In the latter case the sparse fauna of this division could simply be an impoverished Middle Coniacian assemblage. Only evidence from other groups can resolve this problem.

The base of Coniacian IV in Zululand is to be correlated with the base of the European Upper Coniacian *Gauthiericeras margae* Zone on the basis of the close similarities between the *Gauthiericeras* in the two regions. The presence of

several (albeit rare) *Protexanites* and *Paratexanites* species may indicate that the top of Coniacian IV extends into the base of the succeeding *Paratexanites serratomarginatus* Zone, but *P. zeilleri* (de Grossouvre, 1894) is a pre-*P. serratomarginatus* Zone species (the holotype is from the condensed Calcaires Durs de la Ribochère (*petrocoriensis* to *margae* Zones)), and there are records of rare *Protexanites* below the *P. serratomarginatus* Zone.

Coniacian V in Zululand is probably to be correlated with the European Upper Coniacian *P. serratomarginatus* Zone, but the paucity of ammonite species and poor exposure do not permit certainty that it does not extend into the lowest Santonian. While the appearance of *Texanites* in numbers marks the Lower Santonian in both areas, it is still not clear if this is, indeed, the base of the stage.

Madagascar

Coniacian faunas from Madagascar are the richest known, and are described in works by Boule, Lemoine & Thévenin (1906–7), Collignon (1931, 1948, 1954, 1965), Besairie (1936), and Basse (1927, 1931, 1947, etc.).

Well illustrated as the faunas are, their stratigraphic distribution presents many problems and detailed successions are generally lacking.

In 1960 Collignon provided a threefold zonation maintained in his later works:

- Lower Santonian *Texanites oliveti* Zone
- Upper Coniacian *Prionocycloceras guyabanum* and *Gauthiericeras margae* Zone
- Middle Coniacian *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* Zone
- Lower Coniacian *Peroniceras dravidicum* and *P. subtricarinatum* Zone
- Upper Turonian *Romaniceras deveriai* and *Coilopoceras requieni* Zone

In understanding these successions, the faunas from individual localities are more revealing than those of the synthetic accounts.

In the Diego Basin Besairie & Collignon (1972: 49) note that the Senonian consists of sandstones and sandy marls with several limestone beds, and that there are no vertical successions. Faunas recorded indicate both Middle and Upper Coniacian (in the sense used here) to be present.

In the Majunga Basin the same authors record only a fauna with *Barroisiceras* from Antsira. The assemblage consists of *Barroisiceras onilahyense* Basse, 1947, *Lewesiceras beantalyense* Collignon, 1952, and *Peroniceras* sp.

In the Morondava Basin Besairie & Collignon (1972: 249) recognize Coniacian with *Peroniceras rousseauxi* de Grossouvre, 1894, and *Lewesiceras tongoboryense* Collignon, 1952, above post-Lower Turonian basalts. The same relationship is observed between Demoka and Manambolo, with '*Lewesiceras*' *tongoboryense* Collignon, 1952, *Peroniceras rousseauxi* De Grossouvre, 1894, and '*Hyporbulites*' *masiaposensis* Collignon, 1956, east of Bevitsika, and *Peroniceras* sp. *Gaudryceras analabense* Collignon, 1956, and *Tetragonites wieli* Collignon, 1956, north-west of Bemonta. At Ankotrofotsy, a 7–8 m sequence of marls

and reefal limestones resting on basalt yielded (Hourcq 1950) *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine & Thévenin, 1907), *Kossmaticeras* (*Kossmaticeras*) *recurrens* Kossmat, 1897, *Oxybeloceras*, *Phylloceras* (*Hypophylloceras*), *Gaudryceras*, *Puzosia*, and *Pachydiscus*. The first of these faunas was regarded as Lower Coniacian, but the presence of *Peroniceras* at the first two localities and *Forresteria* (*F.*) *alluaudi* at the third all indicate the Middle Coniacian *Peroniceras* (*P.*) *tridorsatum* Zone as defined here.

In the centre of the Morondava Basin the Turonian forms a continuous strip from Manambolo to Andranomena (Besairie & Collignon 1972) with Lower Turonian containing *Fagesia*, and an Upper Turonian containing *Romaniceras*. The facies is mixed, with coarse red sandstones, sometimes with silicified wood.

At Masiaposa, 3 km west of Antsarona, there is a rich fauna with (among other stratigraphically unimportant taxa) *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny, 1841), *Coilopoceras requienianum altesselata* Collignon, 1965, *Kossmaticeras* (*Kossmaticeras*) *recurrens* Kossmat, 1897, *Subprionocyclus nepuni* (Geinitz, 1850), *Subprionocyclus casterasi* Collignon, 1965 (? = *S. normalis* Anderson, 1958), *Masiaposites* spp., and *Hourcquia* spp.

The Turonian and Coniacian are separated by a basaltic interlude, succeeded by 'Coniacien Inférieur'; between Manambolo and Tsiribihina, there are approximately 20 m of yellow-grey marls with sandy limestones, yielding many ammonites referred to the *Peroniceras dravidicum* Zone. Important taxa are *P.* (*Peroniceras*) *dravidicum* Kossmat, 1895, *P.* (*P.*) *subtricarinaratum* (d'Orbigny, 1850), *P.* (*P.*) cf. *tridorsatum* (Schlüter, 1867), *P.* (*P.*) *westphalicum* (von Strombeck, 1859), *P.* (*P.*) *moureti* de Grossouvre, 1894, *P.* (*Zuluiceras*) aff. *czoernigi* (Redtenbacher, 1873), *P.* (*P.*) *besairiei* van Hoepen, 1965, *P.* (*P.*) *tenuis* van Hoepen, 1965, *P.* (*P.*) *guerini* Collignon, 1965, '*Lewesiceras*' spp., *Yabeiceras menabense* Collignon, 1965, and *Y. ankinatsyense* Collignon, 1965 (see full list, by locality, in Besairie & Collignon 1972: 283).

Above, the 'Coniacien Moyen' and 'Supérieur' are represented by 30 m of yellow marls, with the Zone à *Kossmaticeras theobaldi* et *Barroisiceras onilahyense* yielding: *Barroisiceras onilahyense* Basse, 1947, *Subbarroisiceras mahafalense* Basse, 1946, *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine & Thévenin, 1907), *F.* (*F.*) *madagascariensis* (Collignon, 1965), *Yabeiceras bituberculatum* Collignon, 1965, *Y. costatum* Collignon, 1965, *Y. ankinatsyense* Collignon, 1965, *Y. magnumbilicatum* (Basse, 1946), *Kossmaticeras* (*Kossmaticeras*) *theobaldianum* (Stoliczka, 1865) and other species, plus numerous other forms listed by Besairie & Collignon (1972: 283). The 'Coniacien Supérieur' Zone à *Prionocycloceras guyabanum* et *Gauthiericeras margae* yields only the index species and long-ranging taxa (Besairie & Collignon 1972: 284).

The base of the Santonian *Texanites oliveti* Zone is marked by the appearance of the index species and many other taxa.

These observations indicate that there is no ammonite evidence for the Lower Coniacian *F.* (*H.*) *petrocoriensis* Zone of the European standard, and that the 'Coniacien Moyen' *Peroniceras* (*P.*) *dravidicum* Zone is equivalent to

part of the European *P. (P.) tridorsatum* Zone. The paucity of common elements between the succeeding *B. onilahyense* and *K. (K.) theobaldi* Zone and European faunas makes comparison difficult, but *Forresteria (F.) alluaudi* is a common species, suggesting that the zone is also Middle Coniacian and equivalent to part of the *P. (P.) tridorsatum* Zone.

Comparisons with Zululand are close but pose problems. Whereas the peroniceratids of the Madagascan *P. (P.) tridorsatum* Zone indicate correlation with Coniacian II and III, the absence of *Forresteria (Forresteria)* in the *P. (P.) tridorsatum* Zone in Madagascar but its presence in the succeeding *Barroisicerias onilahyense*–*Kossmaticeras theobaldi* Zone is the reverse of the order seen in Zululand where this genus occurs with *Peroniceras* in Coniacian II but is absent in Coniacian III, with *Peroniceras* persisting.

There is insufficient evidence to resolve this apparent inconsistency.

The fauna of the *Prionocycloceras guyabanum*–*Gauthiericeras margae* Zone has little in common with European faunas; the one fragment of *G. margae* figured by Collignon (1965, pl. 435 (fig. 1798)) is so poor as to be indeterminate from the figure. Correlation with the *G. margae* Zone is suggested. Correlation with Zululand is easier: there are *Prionocycloceras* species common to this zone and Coniacian IV.

Japan

Matsumoto (1981) has presented the most recent review of the sequence of ammonite faunas in the Japanese Coniacian, the chief sections being in Hokkaido, Kyushu, and Shikoku. Interpretation of the sequence is often difficult due to complex tectonics and the general rarity of ammonites.

A twofold division based on inoceramids is recognized, with a zone of *Inoceramus uwajimensis* below and *I. mihoensis* above. These species are stratigraphically separated in some areas (e.g. the Ikushumbets, Futaba, and Orogawa areas), but elsewhere (e.g. the Obira area of Hokkaido) they overlap, with *I. mihoensis* being the later species to appear.

Potentially important species for long-term correlation from these divisions are as follows:

Inoceramus uwajimensis Zone

Nowakites mikasaensis Matsumoto, 1979, *Prionocycloceras wrighti* Matsumoto, 1971, *P. sigmoidale* Matsumoto, 1965, *Prionocycloceras* sp. aff. *P. lenti* (Gerhardt, 1897), *Ishikariceras binodatum* Matsumoto, 1965, *Paratexanites serratomarginatus* (Redtenbacher, 1873), *Barroisicerias onilahyense* Basse, 1947, *Pseudobarroisicerias nagaoui* Shimizu, 1932, *Barroisicerias (Basseoceras) inornatum* Matsumoto, 1970, *F. (Muramotoa) yezoensis* Matsumoto, 1970, *F. (M.) muramotoi* Matsumoto, 1970, *Yabeiceras orientale* Tokunaga & Shimizu, 1926, 'Harleites cf. harlei (de Grossouvre, 1894)' (apparently a feebly ornamented *Forresteria (F.) alluaudi*), and *Hourcquia hataii* Hashimoto, 1973. Recorded from either this zone or that succeeding it are *Peroniceras (Peroniceras) yubarense* Matsumoto & Muramoto, 1981 (said to be a close ally of *P. (P.) besairiei*

van Hoepen, 1965) and *P. (P.)* aff. *platycostatum* van Hoepen, 1955 (*P. (P.) dravidicum* Kossmat, 1895, according to the present revision).

Elements undoubtedly from this zone listed above show that it is certainly in part Middle Coniacian, equivalent to the European *tridorsatum* Zone and to Coniacian II of the Zululand sequence. There is no ammonite evidence for Lower Coniacian. The only anomalous record is of *Paratexanites serratomarginatus*, a species known only from the Upper Coniacian *P. serratomarginatus* Zone in Europe and only from the Upper Coniacian elsewhere.

The basis of the record is given in Matsumoto (1970: 260). One specimen was from a fallen nodule near the Coniacian–Santonian boundary, and a second was also collected loose in Hokkaido. The only well-localized specimen is the fragment figured by Matsumoto (1970, pl. 36 (fig. 2)) from his 'Locality IK2112, Go-no-sawa, Pombets, a tributary of the Ikushumbets', zone of *Inoceramus uwajimensis* K5 (Coniacian).

Inoceramus mihoensis Zone

Peroniceras (Peroniceras) latum Matsumoto & Muramoto, 1981 (probably *P. (P.) westphalicum*), *Sornayceras omorii* Matsumoto, 1965 (= *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873)), *P. (Z.) proteus* Matsumoto, 1965, *Paratexanites orientalis* (Yabe, 1925), and *P. mikasaensis* Matsumoto, 1970.

This assemblage appears to be in part equivalent to the European *Peroniceras (P.) tridorsatum* Zone and includes species allied to those of the *Gauthiericeras margae* and *Paratexanites serratomarginatus* zones, indicating it to be in part Middle and in part Upper Coniacian. When compared with the Zululand succession it has common (or closely comparable) species to those of Coniacian III and IV.

Texas

The Coniacian ammonite faunas of this vast region have been described by Young (1963), Wolleben (1967), and Young & Powell (1978).

The Coniacian is represented in the Austin Chalk and its correlatives. Over much of Texas east of the Pecos there is a regional break between the Austin and the underlying Eagle Ford. The base of the Austin is Coniacian (but not lowest Coniacian) in the Dallas area, but becomes progressively older when traced southwards, until it is Upper Turonian along the Rio Grande. The standard zonation proposed by Young is: *Prionocycloceras gabrielense* Zone (youngest), *Peroniceras westphalicum* Zone, and *Peroniceras haasi* Zone (oldest). Faunas of these zones are rather poor in number and species.

Peroniceras (P.) haasi Young, 1963 (less than twenty specimens) and *Coilopoceras austinense* Adkins, 1931 (Adkins 1931: 50, explanation of pl. 4), one specimen, the holotype, are from Bear Creek 'about $\frac{3}{8}$ mile west of Marchaca', which is said to be in both Travis and Hays counties. The only precisely localized *P. (P.) haasi* specimens are fragments from '30 feet above the base of the Austin' from Williamson County, a specimen from the basal '15 feet of the Austin Chalk' on

Boudin Creek, Travis County, and the basal '20 feet of the Austin' at Watters Park, Travis County (Young 1963: 72). *Inoceramus* species collected from 2 m above the base of the Austin at Cedar Hill Scarp, Johnson County, are *Cremnoceramus deformatis* (Meek, 1871) (an early form of Kauffman (OUM KT5386-9)).

According to Kauffman, Cobban & Eicher (1978), *Cremnoceramus deformatis* (early form) characterizes the upper part of the lower half of the *Scaphites preventricosus* Zone of the U.S. Western Interior.

The *Peroniceras* (*P.*) *westphalicum* Zone yielded *P.* (*P.*) *westphalicum* (seven specimens) and *P.* (*P.*) *moureti* (interpreted here as *P.* (*P.*) *tridorsatum*) (two specimens). *Prionocycloceras adkinsae* Young, 1957, was inferred to be from this zone on phylogenetic grounds alone.

The *Prionocycloceras gabrielense* Zone yielded *P. gabrielense* Young, 1957 (five specimens), *P. hazzardi* Young, 1957 (the holotype plus two doubtful juveniles), *Parabevahites sellardsi* Young, 1957 (three specimens), and *Protexanites planatus* (Lasswitz, 1904) (eleven specimens). Wolleben (1967), working in Trans-Pecos Texas, added *Placenticerias colquitti* Wolleben, 1967 (two specimens), and *Prionocycloceras adkinsae* Young, 1963 (one specimen) to the *P. gabrielense* Zone assemblage.

It is concluded that the ammonites of the *Peroniceras haasi* and *P. westphalicum* Zones indicate the Middle Coniacian, and are equivalent to the European *P.* (*P.*) *tridorsatum* Zone. There is no ammonite evidence for the Lower Coniacian.

Northern Spain

A series of papers by Wiedmann (1960, 1964, 1979, 1980) and Wiedmann & Kauffman (1978) have documented the sequence of Upper Cretaceous ammonite faunas in northern Spain, building on early work by Karrenberg (1935), Ciry (1940, 1951), and others.

It is important to note that the highest Turonian ammonites, which include *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny), are generally separated from the first Coniacian ammonites by a rudistid limestone complex that is 25 m thick at Picofrentes in the Celtiberic Ranges and 50–80 m thick in the Nela area of the Vascogetic Ranges. The succeeding Coniacian consists of sandy and glauconitic marls up to 200 m thick in the Vascogetic Ranges. Two important sections are given in detail as a basis for discussion.

Ollogoyen, Navarra (1°32'15"E 42°41'15"N)

The section consists of 110 m of grey clays and silty marls. Details are as follows (after Wiedmann 1960: 718; 1979: 177, with original nomenclature):

1. Upper part of Middle Turonian (Zone VII): more than 10 m with *Romaniceras inerme* (de Grossouvre, 1889), and *Proromaniceras pseudodeverianum* (Jimbo, 1894).

2. Upper Turonian (Zone VII): about 50 m with *Romaniceras ornatissimum* (Stoliczka, 1865), *R.* (*R.*) cf. *deverianum* (d'Orbigny, 1841), *Collignoni-*

ceras? sp., *Pachydesmoceras denisonianum* (Stoliczka, 1865), and *Puzosia* cf. *P. planulata* (J. de C. Sowerby, 1827).

3. Lower Coniacian (I and ?II): about 45 m with *Tissotia* (*Metatissotia*) cf. *robini* (Thiollière, 1848), *Reesideoceras* cf. *R. camerounens* Basse, 1947, and *Proplacenticeras* sp.

4. Middle–Upper Coniacian (Zones ?III and IV): about 50 m of massive limestones.

5. Upper Coniacian (Zone V): sandy marls and marly limestone of the Col d'Ollogoyen with *Paratexanites* cf. *P. emscheris* (Schlüter, 1876), *Gauthiericeras aberlei* (Redtenbacher, 1873), *Gaudryceras vascogeticum* Wiedmann, 1962, and *Scaphites compressus* d'Orbigny, 1842.

Terradillos de Sedano, Burgos (0°8'05"E 42°39'10"N)

1. Middle–Upper Turonian (Zones VII and VIII) massive, well-bedded limestones with *Vaccinites*.

2. Lower Coniacian (Zone I): 32 m marls and marly limestones, glauconitic sandstones and marls with *Tissotioides haplophyllus* (Redtenbacher, 1873), *T. crassus* Ciry, 1940, *Metatissotia robini* (Thiollière, 1848), *M. ewaldi* (von Buch, 1847), *Parapuzosia* cf. *P. corbarica* (de Grossouvre, 1894), to which can be added *Tongoboryceras* sp. (OUM KZ 14001) and *Scaphites meslei* (de Grossouvre, 1894) (OUM KZ 14006).

3. Lower Coniacian (Zone II): 4 m calcarenites and limestones with *Reymentoceras hispanicum* (Wiedmann, 1960) and *Protexanites bourgeoisi* (d'Orbigny, 1850).

4. Middle Coniacian (Zone III): 16 m grey marls with *Gauthiericeras vallei* Ciry, 1940, *G. margae* (Schlüter, 1867), *G. gordum* (Karrenberg, 1935), *Barroisiceras* cf. *B. sequens* (de Grossouvre, 1894), *Texasia iberiense* (Basse, 1947), *Reesideoceras* cf. *camerounense* Basse, 1947, *R.* cf. *R. nicklesi* (de Grossouvre, 1894), *Paratexanites zeilleri* (de Grossouvre, 1894), and *Scaphites* ex aff. *arnaudi* de Grossouvre, 1894.

5. Upper Coniacian (Zone IV): 12 m of brown marls with *Hemitissotia turzoi* Karrenberg, 1935, *Texasia* cf. *dartoni* Reeside, 1932, and *Protexanites* sp. nov.

6. Upper Coniacian (Zone V): 5 m of marls similar to those of Zone IV with *Hemitissotia lenticeratiformis* Wiedmann, 1978.

7. Lower Santonian (Zone I): 7,5 m of marls and 8 m of marly limestones with *Texanites hispanicus* Collignon, 1948, and *Lenticeras* cf. *lissoni* Knetchel, 1947.

8. Upper Santonian: 20 m red limestones with larger benthonic Foraminiferida.

At first sight this succession appears wholly incompatible with the sequence developed by Kennedy (in press) for the French succession. De Grossouvre (1901) had long ago recognized that the acme of Tissotidae in France occurred at least at the level of appearance of *Peroniceras*. Subsequent work has confirmed this and the following species are of the *Tissotioides haplophyllus* Zone: *T. haplophyllus* (of which *T. crassus* is a synonym (Kennedy in press)),

Metatissotia robini and *M. ewaldi*, which are restricted to the *P. (P.) tridorsatum* Zone in France, whereas *Tongoboryceras* and *Scaphites (Scaphites) meslei* are commonest in this zone. It is concluded that the *Tissotioides haplophyllus* Zone of Wiedmann is equivalent to the *P. (P.) tridorsatum* Zone.

The only common element of the *Texanites hispanicum* Zone and the French sequence is *Protexanites bourgeoisi*. In France this is generally uppermost Coniacian, but *Protexanites* does occur low in the Upper Coniacian in Zululand.

The fauna of the *Gauthiericeras vallei* Zone presents most apparent anomalies. It does include *G. margae*, but the other recorded species of '*Gauthiericeras*' (*G. turzoi*, *G. gordum*, *G. vallei*) are all *Prionocycloceras*. So far as can be judged from large new collections, the *Prionocycloceras* at this level includes compressed, flat-sided forms as well as the depressed strongly ribbed types already noted, and *Barroisiceras iberiense* Basse (1947: 118; lectotype herein designated, the original of Basse's pl. 7 (fig. 2)) is one such compressed form; *Barroisiceras* cf. *sequens* of Wiedmann & Kauffman (1978, pl. 11 (fig. 3)) and Wiedmann (1980, pl. 11 (fig. 3)) is probably another, as may be the *Reesideoceras* cf. *came-rounense* recorded from the zone. (Unpublished observations by C. W. Wright on Colombian *Prionocycloceras* show a comparable range of variation from depressed and coarsely ribbed to compressed and feebly ribbed specimens.)

Of other species noted by Wiedmann, *Paratexanites zeilleri* can be dated only as pre-*Paratexanites serratomarginatus* Zone in France, and *Otoscaphtes* ['*Scaphites*'] ex. aff. *arnaudi* is impossible to assess without illustrations. *O. arnaudi* itself appears in the *P. (P.) tridorsatum* Zone. The *Gauthiericeras vallei* Zone is thus directly equivalent to the *G. margae* Zone of the French sequence.

The *Gauthiericeras turzoi* and *Hemitissotia lenticeratiformis* zones cannot be correlated with the sequences in France (or indeed elsewhere), having no described elements in common.

Romania

Szász (1981) presented the most recent review of the Coniacian succession in Romania. Two areas were investigated — the Babadag Basin (north Dobrogea) and the Cheia Valley–Vinturarita (south Carpathians). In the Babadag Basin two successive zones were recognized, a zone of *Barroisiceras haberfellneri* below and one of *Peroniceras moureti* above. In the Vinturarita region, only one zone of *Forresteria (Reesideoceras) petrocoriensis* was recognized, and equated with the *Barroisiceras haberfellneri* Zone of the Babadag Basin.

Details of the zonal assemblages are as follows:

Zone of *Barroisiceras haberfellneri*

Barroisiceras haberfellneri haberfellneri (von Hauer, 1866), *Harleites bentori* Parnes, 1964, *Yabeiceras* sp. (aff. *Yabeiceras orientale* Tokunaga & Shimizu, 1926), *Pseudokossmaticeras* sp. (sp. nov?), *Nowakites? macoveii* Szász, 1981, *Scaphites* ex gr. *compressus* d'Orbigny, 1842, *Gaudryceras* aff. *varagurense* Kossmat, 1891, *Gaudryceras* aff. *mite* (von Hauer, 1866), *Damesites* spp.,

Austiniceras cf. *mobergi* (de Grossouvre, 1894), *Neocrioceras* (*Schlueterella*) *kossmati* (Simionescu, 1899), and *Neocrioceras* sp. Also recorded from this level are *Harleites harlei* (de Grossouvre, 1894), *Gaudryceras denseplicatum* (Jimbo, 1894), and *Pseudokossmaticeras* ?sp. nov.

Zone of *Peroniceras moureti*

Peroniceras moureti de Grossouvre, 1894, *Peroniceras tridorsatum* (Schlüter, 1867), *Peroniceras* sp., *Nowakites carezi* (de Grossouvre, 1894), and *Puzosia* ex. gr. *orientalis* Matsumoto, 1954. Previous records from this level include *Peroniceras czoernigi* (Redtenbacher, 1873), *Peroniceras rousseauxi* de Grossouvre, 1894, *Eupachydiscus sayni* (de Grossouvre, 1894), and '*Anisoceras*' *sertum* Müller & Wolleman, 1904.

Zone of *Forresteria* (*Reesideoceras*) *petrocoriensis*

Forresteria (*Reesideoceras*) *petrocoriensis* (Coquand, 1865), *Sornayceras* aff. *omorii* Matsumoto, 1965, *Nowakites tallavignesi* (d'Orbigny, 1850), *Nowakites lemarchandi* (de Grossouvre, 1894), *Pseudokossmaticeras brandti* (Redtenbacher, 1873), *Neocrioceras* (*Schlueterella*) *kossmati* (Simionescu, 1899), *Hyporbulites* cf. *bizonatus* (Fritsch, 1872), *Gaudryceras* aff. *varagurense* Kossmat, 1895, *Gaudryceras* aff. *mite* (von Hauer, 1866), *Scaphites* ex. gr. *compressus* d'Orbigny, 1842, *Tetragonites* (*Epigonoceras*) sp. nov. (aff. *T. (E.) epigonum*) Kossmat, 1895, *Tetragonites*? sp., and *Puzosia* sp.

The *P. moureti* Zone is clearly equivalent to the Middle Coniacian *P. tridorsatum* Zone as used here. The *F. (R.) petrocoriensis* Zone is also part at least equivalent to the *tridorsatum* Zone (some of Szász's *F. (R.) petrocoriensis* are actually Middle Coniacian *F. (H.) nicklesi* (de Grossouvre) (e.g. Szász 1981, pl. 11 (fig. 1)). The *B. haberfellneri* Zone also presents difficulties; the only common element with faunas we have studied is the *Yabeiceras*, which suggests this zone to be Middle Coniacian.

TABLE 1
Coniacian correlation

SUBSTAGE	FRANCE	ZULULAND	MADAGASCAR	SPAIN
LOWER SANTONIAN	'gallicus'	I	<i>oliveti</i>	<i>hispanicus</i> ? — ? — ? — ?
UPPER CONIACIAN	<i>serratmarginatus</i>	V	<i>guyabanum</i> et <i>margae</i>	<i>lenticeratiformis</i> <i>turzoi</i> <i>vallei</i> ? — ? — ? — ?
	<i>margae</i>	IV		
MIDDLE CONIACIAN	<i>tridorsatum</i>	III + II	<i>theobaldi</i> et <i>onilähynse</i> + <i>dravidicum</i> et <i>subtricarinaratum</i>	<i>hispanicum</i> + <i>haplophyllus</i>
LOWER CONIACIAN	<i>petrocoriensis</i>	? I	—	—

Conclusions

The preceding observations lead to the correlation shown in Table 1. In the following sections the terms Lower, Middle and Upper Coniacian are as used in the present discussion, and not as used by previous authors.

SYSTEMATIC PALAEOLOGY

Phylum MOLLUSCA

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Order AMMONITIDA Hyatt, 1889

Superfamily ACANTHOCERATAEAE de Grossouvre, 1894

Family **Collignoniceratidae** Wright & Wright, 1951

Subfamily Peroniceratinae Hyatt, 1900

Discussion

Wright (1957: L428-429) included four genera in the subfamily Peroniceratinae: *Prionocycloceras* Spath, 1926, *Gauthiericeras* de Grossouvre, 1894, *Peroniceras* de Grossouvre, 1894, and *Yabeiceras* Tokunaga & Shimizu, 1926. The authors follow Matsumoto (1964, 1965) in transferring *Yabeiceras* to the subfamily Barroisiceratinae and *Prionocycloceras* to the subfamily Collignoniceratinae.

Gauthiericeras, with type species *Ammonites margae* Schlüter, 1867, was erected by De Grossouvre (1894: 87) for a series of species 'dont les tours à section subquadrangulaire présentent sur leur bord externe une quille médiane très saillante: en dehors de ce caractère extérieur, les cloisons offrent aussi certaines particularités spéciales qui les placent comme formes de transition entre celles des *Mortoniceras* et celles du genre suivant, *Peroniceras*'.

Peroniceras, with type species *P. moureti* de Grossouvre, 1894, was diagnosed (De Grossouvre 1894: 93) as including a group of species presenting 'd'assez grandes affinités avec les *Mortoniceras* et les *Gauthiericeras*, mais s'en distinguant par leur bord externe orné de trois quilles et par une ligne suturale beaucoup plus découpée et plus élancée qui rapelle celle des *Stoliczkaia*: le premier lobe latéral est, comme dans ce dernier genre, assez étroit et terminé par une fourche bien nette. La troisième selle latérale a aussi son extrémité supérieure bien au-dessus de celles des deux premières.'

Concerning the suture-line of *Peroniceras* [*Schloenbachia*] *dravidicum*, Kossmat (1895: 190) noted that 'der erste Lateralsattel von beiden Seiten her stark eingeschnürt und von sehr zierlicher Gestalt, der zweite Lateralsattel ist nicht mehr selbständig, sondern dem ersten Lateralsattel als grosser schiefer Ast angehängt...'. Kossmat also maintained that all *Peroniceras* species possessed a similar suture-line, though not always as pronouncedly developed. In this respect he mentioned *Peroniceras czoernigi* (Redtenbacher), *P. tridorsatum* (Schlüter) and *P. moureti* de Grossouvre.

The diagnoses of *Peroniceras* and *Gauthiericeras* as given by De Grossouvre and slightly elaborated on by Kossmat remained virtually unchanged during the ensuing 60 years. In 1957 the diagnoses of *Peroniceras* and *Gauthiericeras* were given in the *Treatise* (Wright 1957: L429) as:

Gauthiericeras. 'Rather evolute; whorl section trapezoidal to subquadrate; with entire or feebly crenulate high keel bearing a distinct groove on either side; strong ribs spring at first in pairs, later usually singly, from single or double umbilical tubercles and end in strong ventrolateral tubercles.'

Peroniceras. 'Very evolute, with oval, trapezoidal or square whorl section; venter with 3 entire keels, middle one as high as others or higher; regular rounded or conical umbilical tubercles are joined to slightly larger number of similar ventrolateral ones by short straight rounded ribs; also, lateral tubercles may occur.'

Reyment (1957: 65) added a new subgenus to *Peroniceras*, *P. (Reginaites)*, with type species *P. (Reginaites) quadrituberculatum* Reyment, 1957. This is an evolute form with tricarinate venter but with four rows of tubercles. As the authors have previously shown (Klinger & Kennedy 1980), *Reginaites* is more appropriately referred to the subfamily Texanitinae Collignon, 1948, and is closely allied to and often homoeomorphic with *Plesiotexanites*. In addition, it seems to be restricted to the Upper Santonian and possibly the lowermost Campanian (in Zululand), rather than Coniacian as initially presumed by Reyment.

Wiedmann (1960) described a new subgenus of *Gauthiericeras*, *G. (Ciryella)*, type (and only) species *G. (Ciryella) vascogoticum* Wiedmann, 1960, from the 'Lower' Coniacian of Spain. As shown above, the type species is no older than Middle Coniacian. This is a widely umbilicate form with a single keel, fastigiate venter, two rows of tubercles, and a rather simple suture, in several respects intermediate between *Peroniceras* and *Gauthiericeras*, according to Wiedmann.

In 1965 this relatively simple classification, comprising four genera (or subgenera) only, was extended by the addition of a new subfamily, nine new genera and two subgenera by the independent studies of Van Hoepen and Matsumoto.

Van Hoepen's publication received a rather narrow circulation, and his diagnoses are given here in full; Matsumoto's diagnoses are summarized where appropriate.

Reiterating Kossmat's (1895: 190) views, Van Hoepen (1965: 4) defined *Peroniceras* as 'ammonites with three keels at a full-grown stage and with a suture-line which is deeply incised and of which the third lateral saddle is rooted in the inner lower corner of the second lateral saddle and which is separated from the auxiliary saddles by a more or less horizontal, sometimes deeply penetrating lobe'.

The new subgenera of *Peroniceras*, *P. (Zuluiceras)*, type species *P. Zuluiceras zulu* van Hoepen, 1965, and *P. (Zuluites)*, type species *P. (Zuluites) modestum* van Hoepen, 1965, were defined as follows:

P. (Zuluiceras). 'Ammonites with umbilicus narrower than in *Peroniceras* sensu stricto and whorl section more or less square in the early stages, but increasing more rapidly in height than in *Peroniceras* sensu stricto and tending to become inflated and rounded in later stages; the ribs are stronger relative to the tubercles than in *Peroniceras* sensu stricto' (Van Hoepen 1965: 9);

P. (Zuluites). 'A further development of the trend exhibited by *Zuluiceras*; distinguished from that subgenus by the still greater whorl-height and oval whorl section. Ornamentation gradually becomes weaker and eventually disappears completely.' (Van Hoepen 1965: 23).

In the new subfamily Gauthiericeratinae (ex Gauthiericeratidae van Hoepen (1955), Van Hoepen (1965) included 'ammonites with three keels at a full-grown stage of which the suture-line is little incised; the axes of the three lateral saddles and the two lateral lobes are more or less parallel; the third lateral saddle is short and high up the suture'.

Apart from the nominate genus *Gauthiericeras*, Van Hoepen included five new genera in the subfamily Gauthiericeratinae: *Andersonites*, type species *A. listeri* van Hoepen, 1965; *Fluminites*, type species *F. albus* van Hoepen, 1965; *Hluhluweoceras*, type species *H. fugitivum* van Hoepen, 1965; *Falsebayites*, type species *F. peregrinus* van Hoepen, 1965; and *Fraudatoroceras*, type species *F. besairiei* van Hoepen, 1965. With the exception of *Falsebayites*, the type species of which was based on two specimens, all the other taxa were based on single specimens. In order of pagination they were defined as follows:

Andersonites. 'Ammonites with three keels, wide umbilicus, more or less square section, very strong, straight ribs each with two tubercles, a very large shoulder tubercle and only slightly smaller umbilical tubercle' (Van Hoepen 1965: 29).

Fluminites. 'Ammonites with three keels, wide umbilicus and a section which is at first higher than broad. The ribs are strong and slightly concave forwards. They are at first close together, but later far apart. External saddle very low down, reaching nearly as far back as the first lateral lobe. First lateral saddle and first lateral lobe broad; second lateral saddle narrow; second lateral lobe very short. Axes of these elements more or less parallel' (Van Hoepen 1965: 31).

Hluhluweoceras. 'Ammonites with suture-line consisting of a square, broad first lateral saddle, a narrower second lateral saddle and a broad but very short third lateral saddle. The external saddle is short and fairly high up. The first lateral lobe is deep and narrower than the second lateral saddle. The axes of all these elements are parallel to the keel, with the exception of the axis of the short but robust second lateral lobe which extends obliquely, more or less in the direction of the hind end of the first lateral lobe. There is only one keel which is slightly crenulated; the venter is smooth, the section square' (Van Hoepen 1965: 33).

Falsebayites. 'Ammonites with a suture-line consisting of a square, broad, first lateral saddle, a narrower but still broad first lateral lobe the sides of which are slightly convergent backwards, a short second lateral saddle and a short second lateral lobe (both these elements being narrower than the first lateral lobe); then follows a very short third lateral saddle which is as broad as high, and on the

umbilical surface are another three small lobes and saddles. The axes of all these elements are parallel to the keel. The external saddle is short and fairly low down. The whole suture is a more or less regularly meandering line. The venter is rounded; along its middle there is a broad zone which is ever so slightly raised and might be regarded as representing a keel. The ribs form a broad, very low band passing across the venter in a slightly forward direction' (Van Hoepen, 1965: 34). *Fraudatoroceras*. 'Ammonites with three keels, very wide umbilicus, square section, fairly large, clavate shoulder tubercles and very long, narrow umbilical tubercles reaching up to the middle of the flanks. External saddle is half as high as the first lateral saddle which is as broad as high. First lateral lobe is very narrow. Second lateral saddle is not as broad as the first. Second lateral lobe is narrow and short. Third lateral saddle broad and short, but not as broad as the second and not reaching as far forward nor as far backwards. Third lateral lobe narrow and short not reaching as far forward or backward as the second. The umbilical seam passes through its middle. The dorsal saddle is high and narrow, higher than the first lateral saddle. There is a very small, oblique, internal lateral lobe and a small, first dorsal lateral lobe, just touching the umbilical seam. The axes of all these elements, except that of the internal lateral lobe, are parallel' (Van Hoepen 1965: 35).

According to Matsumoto's interpretation of *Peroniceras*, (Matsumoto 1965: 210) the genus is characterized by '... evolute whorls, distinctly tricarinate venter, bi-tuberculate ribs and deeply incised, particularly specialized sutures', whereas *Gauthiericeras* (Matsumoto 1965: 210) '... typically has less evolute whorls, an entire or feebly crenate ventral keel with a groove on either side, stronger ventrolateral tubercles, often double umbilical tubercles and simpler, normal collignoniceratid sutures'.

Matsumoto (1965: 210) furthermore believed that '*Peroniceras* is clearly separated from *Gauthiericeras* (*s. l.*) by the different pattern of sutures and distinctly tricarinate-bisulcate venter'.

Apart from *Peroniceras* and *Gauthiericeras*, Matsumoto referred *Reginaites* and *Ciryella* to the subfamily Peroniceratinae and added four new genera: *Cobbanoceras*, type species *C. tanakai* Matsumoto, 1965; *Sornayceras*, type species *S. proteus* Matsumoto, 1965; *Ishikariceras*, type species *I. binodosum* Matsumoto, 1965; and *Reymentites*, type species *R. hataii* Matsumoto, 1965. Contrary to the opinions of both Matsumoto and Wiedmann (1978: 670), the authors prefer to place *Reymentites*, a tri- or quadrituberculate form with tricarinate venter, in the subfamily Texanitinae Collignon, 1948, rather than in the subfamily Peroniceratinae. Moreover, *Reymentites* is regarded as possibly a junior synonym of *Reginaites*, which the authors also referred to the subfamily Texanitinae (Klinger & Kennedy 1980).

Cobbanoceras is evolutely coiled with a wide umbilicus, subquadrate whorls and three entire keels on the venter, of which the middle one is higher than the lateral ones. Ribs are mostly single, and each has an umbilical and ventrolateral tubercle. The suture is rather simple.

Sornayceras has a moderate to large shell, consisting of more or less evolute whorls with wide or moderate umbilicus. The whorl section varies from subquadrate to high subrectangular with a roughly fastigate venter. There is a distinct median keel bordered on either side by a shallow groove without distinct lateral keels. The median keel is entire or feebly crenate. The flanks are ornamented by radial ribs which are intercalated or branched, bearing umbilical and ventrolateral tubercles. The suture is deeply and finely incised and much complicated.

Ishikariceras has a shell of moderate size, evolute with wide umbilicus. The whorl section is subquadrate in early stages, but semi-elliptical in the adult. The venter is unicarinate with two shallow lateral grooves. Lateral keels, if present, are virtually indiscernible or very weak. The suture is rather simple with massive and subquadrate elements.

Etayo-Serna (1979: 97) introduced the genus *Gloriaceras*, type species *G. corraei* Etayo-Serna, 1979, which has peroniceratine characteristics. The original diagnosis is as follows:

'Conchs small to moderately large. The earliest whorls observed are discoidal with fastigate, unicarinate median ventral region; the ornament consists of faint falcoid or biconcave ribs that cross the venter in an acute adoral bend; the ribs may bifurcate on the umbilical third of the flank, at this stage no tubercles are developed.

Shortly after, the ribs weaken on the median ventral line and develop a rounded somewhat spirally elongated external lateroventral node; the admedian ventral end of the ribs elongates longitudinally and which soon interconnect forming almost continuous keels on each side paralleling the median keel but the ribs can still be observed crossing the venter. The ribs sporadically develop weak peri-umbilical swellings. With growth the ribs tend to straighten on flanks, become club-like and connect the ventrolateral carinae. The periventral tubercles are much stronger than the peri-umbilical ones which sometimes are missing. The suture line has E/L saddle large, rectangular and bifid with the external branch foliate and narrow at its stem; L lobe is wide, deep, bifid (pseudotrifid), L/U2 saddle is slender, taller than E/L saddle, bifid, phylloid; U2 lobe is digitated, short. U2/U3 and U3/U1 are subequal. U3 lobe is digitated, glove-like; U1 lobe is bifid, narrower but as deep as U2; U1/I saddle is single, with a unique phylloid head.'

Another possible candidate for the subfamily Peroniceratinae is *Neogauthiericeras* Collignon, 1969, type species *N. zafimahovahi* Collignon, 1969, from the basal Campanian of Madagascar, erected for evolute forms with fastigate venter and bituberculate ribs and suture similar to that of *Gauthiericeras*, or very close to it. Collignon did not indicate whether the genus was to be placed in the subfamily Peroniceratinae, but the name seems to imply this. The authors (Klinger & Kennedy 1980: 111) previously suggested that *Neogauthiericeras* may possibly be derived from *Reginaites* at the Santonian-Campanian stage boundary and should thus also be referred to the subfamily Texanitinae.

Patrulius & Szász (1975: 158) described a pentacarinat form of *Peroniceras* from the Coniacian of Romania. The material is fragmentary but, if more complete, would possibly be eligible for separate subgeneric or generic rank.

All these taxa, with the exception of those previously referred to the subfamily Texanitinae by Klinger & Kennedy (1980) and the enigmatic specimen from Romania are summarized in Figure 1. From the diagnoses it appears that the main characteristics for distinguishing between the various taxa are, in unweighted order:

- (i) Unicarinat versus tricarinat venter,
- (ii) Complex versus simple suture-line,
- (iii) Evolute versus involute coiling.

The dividing lines become vague in the cases of *Fluminites*, *Falsebayites*, and *Sornayceras*. The validity of these various taxa and their extent is reviewed below in their proper context, as exemplified by the various species.

Genus *Peroniceras* de Grossouvre, 1894

Type species

Peroniceras moureti de Grossouvre, 1894: 100, by original designation = *Ammonites tridorsatus* Schlüter, 1867: 26.

Diagnosis

Medium-sized to large, moderately to very evolute, whorl section compressed trapezoidal to depressed quadrate. Venter with three subequal entire keels, or with the siphonal keel strongest. Ribs may be simple, prorsiradiate, straight or concave throughout, with or without umbilical bullae that migrate out to an inner flank position at maturity, or may arise in pairs or intercalate on inner whorls. All ribs develop ventrolateral tubercles. Ribs may persist to maturity, or weaken and decline on the adult body chamber.

Suture variable, from simple with short elements, as in ancestral Collignoniceratinae, or complex, with long, deeply incised elements; L more or less bifid; U₂ small and inserted below L/U.

Discussion

The diagnoses given above (pp. 130–5) by various authors indicate confusion in generic distinctions, yet *Peroniceras* is one of the most easily identified taxa if the degree of complexity of the suture is ignored. A detailed description of the type species is given below; it shares with many other species very evolute coiling, a tricarinat venter and ornament of mainly simple ribs each with an umbilical and a ventrolateral tubercle.

Its suture is relatively simple with rather broad, blocky, little-indented saddles E/L and L/U and a narrow L; U₂ and inner elements are all narrow and small. Other species, such as *P. dravidicum* Kossmat, 1895, universally referred to the genus, have much more complex, long, narrow, finely indented saddles

TAXA	COILING		VENTER		SUTURE		SUPPOSED AGE IN ORIGINAL PUBLICATIONS
	EVOLUTE	INVOLUTE	UNI- CARINATE	TRI- CARINATE	SIMPLE	COMPLEX	
<i>Peroniceras</i>	X			X	X	X	M. Coniacian
<i>Gauthiericeras</i>		X	X		X		U. Coniacian
<i>Ciryella</i>	X		X		X		U. Coniacian
<i>Zuluiceras</i>	X			X		X	M-U. Coniacian
<i>Zuluites</i>		X		X		X	M-U. Coniacian
<i>Andersonites</i>	X			X	X		U. Coniacian
<i>Fluminites</i>	X			X	X		U. Coniacian
<i>Hluhluweoceras</i>		X?	X		X		U. Coniacian
<i>Falsebayites</i>		X?	X		X		U. Coniacian
<i>Fraudatoroceras</i>	X			X	X		U. Coniacian
<i>Cobbanoceras</i>	X			X	X		M. Coniacian
<i>Ishikariceras</i>	X		X	----- ?			Santonian?
<i>Sornayceras</i>	X	X			X		Coniacian
							M-U. Coniacian

Fig. 1. Summary of taxa referred to the subfamily Peroniceratinae prior to the present investigation, with identifying characteristics.

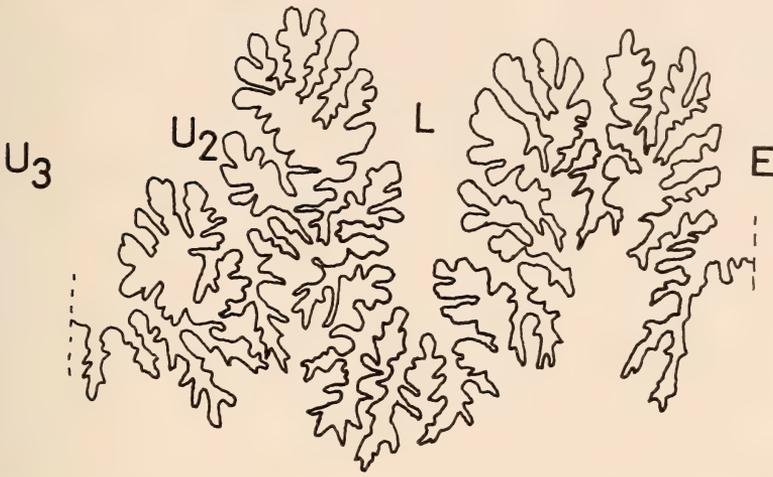


Fig. 2. External suture-line of typical *Peroniceras*, here referred to as *P. (Peroniceras) dravidicum*-type, with highly incised elements and narrow-stemmed saddles and lobes. Note the thin, stemmed saddle U_3/U_2 attached obliquely to the base of saddle L/U_2 . $\times 1$. (After Van Hoepen 1965, fig. 2a.)

with lobe U_2 distinctly inserted below saddle L/U (Fig. 2). There is great variation between species in these characters and it seems absurd to pick out particular degrees in a gradational series to typify subgenera. The simple form of suture closely resembles that of evolute species of *Subprionocyclus* Shimizu, 1926 (Collignoniceratinae) and *Protexanites* Matsumoto, 1955, and other Texanitinae except that the inner elements are narrower to accommodate the more evolute whorl. The evolutionary trend was thus from the collignoniceratine type to the *dravidicum* type.

Fraudatoroceras van Hoepen, 1965, of which *Cobbanoceras* Matsumoto, 1965, is a junior synonym, have type species with sutures that are only very slightly less developed along this line than those of *Peroniceras tridorsatum* (= *P. moureti*) and the species assigned to them, which differ in no other significant characters, should be referred to the group of *Peroniceras* centred round the type species. Indeed, *Fraudatoroceras besairiei*, the type species of Van Hoepen's genus *Fraudatoroceras*, resembles *P. tridorsatum* (= *P. moureti*) much more than do other species always referred to *Peroniceras*, both in the early stage at which tricarination sets in and in the shape of the pinched latero-umbilical bullae.

Occurrence

Middle Coniacian, world-wide. Upper Coniacian of Japan and Zululand, ?Santonian of Japan.

Subgenus *Peroniceras* (*Peroniceras*) de Grossouvre, 1894

(= *Fraudatoroceras* van Hoepen, 1965: 35; *Cobbanoceras* Matsumoto, 1965: 219; *Gloriaceras* Etayo-Serna, 1979: 96)

Diagnosis

Very evolute, keels strong and subequal, ribs and tubercles persist to the end of the adult body chamber.

Discussion

Observations under the discussion of the genus *Peroniceras* (p. 137) explain the basis for regarding *Fraudatoroceras* and *Cobbanoceras* as synonyms of *Peroniceras* (*Peroniceras*).

The genus *Gloriaceras* Etayo-Serna, 1979 (type species *G. correaui* Etayo-Serna, 1979: 97, pl. 13 (fig. 18), pl. 14 (fig. 10), text-fig 9C-D, H) was introduced for two Colombian species that were separated from *Peroniceras* on the basis that they had an early stage with flexuous bifurcating ribs that cross the venter forming chevrons, a character retained in some adults, and also differed in suture-line. This was described as having a large, rectangular and bifid E L saddle with the external branch foliate and narrow at its stem, L lobe wide, deep and bifid (pseudotrifid); saddle L/U₂ slender, taller than saddle E L, bifid and phylloid; U₂ digitated and short; U₂/U₃ and U₃/U₁ subequal; U₃ digitated and glove-like; U₁ bifid, narrower but as deep as U₂; and U₁/I single with a unique phylloid head. This was contrasted with the suture of *P. moureti* on the basis of de Grossouvre's figure, which he described as having a wide E L, with narrow, highly incised digitated L, U₂/U₃ accessory to L/U₂, and a similar interdependency of L/U₂-U₂/U₃ was noted in *P. dravidicum* on the basis of Kossmat's figure (1895, pl. 23 (fig. 3)).

Juvenile *Peroniceras* (*Peroniceras*) of several species have, at 10-15 mm diameter, a strong, entire or undulose siphonal keel flanked by shallow grooves and weak lateral keels, which may also be undulose, strengthening at the termination of the ribs. This stage is rapidly replaced by a distinctly tricarinate one in which undulations are either lost or are irregular and correspond to the ribs. *Gloriaceras correaui* differs only in the more obvious development of this feature and the retention of rather more marked undulations of the lateral keels, in these respects retaining the phylogenetically primitive features of the ancestral Collignoniceratinae a little longer than some other specimens. Etayo-Serna also noted that the ribs extend to the siphonal keel in *Gloriaceras*. This is no more so than in some specimens of the type species of *Peroniceras* (*Peroniceras*): the juvenile SAS Z734, illustrated as Figure 16D-E (the original of Van Hoepen 1965, pl. 2), in fact shows all the supposedly diagnostic features of *Gloriaceras*, which is here treated as a strict synonym.

Zuluiceras van Hoepen, 1965, of which *Zuluites* van Hoepen, 1965, and *Sornayceras* Matsumoto, 1965, are regarded as synonyms, is discussed fully

below (p. 180). They represent a series of progressively more involute forms, the earliest of which, *Zuluiceras uberlei* (Redtenbacher, 1873) and *Z. bajuvanicum* (Redtenbacher, 1873) occur with *Peroniceras* (*Peroniceras*). These early forms (*Zuluiceras* s.s.) are linked by a continuum to much more involute later forms ('*Zuluites*'), the series showing progressive decline in ornament. The earliest species are close to *Peroniceras* (*Peroniceras*) and *Zuluites* is in consequence afforded subgeneric status only. The two differ in the greater involution of *Zuluiceras*, the compressed whorls that tend to round, lateral keels that are weaker than the siphonal one, and adults that retain only weak ornament or none.

Peroniceras (*Peroniceras*) is easily distinguished from *Gauthiericeras* de Grossouvre, 1894, which has a strong, sometimes serrated siphonal keel flanked by grooves and only incipient lateral keels, and strong primary ribs that may branch at umbilical or lateral tubercles.

Ishikariceras Matsumoto, 1965, has inner whorls with a subquadrate section, coarse bituberculate ribs and a strong siphonal keel but no, or only very weak, side keels, the body chamber being oval and virtually smooth with only constrictions and a single keel.

Reginaites Reymont, 1957, of the Texanitinae, of which *Reymentites* Matsumoto, 1965, is a synonym (Klinger & Kennedy 1980), is tricarinate with umbilical and ventrolateral tubercles only on nuclei, the ventrolateral splitting in two at a later stage when feeble lateral tubercles may appear.

Occurrence

Middle Coniacian, world-wide. *P.* (*Peroniceras*) [*'Cobbanoceras'*] *tanakui* Matsumoto, 1965, is questionably dated as approximately Santonian (Matsumoto 1965: 220).

Peroniceras (*Peroniceras*) *tridorsatum* (Schlüter, 1867)

Figs 3–15, 16D–E

Ammonites tridorsatus Schlüter, 1867: 26, pl. 5 (fig. 1).

Ammonites cf. *tridorsatus* Schlüter, 1876: 158, pl. 41 (figs 3–5).

? *Ammonites* (*Schloenbachia*) *czörnigi* Redt: Fallot, 1885: 229, pl. 1 (fig. 1).

Peroniceras subrotundatum var. *tridorsatum* Schlüter (de Grossouvre, 1894: 96, pl. 10 (figs 2–3), pl. 11 (fig. 1).

Peroniceras mourei de Grossouvre, 1894: 100, pl. 11 (figs 3–4), text-figs 37, 39. Pruvost, 1910: 367. Stolley, 1916: 89. Diener, 1925: 150. Venzo, 1936: 101, pl. 9 (fig. 1). Young, 1963: 73, pl. 26 (fig. 5), pl. 27 (fig. 4), text-fig. 13(a). Collignon 1965: 60, pl. 440 (fig. 1807). Szász & Lácátusa, 1974: 209, pl. 6 (fig. 3), pl. 7 (fig. 3). Wiedmann, 1978: 669, pl. 2 (figs 4–5). Amedro & Robaszynski, 1978: 37, pl. 1 (fig. 2). Collignon *et al.* 1979: 392, pl. 2 (fig. 3). Szász, 1981: 106, pl. 9 (figs 3–4).

Peroniceras (*Peroniceras*) *besairiei* van Hoepen, 1965: 4, pl. 1, text-fig. 1a.

Fraudatonoceras besairiei van Hoepen, 1965: 36, pl. 27, text-fig. 9a–b.

Peroniceras besairiei van Hoepen: Collignon, 1965: 54, pl. 437 (fig. 1803), pl. 438 (fig. 1803).

Peroniceras rousteauxi de Grossouvre, 1894: 102, pl. 11 (fig. 5). Diener, 1925: 151.

Peroniceras cf. *mourei* de Grossouvre: Maury, 1907: 87. Diener, 1925: 151.

Peroniceras tridorsatum (Schlüter): Stolley, 1916: 89. Diener, 1925: 152. Van Hoepen, 1965: 7, pl. 2. Amedro & Robaszynski, 1978: 36, pl. 2 (fig. 1), pl. 3 (figs 1–2). Szász, 1981: 107, pl. 9 (fig. 2).

? *Peroniceras tricarinatum* d'Orbigny: Scupin, 1913: 93, pl. 3 (fig. 5).

Peroniceras l'eppei (Fallot): Mirăuță & Mirăuță 1964: 336, pl. 7 (fig. 2), pl. 11. ?Joja & Chiriac, 1964: 46, pl. 1 (fig. 5).

? *Peroniceras* cf. *tridorsatum* (Schlüter): Collignon, 1965: 58, pl. 439 (fig. 1805, *non* 1806).

? *Peroniceras* aff. *tridorsatum* (Schlüter, 1867): Amedro & Robaszynski, 1978: 37, pl. 2 (fig. 2).

Peroniceras sp. (aff. *Peroniceras rousseauxi* Grossouvre): Szász & Lăcătușu, 1974: pl. 2 (fig. 4), pl. 7 (fig. 4).

Peroniceras (*Peroniceras*) *tridorsatum* (Schlüter, 1867): Kennedy, in press.

Type specimens

The holotype of the species, from the Coniacian of Westphalia, is lost. The holotype, by original designation, of *Peroniceras moureti* de Grossouvre, 1894, is the original of De Grossouvre's pl. 11 (fig. 4) from the 'Calcaires tendres gréseaux de la base de la Craie de Villedieu. Courtiras, près Vendôme (Loir-et-Cher)'. It is in the collections of the École des Mines, now in the Université Claude Bernard, Lyon. Paratypes include the specimen figured by De Grossouvre as his pl. 11 (fig. 3), an unregistered specimen in the collections of the Sorbonne (now in the Université Pierre et Marie Curie, Paris) from Assize L¹ of Arnaud at La Boulenerie, near Jonzac (Charente-Maritime) and a specimen (ML 7) from the Coniacian of Lezennes (Nord) in the Musée Gosselet, Lille.

The holotype, by monotypy, of *Peroniceras rousseauxi* de Grossouvre, 1894, is an unregistered specimen in the collections of the Sorbonne from Assize L¹ of Arnaud at St. Simon-de-Jonzac (Charente-Maritime).

The holotype, by original designation, of *Peroniceras* (*Peroniceras*) *besairiei* van Hoepen, 1965, is SAS Z248.

The holotype, by original designation, of *Fraudatoroceras besairiei* van Hoepen, 1965, is SAS Z756.

Material

SAS Z1117, SAS A63, and NMB D1145a–e, all from locality 72, degraded river cliff on the north side of the Mzinene River downstream from the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1590 and Z1522 from locality 91, degraded river cliff and artificial cut near the Hluhluwe River estuary, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, undifferentiated Coniacian debris. SAS Z1623a–b, Z1607, and SAM-PCZ5942 from locality 92, bulldozer scrapings and adjacent hillslopes on the farm Panplaas east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z248, Z730 and Z1120 from locality 73, degraded river cliffs on the north bank of the Mzinene River downstream of the Munywana River junction, Zululand, St. Lucia Formation, Coniacian II and III.

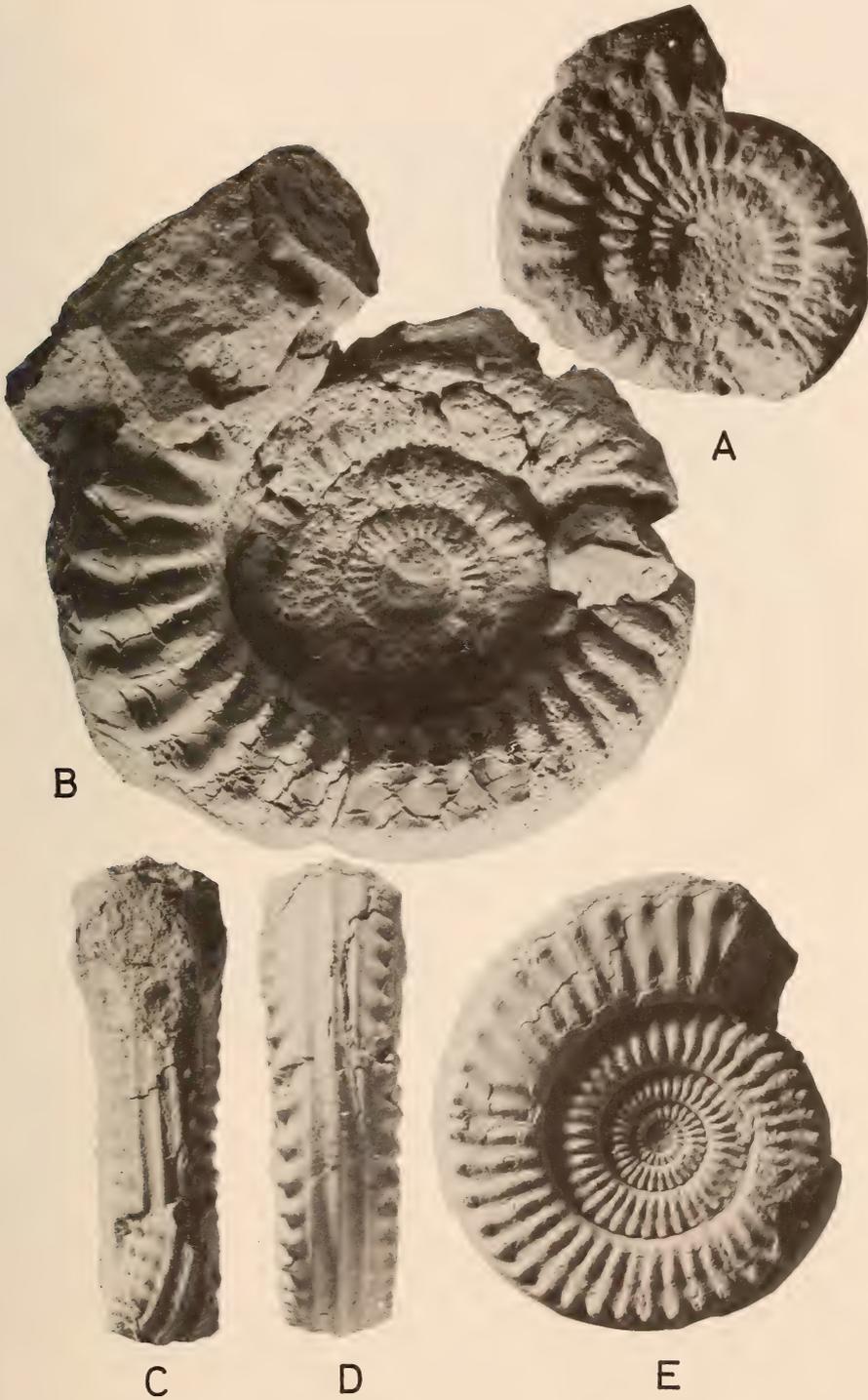


Fig. 3. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). A. SAS A63.
 B. NMB-D1145a. C-E. SAS Z1117. All $\times 1$.



Fig. 4. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). NMB D1145e. Specimen with distinct latero-umbilical tubercles on inner whorls, but indistinct on outer whorls, as in *P. (P.) lepeei* (Fallot, 1885). $\times 1$.



Fig. 5. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). NMB D1145C.
Specimen with narrower umbilical width than usual. $\times 1$

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
D1145a	31,0	9,0(29,0)	9,0(29,0)	1,0	16,0(51,6)	32:34
Z1623b	42,7	13,2(30,9)	12,5(29,2)	1,05	20,5(48,0)	28:28
Z1623a	52,4	17,0(32,4)	12,5(23,8)	1,36	27,0(52,0)	26:26
Z1117	59,0	17,0(28,8)	17,0(28,8)	1,0	31,0(52,5)	38:38
Z1607	60,0	17,0(28,0)	17,7(29,5)	1,04	29,1(48,5)	30:30
Z1120	63,3	19,0(30,0)	19,6(30,9)	0,96	30,5(48,0)	21:21
Z1590	82,8	24,6(29,7)	22,0(26,5)	0,92	48,0(57,9)	28:28
Z730	101,6	25,6(25,1)	23,3(22,9)	1,09	60,0(59,0)	30:30
Z1522	112,0	30,0(26,7)	26,0(23,2)	1,15	65,0(58,0)	24:24
D1145c	119,0	—	40,0(33,6)	—	55,0(46,2)	—
Z756	120,0	33,7(28,0)	27,3(22,7)	1,23	71,0(59,0)	33:33
D1145e	124,0	36,0(29,0)	34,0(27,4)	1,05	66,0(53,2)	38:38
Z248	132,0	33,0(25,0)	33,0(25,0)	1,0	73,0(53,0)	29:29

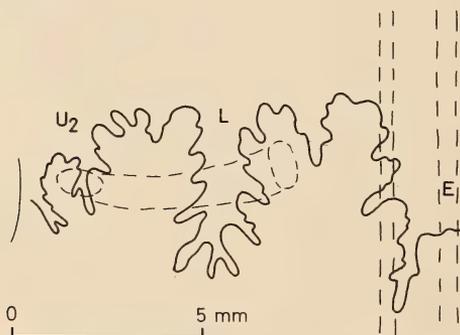


Fig. 6. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). External suture of SAS A63.

Description

Coiling is very evolute, with an umbilical width of the order of 48 to 59 per cent of the diameter, and with the whorls overlapping only slightly.

The whorl section is rounded to subrectangular, varying from compressed to depressed, with the greatest costal width at the umbilical tubercle.

There is an initial smooth stage, which may persist to a diameter of 9 mm; thereafter umbilical tubercles connecting to ventrolateral tubercles via weak ribs appear. With increasing diameter all ornament becomes stronger, with prominent umbilical bullae situated well away from the umbilical edge on the flanks and connected to rounded or slightly clavate ventrolateral tubercles by prominent ribs. The ribs are generally single but occasional bifurcations occur, es-

pecially on the inner whorls. All ribs are slightly prorsiradiate and curved. Strong spiral ridges are commonly developed.

The venter is prominently tricarinate, with the central keel strongest. The suture is relatively simple but variable with blocky elements (Figs 12–13).

Discussion

Kennedy (in press) has discussed the difficulties in interpreting Schlüter's lithograph of the lost holotype, and concluded that the variable, closely and simply ribbed *Peroniceras* (*P.*) with persistent umbilical–umbilicolateral bullae that



Fig. 7. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). SAS Z248, the holotype of *P.* (*Peroniceras*) *besairiei* van Hoepen, 1965. $\times 1$.

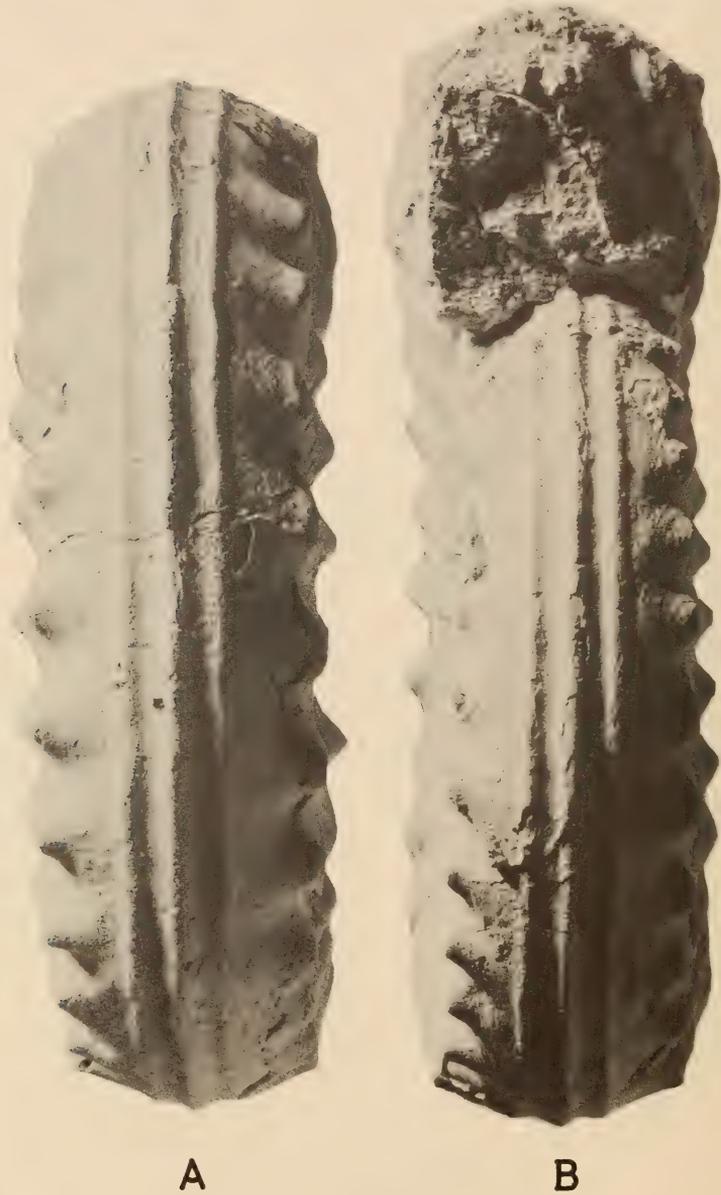


Fig. 8. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z248 the holotype of *P. (Peroniceras) besairiei* van Hoepen, 1965. $\times 1$.

occur in France and Germany (*P. tridorsatum*, *moureti*, and *rousseauxi*) represent but a single species, a view followed here.

P. (P.) lepeei (Fallot, 1885) differs from the present species in having delicate dense ribs that lack umbilical bullae; it is discussed further below. There are, however, transition forms such as NMB D1145e (Fig. 4) that have a more angular whorl section and weakening ornament on the outer whorl.

P. (P.) besairiei van Hoepen, 1965, is based on a depressed variant of this species that is close to the holotype of De Grossouvre's *P. (P.) rousseauxi*, also regarded as a synonym. Van Hoepen was misled in his interpretation of *P. (P.) besairiei* by the illustrations of Besairie (1930, pl. 64 (figs 4–6)) and Venzo (1936,

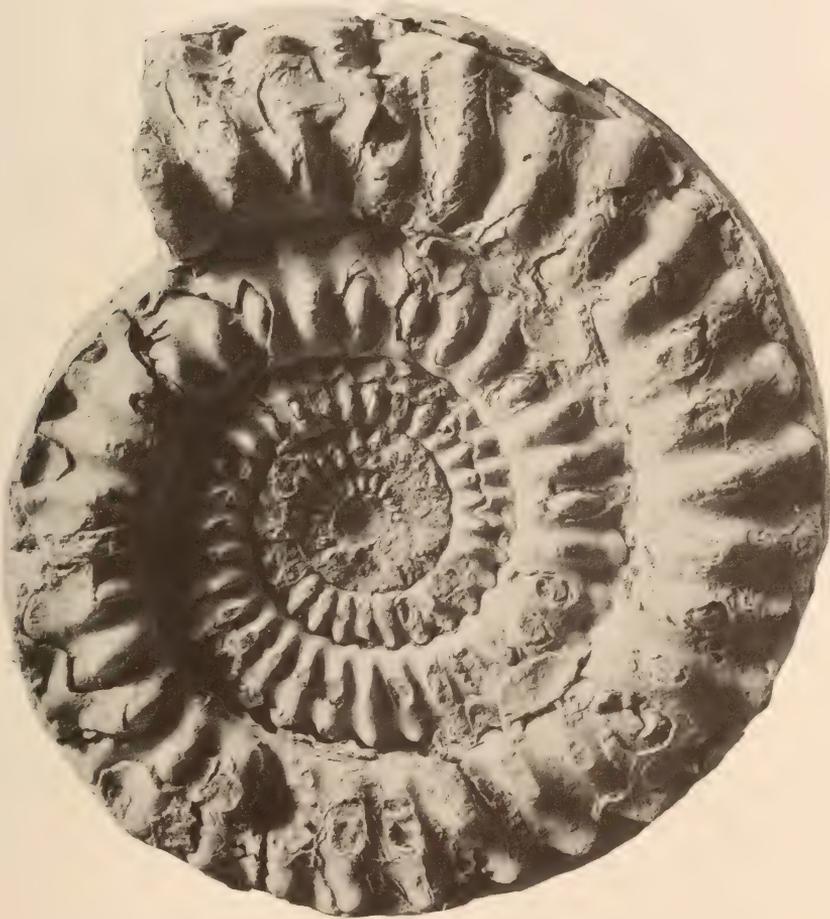


Fig. 9. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). SAS Z786, the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. $\times 1$.



Fig. 10. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). SAS Z786, the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. $\times 1,2$.



Fig. 11. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z1522, with stronger lateral ornament than the other specimens, and distinct spiral ornament. $\times 1$.

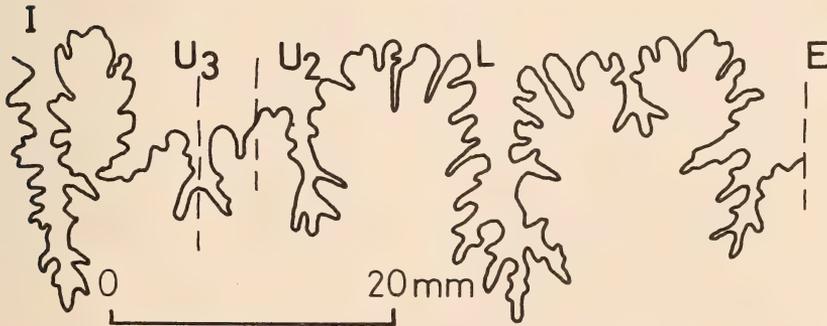


Fig. 12. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). Complete suture-line of SAS Z786.

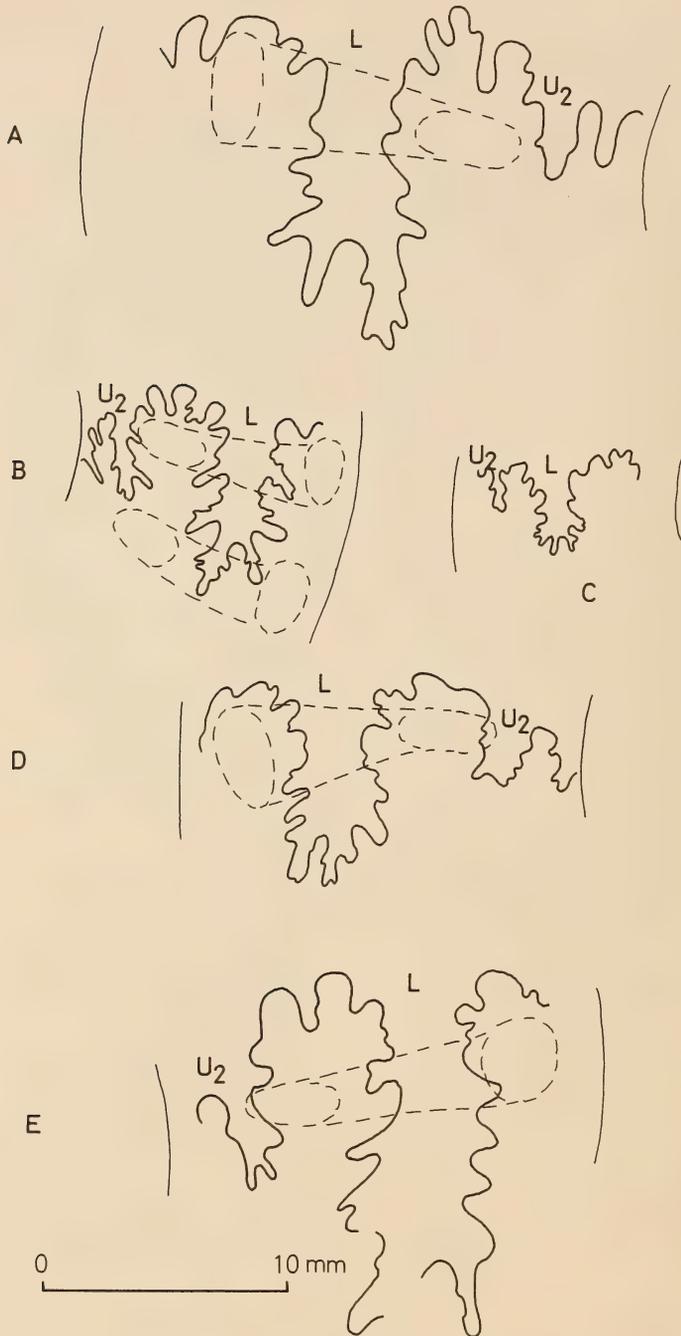


Fig. 13. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). Suture-lines of different specimens. A. SAS Z248, part of the suture-line of the holotype of Van Hoepen's *Peroniceras (Peroniceras) besairiei*, alleged to be of the *P. (P.) dravidicum* type. B-C. SAS Z1623. D. SAM-PCZ5942. E. SAS Z730.

pl. 11 (fig. 9)). According to Van Hoepen (1965: 36), *P. (P.) besairiei* and his *Fraudatoroceras besairiei* are 'practically the same in shape and ornamentation. . . . The only difference is the suture-line'. He believed that *F. besairiei* had a simple block-type suture-line, whereas *P. (P.) besairiei* (interpreted according to Besairie's figures) was alleged to have a complex *Peroniceras (dravidicum)*-like suture-line. Examination of the holotype of *P. (P.) besairiei* shows that the suture-line (which according to Van Hoepen could not be developed) is of the same type as that of *F. besairiei* (Figs 12-13). They are synonyms, homonyms when in the same genus, and both synonyms of *P. (P.) tridorsatum*. Van Hoepen also erred in regarding his *P. (P.) besairiei* as the same as Besairie's (1930: 634, pl. 46 (figs 4-6)) *Peroniceras subtricarinatum* and Venzo's (1936: 99, pl. 10 (fig. 1) pl. 11 (fig. 9)) *Peroniceras dravidicum*, and he assumed that the suture-lines would be identical. The specimens described by Besairie may partially include *P. (P.) tridorsatum* as some specimens were said to have single ribbing, but the figured specimens definitely do not belong to *P. (P.) tridorsatum* as the complex suture-line and bifurcating ribbing shows. The specimen figured by Venzo probably belongs to *P. (P.) dravidicum*. Collignon (1965: 54, pl. 437 (fig. 1803), pl. 438 (fig. 1803)) described and figured a specimen under the name of *Peroniceras besairiei*, but unfortunately did not describe the suture-line; neither is it visible in the figures.

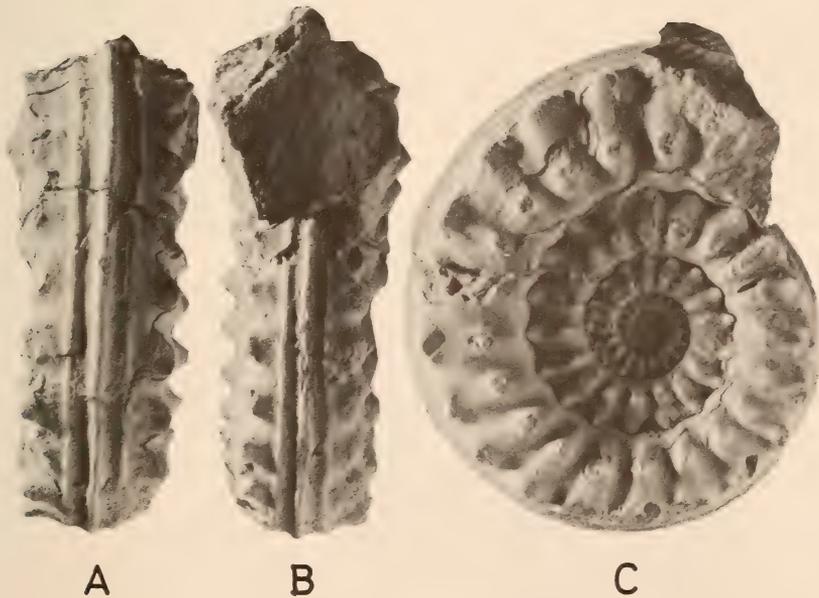


Fig. 14. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). A-C. SAS Z1120. $\times 1$.



Fig. 15. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). SAS Z756, the outer phragmocone whorl of the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. $\times 1$. (See also Figs 9–10.)

Specimens the authors refer to *Peroniceras (P.) subtricarinatum* may resemble *P. (P.) tridorsatum* superficially, but differ in having occasionally bifurcating ribs and a more complex, incised suture-line.

P. (P.) ninakawai (Matsumoto 1965: 223, pl. 37 (fig. 2), text-figs 7–8) from the 'Santonian' of Hokkaido has a narrower umbilicus (41–42 %) than many *P. (P.) tridorsatum* specimens (48–49 %) and develops strong, widely spaced auricular ribs on the outer whorls.

Occurrence

Middle Coniacian *P. (P.) tridorsatum* Zone of western, central and southern Europe, Gulf coast of the United States, Coniacian II and III of Zululand.

Peroniceras (Peroniceras) lepeei (Fallot, 1885)

Figs 16A–C, 17–18

Ammonites (Schloenbachia) L'Epeei Fallot, 1885: 231, pl. 1 (fig. 2).

Peroniceras L'Epeei (Fallot): Desio, 1920: 208, pl. 12, (figs 6–7), pl. 14 (fig. 6). Diener, 1925: 150. Kennedy, in press.

Type specimen

The holotype, by monotypy, is the original of Fallot (1885 pl. 1 (fig. 2)), from the Grès Verts de Dieulefit of Dieulefit, Drôme, south-eastern France, Middle Coniacian, *Peroniceras (P.) tridorsatum* Zone. The specimen is preserved in the collections of the Laboratoire de Géologie of the Faculté des Sciences, Grenoble.

Material

SAS Z1568 from locality 92, bulldozer scrapings and adjacent hillslopes on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II or III. SAS A1989 from locality 72, degraded river cliff on the north side of the Mzinene River downstream from the junction with the Munnywana River, Zululand, St. Lucia Formation, Coniacian II or III.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
Z1568	52,0	15,5(29,8)	14,2(27,3)	1,09	27,7(53,2)

Description

Coiling is polygyral, very evolute with an umbilical diameter of 53 per cent. The whorl section is variable, both between specimens and at different stages of ontogeny (Fig. 18A). It is initially ovoid and compressed, but thereafter rectangular with flattened flanks.

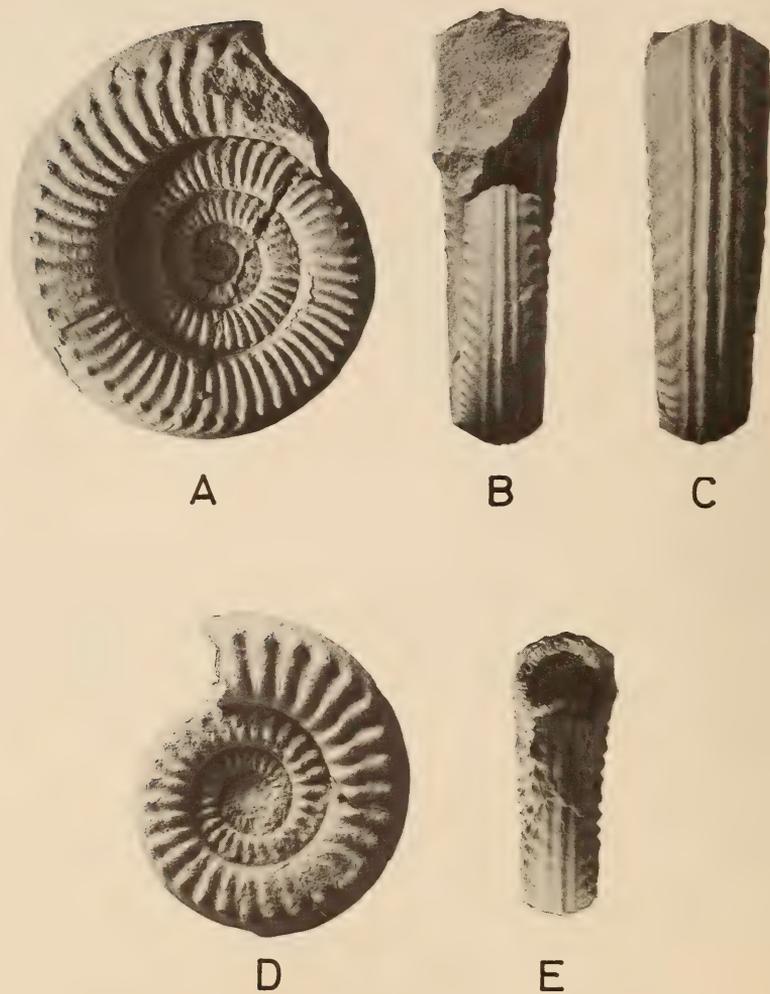


Fig. 16. A-C *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). SAS Z1568.
D-E. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z734.
All $\times 1$.



Fig. 17. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). Large specimen showing the relatively simple suture-line and faint spiral ornament on the body chamber. SAS A1989. $\times 1$.

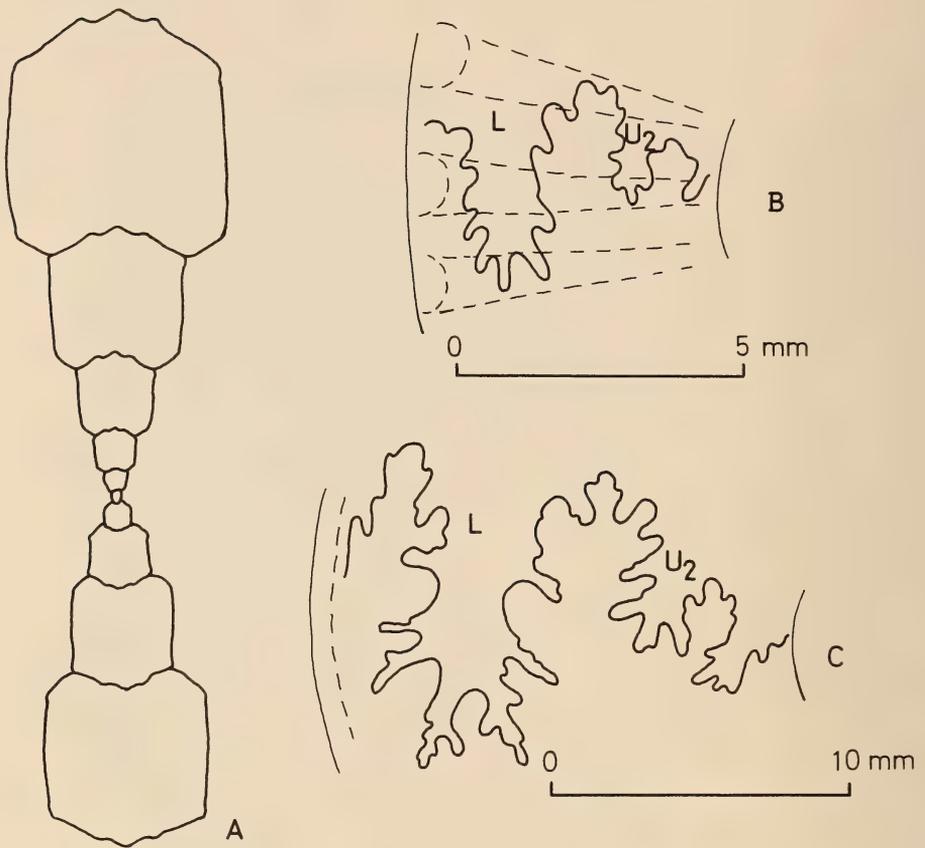


Fig. 18. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). A. Whorl section of SAS Z1568. $\times 1,5$. B. External suture of SAS Z1568. C. External suture of SAS A1989.

It remains so in SAS Z1568 (Fig. 16A–C), but reverts to being rounded in SAS A1989 over the greater part of the phragmocone and body chamber, with no clearly defined umbilical edge (Fig. 17).

On the innermost whorls of SAS Z1568 the flanks are completely smooth up to a diameter of 6 mm, and the venter is fastigate with a feeble siphonal ridge. Beyond that diameter tubercles appear in the umbilical seam of the succeeding whorl, and at a diameter of 18 mm adult ornament is fully developed. This consists of delicate, concave, prorsiradiate ribs each bearing a clavate tubercle. There are 50 ribs per whorl in SAS Z1568 (Fig. 16 A–C). Ribbing is generally simple but occasional bifurcations occur in SAS A1989 (Fig. 17). Parts of the body chamber of both specimens show delicate spiral ornament. The venter is tricarinate, with the median keel strongest. The suture is rather simple, with massive saddles and lobes (Fig. 18 B–C).

Discussion

This is a very poorly known species, thus far described only from the Middle Coniacian of France and Italy. The species is characterized by the delicate, concave prorsiradiate ribs, absence of umbilical tubercles, and flattened flanks.

It is very close to *P. (P.) tridorsatum* (= *P. (P.) moureti*), and the two occur together. De Grossouvre (1894: 101) had already pointed to the similarities between the species, and Desio (1920: 208) even included *P. (P.) moureti* in the synonymy of *P. (P.) lepeei*. The only difference is the absence of umbilical tubercles in *P. (P.) lepeei*. The specimen figured by Schlüter (1876, pl. 4 (figs 3–5)) as *Ammonites* cf. *tridorsatus*, and included in the synonymy of *P. (P.) moureti* by De Grossouvre, has umbilical tubercles on the inner whorls but these become progressively weaker on the outer whorl. Similar though more coarsely ornamented specimens of *P. (P.) tridorsatum* also occur in Zululand and this suggests a close relationship between the two species.

The suture-lines of the two species are similar, having relatively simple blocky elements but lack the narrow-stemmed elements typical of the *P. (P.) dravidicum*-type suture.

Occurrence

Middle Coniacian, *P. (P.) tridorsatum* Zone of Dieulefit (Drôme), Coniacian (precise horizon unknown) of Touraine (condensed Calcaires durs de la Ribochère) in France, Italy, and Coniacian II or III of Zululand.

Peroniceras (Peroniceras) subtricarinatum (d'Orbigny, 1850)

Figs 19A–B, D–E, 20–23

Ammonites tricarinatus d'Orbigny, 1841: 307, pl. 91 (figs 1–2). Schlüter, 1872: 44, pl. 13 (figs 1–4). Fritsch 1872: 26, pl. 1 (figs 1, 3, non 2).

Ammonites subtricarinatus d'Orbigny, 1850: 212. ? Ooster, 1858: 151, pl. 26 (figs 10–11). Drescher, 1863: 331, pl. 8 (figs 2, 4). Non Stoliczka, 1865: 54, pl. 31 (fig. 3).

Ammonites (Schloenbachia) subtricarinatus d'Orbigny: Fritsch, 1889: 70; 1893: 74; 1897: 36.

Peroniceras subtricarinatum d'Orbigny: de Grossouvre, 1894: 94 (pars), pl. 10 (fig. 1, non 2–3), non pl. 11 (figs 1–2). Non Sturm, 1900: 60, pl. 3 (fig. 5). Pervinquière, 1907: 249. Pruvost, 1910: 365. Stolley, 1916: 89. Burckhardt, 1921: 112, pl. 29 (figs 5–6 only). Diener, 1925: 151. Besairie, 1930: 634, pl. 66 (figs 4–6), text-fig. 2.1. Andert, 1934: 406. Collignon, 1965: 58, pl. 439 (fig. 1804). Thomel, 1969: 119, pl. F (figs 1–2). Amedro & Robaszynski, 1978: 35, pl. 1 (fig. 3). Collignon *et al.* 1979: 390, pl. 1 (fig. 1).

Schloenbachia (Peroniceras) subtricarinatum d'Orbigny: Boule, Lemoine & Thévenin, 1907: 22.

Peroniceras aff. *tricarinatum* d'Orbigny: Böse, 1928: 268, pl. 11 (figs 2–4).

Peroniceras tenuis van Hoepen, 1965: 7, pl. 3, text-fig. 1b–e.

Peroniceras tenue van Hoepen: Collignon, 1965: 66, pl. 443 (fig. 1814).

Peroniceras (Peroniceras) subtricarinatum (d'Orbigny, 1850): Kennedy, in press.

Type specimens

D'Orbigny (1841: 308) referred two specimens to his *Ammonites tricarinatus*, which he subsequently (1850: 212) renamed *Ammonites subtricarinatus* be-

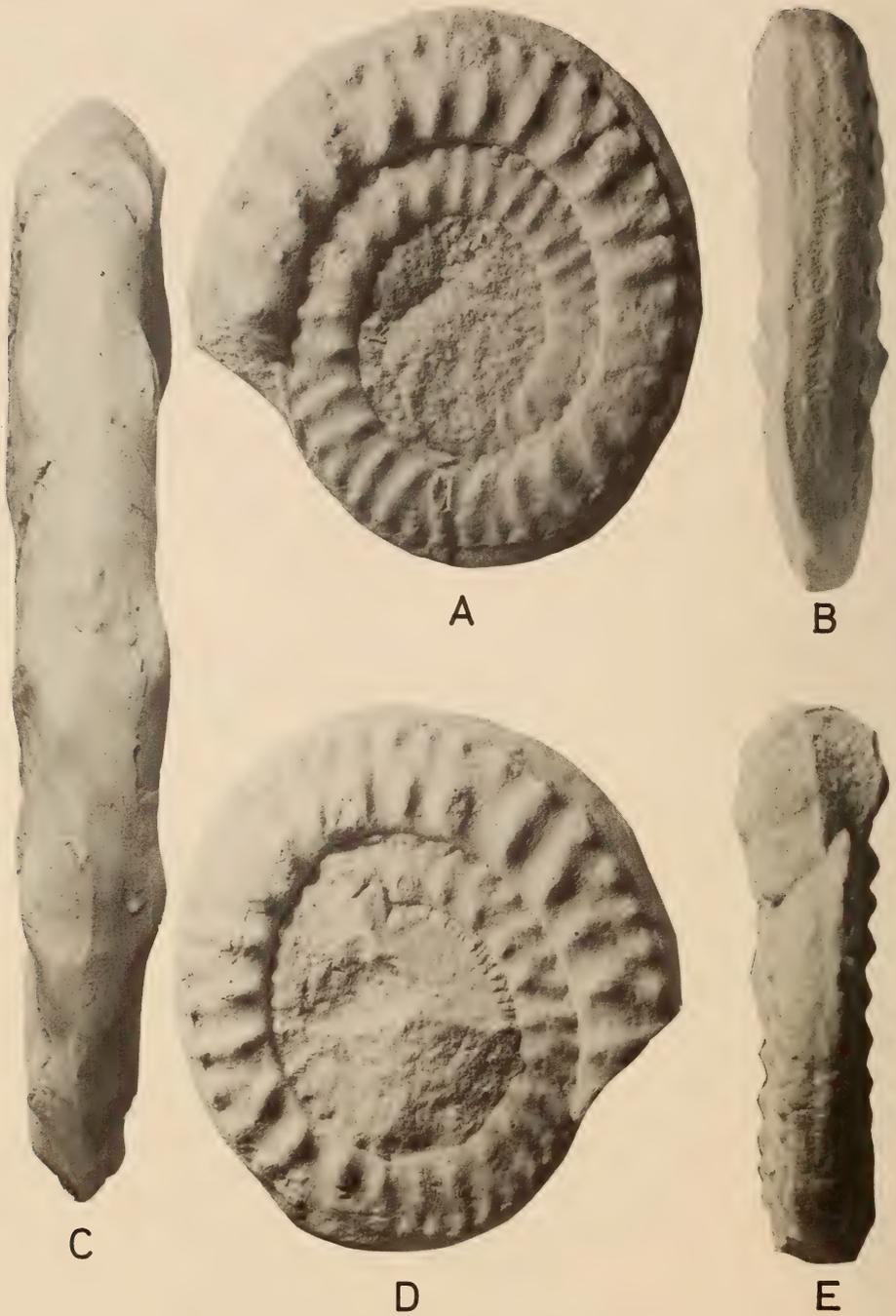


Fig. 19. A-B, D-E. *Peroniceras* (*Peroniceras*) *subtricarinatum* (d'Orbigny, 1850). The lectotype from the Lower Coniacian near Rennes-les-Bains, France. $\times 1$. C. *Gauthiericeras margae* (Schlüter, 1867), holotype. $\times 0,6$. (See Figs 94-95 for details.)

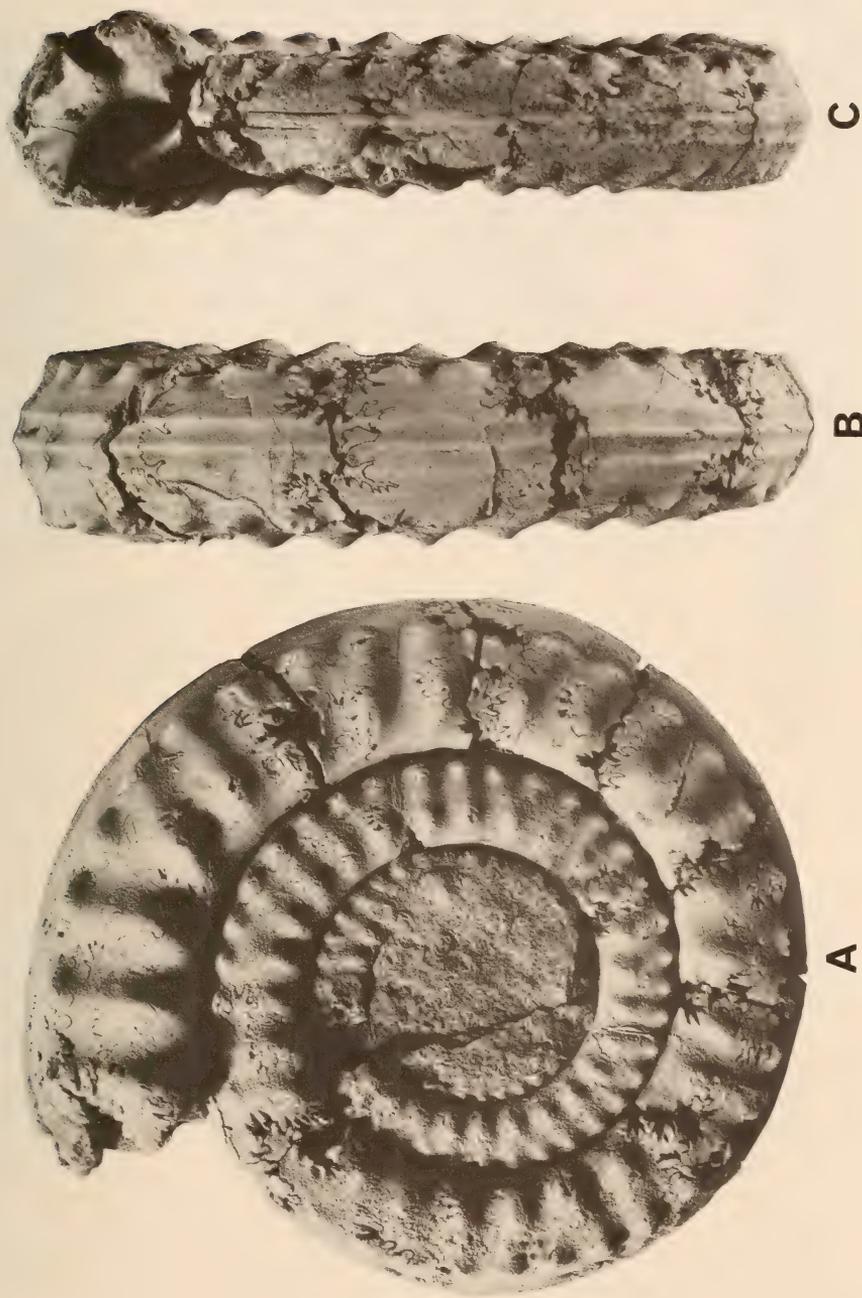


Fig. 20. *Peroniceras (Peroniceras) subtricarinarium* (d'Orbigny, 1850), SAS Z1002. $\times 0,67$.

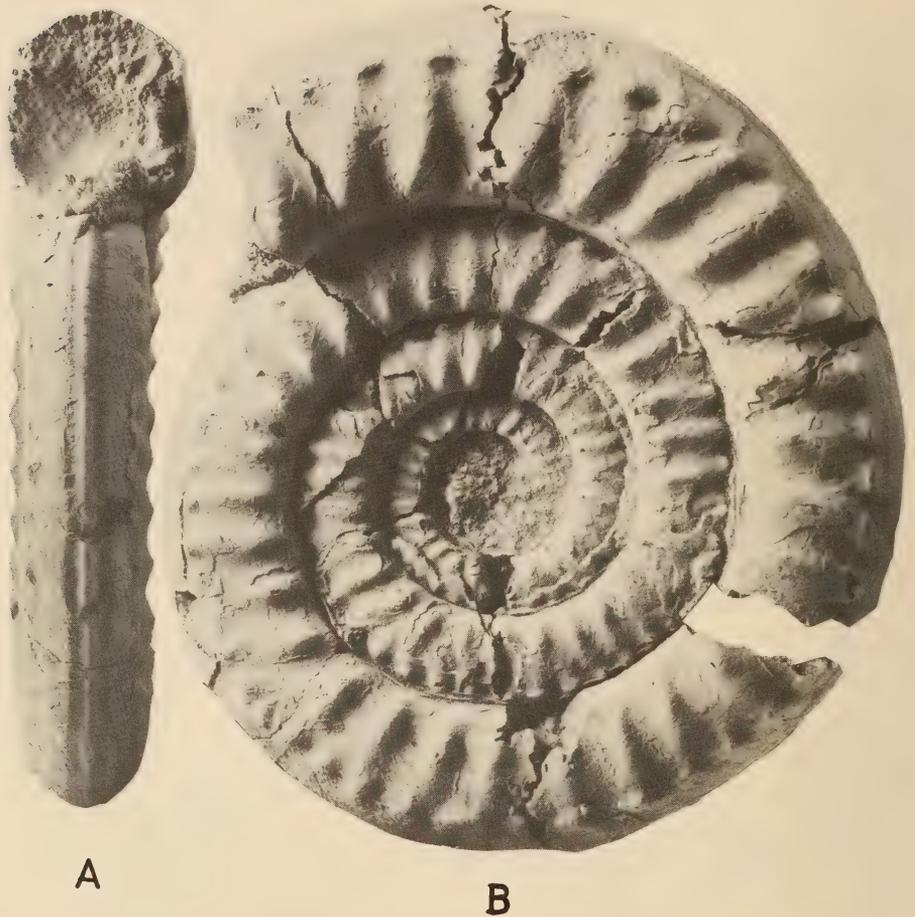


Fig. 21. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). SAS Z511, the holotype of Van Hoepen's *Peroniceras (Peroniceras) tenuis* (1965: 7, pl. 3, text-figs 1b, e); a compressed specimen representing the inner whorls of *P. (P.) subtricarinatum*. $\times 1$. (See also Fig. 22.)

cause of prior usage of the combination *Ammonites tricarinata* by Poitiez & Michaud (1838). The syntypes survive in the D'Orbigny Collection (now in the Muséum Nationale d'Histoire Naturelle in Paris) under the catalogue number 7183. The larger of these, reillustrated here as Fig. 19A–B, D–E is herein designated lectotype of the species. It is from the environs of Sougraines, near Rennes-les-Bains (Aude).

Material

SAS Z1002, Z511, SAM-PCZ5943 from locality 93, hillslopes on the boundary of lots H101 and H102, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II, SAS Z1521 from locality 92, bulldozer scrapings

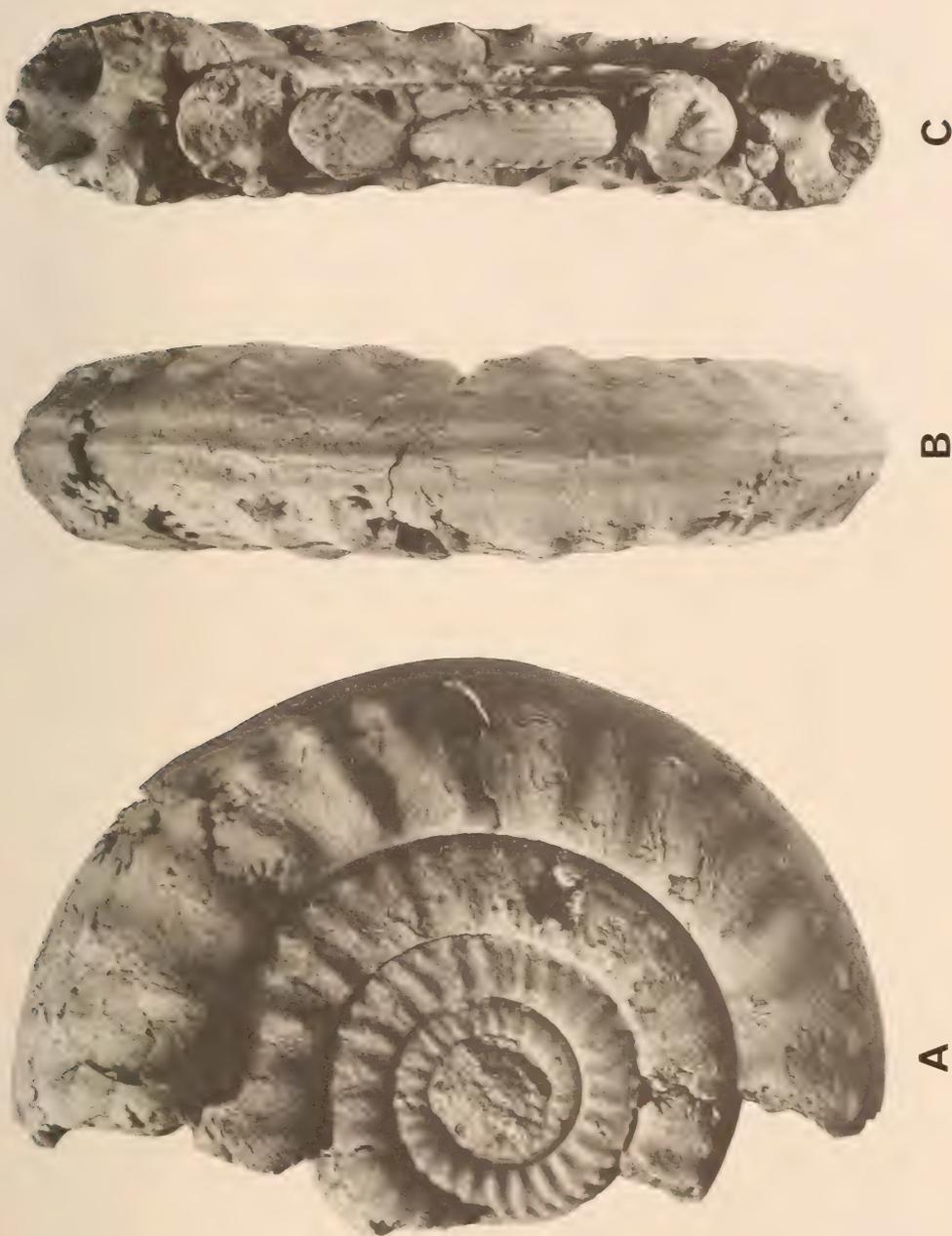


Fig. 22. *Peroniceras* (*Peroniceras*) *subtricarinarium* (d'Orbigny, 1850). SAM-PCZ5943, specimen with inner whorls similar to *P. (P.) tenuis* van Hoepen, 1965. $\times 0,6$. (See Fig. 21.)

and adjacent hillslopes on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z511	132,0	37,0(28,0)	34,0(35,8)	1,08	73,0(55,3)	29:42
Z1002	152,0	33,0(21,7)	31,5(20,7)	1,05	92,0(60,2)	26:36
PCZ5943	195,0	40,0(20,5)	41,0(21,0)	0,97	113,0(57,9)	12 × 2:18 × 2
at	120,0	27,0(22,5)	'27,0(22,5)'	1,0	70,0(58,3)	14 × 2:19 × 2

Description

Coiling is polygyral and evolute with an umbilical diameter of 55 to 60 per cent of the total diameter. The adult whorl section is depressed, fastigiate with a prominent central keel and subordinate lateral keels and more or less parallel flanks in intercostal section. The dorsal zone of impression is very shallow and whorl overlap minimal. In the juvenile stage the whorl section is more rounded and the venter appears unicarinate. In costal section maximum width is across the dorsal third of the flanks.

Ornament consists of prominent rounded to bullate umbilical tubercles and smaller spirally elongated ventrolateral tubercles connected by weak ribs. Bifurcations are present both on the inner and outer whorls and in some cases one of the ribs of a bifurcating pair is weaker than the other, thus creating the appearance of intercalated ventrolateral tubercles. On the outer phragmocone whorls the umbilical tubercles may enlarge considerably and migrate away from the umbilical edge. Strength of ornament in the various specimens studied varies considerably as the figures show. In SAS Z511 (Fig. 21) faint spiral ornament is visible in the area between the ventral tubercles and the lateral keel.

The suture is finely subdivided. Details may vary considerably in response to position relative to ornamentation which affects mainly width and incision of the elements (Fig. 23).

Discussion

This species has been treated in various ways since its original description. De Grossouvre (1894: 94 et seq.) included Schlüter's *Ammonites tridorsatus* in the synonymy of *P. (P.) subtricarinatum*. According to De Grossouvre's interpretation they could, however, be separated at varietal rank. The typical *P. (P.) subtricarinatum* has a nearly equal number of single and bifurcating ribs, whereas *P. (P.) tridorsatum* has all the ribs simple. The lectotype of *P. (P.) subtricarinatum*, here refigured as Figure 19A–B, D–E shows D'Orbigny's figures to be considerably restored, especially as far as the inner whorls are concerned. The specimen does, however, show the typical common and distinctive bifurcations on the outer whorls.

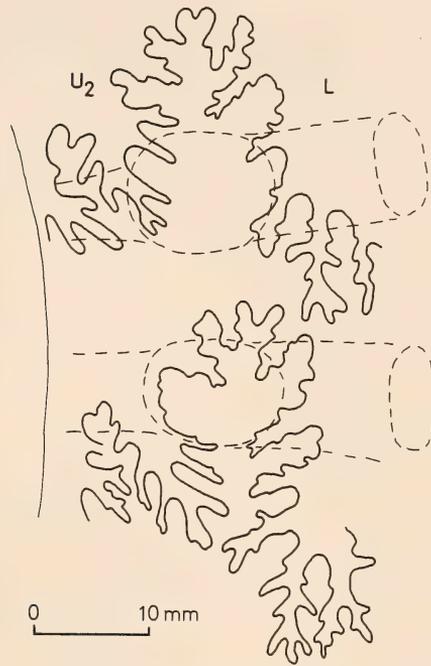


Fig. 23. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). Two successive sutures of SAS Z1002 to illustrate influence of ornament on details of suture, in this case especially the width of the stem of saddle L/U₂.

Desio's (1920: 206, pl. 25 (fig. 3)) *P. subtricarinatum* var. *etruscum* has weak ornament on the inner whorls, and lacks umbilical tuberculation on the outer whorls. Furthermore, the whorl section is much higher than wide. As Desio (1920: 207) pointed out, the specimen is very close to *P. (P.) dravidicum*.

P. cf. subtricarinatum var. *tridorsatum* of Desio (1920: 205, pl. 12 (fig. 10)) is poorly preserved, but because of the single ribbing falls beyond the limits of this species.

P. (P.) tenuis van Hoepen (1965: 7, pl. 3, text-figs 1b–e) merely represents the inner whorls of a weakly ornamented form of *P. (P.) subtricarinatum* as Figures 21–22 show, and is thus included in the synonymy.

P. haasi Young (1963: 72, pl. 34 (figs 3–4), pl. 35 (figs 1–2)) from the Coniacian of Texas has the general appearance of *P. (P.) subtricarinatum* but weaker ornament. Given more material it might be possible to include it in the strict synonymy of *P. (P.) subtricarinatum*, as was done with *P. (P.) tenuis* van Hoepen.

Occurrence

Middle Coniacian *P. (P.) tridorsatum* Zone of western and central Europe, north Africa, Madagascar, and Mexico. Coniacian II and III of Zululand.

Peroniceras (Peroniceras) westphalicum (von Strombeck, 1859)

Figs 24–28

Ammonites westphalicus von Strombeck, 1859: 56. Schlüter, 1867: 30, pl. 6 (fig. 2); 1872: 45, pl. 13 (figs 5–6).

Peroniceras westphalicum (Schlüter): de Grossouvre, 1894: 98, pl. 12 (figs 1, 4), text-fig. 38. Pruvost, 1910: 366. Non Scupin, 1913: 94, pl. 4 (fig. 8). Desio, 1920: 214, pl. 12 (fig. 2), pl. 13 (fig. 3). Diener, 1925: 152. Adkins, 1933: 407, 453. ? Andert, 1934: 407. Young, 1963: 74, pl. 28 (figs 2–4), pl. 29 (figs 1–2), text-fig. 15d. Collignon, 1965: 60, pl. 440 (fig. 1807).

Peroniceras westphalicum (Schlüter) var. *australis* Venzo, 1936: 100, pl. 9 (fig. 4), pl. 11 (fig. 8).

Peroniceras stephaninii Venzo, 1936: 102, pl. 9 (fig. 3), pl. 11 (fig. 10).

Peroniceras guerini Collignon, 1965: 64, pl. 442 (fig. 1811).

Peroniceras cf. *westphalicum* (Schlüter), 1867: Amedro & Robaszynski, 1978: 37, pl. 1 (fig. 1). ? *Peroniceras latum* Matsumoto & Muramoto, 1981: 52, pl. 6 (fig. 1), pl. 7 (fig. 1), text-fig. 1.

Type specimens

Von Strombeck's originals, from the Coniacian of Westphalia, have not been traced. They were presumably in Berlin.

Material

NMB D1146, D1145, D1060, SAS A2941, A1972, all from locality 72, degraded river cliffs on the northern banks of the Mzinene River downstream of the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1616 from locality 93, bulldozer scrapings and adjacent hillslopes around the pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z696	144,0	41,0(28,4)	43,0(29,8)	0,95	85,0(59,0)	15 × 2:16 × 2
A1972	155,0	35,0(22,5)	40,0(25,8)	0,87	89,0(57,4)	—
Z1616	195,0	—	50,0(25,6)	—	100,0(51,2)	16 × 2:16 × 2
D1146	195,0	49,0(25,2)	56,0(28,0)	0,87	97,0(49,7)	21:21

Description

Coiling is evolute with an umbilical diameter of about 50 to 60 per cent of the total diameter. The whorl section is compressed throughout, higher than wide with little-inflated flanks, and has a very low umbilical wall and broadly rounded venter.

Ornament on the inner whorls is more or less of the *P. (P.) dravidicum* type with frequently bifurcating ribs, though not as strongly developed as in the latter species. With increasing diameter the umbilical tubercles become progressively

weaker, and eventually lateral ornament consists of broad, low ribs that end or weaken considerably before reaching the clavate ventrolateral tubercles. At the same time there is a tendency towards a decrease in the number of bifurcations. On the outer whorls of the specimens available, virtually all ribs are single. Detail of the ornament varies considerably, from densely costate as in SAS Z1616 (Fig. 27) to sparsely costate in NMB D1146 (Fig. 24).

The species may grow to a very large size. The suture is highly incised (Fig. 28).

Discussion

In the absence of type specimens, interpretation of this species presents difficulties. It is here interpreted in terms of the specimen from near Altenessen

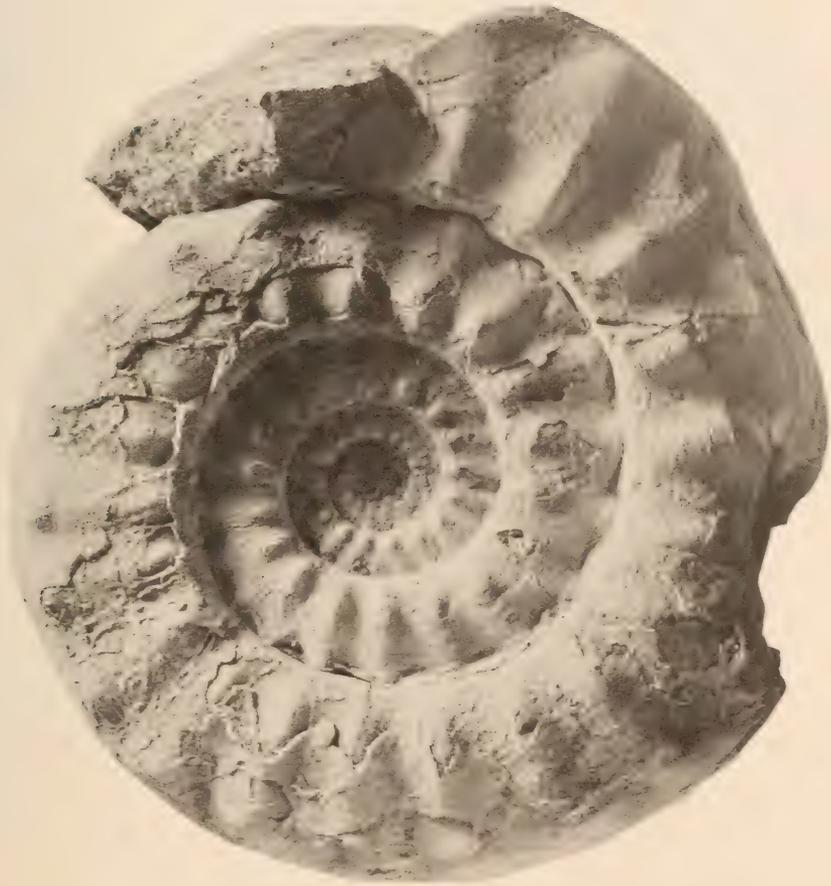


Fig. 24. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). NMB D1146, specimen with typical ornament consisting of low, broad ribs. $\times 0,6$.



Fig. 25. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). NMB D1060. Evolute specimen with typical ornament.
× 0,69.



Fig. 26. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). SAS Z696, specimen with ornament approaching that of *P. (P.) dravidicum* Kossmat, 1895. $\times 0,77$.



Fig. 27. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). SAS Z1616, specimen with ornament transitional to *P. (P.) dravidicum* Kossmat, 1895. $\times 0,70$.

figured by Schlüter (1872, pl. 13 (figs 5–6)). This clearly shows the low, rounded and broad bullae, which clearly distinguish the species from the majority of other peroniceratids.

One of the specimens figured by De Grossouvre (1894, pl. 12 (fig. 1)), from the Craie de Villedieu of Touraine, lacks the typical broad lateral ornament and may possibly be a transition towards *P. (P.) subtricarinatum*.

P. westphalicum var. *italicum* Desio (1920: 216, pl. 16 (fig. 4)) lacks the bullae of typical *P. (P.) westphalicum* and has, instead, sharp-crested, narrow, widely spaced lateral ribs. In this respect it bears resemblance to *P. stefaninii*

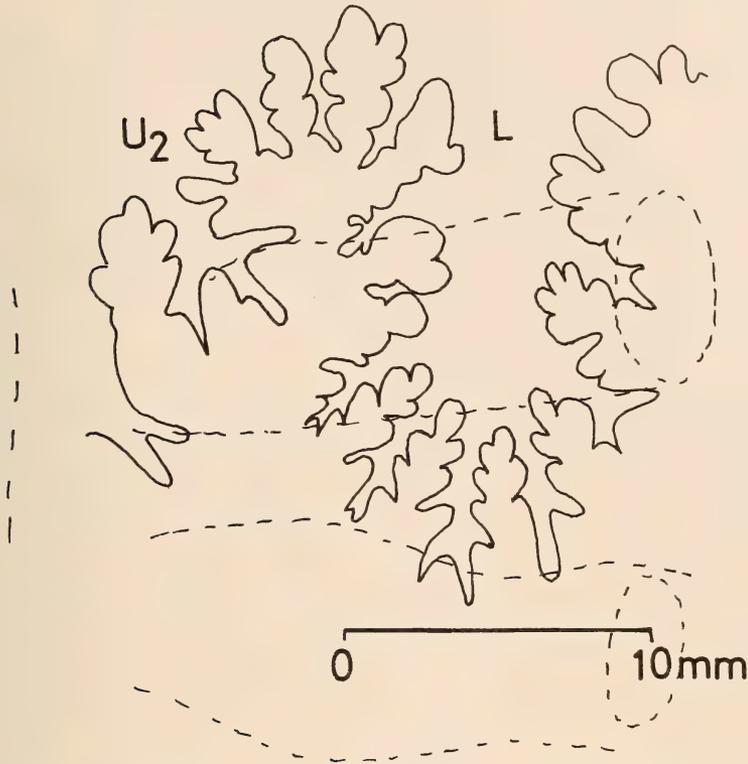


Fig. 28. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859).
Partial suture-line of SAS Z996.

Venzo (1936: 102, pl. 9 (fig. 3)) from the Coniacian of Zululand. Specimen NMB D1146 (Fig. 24) also shows a tendency towards narrowing of the ribs as in these forms. They may thus safely be included in the strict synonymy of *P. (P.) westphalicum*, in contrast to the conclusions of Matsumoto & Muramoto (1981: 55).

P. westphalicum var. *australis* Venzo (1936: 100, pl. 5 (fig. 4)), also from the Coniacian of Zululand, resembles the specimen figured by De Grossouvre (mentioned above) in having a rather prominent umbilical tubercle and a more quadrate whorl section than typical *P. (P.) westphalicum*. It is morphologically transitional to *P. (P.) subtricarinatum*.

P. guerini Collignon (1965: 64, pl. 442 (fig. 1811)) has typical *P. (P.) westphalicum* ornament, and differs only in possessing a prominent depression separating the lateral ribs from the ventrolateral tubercles. The authors doubt if this feature merits specific separation, and include the species in the strict synonymy of *P. (P.) westphalicum*.

P. latum Matsumoto & Muramoto (1981: 52, pl. 6 (fig. 1), pl. 7 (fig. 1), text-fig. 1) was considered to be a close ally of *P. stefaninii* Venzo, 1936, differing only in a wider umbilicus (U = 63 %) and numerous (twenty-eight) ribs on the outer whorl. It is also a probable synonym of the present species.

Occurrence

Middle Coniacian of western Europe, Madagascar, Zululand, and the Gulf Coast of North America.

Peroniceras (Peroniceras) dravidicum Kossmat, 1895

Figs 29–42

- Ammonites subtricarinatus* d'Orbigny: Stoliczka, 1865: 54, pl. 31 (fig. 3)
Schloenbachia (Peroniceras) dravidica Kossmat, 1895: 190, pl. 22 (fig. 3).
Peroniceras dravidicum Kossmat: Solger, 1904: 181, figs 71–72. Lombard, 1930: 294, pl. 30 (fig. 1). Venzo, 1936: 99, pl. 10 (fig. 1), pl. 11 (fig. 9). Non Ciry, 1940: 212. Reyment, 1958: 65. Collignon, 1965: 52, pl. 436 (fig. 1802), p. 62, pl. 441 (fig. 1809); 1978: 63, pl. 28 (fig. 1).
Peroniceras cfr. *subtricarinatum* d'Orbigny var. *dravidicum* Kossmat: Desio, 1920: 207, pl. 12 (fig. 9).
Peroniceras cf. *dravidicum* Kossmat: Spath, 1921: 295, pl. 23 (fig. 1).
Peroniceras sp. aff. *dravidicum* Kossmat: Collignon, 1967: 51, pl. 30 (fig. 6).
Peroniceras platycostatum van Hoepen, 1955: 367, figs 15–17.
Peroniceras spathi van Hoepen, 1955: 368.
Peroniceras (Peroniceras) multinodatum van Hoepen, 1965: 8, pl. 4; text-fig. 1f.
Peroniceras (Zuluiceras) obliquenodatum van Hoepen, 1965: 14, pl. 8; text-fig. 3f.
Peroniceras (Zuluiceras) bessiae van Hoepen, 1965: 18, pl. 13.

Type specimen

The lectotype is the original of Kossmat (1895, pl. 23 (fig. 3a–d)) by the subsequent designation of Matsumoto (1965: 213).

Material

SAS A536, Z253, Z753, Z1017, SAM-PCZ5944, PCZ5495, K5494, K4950, NMB D2145b, D1148 from locality 72, degraded river cliff and northern banks of the Mzinene River downstream from the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z663, Z811, Z1607, Z1521, Z1521c, Z1616, Z1632, Z1650, Z1662, Z1672, Z1674 from locality 92, bulldozer scrapings and adjacent hillslopes around the pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1 and Z892 from locality 93, hillslopes on either side of the boundary fence separating lots H101 and H102, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS A609 from locality 24, caisson excavations for new Nyalazi River bridge, Zululand, St. Lucia Formation, inferred to be Coniacian II and III. Numerous fragments and uncatalogued material from the above localities.



Fig. 29. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1017 showing details of ontogeny up to the body chamber. Note especially the uncarinate venter on the inner whorls. $\times 0.9$.

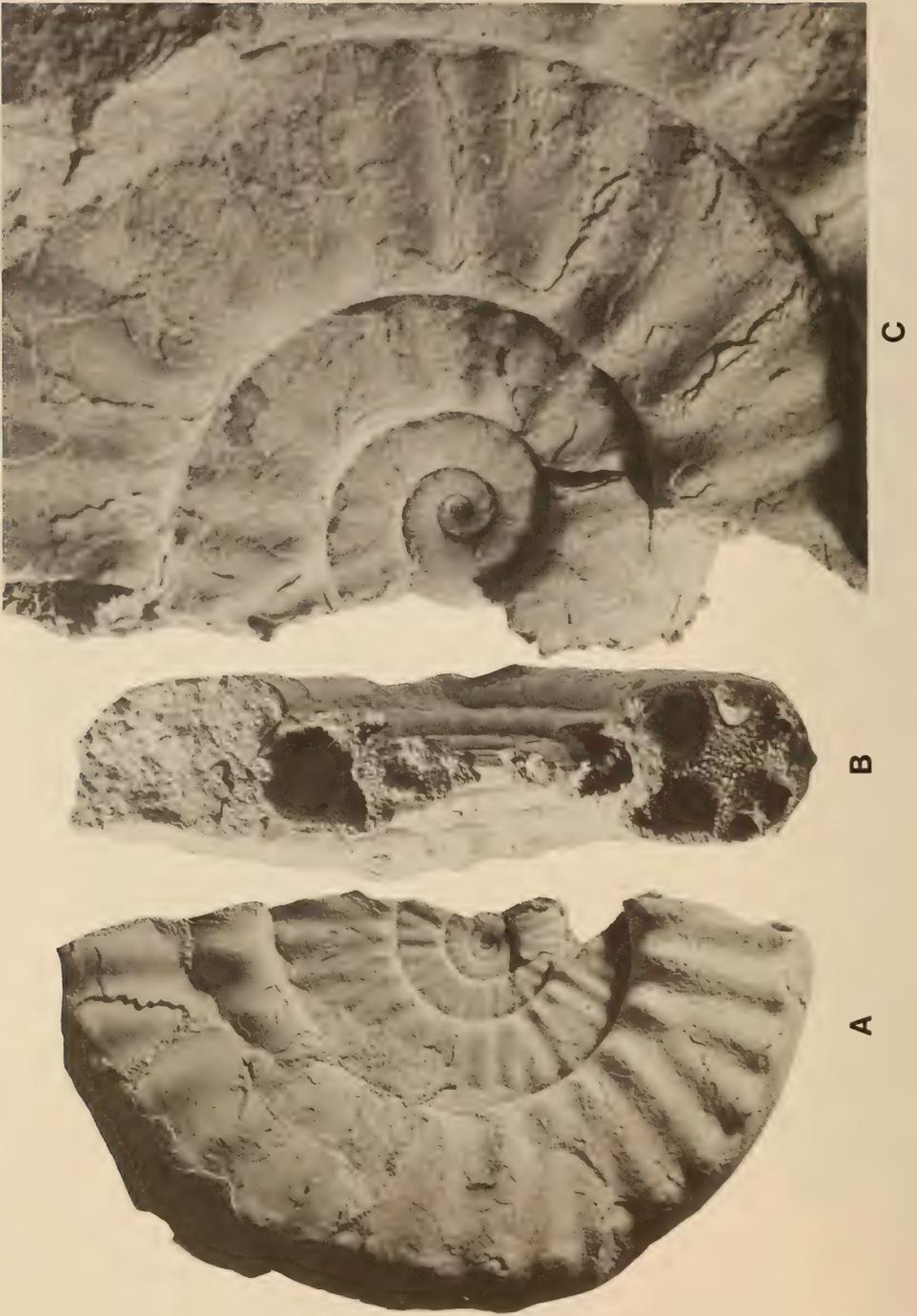


Fig. 30. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS PCZ5945 showing details of ontogeny. Note especially the smooth, uncarinate inner whorls. A-B $\times 1$, C $\times 3$.

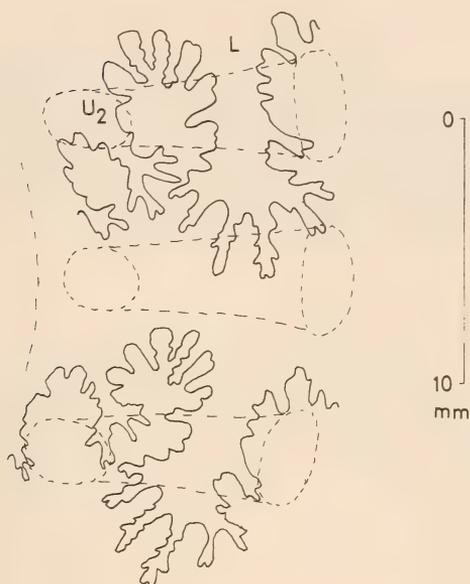


Fig. 31. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1633 partial suture-line showing effect of ornamentation on details of elements, in this case saddle U_2/U_3 .

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
D1148	44,0	11,0(25,0)	14,0(31,8)	0,79	19,0(43,2)	19:30
Z1607	46,0	13,0(28,3)	14,0(30,4)	0,92	21,0(45,6)	19:24
Z1672	46,0	12,0(26,1)	13,1(28,3)	0,92	23,0(50,0)	27:38
Z253	65,0	18,0(27,7)	21,0(32,3)	0,86	29,0(44,6)	20:32
Z892	74,0	20,0(27,0)	21,0(28,4)	0,95	37,0(50,0)	—
Z811	75,0	24,0(32,0)	24,0(32,0)	1,0	34,0(45,3)	26:29
K5494	78,0	20,0(25,6)	24,0(30,8)	0,83	37,0(47,4)	20:34
Z1632	80,0	20,0(25,0)	23,0(28,7)	0,87	40,0(50,0)	23:27
Z1662	80,0	19,0(23,7)	23,0(28,7)	0,83	39,0(48,8)	20:31
Z663	81,0	18,0(22,2)	29,0(35,8)	0,62	39,0(48,1)	15:34
Z1521	82,0	20,0(24,4)	25,0(30,5)	0,80	37,0(45,1)	24:35
A536	87,0	22,0(25,3)	27,0(31,0)	0,81	39,0(44,8)	20:36
Z1521c	87,0	22,0(25,3)	27,0(31,0)	0,82	40,0(45,9)	18:24
PCZ5944	97,0	26,0(26,8)	25,0(25,8)	1,04	51,0(52,6)	23:31
D1145b	104,0	29,0(27,9)	29,0(27,9)	1,0	54,0(51,9)	20:26
D1145a	116,0	33,0(28,5)	34,0(29,3)	0,97	57,0(49,1)	26:32
A912	122,0	31,0(25,4)	32,0(26,2)	0,97	66,0(54,1)	34:34

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z753	124,0	31,0(25,0)	41,0(33,1)	0,75	55,0(44,3)	—
Z1616	141,0	38,0(26,9)	45,0(31,9)	0,84	62,0(43,9)	20:35
Z1674	151,0	37,0(24,5)	49,0(32,5)	0,75	72,0(47,7)	29:29
PZ5495	150,0	35,0(23,3)	37,0(24,7)	0,95	83,0(55,3)	28:35
Z1017	183,0	—	45,0(24,6)	—	104,0(56,8)	37:37
Z1650	203,0	—	55,0(27,1)	—	114,0(56,1)	34:34

Description

This is the largest known collection of *P. (P.) dravidicum*, and exhibits all stages of ontogeny, as well as the extensive intraspecific variation.

Coiling is generally evolute, the umbilicus comprising up to 56 per cent of the diameter in large individuals, but it may be as low as 43 per cent in smaller specimens and what appear to be stratigraphically younger representatives of the species.

The whorl section is generally rectangular, higher than wide throughout, but may be quadrate or even slightly wider than high in some individuals.

Details of the early ontogeny can be seen in SAS Z1017 (Fig. 29), NMB D1148 and SAM-PCZ5945 (Fig. 30). The early whorls are smooth, with parallel flanks converging to an acute, unicarinate venter. The smooth stage lasts up to about 8 mm, whereafter rounded tubercles start appearing at the umbilical edge and clavate ventrolateral ones in the umbilical suture of the succeeding whorl. They are connected by weak, inconspicuous bifurcating and single ribs. This ornament remains basically the same throughout, except on the later part of the phragmocone and on the body chamber of the larger specimens, where the ribs become more club-shaped and predominantly single, and the umbilical tubercles become indistinct. This latter ornament is very reminiscent of *P. (P.) westphalicum*.

The central keel is strongest throughout ontogeny.

The suture-line is complex, generally with highly incised elements. Details differ, however, according to the relative position of the sutural elements to ornament (Fig. 31). If saddles coincide with tubercles, they tend to be rather broad, whereas if situated in the interspaces, they are narrow-stemmed as in typical *Peroniceras*. The attachment of the U_2/U_3 saddle to the base of the saddle L/U_2 is prominent in the species.

Discussion

Specimens referred to this species form the bulk of the *Peroniceras* material before us. Variants show gradations in some characters, both in contemporary and successive populations, towards other species. It is easily recognized, however, by the numerous bifurcating ribs on the inner whorls, compressed rectangular whorl section, evolute coiling and weak lateral keels.

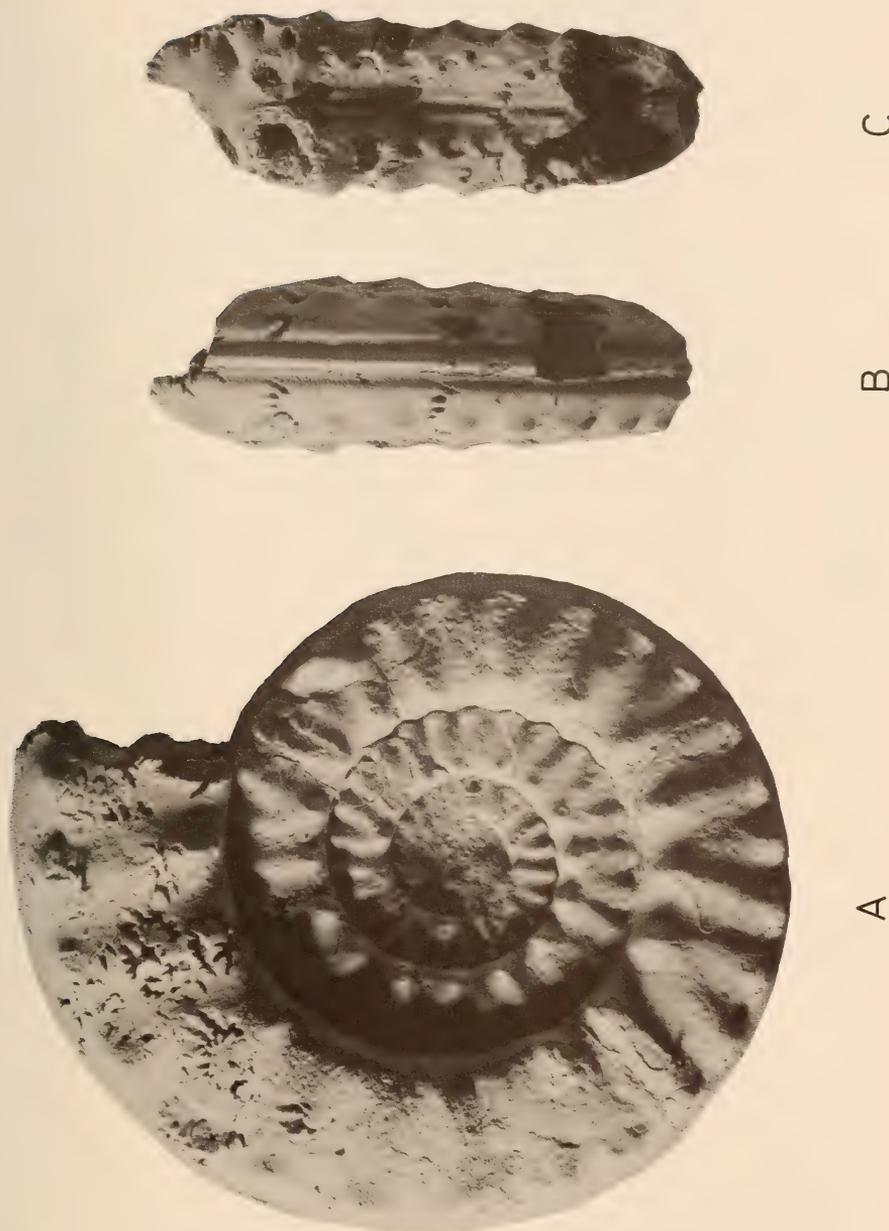
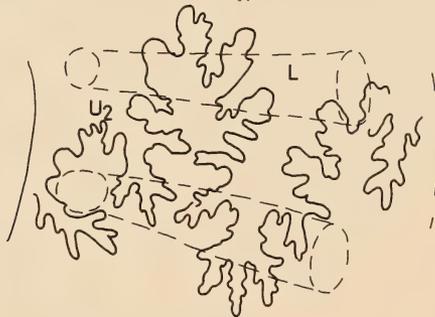


Fig. 32. *Peroniceras* (*Peroniceras*) *dravidicum* Kossmat, 1895. A. SAM-PCZ5946. B-C. The specimen figured and described by Spath (1921: 295, pl. 23 (figs 1a-d)) as *Peroniceras* cf. *dravidicum*, and named *Peroniceras spathi* by Van Hoepen (1955: 368). All $\times 1$.



Fig. 33. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1, the holotype of *P. (P.) platycostatum* van Hoepen, 1955. This is merely a compressed variety of *P. (P.) dravidicum*.
× 1.



0 10 mm

Fig. 34. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895.
Suture-line of SAS Z1119.

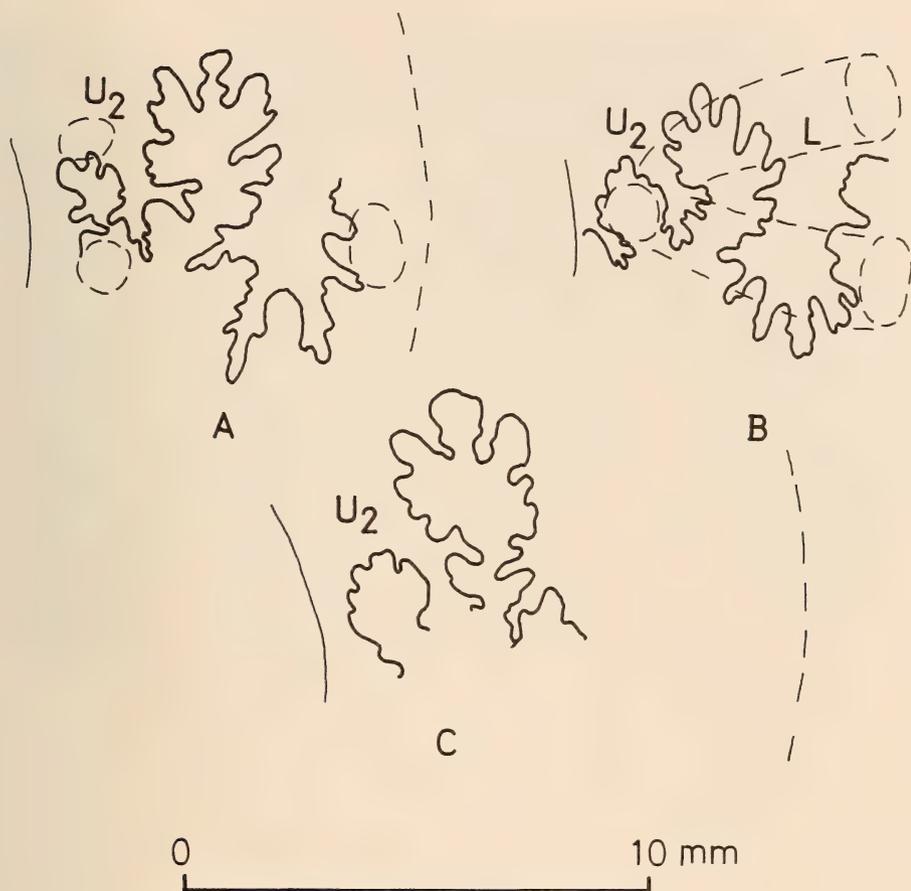


Fig. 35. *Peroniceras (P.) dravidicum* Kossmat, 1895. Suture-lines of juvenile specimens. A. SAS Z1633. B. SAS Z1615. C. Uncatalogued fragment.

A number of species described by Van Hoepen (1955, 1965) are here regarded as synonyms of this species. *Peroniceras spathi* van Hoepen (1955: 368 = *Peroniceras* cf. *dravidicum* Stoliczka of Spath, 1921: 295, pl. 23 (fig. 1a-d)) (Fig. 32B-C herein) is clearly a synonym of *P. (P.) dravidicum*. *P. platycostatum* van Hoepen (1955: 367, figs 15-17) (Fig. 33 herein) was said to differ from *P. (P.) dravidicum* in having slightly converging flanks and somewhat differently disposed umbilical and ventrolateral tubercles. Van Hoepen also considered his species to differ from the specimen of *P. (P.) dravidicum* figured by Venzo (1936, pl. 10 (fig. 1), pl. 11 (fig. 2)) on the basis of the denser ribbing and higher whorl section. Given the variation shown by the material at the authors disposal, these differences are obviously within the limits of intraspecific variation, and *P. platycostatum* is included in the strict synonymy of *P. (P.) dravidicum*.

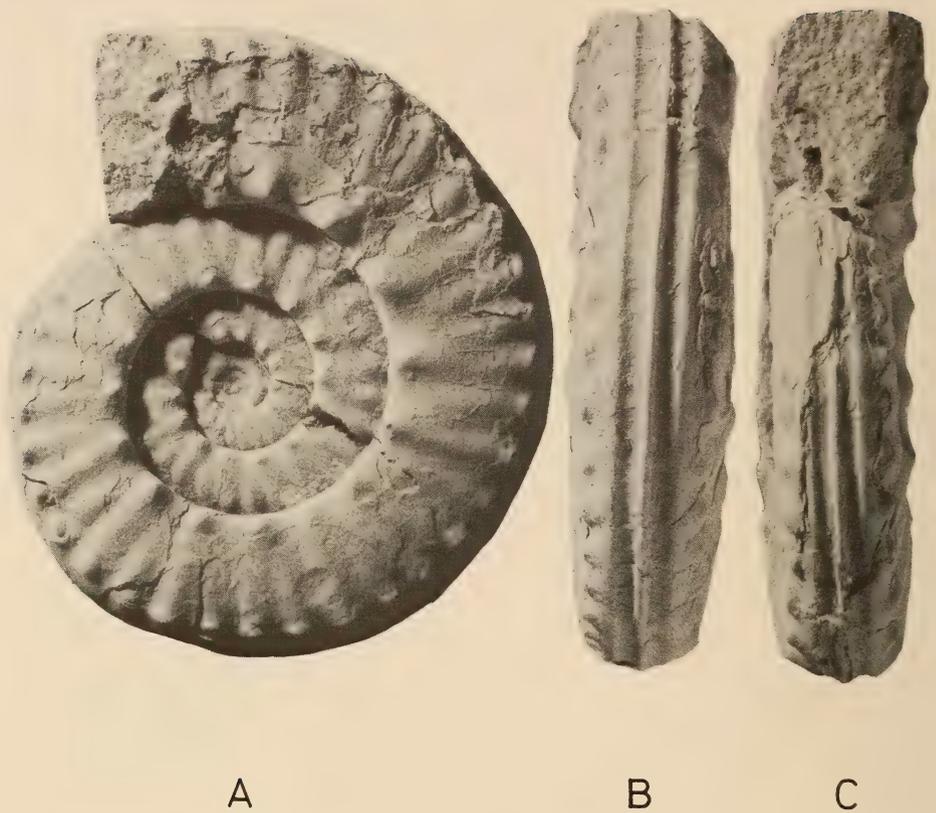


Fig. 36. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z663, the holotype of Van Hoepen's *P. (P.) multinodatum*. $\times 1$.

P. (P.) multinodatum van Hoepen (1965: 8, pl. 4, text-fig. 1f) (Fig. 36 herein) differs from the commoner forms of *P. (P.) dravidicum* in having an unusually high ratio of ventral to umbilical tubercles (34:15), but has all the other characteristics of the species.

P. (Zuluiceras) obliquenodatum van Hoepen (1965: 14, pl. 8, text-fig. 3f) (Fig. 37 herein) is nothing more than a coarsely ornamented variant of *P. (P.) dravidicum*, although the narrow umbilical width (45%) suggests that it is in this respect transitional to *P. (Zuluiceras)*. Another form transitional to *P. (Zuluiceras)*, but which still falls within the limits of *P. (P.) dravidicum*, is *P. (Zuluiceras) bessiae* van Hoepen (1965: 18, pl. 13) (Fig. 38 herein).

Some of the very large forms of *P. (P.) dravidicum* here figured (e.g. Figs 39–40, with very evolute whorls and club-like, simple ribs on the outer whorls, are reminiscent of *P. (P.) westphalicum*. In typical *P. (P.) westphalicum*, however, the ribs are broad and widely spaced. The inner whorls of both species are remarkably similar, suggesting a close relationship.



Fig. 37. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z753, the holotype of *P. (Zuluiceras) obliquenodatum* van Hoepen, 1965. This specimen is transitional to subgenus *P. (Zuluiceras)*. $\times 1$.

Specimens of *P. (P.) dravidicum* with more quadrate whorl sections and stronger ornament are in these respects transitional to *P. (P.) subtricarinaratum*, e.g. SAS A609 and SAM-PCZ5946 (Fig. 32A). Typically, however, *P. (P.) subtricarinaratum* has a quadrate to depressed whorl section with very strong umbilical bullae. In addition, the venter is generally more rounded and the coiling more evolute.

P. (P.) dravidicum is the ancestor of *P. (Zuluiceras)*. The transition involved the development of tighter coiling, retention of a single keel to greater diameters, and more prominent development of rounded ribbing on the outer whorls (Fig. 41). In fact, one of the paratypes of *P. (Z.) zulu*, SAS Z14 (Fig. 45), is still very close to *P. (P.) dravidicum*.

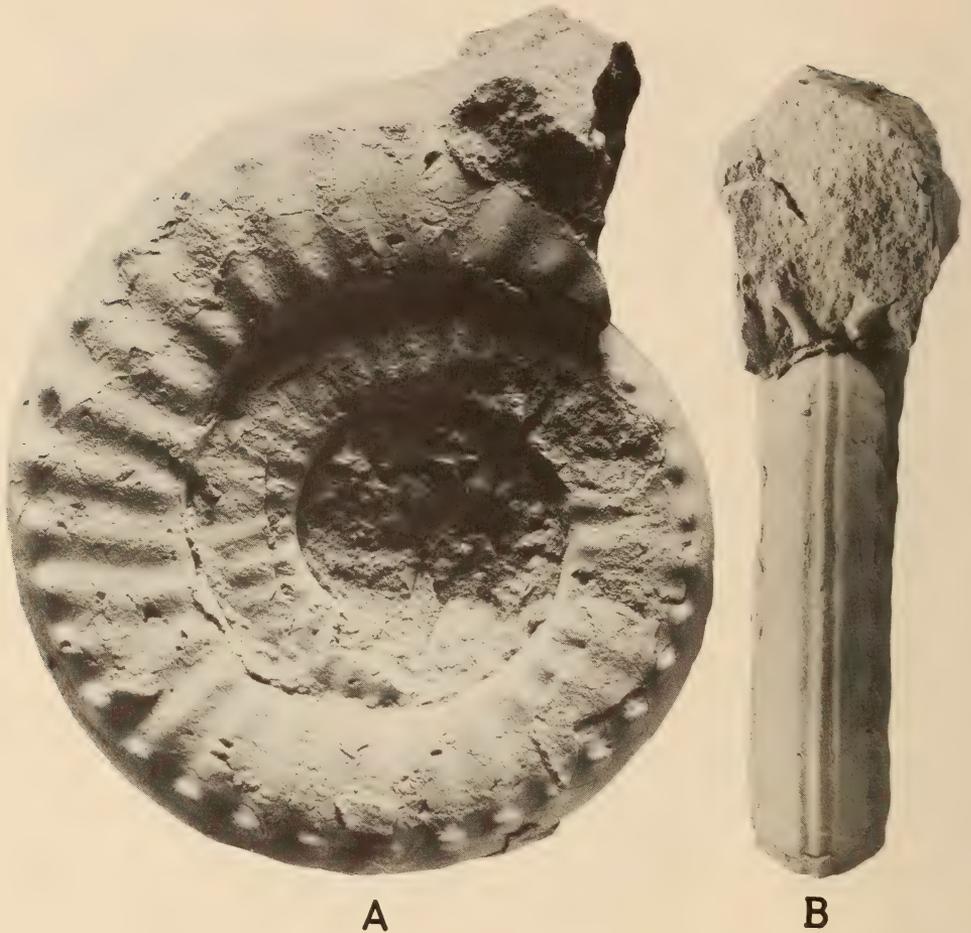


Fig. 38. *Peroniceras* (*Peroniceras*) *dravidicum* Kossmat, 1895. SAS Z255, the holotype of *P.* (*Zuluiceras*) *bessiae* van Hoepen, 1965, another specimen transitional to subgenus *P.* (*Zuluiceras*). $\times 1$.

In addition to the above changes, there appears to have been a general increase in overall size.

Occurrence

Coniacian of Italy, north, west and central Africa, Madagascar and India, Coniacian II and III of Zululand.

Subgenus *Peroniceras* (*Zuluiceras*) van Hoepen, 1965

(= *Zuluites* van Hoepen, 1965: 23; *Sornayceras* Matsumoto, 1965: 226)

Type species

Peroniceras (*Zuluiceras*) *zulu* van Hoepen, 1965: 23, by original designation.



Fig. 39. *Peroniceras* (*Peroniceras*) *dravidicum* Kossmat, 1895. SAS Z1650, a large form with club-like simple ribs on outer whorls. $\times 0.6$.

Diagnosis

Progressively more involute than *Peroniceras* (*Peroniceras*) with adult whorls tending to become rounded and smooth. Lateral keels are weak to absent on outer whorls and siphonal keel may be entire or serrated. Suture complex, of *P. (P.) dravidicum* type.

Discussion

Van Hoepen separated *P. (Zuluiceras)* from *P. (Zuluites)* on the basis of the greater involution and loss of ornament in adults of the latter. Stratigraphic work shows that there is a progression from early, relatively evolute Middle Coniacian species with persistent ornament that are close to *Peroniceras* (*Peroniceras*) (e.g. *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873),

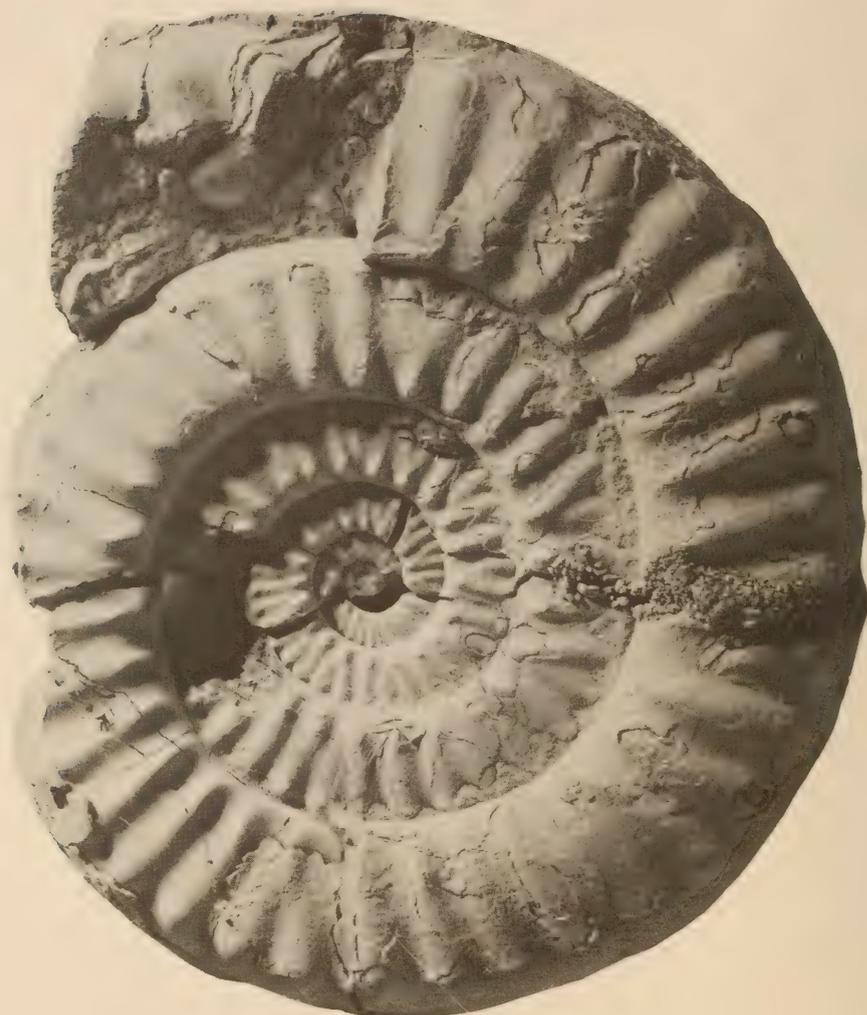


Fig. 40. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1663 a large form with club-like ribs on outer whorls. $\times 0,84$.



Fig. 41. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1674, specimen with narrower umbilical width transitional to subgenus *P. (Zuluiceras)*. $\times 0,75$.

P. (Z.) aberlei (Redtenbacher, 1873), *P. (Z.) isamberti* (Fallot, 1885)) to Upper Coniacian species that are much more involute and lose ornament when adult. There is no morphological break between the members of the series, and the separation proposed by Van Hoepen is considered unnecessary.

Sornayceras Matsumoto, 1965, is a further, junior synonym of *P. (Zuluiceras)*. The type species, *Sornayceras proteus* Matsumoto, 1965, is evolute and coarsely ribbed, the ribs persisting, suggesting that it is an early member of the lineage. Matsumoto (1965: 227) also mentioned that *P. undulatocarinatum* van Hoepen, 1955, here regarded as a good example of *P. (Zuluiceras)*, was a *Sornayceras*, which supports the present conclusions.

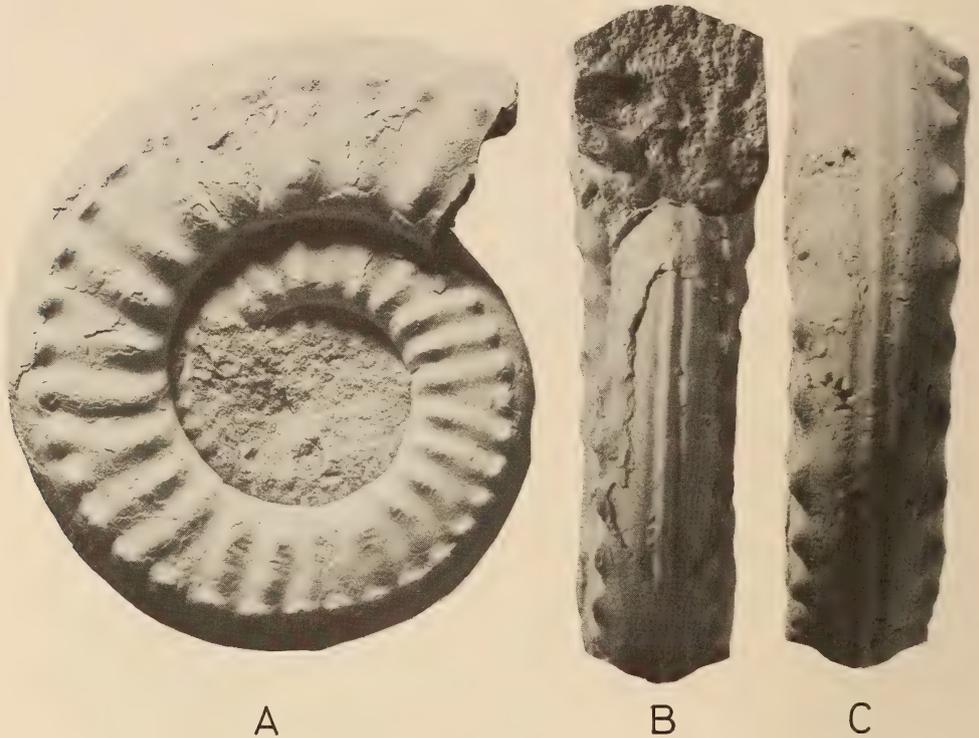


Fig. 42. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895.
A. SAS Z1521. B-C. SAS Z1521c. All $\times 1$.

P. (Zuluiceras) most closely resembles *P. (Peroniceras)* amongst the Peroniceratinae. The more involute coiling, compression, lateral keels subsidiary to the siphonal, and loss or weakening of ornament at maturity distinguishes them.

Occurrence

Middle Coniacian of Touraine, Aquitaine, Dieulefit (Drôme), the Corbières (Aude), Var, and Provence in France, Germany, Czechoslovakia, Austria, Italy, Romania, Armenia, north Africa, Zululand, Madagascar, and Japan. Upper Coniacian of Zululand and, possibly, Japan.

Peroniceras (Zuluiceras) zulu van Hoepen, 1965

Figs 43-52

Peroniceras sp. α Crick, 1907: 226, text-fig. to p. 226.

Peroniceras sp. β Crick, 1907: 227.

Peroniceras (Zuluiceras) zulu van Hoepen, 1965: 9, pl. 5, text-figs 1 g-i, 2b.

Peroniceras (Zuluiceras) charliei van Hoepen, 1965: 11, pl. 6, text-fig. 1j.

Peroniceras (Zuluiceras) regularis van Hoepen, 1965: 14, pl. 9, text-fig. 3d-e.

Peroniceras (Zuluiceras) multilineatum van Hoepen, 1965: 23, pl. 18, text-fig. 5d-e.



Fig. 43. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z746, the holotype. $\times 0.46$.

Type specimen

The holotype, by original designation, is SAS Z746 (Figs 43–44), from locality 91, degraded river cliffs and artificial cut west of the boundary of the St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand. This area is strewn with rubble derived from the St. Lucia Formation, Coniacian IV and V, and the precise age of the holotype is thus unknown.



Fig. 44. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z746, the holotype. $\times 0,62$.



Fig. 45. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z14, one of Van Hoepen's paratypes, still close to *P. (P.) dravidicum*. $\times 0.8$.

The type specimens of Van Hoepen's *P. (Z.) charliei*, *P. (Z.) regularis*, and *P. (Z.) multilineatum*, SAS Z735, Z736, and Z758 respectively, are all from the same locality as the holotype of *P. (Z.) zulu*. Their precise age is thus uncertain.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z735	110,0	39,0(35,5)	38,0(34,5)	1,03	53,0(48,2)	—
Z736	141,0	55,0(39,0)	44,0(31,2)	1,25	68,0(48,2)	22:23
Z758	158,0	52,0(32,9)	47,0(29,7)	1,10	74,0(46,8)	23:23
Z746	296,0	87,0(29,4)	92,0(31,1)	0,94	146,0(49,3)	25:25

Description

Coiling is polygyral, evolute with an umbilical diameter of 47 to 50 per cent of the total diameter. Successive whorls overlap to the ventrolateral row of tubercles.

The whorl section varies from slightly compressed to slightly depressed with a rounded to overhanging umbilical wall, slightly converging flanks and a broadly fastigate venter with a distinct median keel (which may be serrated) as well as weaker lateral keels. The latter may disappear completely in adults.

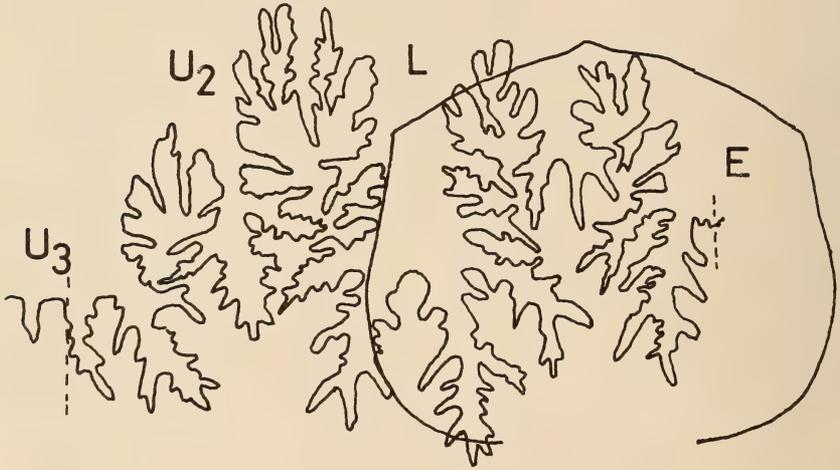


Fig. 46. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. Suture line and whorl section of holotype. $\times 1$. (After Van Hoepen 1965, figs 1g, 2b.)

Ornament consists of rounded to radially elongated umbilical tubercles connected by ribs of varying strength to clavate ventrolateral tubercles. On the inner whorls the ribs may bifurcate or intercalate occasionally. On the outer whorls they are generally single, stronger and more distantly spaced than on nuclei. The ventral area between the row of ventral tubercles and the median keel is often ornamented by faint spiral striae. Where preservation is good, spiral ornament may also be observed on the flanks.

The suture is highly incised and of the *P. (P.) dravidicum* type (Fig. 46). The maximum body chamber length observed is half a whorl.

Discussion

This species appears to include the two specimens described by Crick (1907: 226–228) as *Peroniceras* spp. α and β , here refigured as Figures 51–52. Van Hoepen's choice of the holotype is unfortunate as this is a large, septate

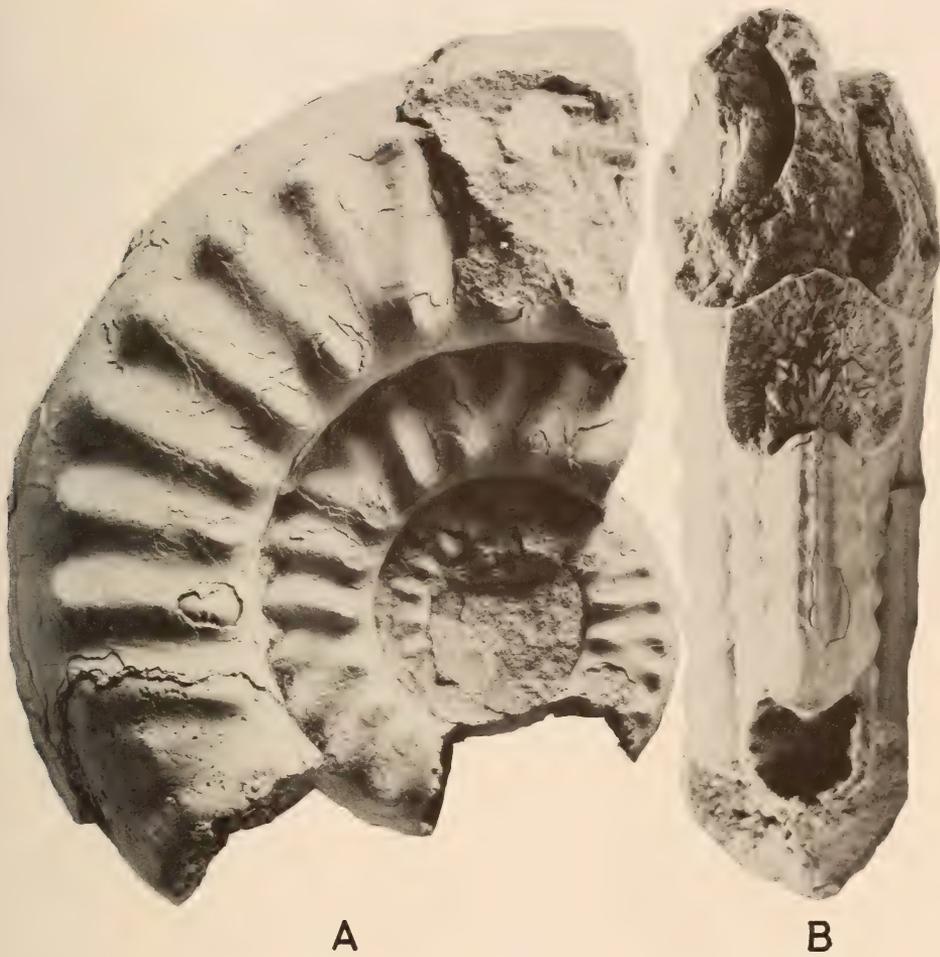


Fig. 47. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z735, the holotype of Van Hoepen's *P. (Z.) charliei*. $\times 1$.

specimen lacking the inner whorls (Figs 43–44) and thus difficult to compare with the other material. However, as interpreted here, *P. (Z.) zulu* is an evolute form with an umbilical diameter between 45 and 50 per cent of the total diameter with whorls more or less as wide as high.

One of Van Hoepen's syntypes, SAS Z14 (Fig. 45) differs from the typical form of the species in having a more rectangular whorl section and more distinct lateral keels, and probably being in those respects transitional to *Peroniceras* (*Peroniceras*) of the *dravidicum* group.

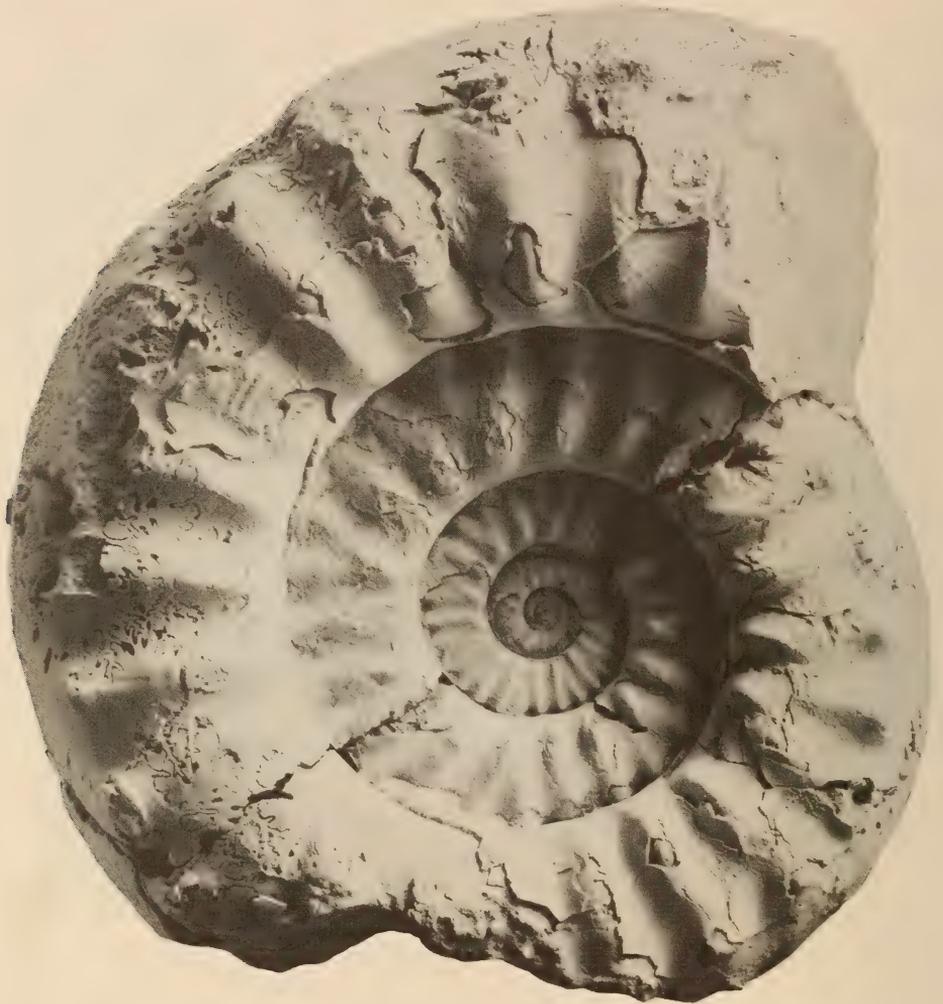


Fig. 48. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z736, the holotype of Van Hoepen's *P. (Z.) regularis*. $\times 0,92$.

P. (Z.) zulu includes *P. (Z.) charliei* (Fig. 47), *P. (Z.) regularis* (Fig. 48), and *P. (Z.) multilineatum* (Figs 49–50), all of which are from the same locality as the holotype and have comparable proportions and ornament: the differences cited by Van Hoepen are trivial and within the range of intraspecific variation shown by other peroniceratids.

P. (Z.) zulu differs from *P. (Z.) henniei* in having a wider umbilicus and more angular whorl section, but it is clear that the latter is derived from *P. (Z.) zulu* through progressive increase in involution and rounding of the whorl section. In addition, there is a reduction of the lateral keels and progressive serration of the median keel.

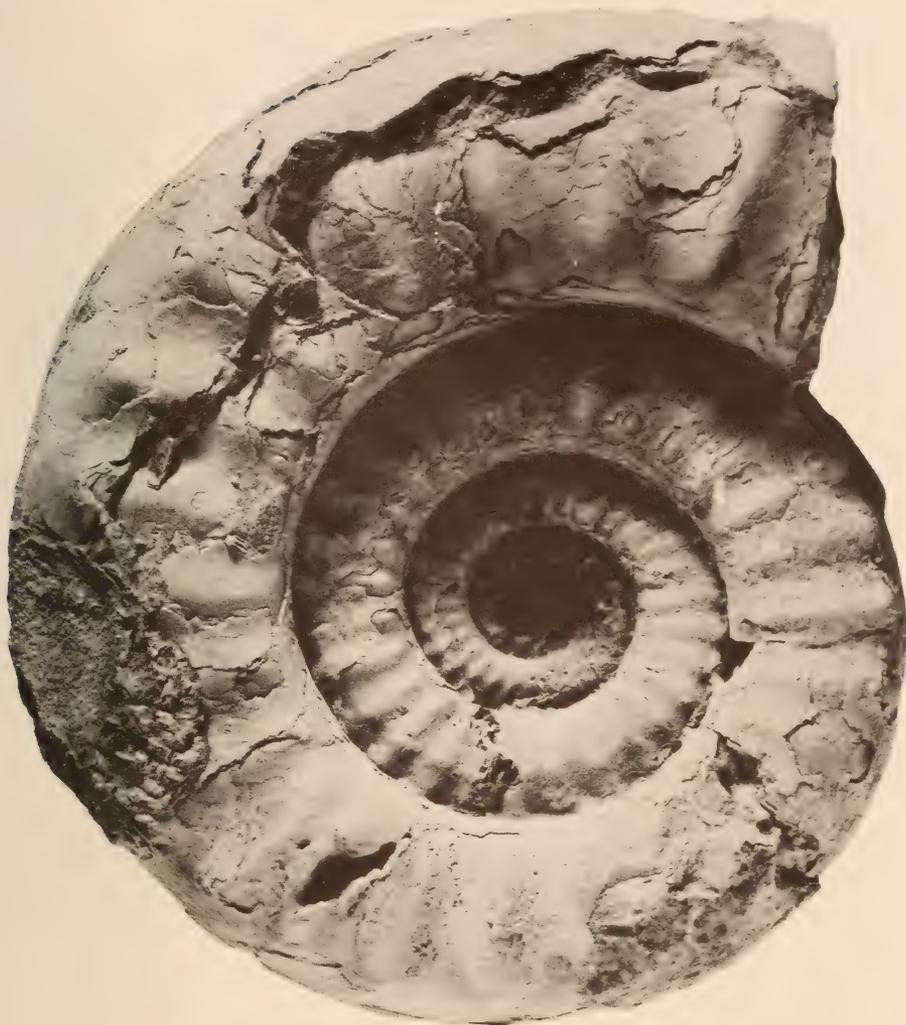


Fig. 48. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z736, the holotype of Van Hoepen's *P. (Z.) regularis*. $\times 0,92$.

In *P. (P.) dravidicum* the whorl section is more rectangular and the coiling more evolute.

Occurrence

The horizon of the type material is difficult to establish as the specimens were collected loose. Material collected *in situ* is restricted to Coniacian IV, which is presumed to be the level of the type specimens. The species is restricted to Zululand.

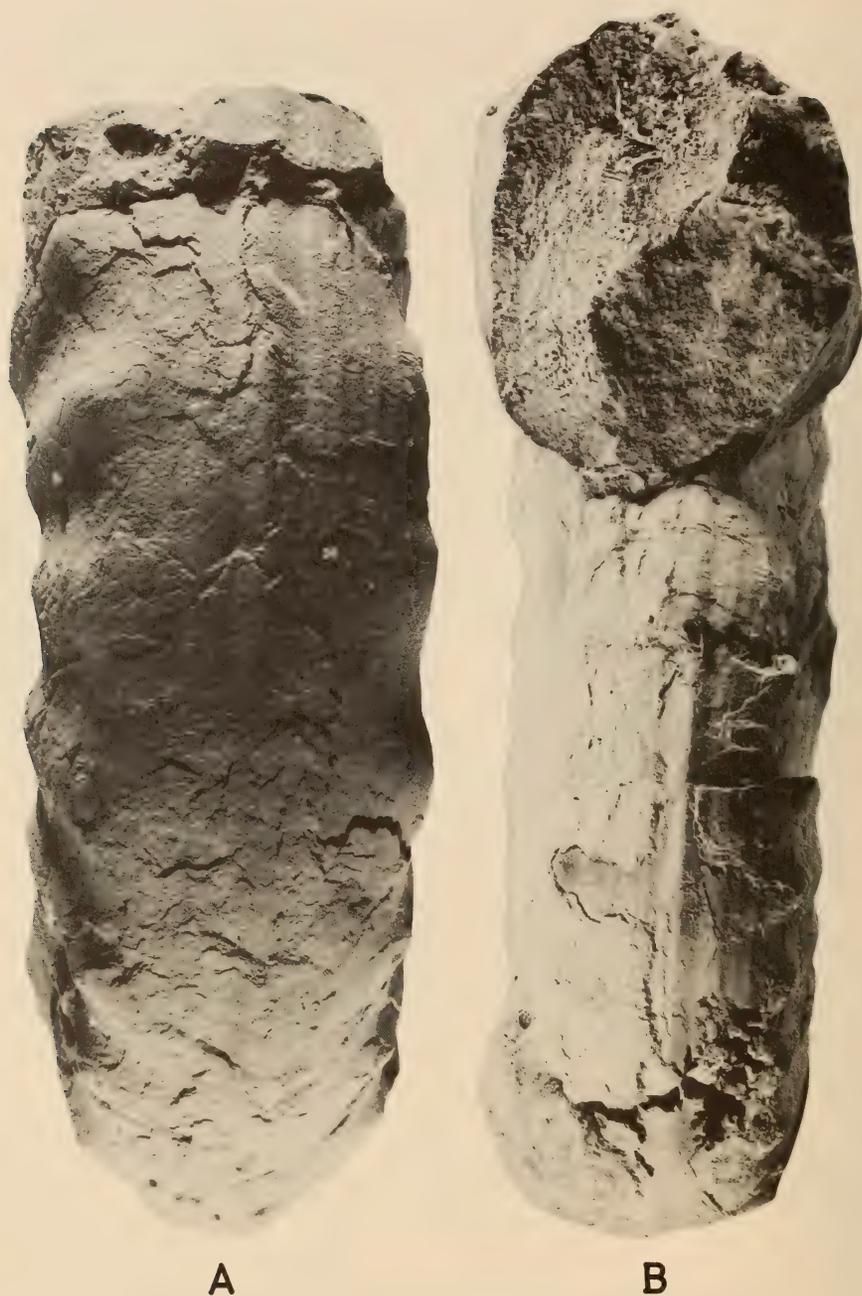


Fig. 50. *Peroniceras* (*Zuluiceras*) *zulu* van Hoepen, 1965. SAS Z758, the holotype of Van Hoepen's *P. (Z.) multilineatum*. $\times 0,8$.

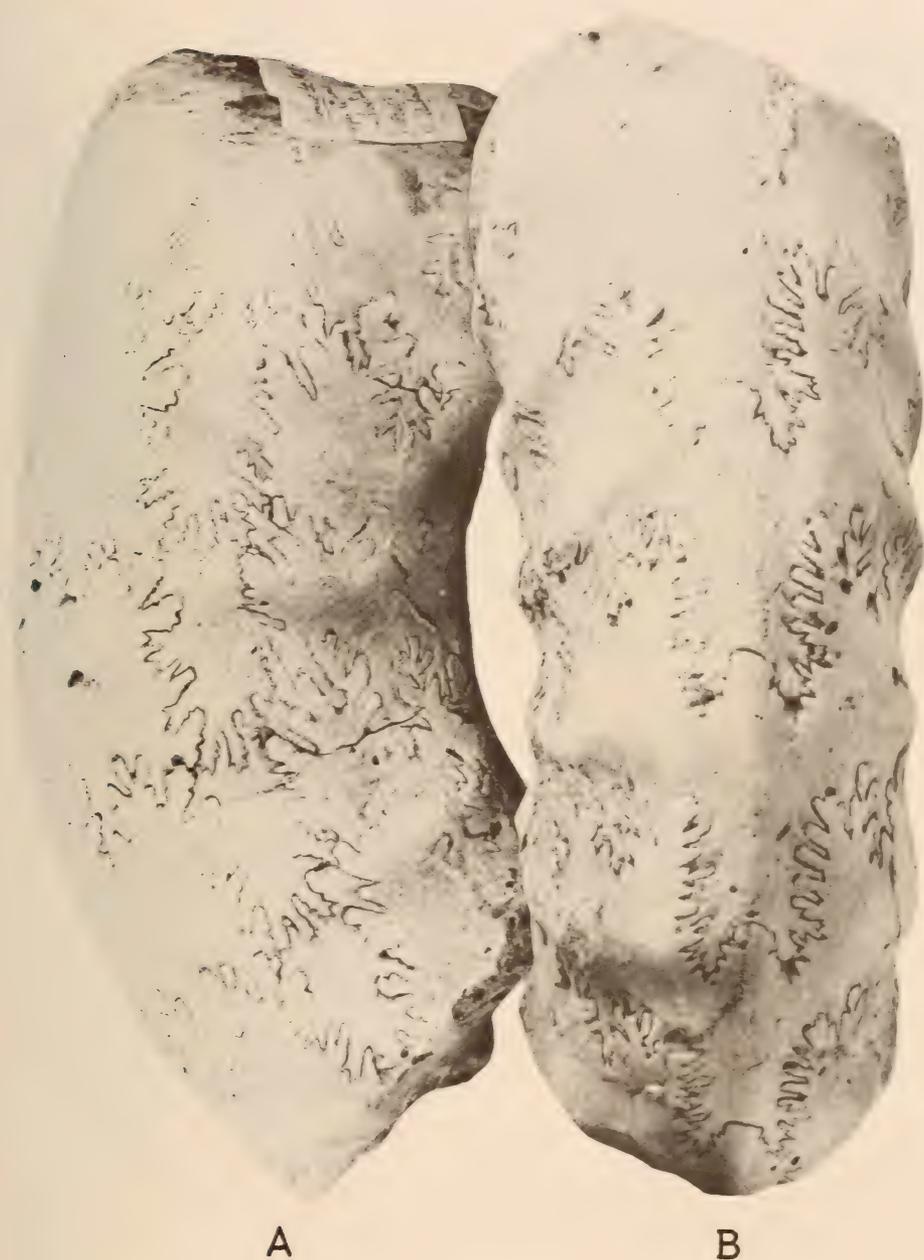


Fig. 51. *Peroniceras* (*Zuluiceras*) *zulu* van Hoepen, 1965.
The original of Crick's (1907) *Peroniceras* sp. α . $\times 0.85$.

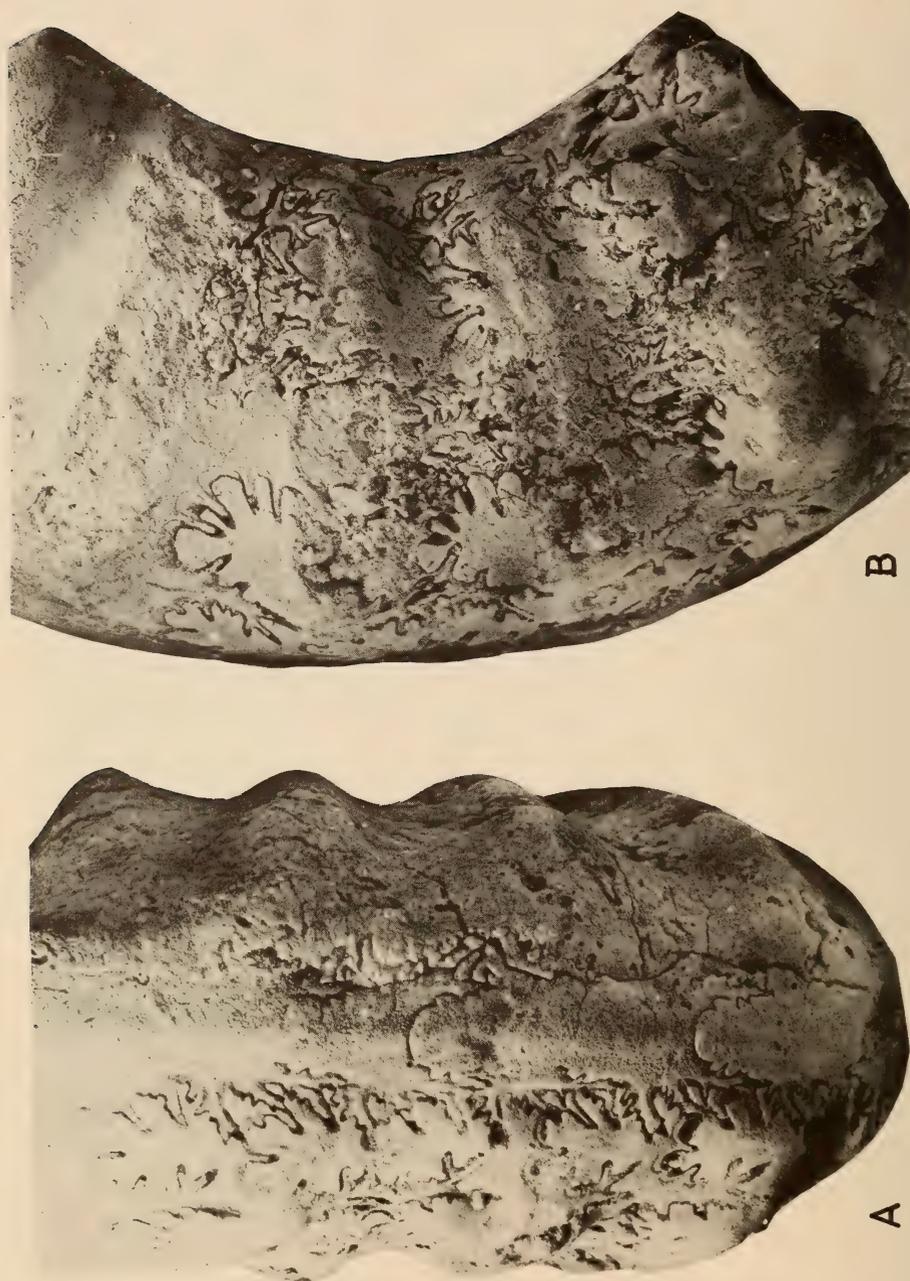


Fig. 52. *Peroniceras* (*Zuluiceras*) *zulu* van Hoepen, 1965. The original of Crick's (1907) *Peroniceras* sp. β . \times 1.

Peroniceras (Zuluiceras) rarum van Hoepen, 1965

Fig. 53

Peroniceras (Zuluiceras) rarum van Hoepen, 1965: 16, pl. 12, text-fig. 4(c).*Type specimen*

Holotype, by monotypy, is SAS Z742 from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV or V, probably the former.

Material

BMNH C83865, from locality 83, foreshore exposures around Mason's Camp, western shores of False Bay, east-north-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z742	100,0	32,0(32,0)	36,0(36,0)	0,89	38,0(38,0)	—

Description

The holotype consists of part of a septate, crushed whorl. Coiling is rather involute with an umbilical diameter of 38 per cent. The whorl section through-out is compressed with little inflated, parallel flanks and a gently rounded, fastigiate venter bearing a distinct crenulate central keel and poorly defined lateral keels.

Lateral ornament consists of weak umbilical bullae, narrow, rectiradiate, occasionally bifurcating ribs, and rounded to clavate ventrolateral tubercles. Faint traces of spiral ornament are visible in the area between the ventrolateral tubercles and the faint lateral keels.

The suture is only partially exposed, but appears to be of the general *P. (P.) dravidicum* type.

Discussion

It is regrettable that Van Hoepen erected a new species on such incomplete material, which renders interpretation difficult. As far as the whorl section is concerned, the species is allied to the group of *P. (P.) dravidicum*, but the crenulate keel and more involute coiling places it closer to the group of *P. (Zuluiceras)*. It differs from *P. (Z.) zulu* by the tighter coiling. The more tightly coiled group of *P. (Z.) henniei* differs from *P. (Z.) rarum* in having a more inflated whorl section at comparable diameters.

Lacking more material for additional observations, the species is here maintained with doubt.

Occurrence

The type locality includes rubble derived from Kennedy & Klinger's (1975) divisions Coniacian IV and V, so that the precise age is unknown. The second specimen is firmly dated as Coniacian IV. The species is known only from Zululand.

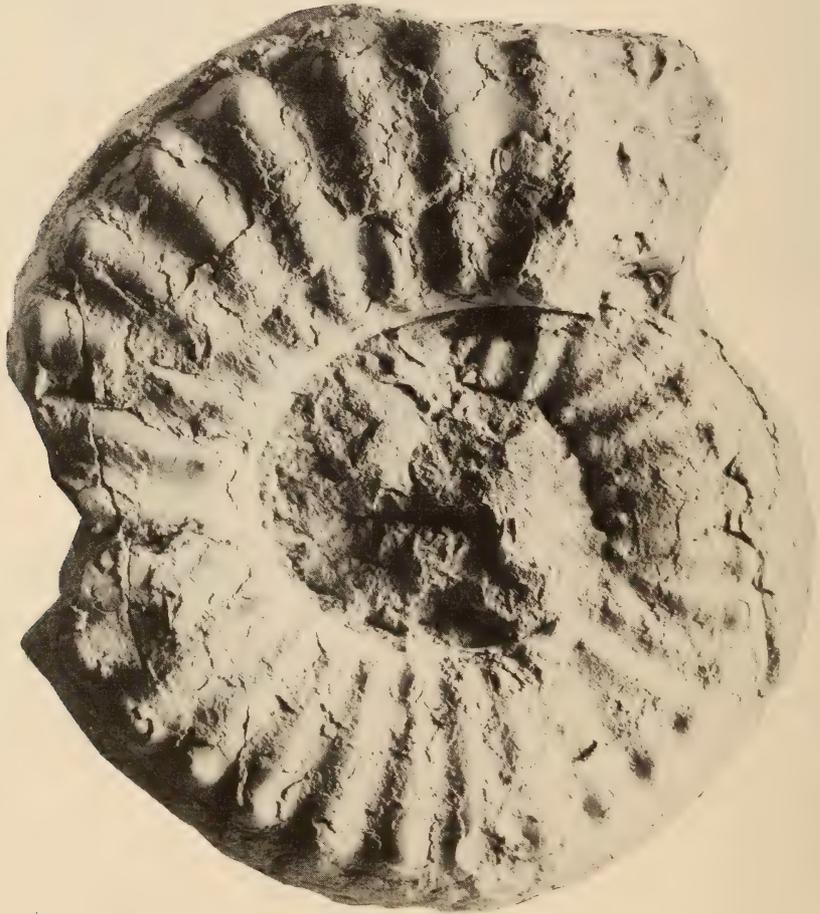


Fig. 53. *Peroniceras (Zuluiceras) rarum* van Hoepen, 1965.
SAS Z742, the holotype. $\times 1$.

Peroniceras (Zuluiceras) henniei van Hoepen, 1965

Figs 54–64

Peroniceras (Zuluiceras) henniei van Hoepen, 1965: 12, pl. 7, text-fig. 1k.*Peroniceras (Zuluiceras) alfredmeintjesi* van Hoepen, 1965: 15, pl. 10, text-fig. 3b–c.*Peroniceras (Zuluiceras) simplicicostatum* van Hoepen, 1965: 16, pl. 11, text-fig. 3a, g.*Peroniceras (Zuluiceras) undulatocostatum* van Hoepen, 1965: 19, pl. 14, text-fig. 4a–b.? *Peroniceras (Zuluiceras) similis* van Hoepen, 1965: 19, pl. 15, text-figs 2a, 4d.*Peroniceras (Zuluiceras) proximum* van Hoepen, 1965: 20, pl. 16 text-fig. 5a–b.*Peroniceras (Zuluiceras) ultimum* van Hoepen, 1965: 22, pl. 17, text-fig. 5c.*Type specimens*

The holotype, by original designation, is SAS Z638 from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV or V. The type specimens of *P. (Z.) alfredmeintjesi*, SAS Z738, *P. (Z.) simplicicostatum*, SAS Z740, *P. (Z.) proximum*, SAS Z747, *P. (Z.) ultimum*, SAS Z752, *P. (Z.) undulatocostatum*, SAS Z744, *P. (Z.) similis*, SAS Z745 and SAS 104, are all from the same locality as the holotype, and are equally imprecisely dated.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z638	115,0	41,0(35,6)	42,0(35,6)	0,98	46,0(40,0)	12×12:12×2
Z752	130,0	46,0(35,4)	44,0(33,8)	1,04	56,0(43,1)	21:34
Z738	150,0	54,0(36,0)	53,0(35,3)	1,02	64,0(42,7)	26:31
Z745	178,0	61,0(34,3)	60,0(33,7)	1,02	79,0(44,4)	—
Z747	262,0	81,0(30,9)	87,0(33,2)	0,93	115,0(43,9)	—
Z740	283,0	88,0(31,1)	97,0(34,3)	0,91	115,0(40,6)	23:25
Z744	345,0	139,0(40,3)	125,0(36,3)	1,11	140,0(40,6)	—

Description

The species has an umbilical diameter varying between 40 and 45 per cent of the total diameter. The whorls are slowly expanding, overlapping up to or beyond the ventrolateral tubercle. The whorl changes through ontogeny; it is initially quadrate with flattened flanks, but in later stages the umbilical wall becomes rounded and the flanks inflated. The venter is broadly rounded with a serrated central keel and weak lateral keels.

The adult whorl section varies among specimens as discussed below.

Ornament on the inner whorls is of *P. (P.) dravidicum* type, with umbilical bullae giving rise to one or two ribs that link ventrolateral clavi. On the outer whorls ribbing becomes bolder, and bifurcations rather rare. The ventral area between the ventrolateral tubercles and the central keel is ornamented by fine, spiral, interrupted striae. The undulations on the keel are far more numerous than the ventrolateral clavi.

The suture-line is of the *P. (P.) dravidicum* type (Fig. 61).

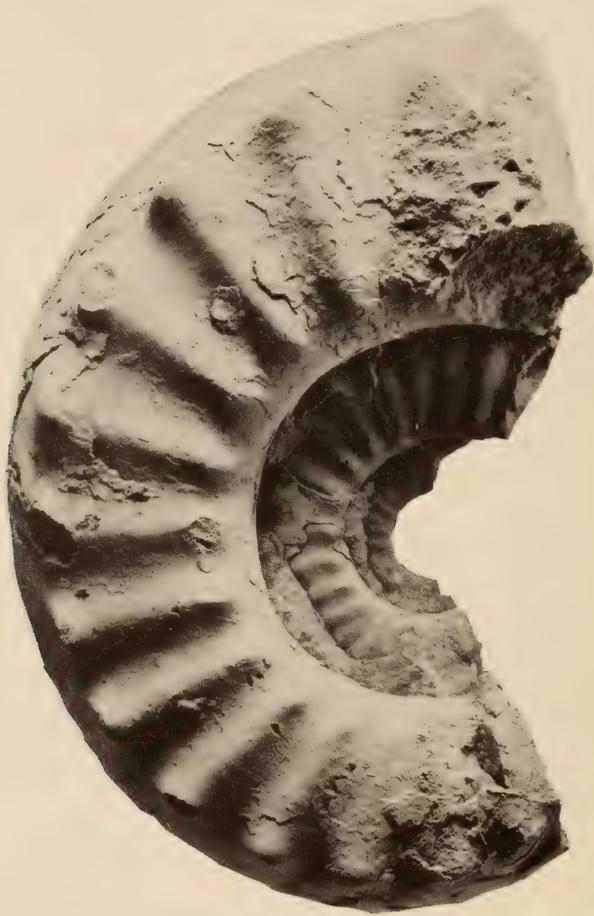


Fig. 54. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965.
SAS Z638, the holotype. $\times 1$.

Discussion

The authors' interpretation of the species is somewhat different from that of Van Hoepen (1965) and includes all forms with an umbilical diameter of between 40 and 45 per cent, more or less equal whorl breadth and height, serrated central keel, and very weak or no lateral keels. This species continues the morphological trend set by *P. (Z.) zulu* towards tighter coiling and loss of ornament on the outer whorls.

The description given above covers a number of species described by Van Hoepen, all collected from the same locality. These species (listed in the synonymy) take the name *P. (Z.) henniei*.



Fig. 55. *Peroniceras (Zuluiceras) henniei* van Hoepen. This specimen and that in Figure 57 show the features of the species to the best advantage. $\times 0,8$.

The holotype of *P. (Z.) henniei* (Fig. 54) consists of parts of three consecutive whorls, of which the last quarter of the outermost one is body chamber. The impression of an earlier whorl shows that the venter is already unicarinate and serrated at a diameter of 12,5 mm. As far as the angular whorl section is concerned, this specimen is perhaps closest to *P. (Z.) zulu*.

The holotype of *P. (Z.) alfredmeintjesi* (Figs 55–56A) is the best preserved of all the specimens and shows the main features of the species. The inner whorls are typically quadrate, whereas the outer whorls are more rounded. A

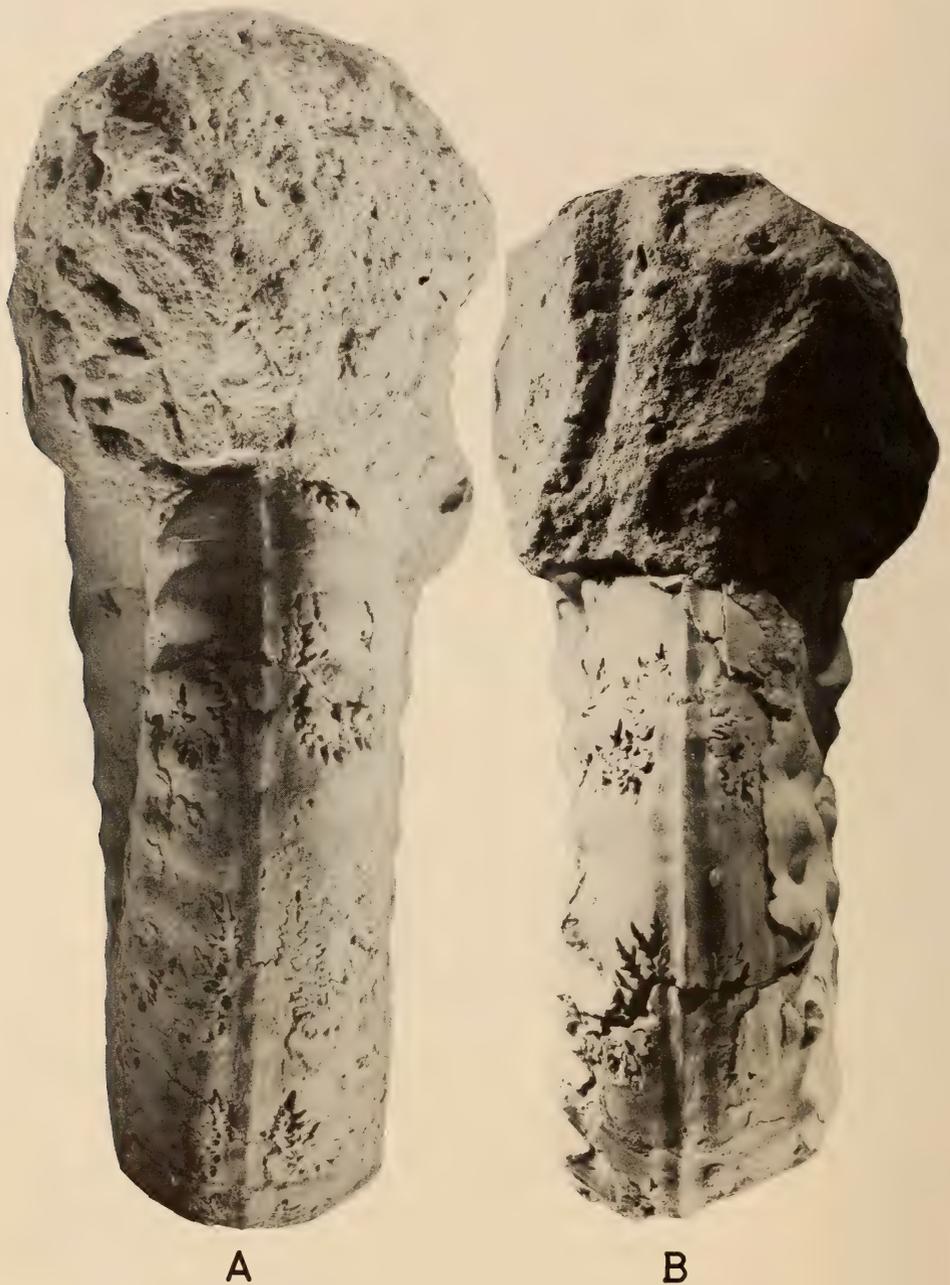


Fig. 56. A. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z738, the holotype of Van Hoepen's *P. (Z.) alfredmeintjisi*. $\times 0,9$. B. *Peroniceras (Zuluiceras) zulu* van Hoepen. $\times 0,88$.



Fig. 57. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS A374. $\times 1$.

nodate *Baculites*, presumably of the group *B. capensis* Woods, is present in the body chamber of this specimen.

The holotype of *P. (Z.) simplicicostatum* (Figs 58–59) is an enormous individual, still septate at a diameter of 306 mm. Unfortunately the inner whorls up to a diameter of 90 mm are not preserved. The whorls are much more massive and increase in size more rapidly than in the preceding specimens. Also, whorl height exceeds whorl breadth considerably. In this respect the specimen is closer to *P. (Z.) undulatocarinatum* described below, but has a slightly greater umbilical width than the latter species. The specimen figured by De Grossouvre (1894,



Fig. 58. *Peroniceras* (*Zuluiceras*) *henniei* van Hoepen, 1965. SAS Z740, the holotype of *P. (Z.) simplicicostatum* van Hoepen. $\times 0,47$.



Fig. 59. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z740, the holotype of *P. (Z.) simplicicostatum* van Hoepen, 1965. $\times 0,53$.

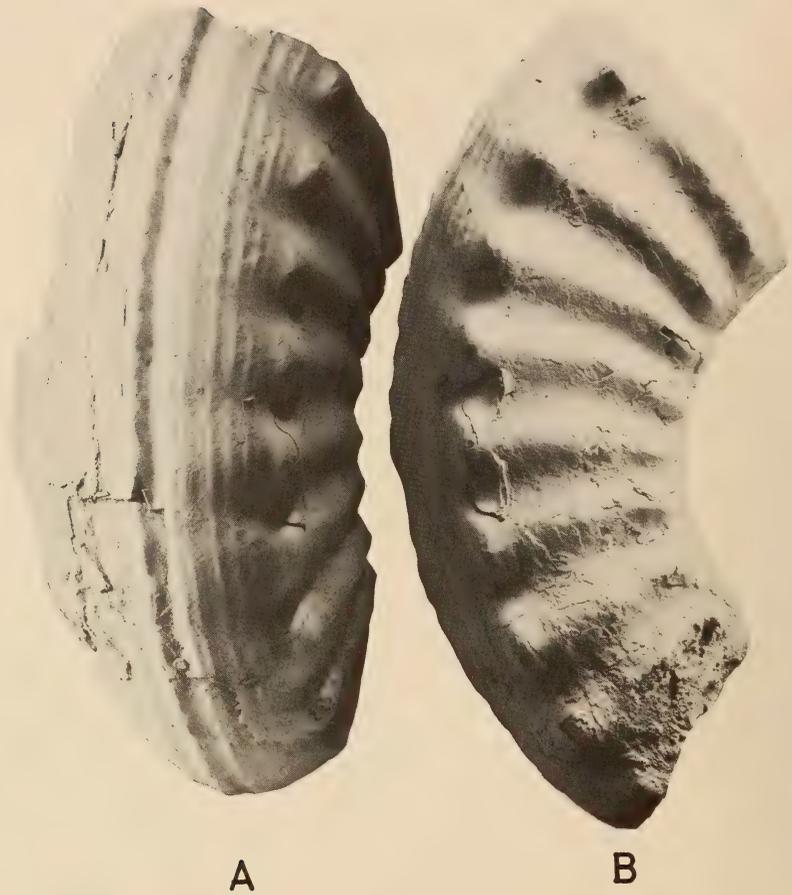


Fig. 60. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z744, inner whorls of the holotype of *P. (Z.) undulatocostatum* van Hoepen, 1965. $\times 1$.



Fig. 61. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. Suture line and whorl section of SAS Z744. $\times 1$. (After Van Hoepen 1965, fig. 4a-b.)



Fig. 62. *Peroniceras* (*Zuluiceras*) *henniei* van Hoepen, 1965. SAS Z747, the holotype of *P. (Z.) proximum* van Hoepen, 1965. $\times 0.6$.

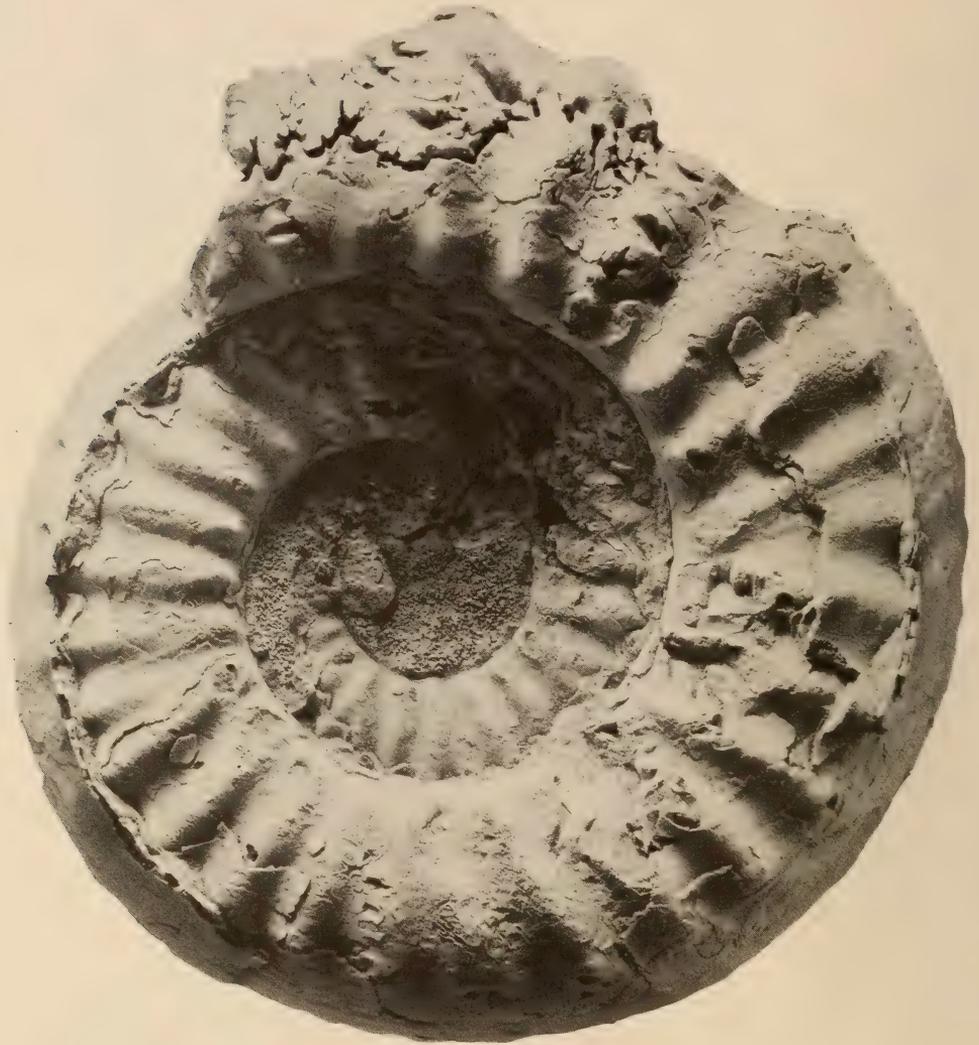


Fig. 63. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z752, the holotype of *P. (Z.) ultimum* van Hoepen, 1965. $\times 1$.

pl. 9 (fig. 1)) as an adult of *Gauthiericeras bajuvaricum* is a comparable but poorly preserved European analogue.

The holotype of *P. (Z.) undulatocostatum* is another gigantic specimen with a maximum measured diameter of 533 mm. Unfortunately only part of the inner whorls survive, but Van Hoepen's figure of the holotype is adequate also to show it as a transitional form between *P. (Z.) henniei* and *P. (Z.) undulatocarinatum*. Part of the inner whorl is preserved with some of the shell still intact. This shows the finely serrated central keel and finely striate radial ornament in the ventral area between the keel and the ventrolateral tubercles (Fig. 60).



Fig. 64. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS 104, a loosely coiled specimen transitional to *P. (Z.) zulu*. $\times 0,73$.

The holotype of *P. (Z.) similis* is not available for study, but from the descriptions and figures it seems to be a more evolute form connecting *P. (Z.) henniei* with *P. (Z.) zulu*. The holotype of *P. (Z.) proximum* (Fig. 62) is also a large specimen consisting of part of two successive whorls of which only a small part is body chamber. Again the looser coiling suggests that it connects morphologically with *P. (Z.) zulu*.

The holotype of *P. (Z.) ultimum* (Fig. 63) is a septate disc 130 mm in diameter. Apart from details of preservation, the outer whorls of this specimen are indistinguishable from the inner whorls of the holotype of *P. (Z.) undulato-costatum*, and is thus a further clear synonym of *P. (Z.) henniei*.

The species is here interpreted more widely than by Van Hoepen, but the authors doubt if the differences between the various 'species' given by that author are of specific significance. All the species are based on single specimens that occur at essentially the same stratigraphic level, which further causes one to doubt their validity. In consequence they are all here included in *P. (Z.) henniei*.

The next species to be discussed, *P. (Z.) undulato-carinatum*, continues the trend towards closer coiling, but here a progressive loss of ornament on the outer whorls spans the boundary between Van Hoepen's 'subgenera' *P. (Zuluiceras)* and *P. (Zuluites)*.

Occurrence

The type locality is strewn with rubble from Coniacian IV and V; the species is probably from the former. It may possibly also occur in France.

Peroniceras (Zuluiceras) undulato-carinatum van Hoepen, 1955

Figs 65–75

Peroniceras undulato-carinatum van Hoepen, 1955: 369, figs 18–21.

Peroniceras (Zuluites) georgemeintjesi van Hoepen, 1965: 25, pl. 20, text-fig. 6c–e.

Peroniceras (Zuluites) lettiae van Hoepen, 1965: 27, pl. 21, text-fig. 7a–d.

? *Peroniceras (Zuluites) dubium* van Hoepen, 1965: 28, pl. 22, text-fig. 7b–c.

Type specimens

The holotype, by original designation, is SAS Z15 (Fig. 73) from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand. This locality is strewn with rubble from the St. Lucia Formation, Coniacian IV and V, and the specimen cannot be precisely dated, although it is probably from Coniacian IV. The holotype of *P. (Zuluites) georgemeintjesi* is SAS Z733; the holotype of *P. (Z.) lettiae* is SAS Z185; the holotype of *P. (Z.) dubium* is SAS Z750. Other specimens are SAS Z19, Z631, Z742, and Z868, all from the same locality. Some specimens are associated with nodose *Baculites*, suggesting that they are from Coniacian IV.



Fig. 65. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z19, inner whorls of paratype of Van Hoepen (1955). $\times 0,95$.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z19	142,0	49,0(34,5)	55,0(38,7)	0,89	55,0(38,7)	13 \times 2:30
Z750	148,0	42,0(28,3)	54,0(36,5)	0,78	58,0(39,2)	11 \times 2:13 \times 2
Z15	159,0	54,0(34,0)	59,0(37,1)	0,95	64,0(40,2)	14 \times 2:14 \times 2
Z733 at	154,0	48,0(31,2)	60,0(39,0)	0,80	55,0(35,7)	—
at	218,0	63,0(28,9)	87,0(39,9)	0,72	84,0(38,5)	—
Z185	174,0	62,0(35,6)	68,0(39,1)	0,91	72,0(41,4)	—

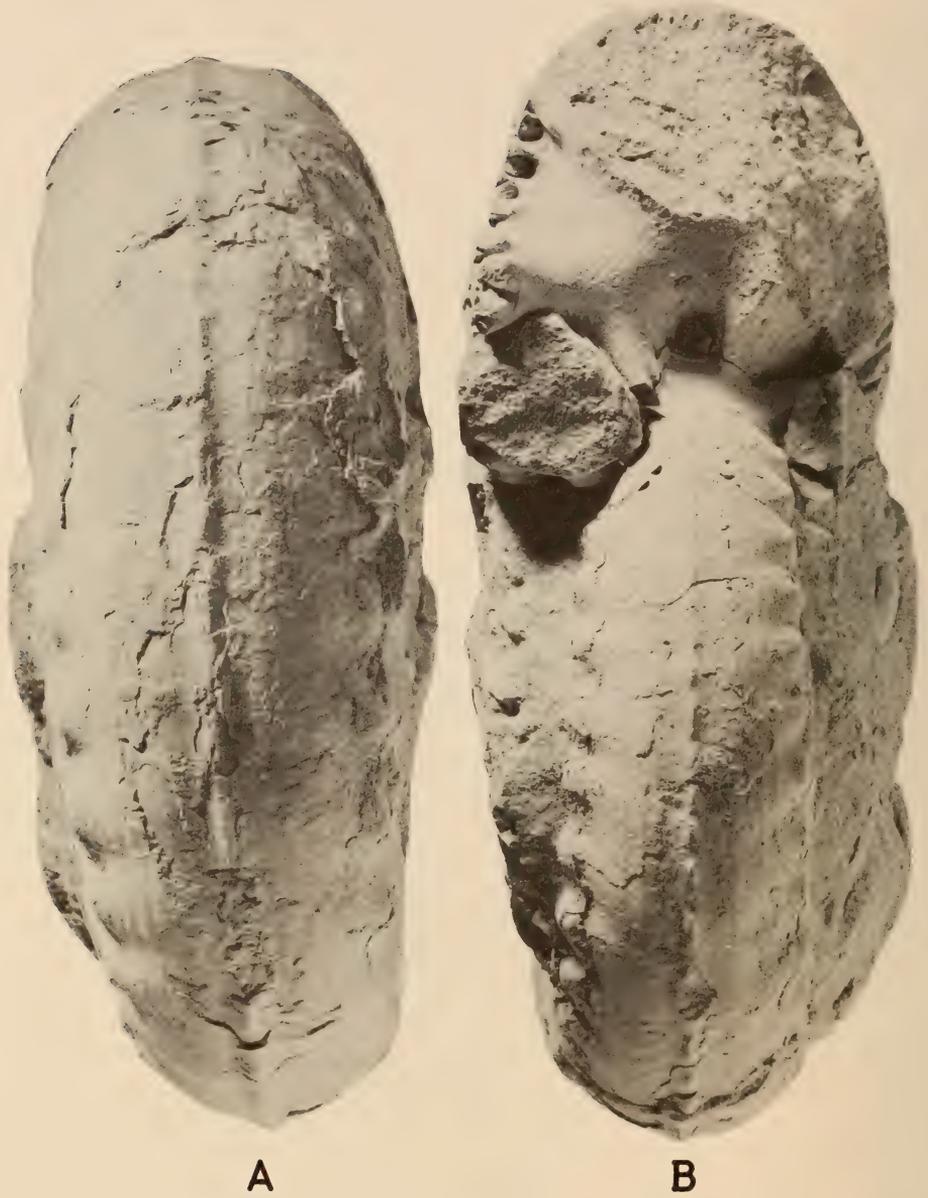


Fig. 66. A-B. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955 SAS Z19, inner whorls of paratype of Van Hoepen (1955). $\times 1$.



Fig. 67. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1965. SAS Z19, outer whorl of paratype of Van Hoepen (1955). $\times 0,75$.



Fig. 68. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line and whorl section of the holotype, SAS Z15. $\times 1$. (After Van Hoepen 1955, figs 19–20.)

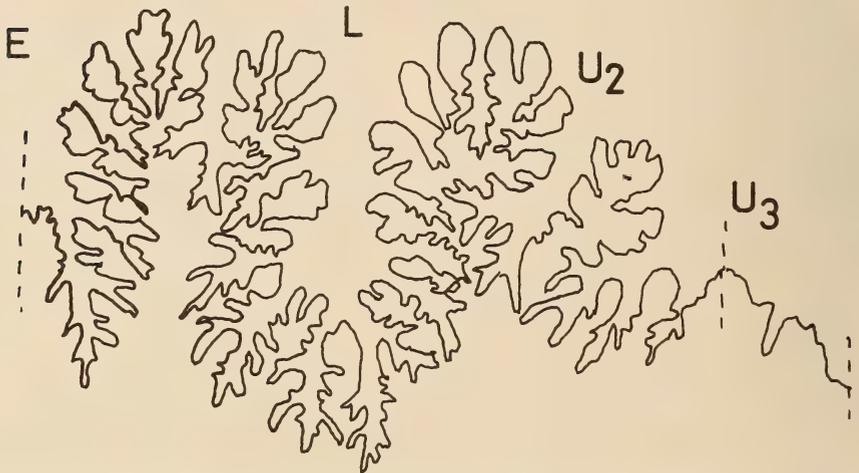


Fig. 69. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line of paratype SAS Z19. $\times 1$. (After Van Hoepen 1955, fig. 22.)

Coiling is involute for *Peroniceras*, with an umbilical diameter of between 35 and 40 per cent of the total diameter. Successive whorls overlap up to and beyond the ventrolateral tubercles.

The whorl section is distinctly compressed, with a vertical to overhanging rounded umbilical wall, little-inflated, rounded flanks converging to a broadly rounded-fastigiate venter (Fig. 68).

Ornament on the inner whorls consists of prominent bullate to auricular umbilical tubercles, weak prorsiradiate ribs and rounded to clavate ventrolateral tubercles. The latter are situated near the ventral third of the flanks. In the



Fig. 70. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z733, the holotype of Van Hoepen's *P. (Zuluites) georgemeinijesi*. $\times 0,66$.



Fig. 71. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z185, the holotype of *P. (Zuluites) lettiae* van Hoepen, 1965. $\times 1$.

fastigiate area between the ventrolateral tubercles and the central keel, numerous spiral striae occur. In some specimens, e.g. SAS Z15 (Fig. 73), these striae also cover the ventrolateral tubercles. The central keel undulates, but the undulations do not coincide with ventrolateral clavi. The central keel is bounded on either side by a shallow depression producing slight spiral ridges, but these can hardly be termed lateral keels.

On the outer whorls of the specimens available (nearly all of them are still septate), all ornament weakens and the whorls become nearly smooth.

Discussion

P. (Zuluiceras) undulatocarinatum continues the trend towards increased involution and compression, forming a link between *P. (Z.) henniei* and *P. (Z.) modestum*. In addition, loss of ornament on the outer whorls is obvious. This is comparable to that found in the transition from *Texanites* to *Submortonoceras* (Klinger & Kennedy 1980: 172).

Differences between *undulatocarinatum*, *henniei* and *modestum* are gradual in some respects. There is no clear-cut boundary between them in respect of umbilical diameter: *P. (Z.) henniei* has an umbilical width of 40 to 45 per cent, *P. (Z.) undulatocarinatum* between 35 and 40 per cent, whereas *P. (Z.) modestum* has an umbilical width below 30 per cent. These reductions in umbilical width are, however, accompanied by changes in whorl section and loss of ornament.

P. (Zuluiceras) undulatocarinatum, as here interpreted, includes *P. (Zuluites) georgemeintjesi* van Hoepen and *P. (Z.) lettiae* van Hoepen. Differences between these latter 'species' and *P. (Zuluiceras) undulatocarinatum* are minor and restricted to details of the inner whorls.

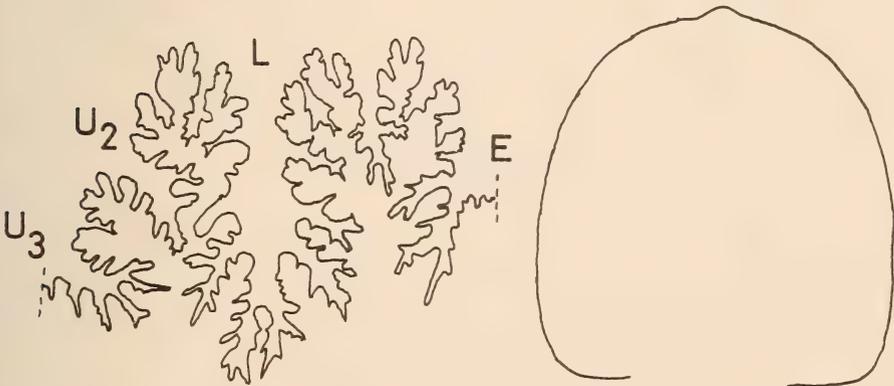


Fig. 72. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line and whorl section of SAS Z185, the holotype of *P. (Zuluites) lettiae* van Hoepen, 1965. $\times 1$. (After Van Hoepen 1965, figs 7d, a.)

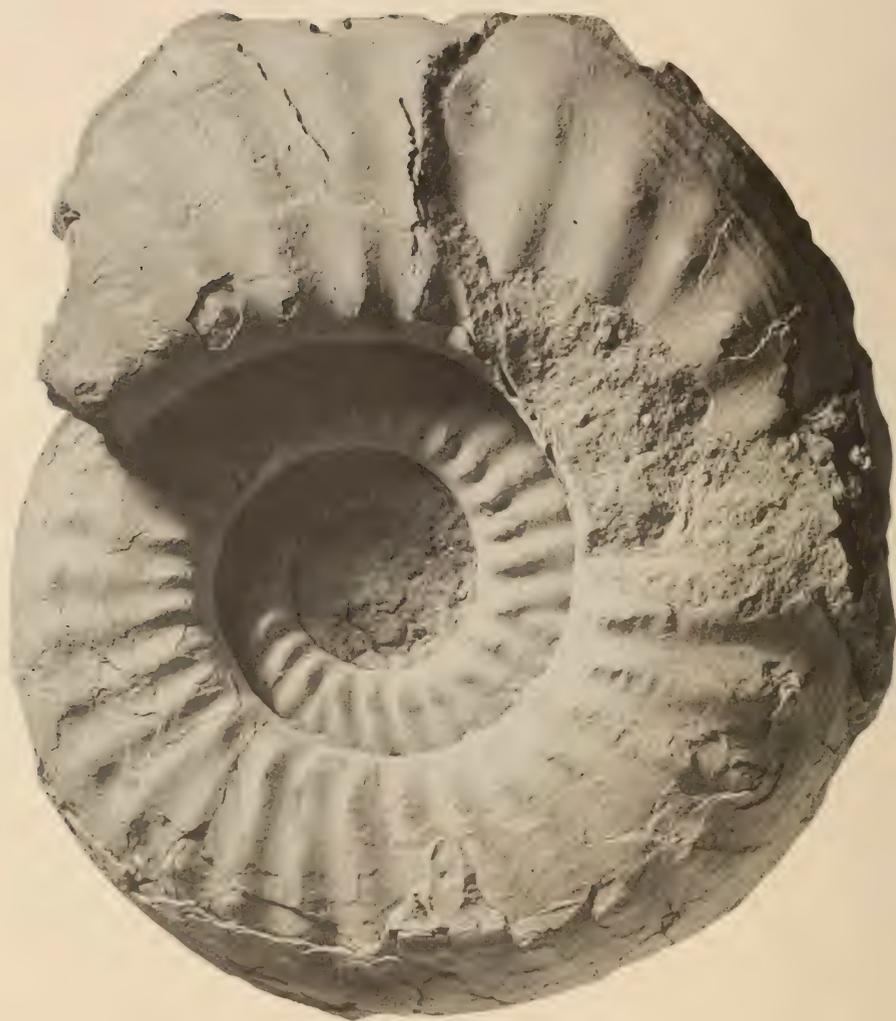


Fig. 73. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955.
SAS Z15, the holotype. $\times 0,72$.

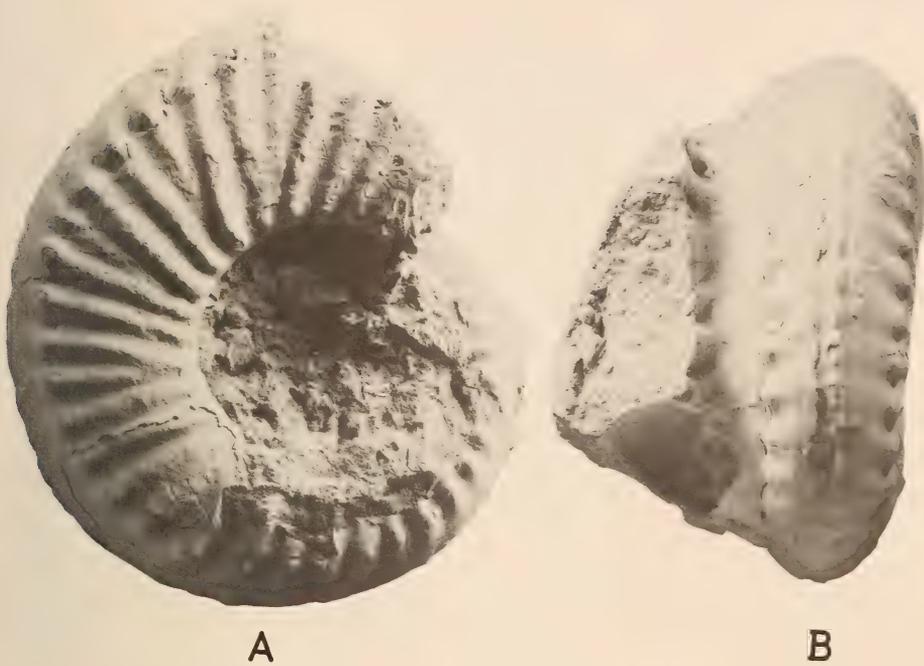


Fig. 74. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z733, the inner whorls of *P. (Zuluites) georgemeintjesi* van Hoepen, 1965. $\times 1$.

P. (Zuluites) dubium (Fig. 75) is more compressed than the holotype of *P. (Zuluiceras) undulatocarinatum* and has finer ornament. It bears great similarity to the inner whorls of the holotype of *P. (Zuluites) georgemeintjesi* (Fig. 74), The outer whorls of the latter are, however, virtually identical with those of *P. (Zuluiceras) undulatocarinatum*. The holotype of *P. (Zuluites) lettiae* (Figs 71–72) has stouter, more quadrate inner whorls than the holotype of *P. (Zuluiceras) undulatocarinatum* and is in these respects transitional to *P. (Z.) henniei* and *P. (Z.) zulu*.

In summary, inner whorls are rather variable as far as dimensions and ornament are concerned; this is analogous to the situation in the similarly compressed *Submortonicerias condamyi* Collignon, 1948, and *S. woodsi* (Spath, 1921), from Zululand and Pondoland (Klinger & Kennedy 1980).

Occurrence

The type locality is strewn with rubble from divisions Coniacian IV and V, the species probably coming from the former level.

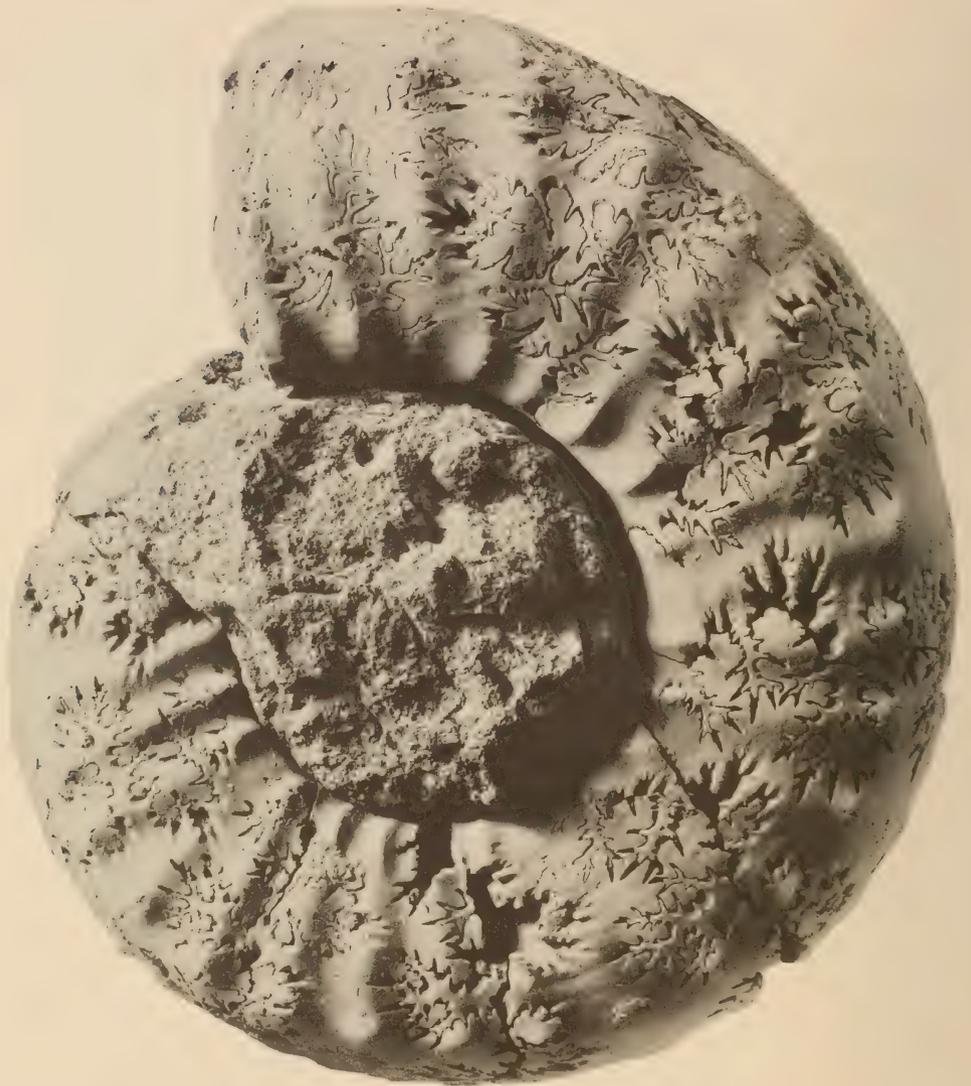


Fig. 75. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955.
SAS Z750, the holotype of *P. (Zuluites) dubium* van Hoepen, 1965. $\times 1$.

Peroniceras (Zuluiceras) modestum van Hoepen, 1965

Figs 76–85

Peroniceras (Zuluites) modestum van Hoepen, 1965: 24, pl. 19, text-fig. 6a–b.*Type specimen*

The holotype, by original designation, is SAS Z739 (Fig. 76, 77A) from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, probably Coniacian IV.

Material

SAS Z21, Z104, Z379, Z631, and Z868 from the same locality and inferred horizon as the holotype, SAS 106 from locality 89, St. Lucia Formation, Coniacian IV. BMNH C83863 and C83864 from the same horizon at locality 82.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z868	145,0	49,0(33,8)	59,9(40,7)	0,83	49,0(33,8)	28:35
SAS106	152,0	51,0(33,6)	67,0(44,1)	0,76	42,0(27,6)	—
Z739	160,0	57,0(35,6)	72,0(45,0)	0,79	46,0(28,7)	—
Z379	165,0	56,0(33,9)	74,0(44,8)	0,76	50,0(30,3)	—
SAS104	229,0	64,0(27,9)	102,0(44,5)	0,63	59,0(25,8)	—

Description

Coiling is very involute, the umbilical diameter varying between 25 and 33 per cent, and up to 50 per cent of the previous whorl being covered.

The whorl section is compressed ovoid throughout ontogeny, with a vertical to distinctly overhanging umbilical wall, slightly inflated flanks converging to a broadly rounded venter, with no distinct demarcation between the latter and the flanks. The venter bears one narrow, serrated keel. Slight depressions occur on either side of the keel, especially on the inner whorls, but distinct lateral keels are not developed. On the outer whorls of the phragmocone these depressions virtually disappear and the venter is unicarinate without sulci.

Ornament on the inner whorls is as in *P. (Z.) undulatocarinatum*, but rapidly disappears on the outer whorls, leaving the shell completely smooth but for slight undulations representing the umbilical tubercles. Spiral striae occur on the ventral regions where the shell is well preserved.

All the specimens are still septate, indicating that the species grew to a very large size. The suture is of the *P. (P.) dravidicum* type.

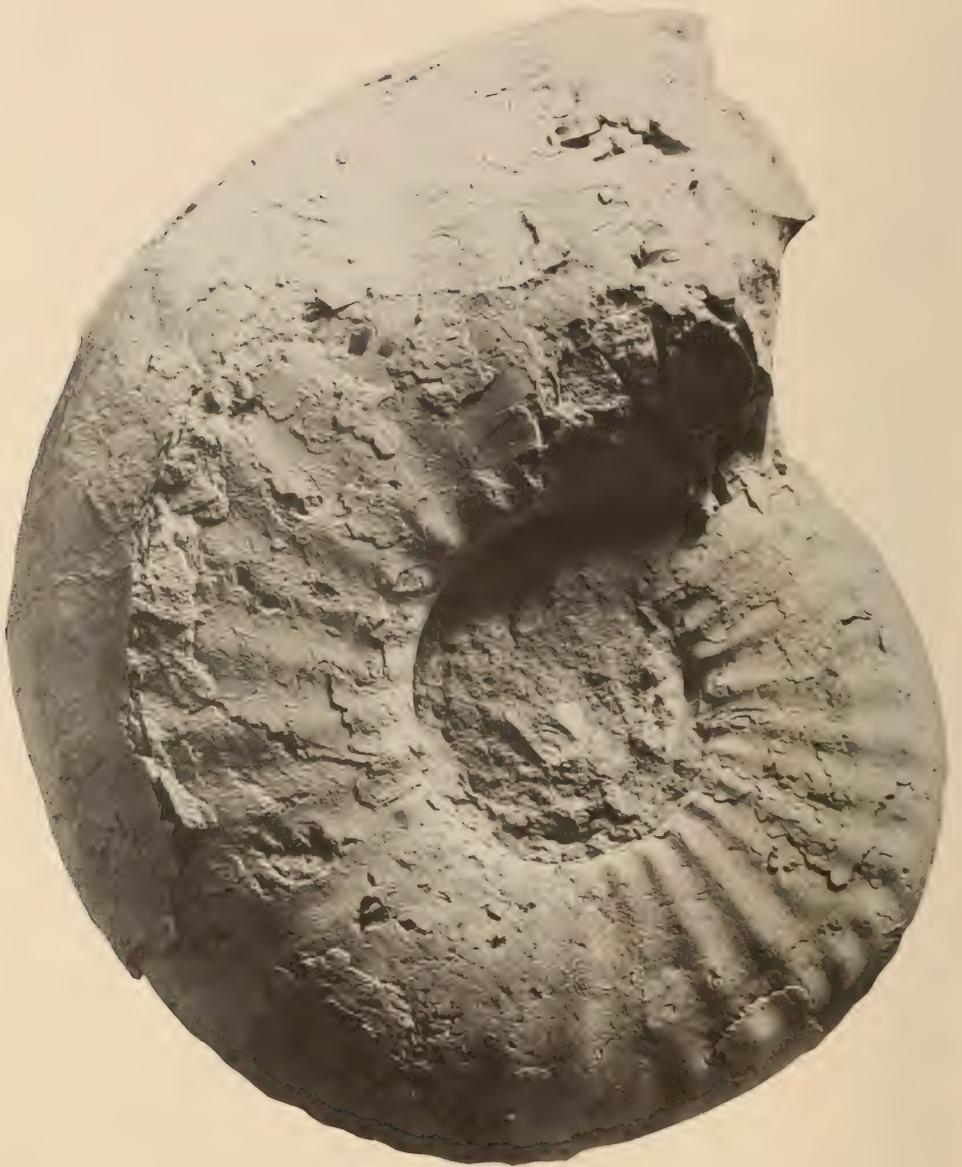


Fig. 76. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z739, the holotype. $\times 1$.



Fig. 77. A. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z739.
B. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1965. SAS Z750, the
holotype of *P. (Zuluities) dubium* van Hoepen, 1965. Both $\times 0,92$.

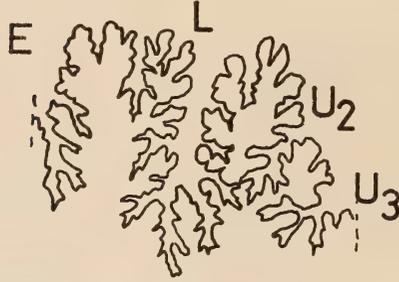


Fig. 78. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965.
Suture-line of the holotype. $\times 1$.
(After Van Hoepen 1965, fig. 6a.)

Discussion

This species is easily distinguished from the preceding *Peroniceras (Zuluiceras)* species by the high degree of involution and virtual lack of ornament on the later whorls of the phragmocone.

This appears to be the last species of the *P. (P.) dravidicum* stock, a line that evolved rapidly through the Middle and lower Upper Coniacian in Zululand, becoming progressively larger and showing increasing involution and whorl compression, losing lateral ornament and the pair of lateral keels. Although the end member is very different from the ancestral *P. (P.) dravidicum*, the suture-line remained remarkably similar throughout, especially the U_2/U_3 lateral saddle, which remained attached obliquely by a thin stem to the root of the lateral L/U_2 saddle.

Occurrence

Coniacian IV of Zululand.

Peroniceras (Zuluiceras) matsumotoi sp. nov.

Figs 86–88

Type specimen

The holotype is NMB D1140 from locality 73, degraded river cliffs on the north bank of the Mzinene River downstream of the junction with the Munywana River, Zululand, St. Lucia Formation, probably Coniacian IV.

Etymology

The species is named for Emeritus Professor Tatsuro Matsumoto of Kyushu University.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
D1140	168,0	40,0(23,8)	52,0(30,9)	0,77	76,0(45,2)	—



Fig. 79. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z743. Note the similarity to *P. (Z.) matsumotoi* sp. nov. (Figs 86–88) apart from the more inflated whorl section and narrower umbilical width. $\times 0.68$.



Fig. 80. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z743. Note the serrated, uncarinate venter already present on the inner whorls. $\times 0,71$.



Fig. 81. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 104. $\times 0,67$.



Fig. 82. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965.
A. SAS Z868. $\times 1$ B. SAS 104. $\times 0,69$.



Fig. 83. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z868. $\times 1$.



Fig. 84. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 106. $\times 1$.

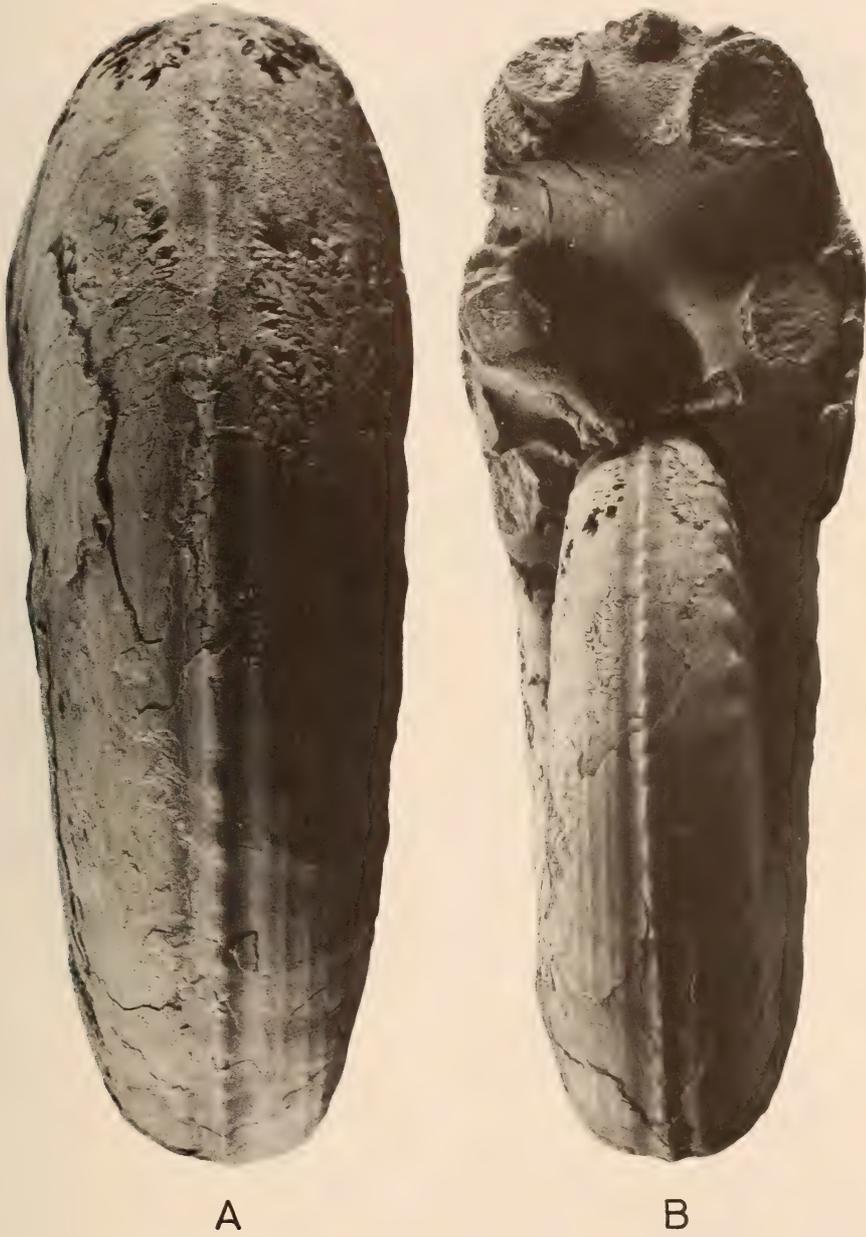


Fig. 85. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 106. $\times 1$.



Fig. 86. *Peroniceras (Zuluiceras) matsumotoi* sp. nov. Holotype NMB D1140. $\times 1$.



Fig. 87. *Peroniceras (Zuluiceras) matsumotoi* sp. nov.
 Holotype NMB D1140. $\times 1$.

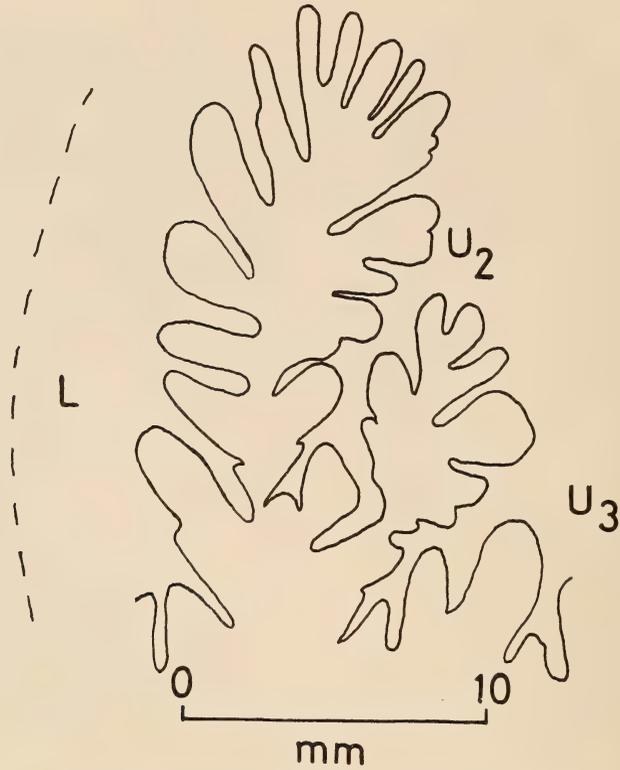


Fig. 88. *Peroniceras* (*Zuluiceras*) *matsumotoi* sp. nov.
Suture-line of holotype NMB D1140.

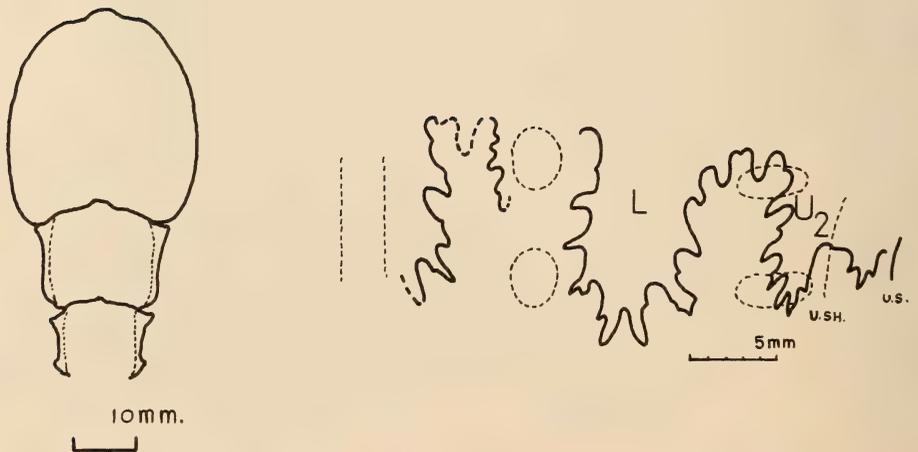


Fig. 89. *Ishikariceras binodosum* Matsumoto, 1965. Whorl section and partial suture. $\times 1$.
(After Matsumoto 1965, text-figs 17-18.)

Description

Coiling is very evolute, with only 25 to 33 per cent of the preceding whorl covered, the degree of overlap increasing through development. The umbilical diameter is 45 per cent of the total diameter.

The whorl section is compressed throughout, with subparallel, slightly inflated flanks and a broadly rounded unicarinate venter. The venter is unicarinate at the smallest diameter observed but in later growth it is bound by shallow depressions, although no distinct lateral keels develop. The keel is serrated on the inner whorls but entire on the internal mould of the outer whorls.

The ornament of inner whorls consists of umbilical bullae and rounded ventrolateral tubercles. These are linked by radial ribs, most of which are single, with only occasional bifurcations at or near the umbilical tubercle. Ornament weakens progressively in later growth and, at the greatest diameter preserved, the flanks bear only feeble undulations. The suture is incompletely exposed (Fig. 88) but is of the *P. (P.) dravidicum* type. The body chamber is unknown.

Discussion

P. (Z.) matsumotoi differs from all the other Zululand species in being both compressed and very evolute.

The precise relationship of this species to other *P. (Zuluiceras)* species is not clear, as transitional or superficially similar forms do not occur.

The most similar form occurs in Madagascar: '*Schloenbachia*' *schneeblii* Boule, Lemoine & Thévenin (1907: 36, pl. 5 (figs 2–2a), text-fig. 20). It resembles *P. (Z.) matsumotoi* in having coarse ornament on the inner whorls but virtually smooth, unicarinate outer phragmocone whorls. At comparable diameters, however, the suture-lines are totally different. That of '*Schloenbachia*' *schneeblii* is very simple, with broad parallel saddles and lobes, markedly different from the highly incised, narrow saddles and lobes of *P. (Z.) matsumotoi*. Moreover, the siphonal keel of '*Schloenbachia*' *schneeblii* is both broader and more prominent than that of *P. (Z.) matsumotoi*.

Another comparable form is *Ishikariceras binodosum* Matsumoto (1965: 236, pl. 43 (fig. 1), text-figs 17–18) from the Coniacian of Hokkaido, Japan. The inner whorls have a more quadrate section but the Japanese species show the same loss of ornament on the outer whorls. The suture of the Japanese species is strikingly different from that of *P. (Z.) matsumotoi* and is simple, with little-incised, broad elements (Fig. 89). This is a situation comparable to that between the extremes of *Peroniceras* s.s. Here, however, no intermediate forms linking *Ishikariceras* to *Peroniceras* are known. Although it seems probable that such forms will turn up, retention of *Ishikariceras* as a separate genus seems wise at present.

Other comparable forms are two specimens described by Matsumoto (1965: 233) as *Sornayceras* sp. cf. *propoetidum* from the 'Upper' Coniacian of Hokkaido, Japan. These specimens have suture-lines and whorl sections like

those of the present species, but are more narrowly umbilicate (U = only 30 per cent of the total diameter as against 45 per cent in *P. (Z.) matsumotoi*)

Occurrence

Coniacian IV of Zululand only.

Peroniceras (Zuluiceras) cf. aberlei (Redtenbacher, 1873)

Figs 90–91, 92A

Compare

Ammonites aberlei Redtenbacher, 1873: 111, pl. 25 (fig. 4a–e).

De Grossouvre, 1894: 89.

Type specimen

Redtenbacher failed to designate a holotype for this species. A lectotype designation will be undertaken in a pending version of some of the Gosau faunas (Kennedy & Summesberger in preparation).

Material

NMB D1147 from locality 72, degraded river cliff and stream sections on the north side of the Mzinene River downstream of the junction of the Munywana River, Zululand, St. Lucia Formation, Coniacian II or III.

Description

A single specimen consisting of parts of two successive septate whorls is referred to Redtenbacher's species. The section of both whorls is distinctly compressed, with a fastigiate venter bearing a single keel. The keel appears entire and is bounded on either side by distinct grooves, creating the appearance of weak lateral keels. Ornament on the inner whorls consists of fine, frequently bi-



Fig. 90. *Peroniceras (Zuluiceras) cf. aberlei* (Redtenbacher, 1873).
NMB D1147. $\times 1$.

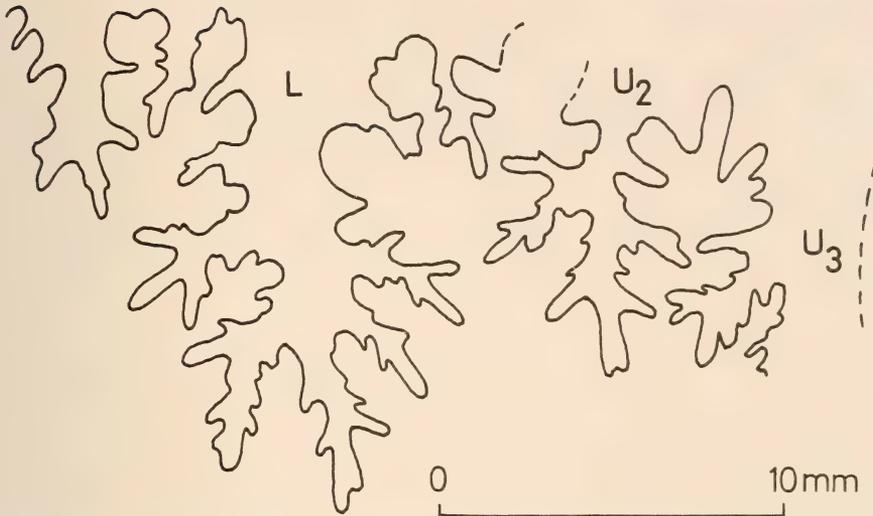


Fig. 91. *Peroniceras (Zuluiceras) cf. aberlei* (Redtenbacher, 1873). Suture-line of NMB D1147.

furcating, prorsiradiate ribs. On the outer whorl, ornament is coarser and the umbilical tubercles are very prominently rounded to slightly auricular.

The suture is highly incised and of the *P. (P.) dravidicum* type (Fig. 91).

Discussion

Redtenbacher based this species on a series of specimens; a cast of one of these is here illustrated as Figure 92A. A full discussion of the species is to be given in a forthcoming revision of the Gosau Fauna (Kennedy & Summesberger in preparation). *P. (Z.) aberlei* can be distinguished from the similarly compressed *P. (Z.) propoetidum* (Redtenbacher, 1873) and *P. (Z.) bajuvaricum* (Redtenbacher, 1873) by virtue of its fewer, coarser ribs and tubercles, more of which arise in pairs from the umbilical bullae. *P. (Z.) proteus* (Matsumoto, 1965) is much more coarsely ornamented than *P. (Z.) aberlei*.

Occurrence

Coniacian of western and southern Europe, and Zululand.

Peroniceras (Zuluiceras) bajuvaricum (Redtenbacher, 1873)

Figs 92B–C, 93

Ammonites bajuvaricus Redtenbacher, 1873: 107, pl. 24 (fig. 2a–c).

Gauthiericeras bajuvaricum (Redtenbacher): de Grossouvre, 1894: 88, pl. 9 (fig. 1), pl. 12 (figs 2a–b, 3a–b), text-fig. 35.

Schloenbachia (Gauthiericeras) bajuvarica (Redtenbacher): Boule, Lemoine & Thévenin, 1907: 22, pl. 12 (fig. 1–1a), text-fig. 22.

Gauthiericeras bajuvaricum (Redtenbacher): Diener, 1925: 152 (with synonymy).

Gauthiericeras bajuvaricum (Redtenbacher) var. *skoenbergensis* Venzo, 1936: 105, pl. 9 (fig. 5), pl. 11 (fig. 7).

Sornayceras bajuvaricum (Redtenbacher): Matsumoto, 1965: 226 et seq.

Sornayceras omorii Matsumoto, 1965: 230, pl. 42 (figs 1–2), text-figs 13–15.

Sornayceras aff. *bajuvaricum* (Redtenbacher): Szász, 1976: 208, pl. 5 (fig. 2).

Sornayceras cf. *bajuvaricum* (Redtenbacher): Atabekjan & Akopjan, 1972: 10, pl. 3 (figs 4–5).

Type specimen

The lectotype is Redtenbacher's (1873 pl. 24 (fig. 2a–c)) original figured specimen from the Gosau Beds of Austria, designated by Reymont (1958: 43).

Material

NMB D1059 and SAS A343 from locality 72, degraded river cliff and northern banks of the Mzinene River downstream of the Munywana River, Zululand, St. Lucia Formation, Coniacian II or III. SAS Z1632a–b from locality 92, bulldozer scrapings and adjacent hillslopes around pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II or III.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z1632a	55,0	16,0(29,1)	19,0(34,5)	0,84	22,0(40,0)	11 × 2:18 × 2
Z1632b	60,0	17,0(28,3)	21,0(35,0)	0,85	23,0(38,3)	21:31
A343	77,0	19,0(24,7)	26,0(33,8)	0,73	30,0(39,0)	—
D1059	87,0	23,0(26,4)	32,0(36,8)	0,71	35,0(40,2)	—

Description

Coiling is involute with an umbilical diameter of about 38 to 40 per cent of the total diameter, each whorl covering the ventral third of the preceding one. The whorl section is compressed throughout, with flat parallel flanks and a fastigiate venter. The venter bears a strong central keel bounded on either side by a slight depression. There are weak lateral ridges that cannot be termed true lateral keels. The umbilical wall is vertical to overhanging.

Ornament consists of weak umbilical bullae connected to clavate to rounded ventrolateral tubercles by numerous single and bifurcating ribs.

The suture-line is complex with narrow-stemmed saddles of the *P. (P.) dravidicum* type (Fig. 93).

Discussion

In Zululand the species is easily identified by the narrow umbilicus, high, compressed whorl section, unicarinate, fastigiate venter, and ornament consisting of single and bifurcating ribs.

Venzo (1936: 105–106) commented on the simplicity of the suture-line, but sutures that he described appear to be those of juveniles. Suture-lines of specimens of *P. (P.) dravidicum* taken at similar diameters (Fig. 35) appear identical

and there can be no doubt that this is, indeed, a representative of *P. (Zuluiceras)*.

Pending the revision of the Gosau material, a discussion of the affinities of the species is omitted, except that the possibility exists that a number of superficially similar, compressed species such as *P. (Z.) omorii* (Matsumoto) (1965: 230, pl. 42 (figs 1a-b, 2a-b)) and *P. (Z.) isamberti* (Fallot) (1885: 232, pl. 2 (fig. 1)) may be mere variants of the species or subspecies only. *P. (Z.) aberlei* is more sparsely ribbed on the outer whorls, as is *P. (Z.) propoetidum* (Redtenbacher, 1873).

Occurrence

Middle Coniacian of western and southern Europe, Armenia and possibly Japan; Coniacian II of Zululand.

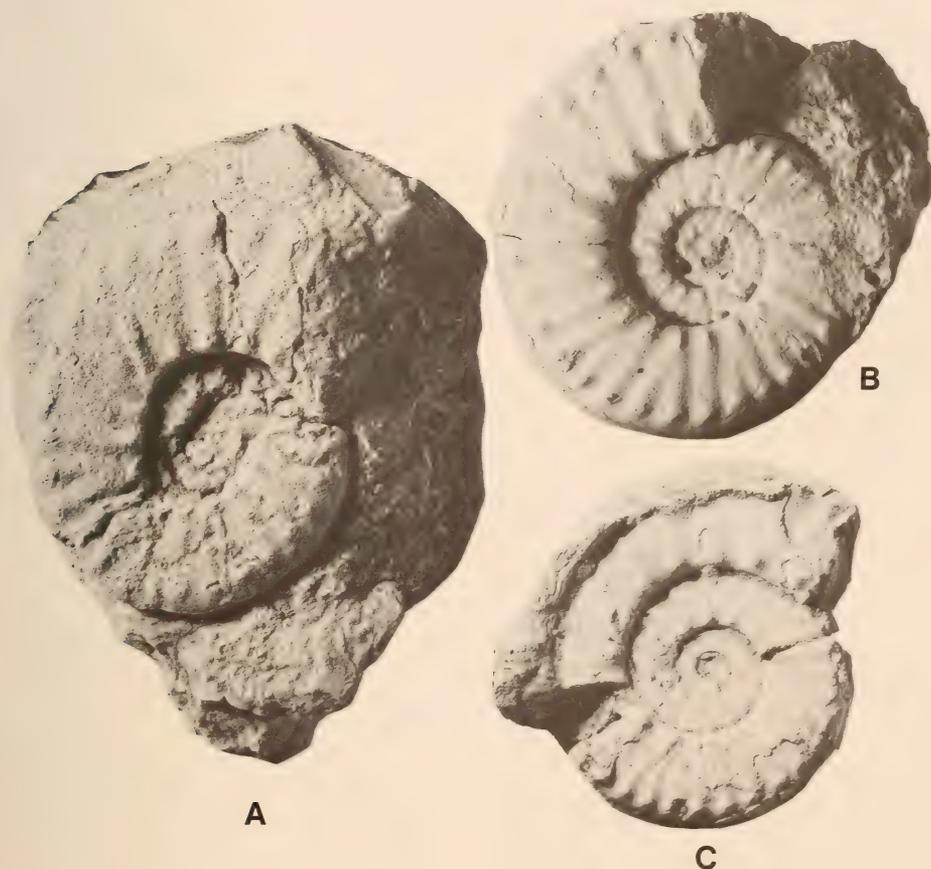


Fig. 92. A. *Peroniceras (Zuluiceras) aberlei* (Redtenbacher, 1873). Cast of one of Redtenbacher's original specimens from the Oberösterreichisches Landesmuseum, Linz. B-C. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). B. SAS Z1632a C. SAS A343. All $\times 1$.

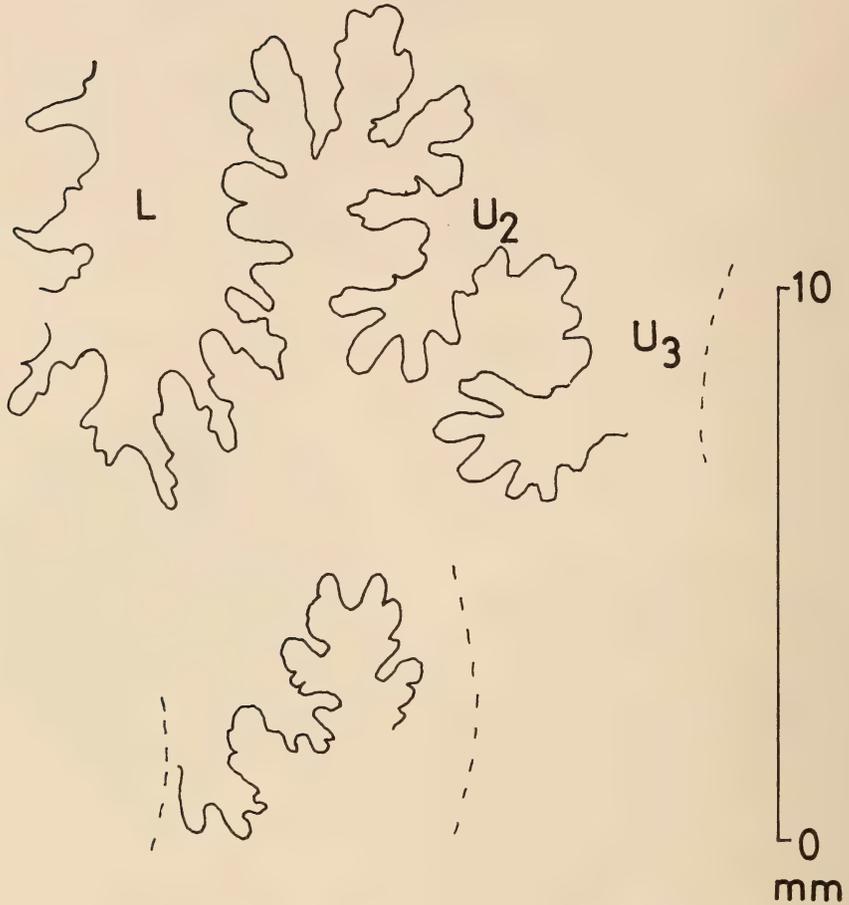


Fig. 93. *Peroniceras* (*Zuluiceras*) *bajuvaricum* (Redtenbacher, 1873).
Suture-lines of SAS Z1632a.

Genus *Gauthiericeras* de Grossouvre, 1894

(= *Ciryella* Wiedmann, 1960: 763; *Andersonites* van Hoepen, 1965: 29; *Fluminites* van Hoepen, 1965: 31; *Hluhluweoceras* van Hoepen, 1965: 33; *Falsebayites* van Hoepen, 1965: 34)

Type species

Ammonites margae Schlüter, 1867: 29, pl. 5 (fig. 2) by original designation of de Grossouvre, 1894: 87.

Diagnosis

Medium sized to large, moderately evolute to involute, whorl section depressed to compressed, trapezoidal to quadrate with strong, entire, undulating or serrated siphonal keel flanked by a groove on either side, the outer edge of



Fig. 94. *Gauthiericeras margae* (Schlüter, 1867). Holotype, the specimen figured by Schlüter (1867, pl. 5 (fig. 2)). $\times 0.6$. (See also fig. 19c.)

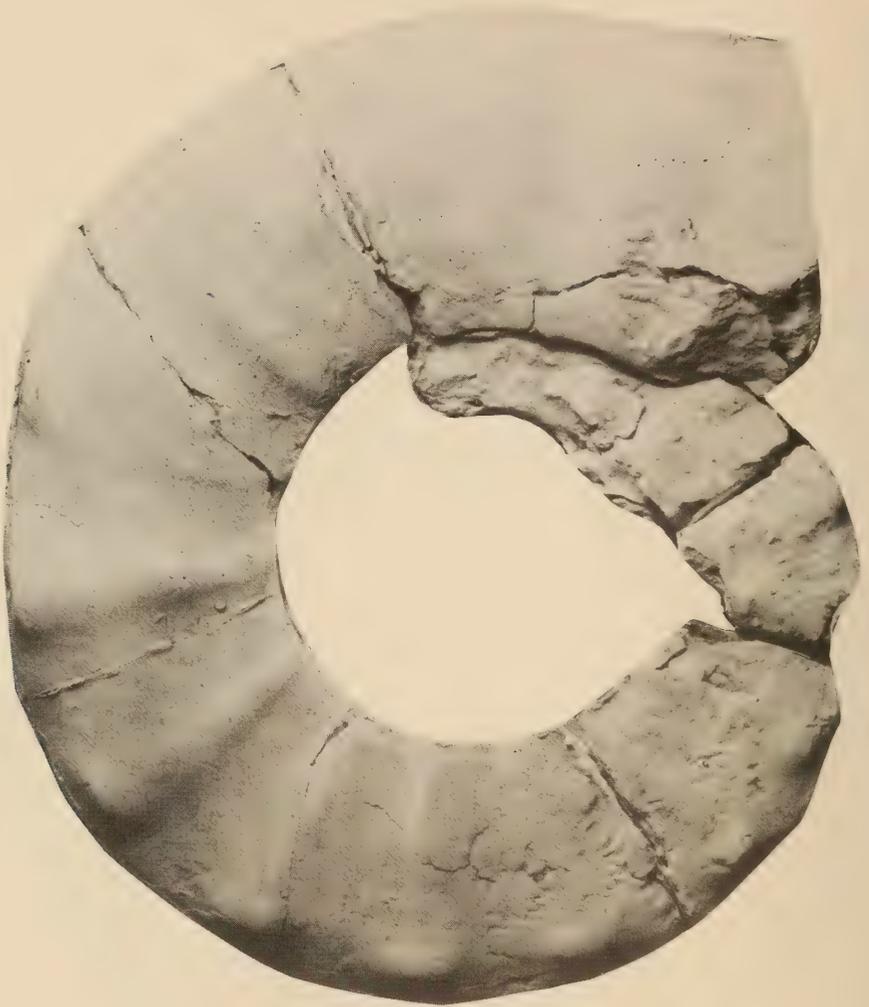


Fig. 95. *Gauthiericeras margae* (Schlüter, 1867). Holotype, the specimen figured by Schlüter (1867, pl. 5 (fig.2)). $\times 0.6$.

which may be strengthened into a low ridge, but not a lateral keel. Strong ribs arise from umbilical bullae in pairs or singly and may branch again from inner to mid-lateral bullae, if present. Shorter intercalated ribs sometimes present. All ribs terminate in strong ventrolateral clavi.

Suture rather simple, with little-incised elements; saddles square.

Discussion

Gauthiericeras is easily distinguished from other peroniceratids by its strong siphonal keel, lack of true lateral keels, strong ribs and the presence, in the type

species and some others, of a lateral tubercle. Persistent ornament and paired or branching ribs distinguished it from *Ishikariceras*.

Wiedmann (1960: 763, pl. 8 (figs 1–4), text-fig. 16) introduced the subgenus *Gauthiericeras* (*Ciryella*), type species *G. (C.) vascogoticum*. The original diagnosis is as follows: 'Coquille à enroulement extrêmement évolutive qui laisse voir les tubercles marginaux. Section de tours rectangulaire. Les côtes restent simples et serrées chez l'adulte et sont munies d'un tubercle ombilical allongé dans le sens de la côte et d'un tubercle marginal en massue. Au stade jeune, les côtes qui couvrent seulement les flancs sont bifurquées sur le tubercle ombilical ou simples. Région siphonale tectiforme et avec une carène siphonale entière. Cloisons, comme *Gauthiericeras* et *Peroniceras*.'

In Wiedmann's discussion, *Ciryella* was suggested as an intermediate form between *Gauthiericeras* and *Peroniceras*, with the general coiling and evolute umbilicus of the latter (U = 40 % at D = 42 mm, 51 % at D = 73 mm, and 52 % at D = 125 mm) and similar ribbing. The features recalling *Gauthiericeras* were said to be the single, entire siphonal keel.

Wiedmann gave the age of his species as Lower Coniacian, and it is based on a specimen recorded by Ciry (1940: 217). As discussed previously (p. 128), the earliest Coniacian ammonite zone recognized by Wiedmann in his 1960 paper and subsequently, that of *Tissotioides haplophyllus*, would appear to be Middle Coniacian, while Wiedmann's Zone III of *Gauthiericeras vallei*, also placed in the Lower Coniacian in 1960, is Upper Coniacian. It is suggested here that *Ciryella* is actually an Upper Coniacian form. It differs from *Gauthiericeras* only in being very evolute, yet specimens of *Gauthiericeras margae* from France have U = up to 42 %. *G. nouelianum* (d'Orbigny, 1850) has U = as little as 20 % and *G. obesum* van Hoepen, 1955, has U = up to 46.5 %. *Ciryella* thus stands in the same relationship to *Gauthiericeras* as does *Peroniceras* (*Peroniceras*) to the more involute *P. (Zuluiceras)*, but without the distinctive differences in ornament shown by these two subgenera. At most it is a subgenus of *Gauthiericeras*, and even this seems unnecessary.

Van Hoepen (1965) was led astray by the wide extent of intraspecific variation shown by the Zululand *Gauthiericeras*, the numbers of which by far exceed that of all other described *Gauthiericeras* collections. This led to his erection of a series of genera: *Andersonites*, *Hluhluweoceras*, *Falsebayites*, and *Fluminites*. In 1970 and 1971 low water-levels in False Bay permitted the authors to collect a range of material *in situ*, on the basis of which it is possible to demonstrate a series from very evolute individuals close to *G. roquei* (Peron, 1897) via more narrowly umbilicate forms referred to *G. obesum* van Hoepen, 1955, to narrowly umbilicate forms with rapidly expanding whorls that include Van Hoepen's *Andersonites*, *Falsebayites*, and *Hluhluweoceras*, the type species of which are all regarded as synonyms, the name *Gauthiericeras* [*'Andersonites'*] *listeri* van Hoepen, 1965, having priority. The type species of *Fluminites*, *F. albus* van Hoepen, 1965, is retained as a further species of *Gauthiericeras*, allied to a very involute species *G. albiforme* sp. nov. *Gauthiericeras libertae* van Hoepen,

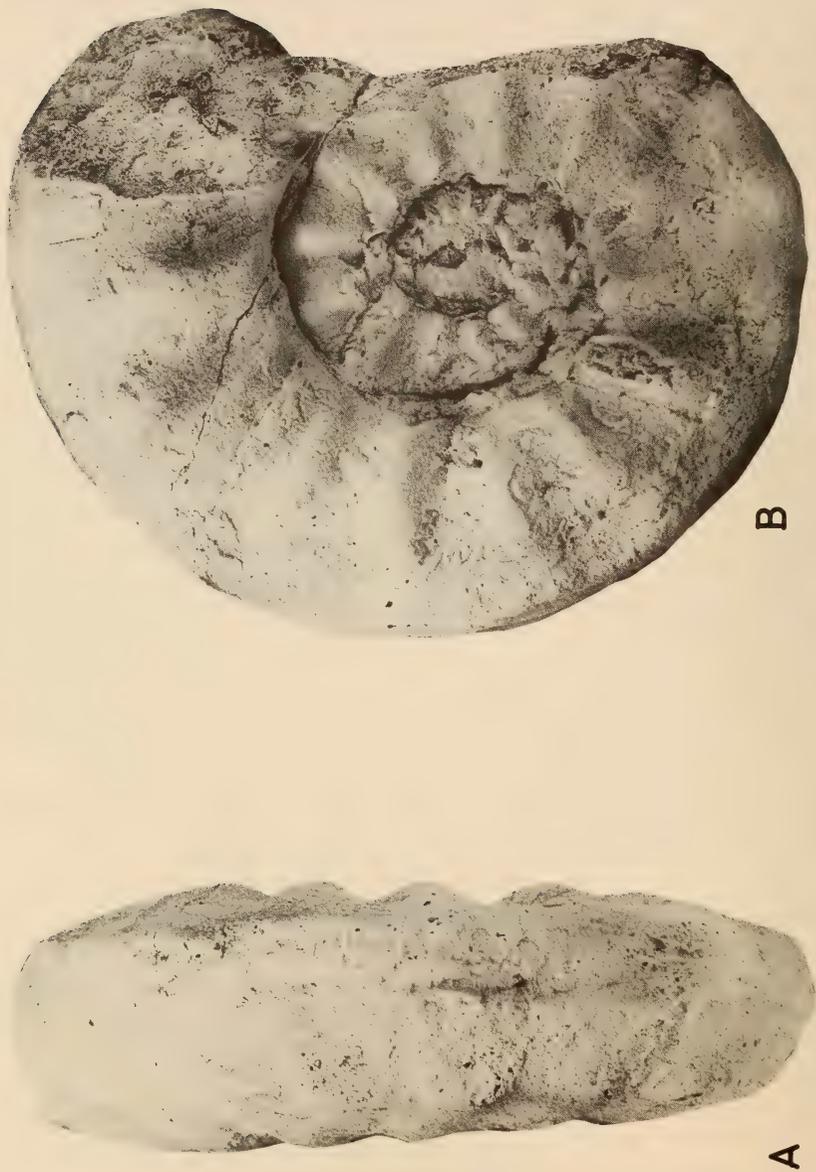


Fig. 96. *Gauthiericeras margae* (Schlüter, 1867). The specimen figured by Redtenbacher (1873, pl. 25 (fig. 1a-c)). $\times 1$.

1955, of which *G. planatum* van Hoepen, 1955 is a synonym, is also maintained as a separate species. *Gauthiericeras* shows a number of similarities to *Prionocycloceras* Spath, 1926, and, indeed, Spath (1926: 80) considered it as transitional between *Collignoniceras* and *Gauthiericeras*. The type species differ in the strong umbilical and lateral tubercles of *Gauthiericeras margae*, and the absence of the huge spines of adult *Prionocycloceras guyabanum*. Both share a simple suture and strongly serrated keel flanked by shallow grooves but, whereas the ribs extend from the ventrolateral tubercles to the siphonal keel in *Prionocycloceras*, they decline in *Gauthiericeras*. Many *P. guyabanum* specimens have fine intercalated flank ribs.

Some species show intermediate features, but the two genera are distinct.

Prionocycloceras may well be the link between Upper Turonian *Prionocyclus* and Upper Coniacian *Gauthiericeras*. Of species referred to *Gauthiericeras* by recent workers, *G. margae peruanum* Brüggem, 1910, is a *Forresteria* (*Forresteria*), as is *Gauthiericeras hoepeni* Collignon, 1965. Of Spanish species, *Gauthiericeras margae turzoi* Karrenberg, 1935, *G. margae gorda* Karrenberg, 1935, *G. vallei* Ciry, 1940, and *G. vallei gorda* Ciry, 1940, are *Prionocycloceras*.

Occurrence

Upper Coniacian of France, Spain, central Europe, north, east and west Africa, Madagascar, New Caledonia, Mexico, Colombia, and Peru. Middle Coniacian records are doubtful.

Gauthiericeras obesum van Hoepen, 1955

Figs 97–114

Gauthiericeras margae (Schlüter): Besairie, 1936: 203, pl. 24 (figs 17–18). Venzo, 1936: 104, pl. 10 (fig. 2). ? Collignon, 1965: 49, pl. 435 (fig. 1798).

Gauthiericeras obesum van Hoepen, 1955: 374, figs 25–28.

Type specimen

The holotype, by monotypy, is SAS Z12, (Figs 107–108), collected loose from the mouth of the Hluhluwe River, Zululand.

Material

SAS 85, 92/2, H200/33, H200/37, H200/76, H200/94, H200/109, SAS Z200, Z872–75, Z877, Z2015, Z2031, Z2035, BMNH C83760–C83790, and SAM-PCZ5947–50, from locality 83 locally known as Mason's Camp, Zululand, St. Lucia Formation, Coniacian IV. SAS H203/8, SAS Z12, SAM-PCZ5951 from boulder- and concretion-strewn slopes west of the St. Lucia Game Park fence, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV. SAS Z1055 and Z1057 from locality 73, degraded river cliffs and stream sections on north side of the Mzinene River downstream of the Munywana River,

Zululand, St. Lucia Formation, Coniacian IV. SAS A1510 and BMNH C83801–C83806 from locality 22, on the north side of the Nyalazi River near Nyalazi River Trading Store, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
A1754	98,0	35,0(35,7)	37,0(37,7)	0,95	38,0(38,8)	—:17
H200/76	81,0	27,0(33,3)	31,0(38,3)	0,87	31,0(38,3)	—:—
PCZ-5948	85,0	27,0(31,8)	30,0(35,3)	0,90	35,0(41,2)	18:18
H200/34	108,0	36,0(33,3)	40,0(37,0)	0,90	40,0(37,0)	—:—
PCZ5497	108,0	37,0(34,2)	42,0(38,9)	0,88	41,0(40,0)	—:17
PCZ5949	108,0	38,0(35,2)	39,0(36,1)	0,97	43,0(39,8)	10×2:10×2
Z200	123,0	45,0(36,6)	50,0(40,6)	0,90	48,0(39,0)	—:20
SAS-85	124,0	—	47,0(37,9)	—	48,0(38,9)	—:16
Z1055	127,0	40,0(31,5)	46,0(36,2)	0,87	53,0(41,7)	20:20
Z473	129,0	44,0(34,1)	47,0(36,4)	0,94	53,0(41,1)	17:—
H203/8	130,0	41,0(31,5)	47,0(36,1)	0,87	57,0(43,8)	18:18
H200/33	134,0	45,0(33,6)	48,0(35,8)	0,94	53,0(39,6)	—:—
Z1057	134,0	39,0(29,1)	45,0(33,6)	0,87	52,0(38,8)	21:21
Z873	140,0	48,0(35,0)	52,0(37,1)	0,92	52,0(37,1)	19:19
Z191	150,0	4,0(29,3)	51,0(34,0)	0,86	64,0(42,7)	16:—
Z12	150,0	52,0(34,7)	57,0(38,0)	0,91	59,0(39,3)	18:18
H200/94	164,0	—	61,0(37,2)	—	61,0(37,2)	17:18
Z2021	167,0	54,0(32,3)	58,0(34,7)	0,93	69,0(41,3)	—:—
Z872	167,0	55,0(32,9)	59,0(35,3)	0,93	67,0(40,1)	23:23
PCZ5950	185,0	59,0(31,9)	66,0(35,7)	0,82	76,0(41,1)	20:20
Z2035	190,0	58,0(30,5)	67,0(35,3)	0,87	82,0(43,2)	19:19
Z874	204,0	60,0(29,4)	71,0(34,8)	0,84	91,0(44,6)	21:21
92/2	221,0	—	71,0(32,1)	—	101,0(45,7)	—:—
Z2030	225,0	65,0(28,9)	74,0(32,9)	0,88	98,0(43,6)	18:18
92	235,0	70,0(29,8)	80,0(34,0)	0,87	103,0(43,8)	21:21
H200/109	237,0	73,0(30,8)	85,0(35,9)	0,86	100,0(42,2)	17:17
Z2015	245,0	72,0(29,4)	80,0(32,5)	0,90	106,0(43,3)	17:17
Z877	285,0	75,0(26,3)	90,0(31,6)	0,83	136,0(43,7)	19:19
PCZ5951	308,0	83,0(26,9)	101,0(32,8)	0,82	141,0(45,8)	18:18
Z875	311,0	83,0(26,7)	98,0(31,5)	0,85	144,0(46,3)	—:—

Description

The umbilical width of the species varies between 37 and 46 per cent of the total diameter, but the majority of specimens have umbilical widths of 39 to 44 per cent (Fig. 97). Coiling is very evolute and the whorls are only slightly overlapping, so that the dorsal zone of impression is very shallow. It appears that the more widely umbilicate specimens grew to a larger size than the more narrowly umbilicate ones, but this may possibly be only an artefact of preservation rather than an indication of dimorphism. The whorl section is compressed throughout, *Wb/Wh* ratios ranging from 0,82 to 0,97.

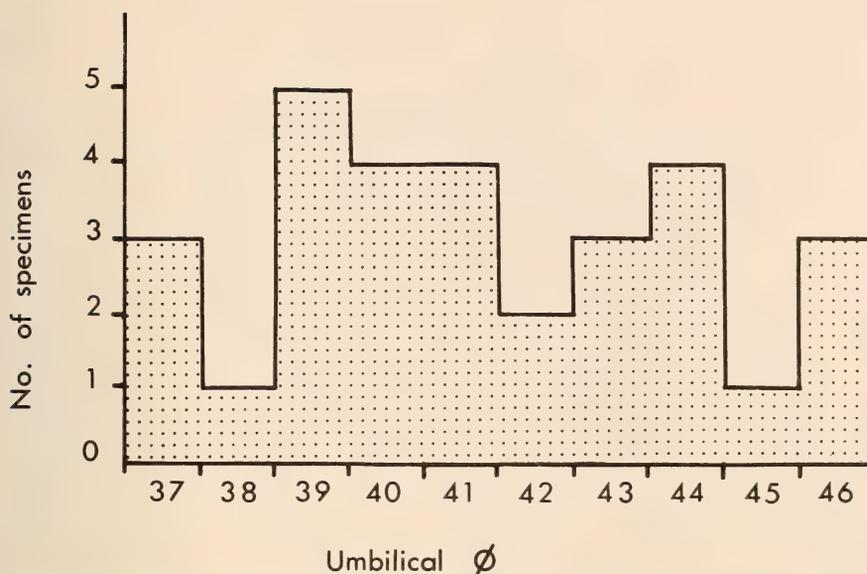


Fig. 97. Histogram illustrating distribution of umbilical width in Zululand population of *Gauthiericeras obesum* van Hoepen, 1955.

Density of ribbing in the population is reasonably constant, varying between 16 and 23 per whorl, but the majority of specimens have a rib density of 17 to 18 per whorl. Strength of ornament is variable, but this depends to some extent on preservation, and is often accentuated through abnormal thickening of the shell as a result of diagenetic growth of calcite. Specimen SAS Z473 (Fig. 98) has much of the inner whorls preserved. Here ornament consists of radial to slightly rursiradiate, very strong ribs, apparently all single, each bearing two rows of tubercles. The umbilical ones are pinched bullate, protruding far beyond the level of the ribs, especially in places where the shell has been thickened diagenetically. The ventrolateral tubercles are clavate and pointed, and lean against and impress into the umbilical wall of the succeeding whorl. On the outer whorls, the ventrolateral tubercles become weaker and rounded clavate, whereas the umbilical tubercles remain prominently bullate and merge into the ribs.

Differences in strength of ornament in the adult stage become obvious when comparing specimens SAS Z869 (Fig. 99) and SAS Z2030 (Fig. 100), the latter with strong ribbing and tuberculation, and the former with virtually smooth flanks.

Some specimens retain the body chamber (e.g. SAM-PCZ5951) (Figs 101-102), consisting of about three-quarters of a whorl. Here ribbing becomes bolder and wider spaced. The umbilical bullae may disappear completely, fusing with the rib. The ribs may also curve gently forward or become slightly sinuous.

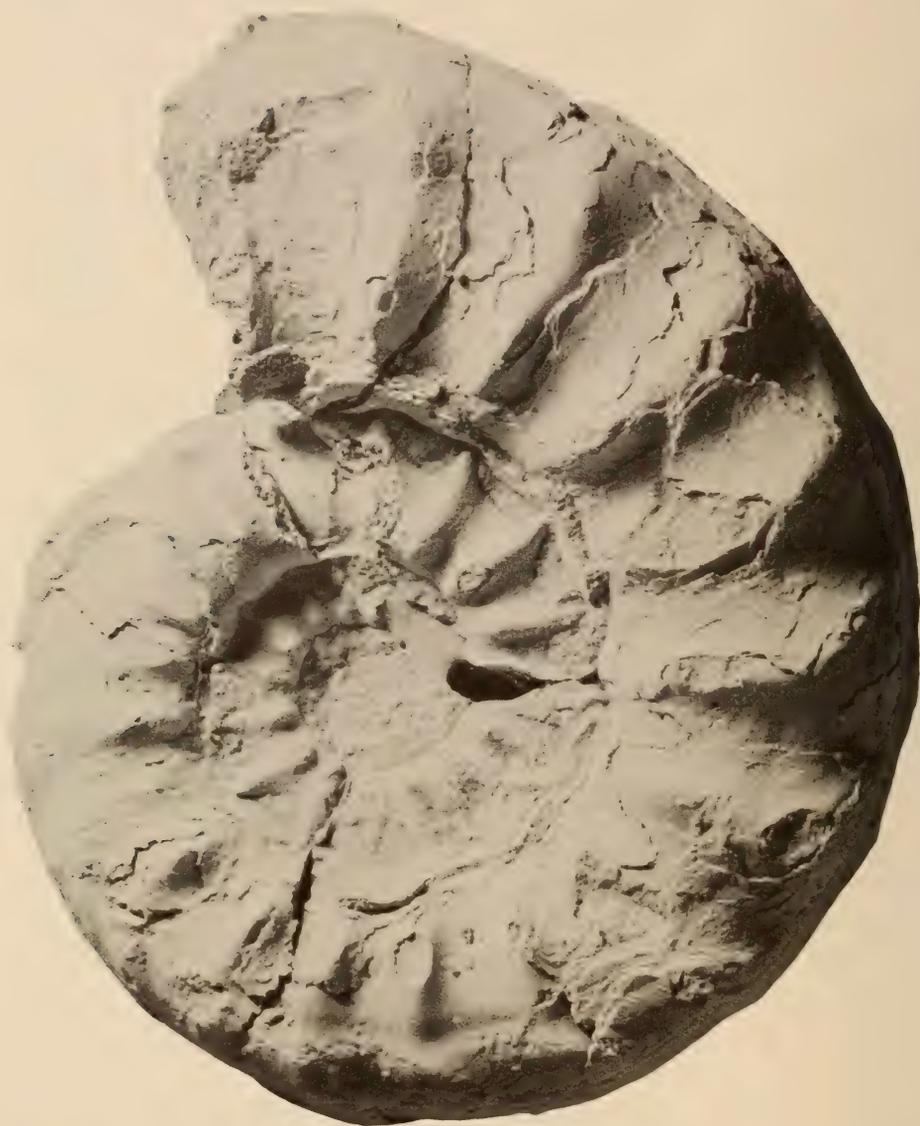


Fig. 98. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z473. Specimen with part of inner whorls preserved, showing early strong ornament. $\times 1$.



Fig. 99. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z869. Specimen with weak ornament compared to Figure 100. $\times 0,67$.

A very large body chamber fragment, NMB D1060 (Fig. 103), with two strong ribs but distinct umbilical and ventrolateral tubercles, may belong here or perhaps to *G. listeri* described below.

The suture lines are very simple as shown in Figures 99–100, and 105.

Discussion

Gauthiericeras obesum most closely resembles the type species, *G. margae* (Schlüter, 1867). Schlüter's figure is highly idealized, and a cast of the basis of Schlüter's figure is shown in Figures 20C and 94–95. The outer whorl is crushed almost flat and the inner whorls survive only as an external mould. A topotype specimen, also in Schlüter's collection, the specimen figured by Redtenbacher (1873: 109, pl. 25 (fig. 1a–c)) from the Gosau Beds of Austria, De Grossouvre's material (1894: 90, pl. 15 (figs 1–2)) (see Fig. 96 herein), plus new material from Touraine show that *G. margae* differs from *G. obesum* in several respects. The ribs commonly arise from bullae in pairs in juveniles, a feature not seen in *G. obesum*; there is a lateral tubercle from which the ribs also branch, and the siphonal keel is strongly serrated. Adults are more closely comparable but, whereas the umbilical bullae perch on the umbilical shoulder in *G. obesum*, they migrate outward to an inner flank position in *G. margae*.

G. nouelianum (d'Orbigny, 1850) has been illustrated by Sornay (1955); it is much more involute than *G. obesum* ($U = 20\text{--}27,5\%$; see Kennedy in press for details). It co-occurs with *G. margae* and, like that species, has branching ribs, lateral tubercles, and a serrated keel, all of which render it easily separable from *G. obesum*. *G? boreau* (de Grossouvre) (1894: 111, pl. 7 (fig. 3)) is a diminutive species, involute, feebly and flexuously ribbed, and lacks ventrolateral tubercles.

Gauthiericeras roquei Peron, 1897: 52, pl. 8 (fig. 1), pl. 9 (figs 1–2), pl. 17 (fig. 6)) (Fig. 115 herein) is a very evolute species ($U = 43\text{--}44\%$). Ornament is very distant, with only ten ribs on the outer whorl compared with nearly double that number in similarly evolute *G. obesum*.

Gauthiericeras listeri (van Hoepen, 1965), of which *Hluhluweoceras fugitivum* van Hoepen, 1965, *Falsebayites peregrinus* van Hoepen, 1965, and *Gauthiericeras listeriforme* Collignon, 1965, are synonyms, is a contemporary of *G. obesum*. It differs in being more involute ($U = 32\text{--}36\%$) with a compressed whorl section in most specimens. It stands in the same relationship to *G. obesum* as does *G? nouelianum* to *G. margae*. These involute and evolute forms may be dimorphs, but this cannot be proven.

Occurrence

Coniacian IV of Zululand. Upper Coniacian *Gauthiericeras margae* and *Prionocycloceras guyabanum* Zone of Madagascar.



Fig. 100. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z2030.
Specimen with strong ornament compared to Figure 99. $\times 0,63$

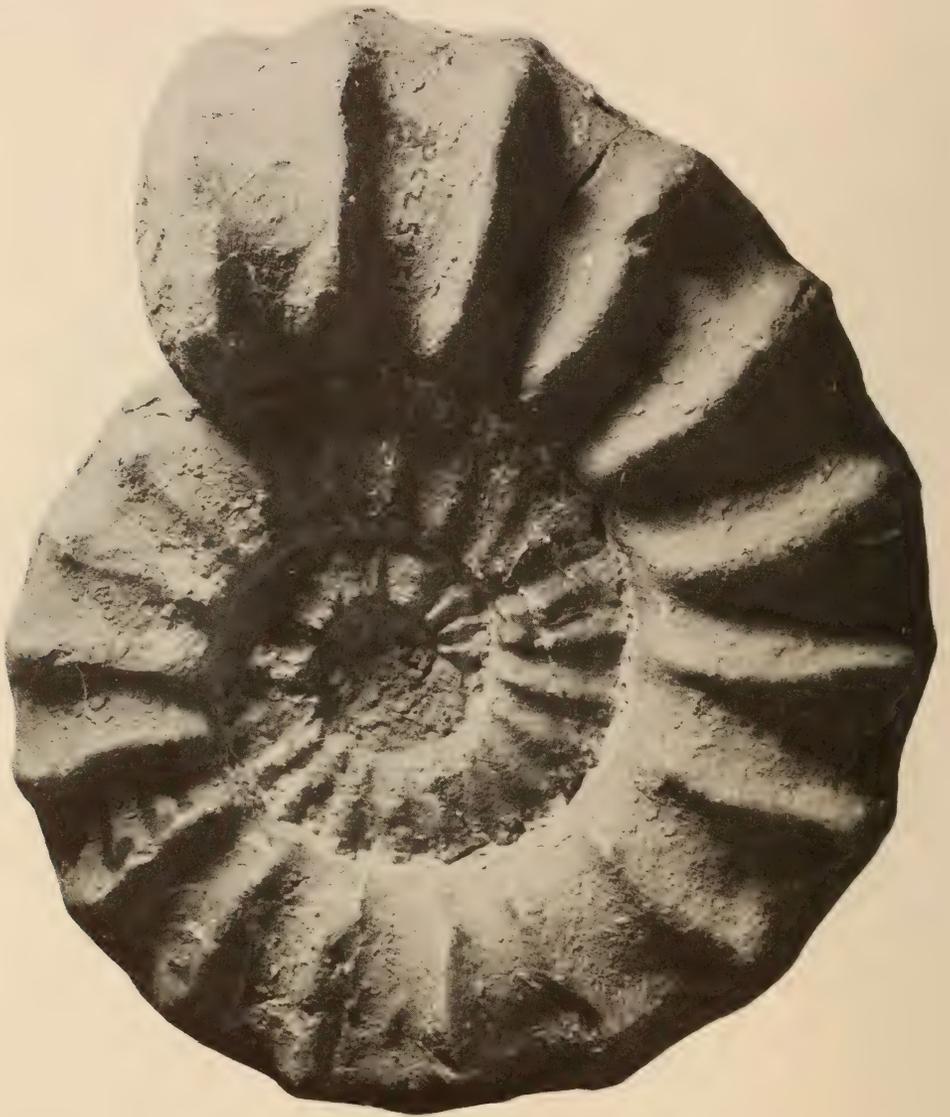


Fig. 101. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5951. Large, evolute specimen with body chamber up to three-quarters of a whorl in length. $\times 0,48$.



Fig. 102. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5951, dorsal views of two sections of the body chamber. $\times 0,6$



Fig. 103. ?*Gauthiericeras obesum* van Hoepen, 1955. NMB D1060, large body chamber fragment. $\times 0.72$.



Fig. 104. *Gauthiericeras obesum* van Hoepen, 1955. SAS A1510. Individual differing from most Zululand specimens in showing numerous rib bifurcations. $\times 0.82$.



Fig. 105. *Gauthierceras obesum* van Hoepen, 1955. SAS Z877, large specimen with wide umbilicus. $\times 0,5$.



Fig. 106. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z877, large specimen with wide umbilicus. $\times 0,61$.

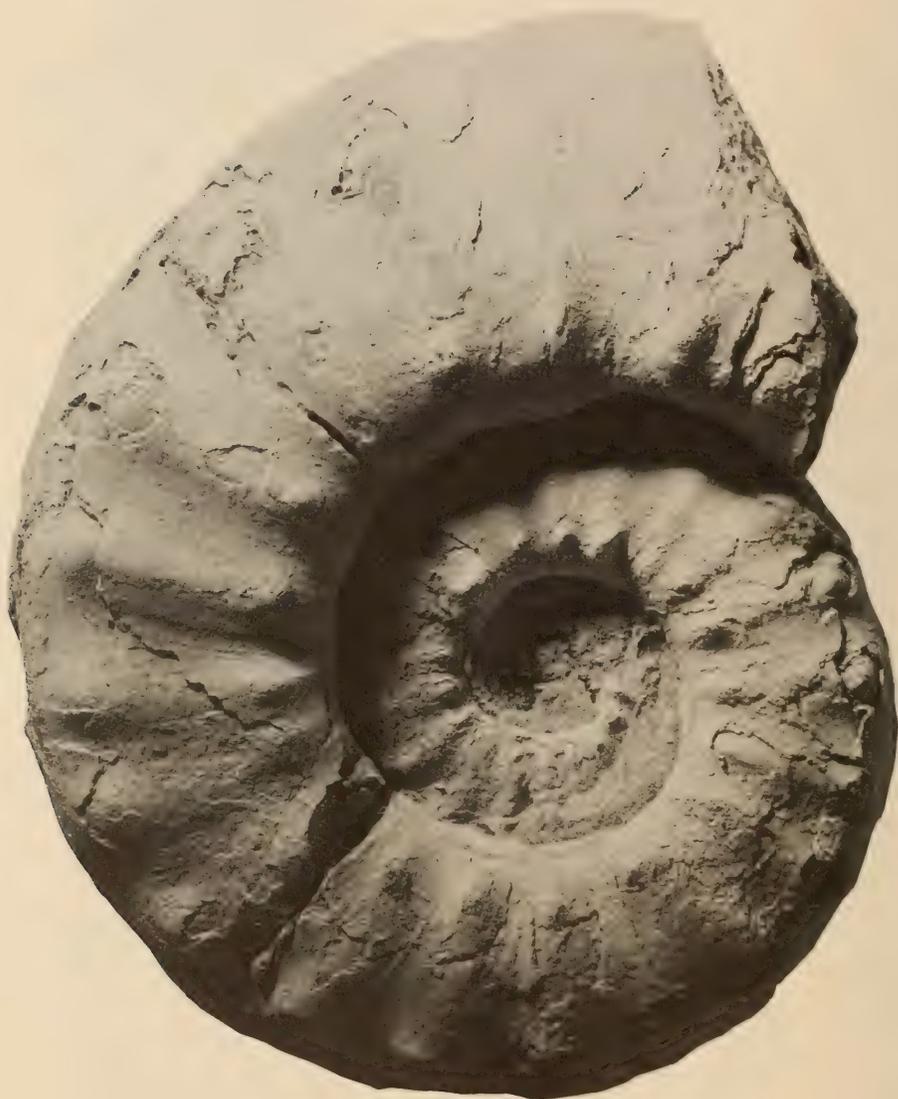


Fig. 107. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z12, the holotype. $\times 0,8$.



Fig. 108. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z12, the holotype. $\times 1$.

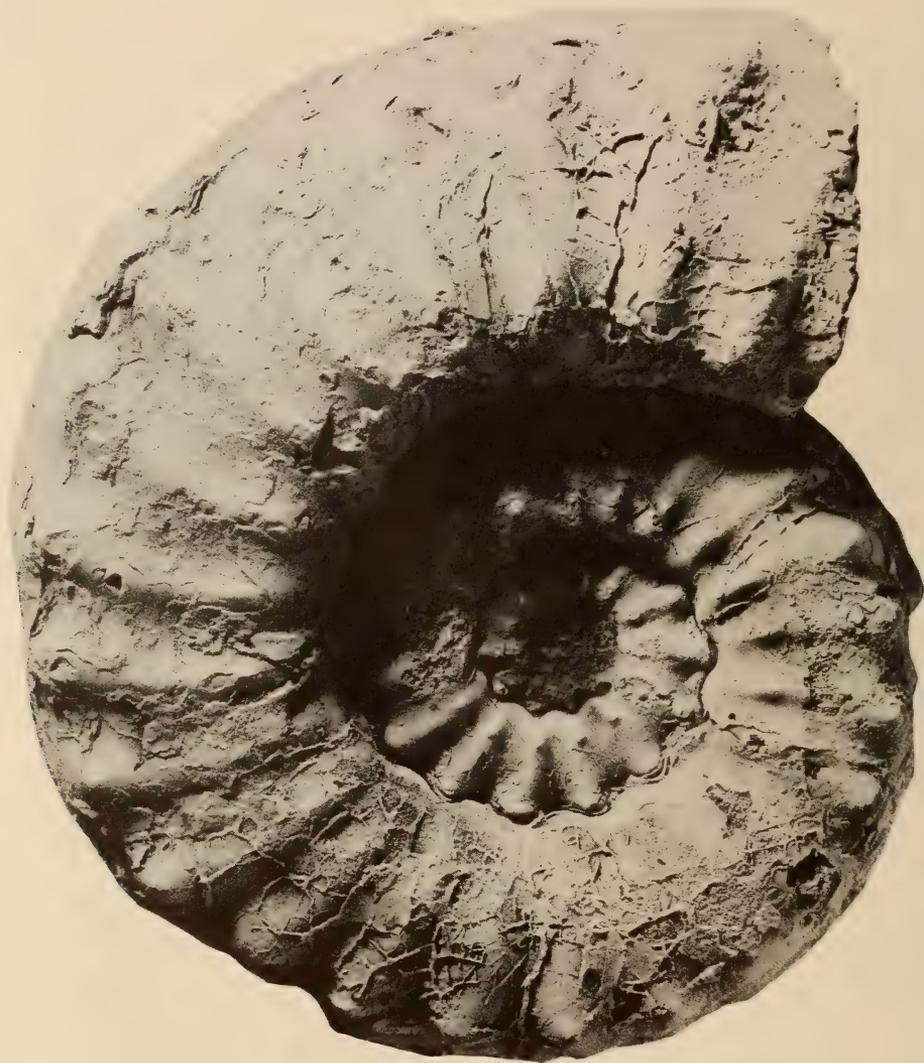


Fig. 109. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z872. $\times 0,88$.



Fig. 110. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z872. $\times 1$.

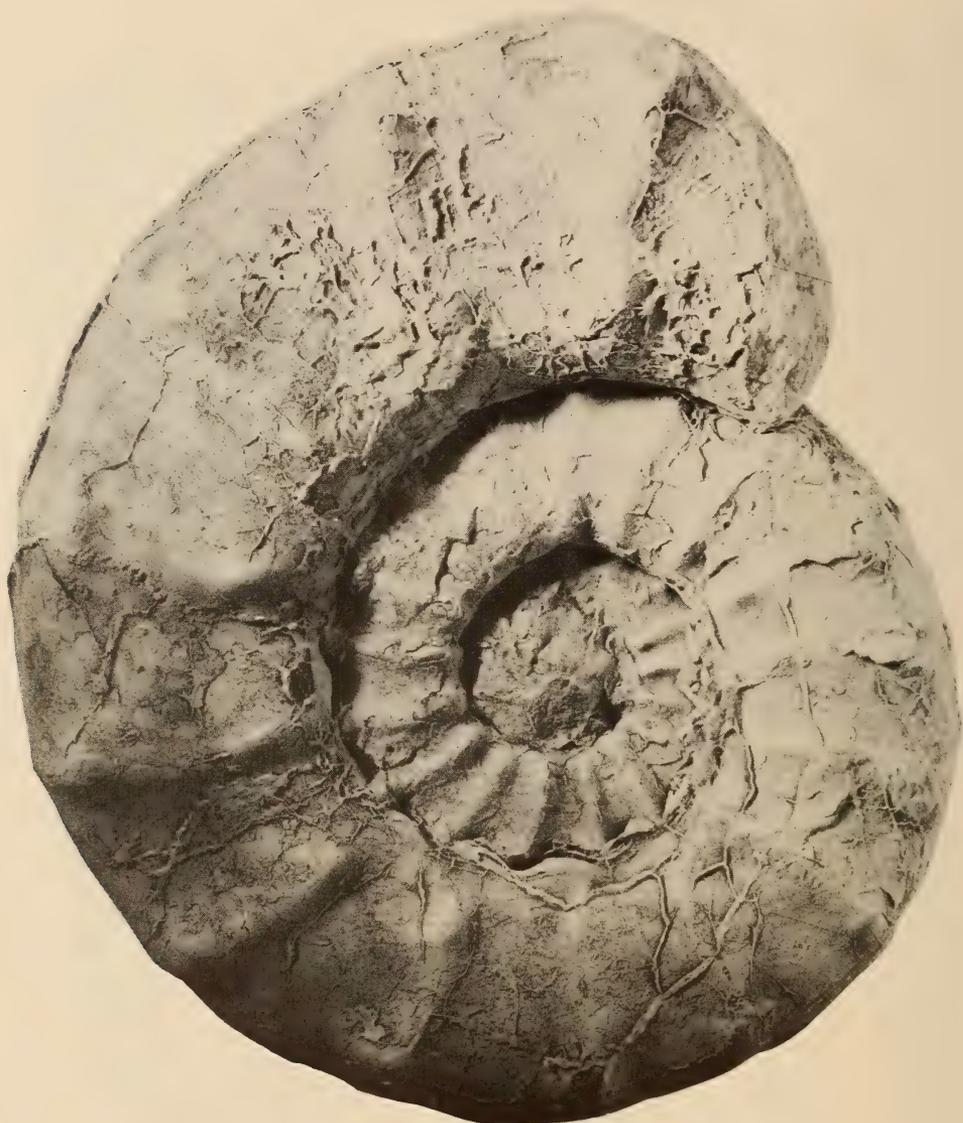


Fig. 111. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z2015. $\times 0.6$.

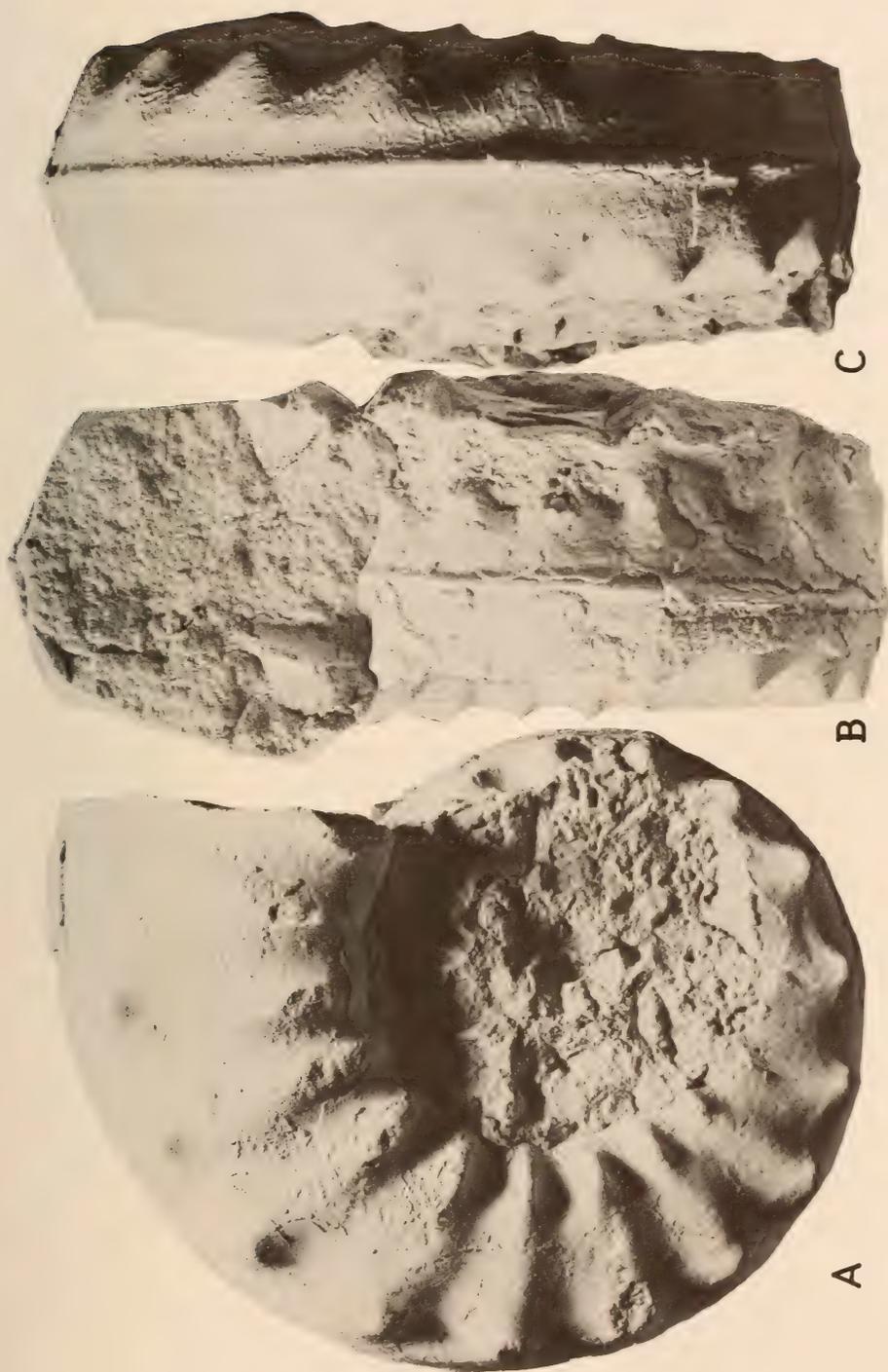


Fig. 112. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5497. $\times 1$.

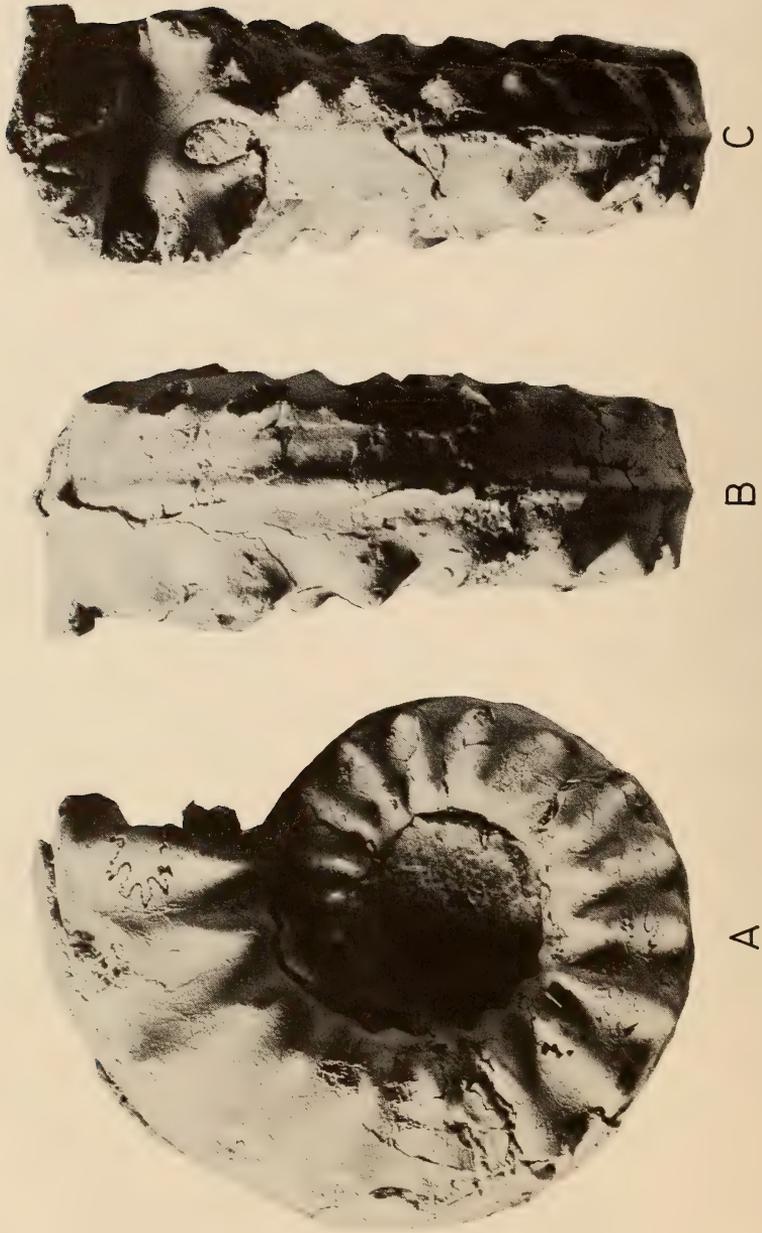


Fig. 113. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5948. $\times 1$.

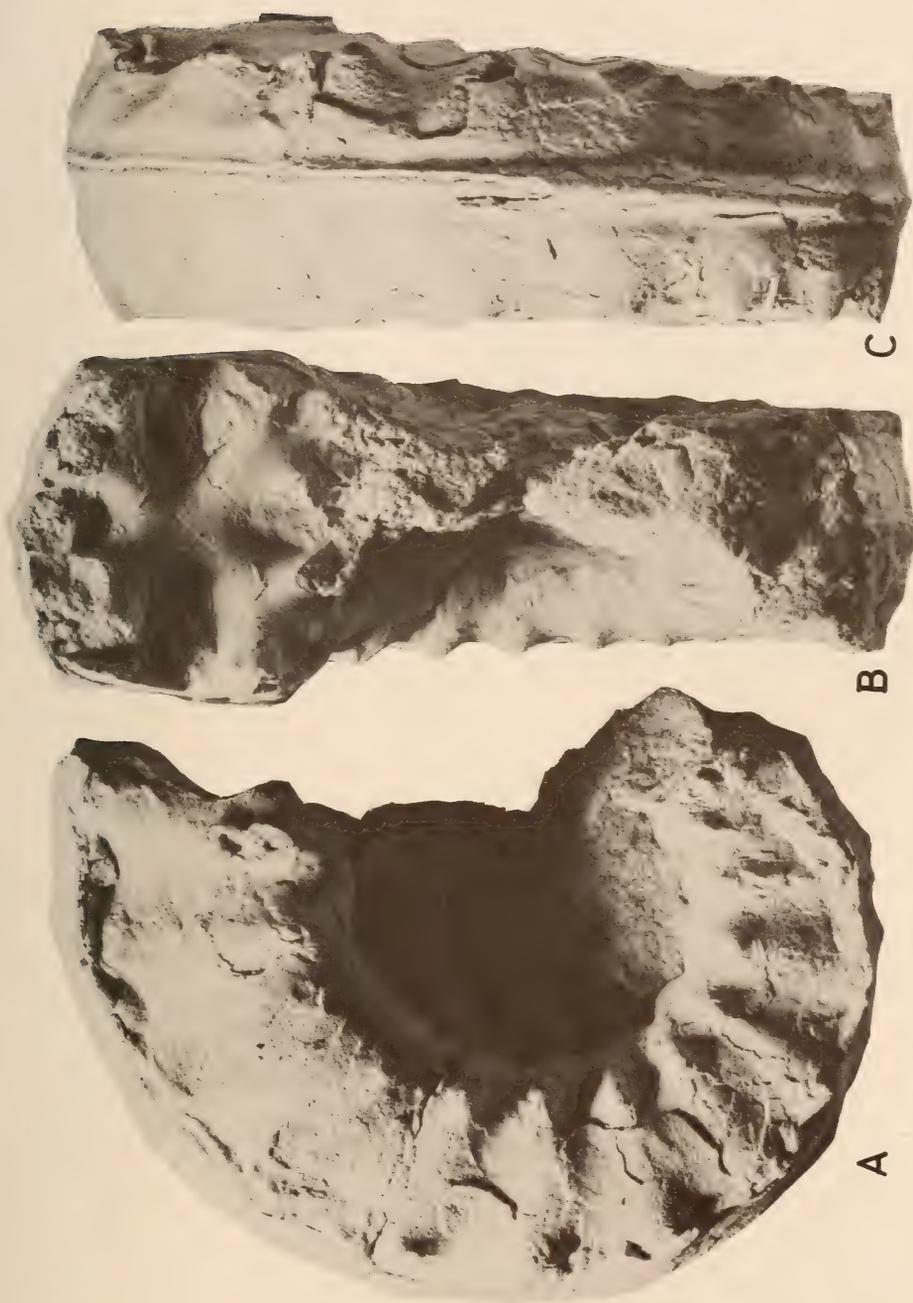


Fig. 114. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5940. $\times 1$.



Fig. 115. *Gauthiericeras roquei* Peron. (After Peron, 1896, pl. 8 (fig. 1). Reduced.)

Gauthiericeras listeri (van Hoepen, 1965)

Figs 116–123

- Andersonites listeri* van Hoepen, 1965: 31, pl. 23, text-fig. 8b, d.
Hluhluweoceras fugitivum van Hoepen, 1965: 33, pl. 25, text-fig. 8a, c.
Falsebayites peregrinus van Hoepen, 1965: 34, pl. 26, text-fig. 9f–g.
Gauthiericeras listeriforme Collignon, 1965: 49, pl. 435 (fig. 1797).

Type specimens

The holotype, by original designation, is SAS Z754 (Figs 116–117B), from locality 91, degraded river cliffs and artificial cut west of the boundary fence of St. Lucia Game Reserve, east-south-east of Hluhluwe, Zululand. This area is strewn with rubble derived from the St. Lucia Formation, Coniacian IV and V, and the precise horizon cannot be stated. The holotype of *Hluhluweoceras fugitivum* is SAS Z755, from the same horizon as the holotype of *Gauthiericeras listeri*. The holotype of *Falsebayites peregrinus* is SAS Z341, the paratype is SAS Z339, both from a little to the north of the previous site. Their precise horizon is similarly uncertain.

Material

SAS H206/2, a topotype, was also collected loose; SAS Z342 is from 'close by'. BMNH C83791 is from locality 83, where it is firmly dated as Coniacian IV.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
H206/2	119,0	42,0(35,3)	48,0(40,3)	0,87	43,0(36,1)	18:19
Z755	180,0	65,0(36,1)	71,0(39,4)	0,91	64,0(35,6)	—
Z341	c.190,0	c.68,0(35,8)	c.72,0(37,9)	c.0,94	c.65,0(34,2)	—
Z754	195,0	74,0(37,9)	73,0(37,4)	1,01	70,0(35,9)	—
<i>G. listeriforme</i> (after Collignon)	102,0	47,0(46,0)	42,0(41,2)	1,12	35,0(34,3)	9:10

Description

The whorls expand rapidly and the umbilicus is narrow, comprising 32 to 36 per cent of the total diameter. The whorl section is compressed in the majority of specimens but may become slightly depressed on the later septate whorls. The umbilical wall is generally rounded, the flanks are very little inflated, and the venter is broadly rounded.

Only one specimen has the inner whorls preserved (SAS H206/2 Fig. 122). The ventrolateral tubercles are concealed in the umbilical seam and the umbilical tubercles are displaced somewhat up the flanks, as in *G. margae*. They are conical to radially elongated, but very irregularly developed. Intercalatory ribs, which do not bear umbilical tubercles, sometimes occur.



Fig. 116. *Gauthiericeras listeri* (van Hoepen, 1965). Holotype SAS Z754. $\times 1$.



Fig. 117. *Gauthiericeras listeri* (van Hoepen, 1965). A. SAS Z342, inner whorls of paratype of *Falsebayites peregrinus* van Hoepen. $\times 1$. B. SAS Z754, inner whorls of holotype of *G. listeri*. $\times 2$.



Fig. 118. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z342, paratype of Van Hoepen's *Falsebayites peregrinus*. $\times 0,64$.



Fig. 119. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z342, paratype of Van Hoepen's *Falsebayites peregrinus*; section on body chamber showing fastigate venter and slight constriction. $\times 1$.



Fig. 120. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z341, holotype of Van Hoepen's *Falsebayites peregrinus*. $\times 1$.



Fig. 121. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z755. Holotype of Van Hoepen's *Hluhluweoceras fugitivum*. $\times 0,71$.

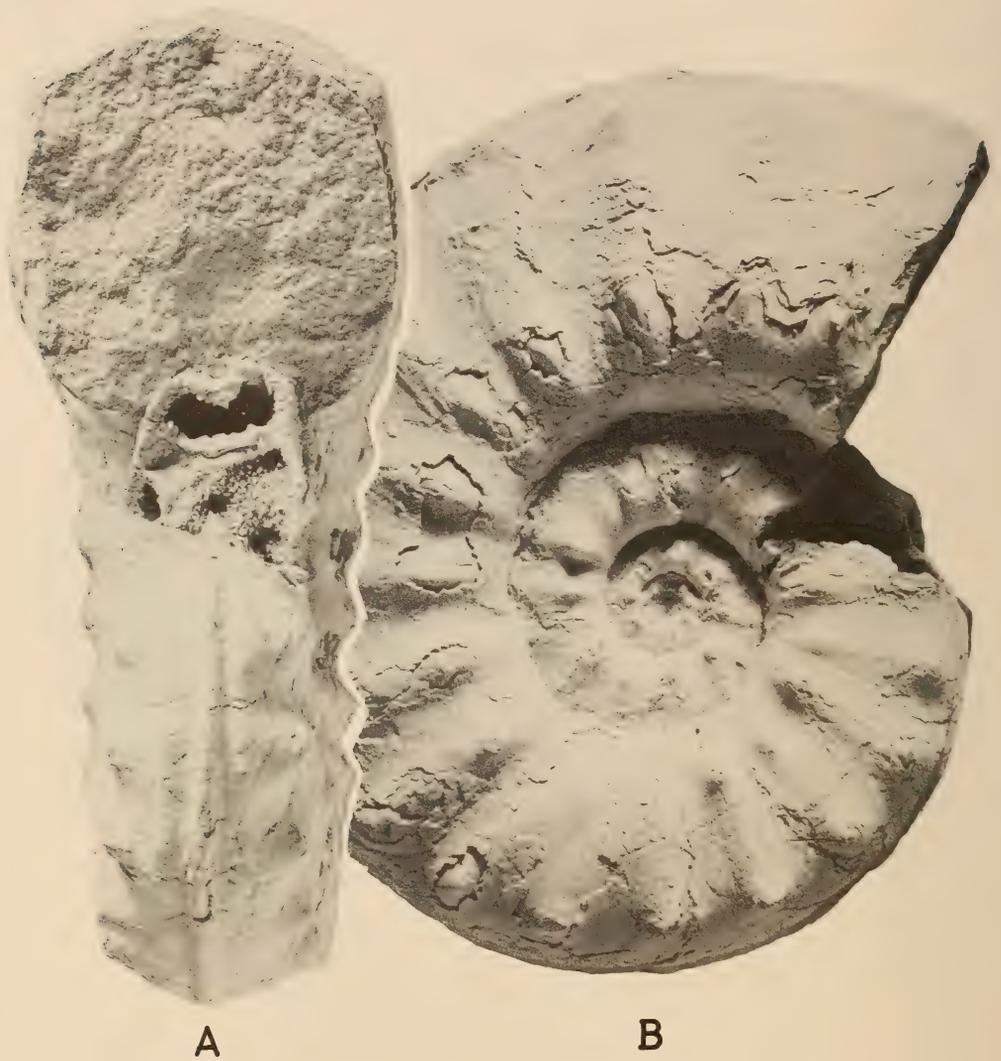


Fig. 122. *Gauthiericeras listeri* (van Hoepen, 1965). SAS H206/2, specimen showing early whorls. $\times 1$.

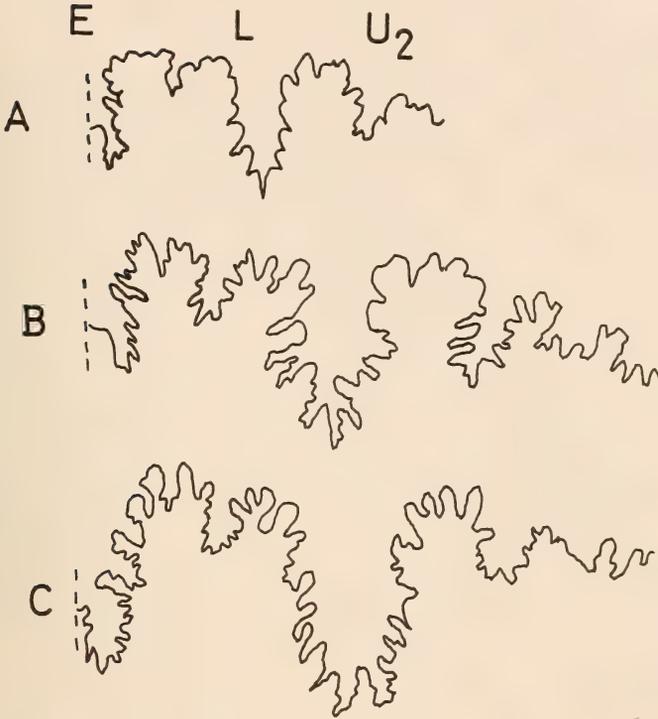


Fig. 123. *Gauthiericeras listeri* (van Hoepen, 1965). Suture-lines of Z755, Z754, Z341. $\times 1$. (After Van Hoepen 1965, figs 8a-b, 9g.)

The venter is distinctly unicarinate, with a single, strong central keel bounded on either side by a depression of variable strength. The ribs often continue beyond the ventrolateral tubercle to the area of these depressions, thus creating the impression of wavy lateral keels, but these are not true keels.

Adult ornament is very variable as the figures show, but differences are all within bounds of specific variation. It ranges from weak (SAS Z755) (Fig. 121) through fairly well developed (as in SAS Z341) (Fig. 120) to very strong (SAS Z754) (Fig. 116).

A large part of the body chamber is preserved in SAS Z342, occupying about three-quarters of a whorl. At the apertural end of this specimen the ribs become increasingly prorsiradiate, the central keel less prominent, and prorsiradiate striae cross the venter (Fig. 119).

Suture-lines are shown in Figure 123A-C.

Discussion

The species as here interpreted comprises virtually the whole of Van Hoepen's subfamily Gauthiericeratinae and includes the type species of his 'genera' *Andersonites*, *Hluhluweoceras*, and *Falsebayites*. This species is probably

derived from *G. obesum* through reduction of the umbilical width and increase in rate of whorl expansion.

'*Andersonites*' *listeri* is the most strongly ornamented morphological variant of the species and the inner whorls are somewhat reminiscent of *Peroniceras* (*P.*) *subtricarinatum* as far as lateral ornament is concerned. The venter, however, is distinctly unicarinate, and not tricarinate as stated by Van Hoepen (1965: 29) (Fig. 117B). There is only one central keel with a spiral furrow on either side. A slight extension of the lateral ribs to these depressions creates the appearance of wavy lateral keels. This together with imperfect shell preservation, probably led Van Hoepen to believe that the specimen was tricarinate.

'*Hluhluweoceras*' *fugitivum* (Fig. 121) has massive quadrate inner whorls with weak lateral ornament, but can be connected to *G. listeri* by transitional forms, so that separation is artificial.

'*Falsebayites*' *peregrinus* (Figs 117A, 118–119) the only species in Van Hoepen's subfamily Gauthiericeratinae based on more than one specimen, shows a very rapid increase in whorl height and an umbilical diameter of only 32 per cent. The general pattern of ornament, however, is that of *G. listeri*.

Collignon (1965: 49, pl. 435 (fig. 1797)) reported a species from the Middle Coniacian of Madagascar *G. listeriforme*, that is very much like *G. listeri*. The whorl section is much wider than high, the whorl breadth to height ratio being 1,12. It, too, is a synonym of *G. listeri*.

Occurrence

In Zululand well-dated specimens are restricted to Coniacian IV. The Madagascar specimen referred to the species is said to be from the 'Coniacian Moyen'.

Gauthiericeras album (van Hoepen, 1965)

Figs 124–126

Fluminites albus van Hoepen, 1965: 31, pl. 24, text-fig. 9c–e.

Type specimen

The holotype is SAS Z757 (Fig. 124) from localities 91 or 92 near the estuary of the Hluhluwe River, Zululand, St. Lucia Formation, Coniacian IV or V.

Material

BMNH C83792 is from locality 83 and is precisely localized as Coniacian IV. A more complete specimen, SAS Z871, is from the same locality and horizon as the holotype.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z871	243,0	69,0(28,4)	86,0(35,4)	0,80	86,0(35,4)	17:17
Z757	—	31,0	40,0	0,77		



Fig. 124. *Gauthiericeras album* (van Hoepen, 1965). Holotype SAS Z757. $\times 1$.

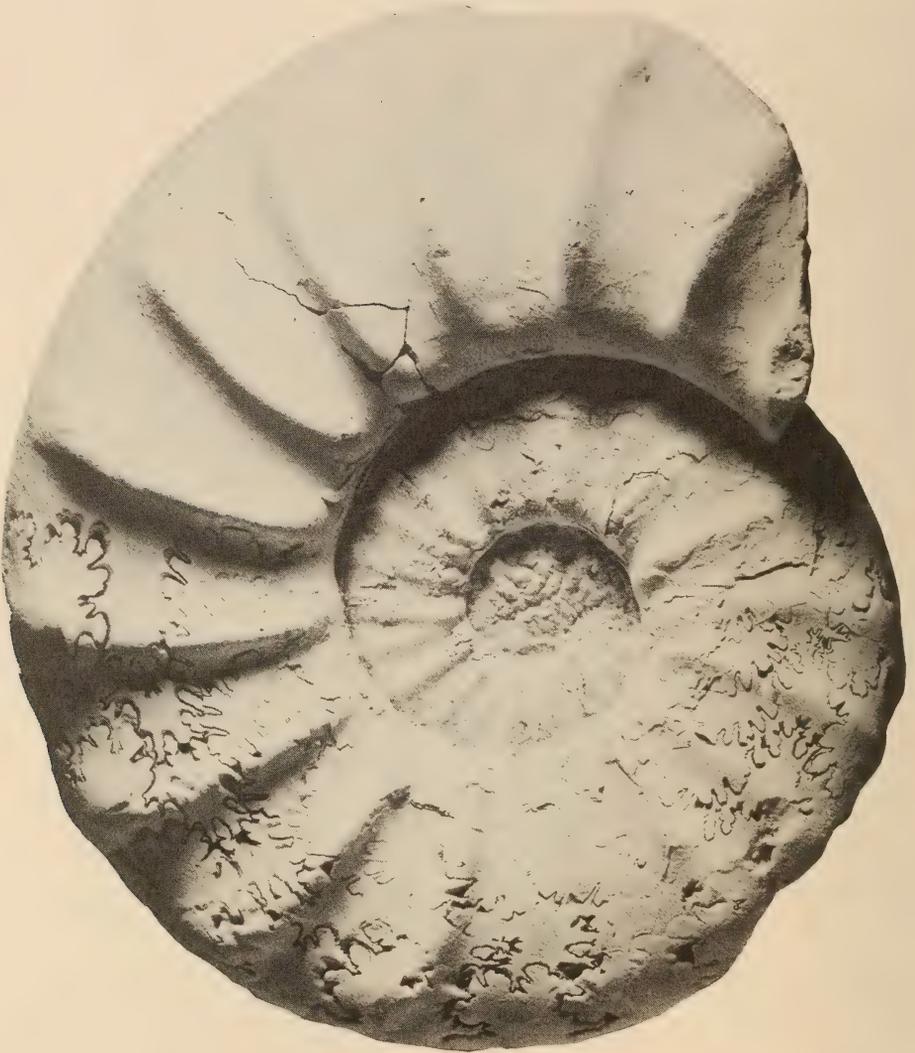


Fig. 125. *Gauthiericeras album* (van Hoepen, 1965). SAS Z871. $\times 0,56$.

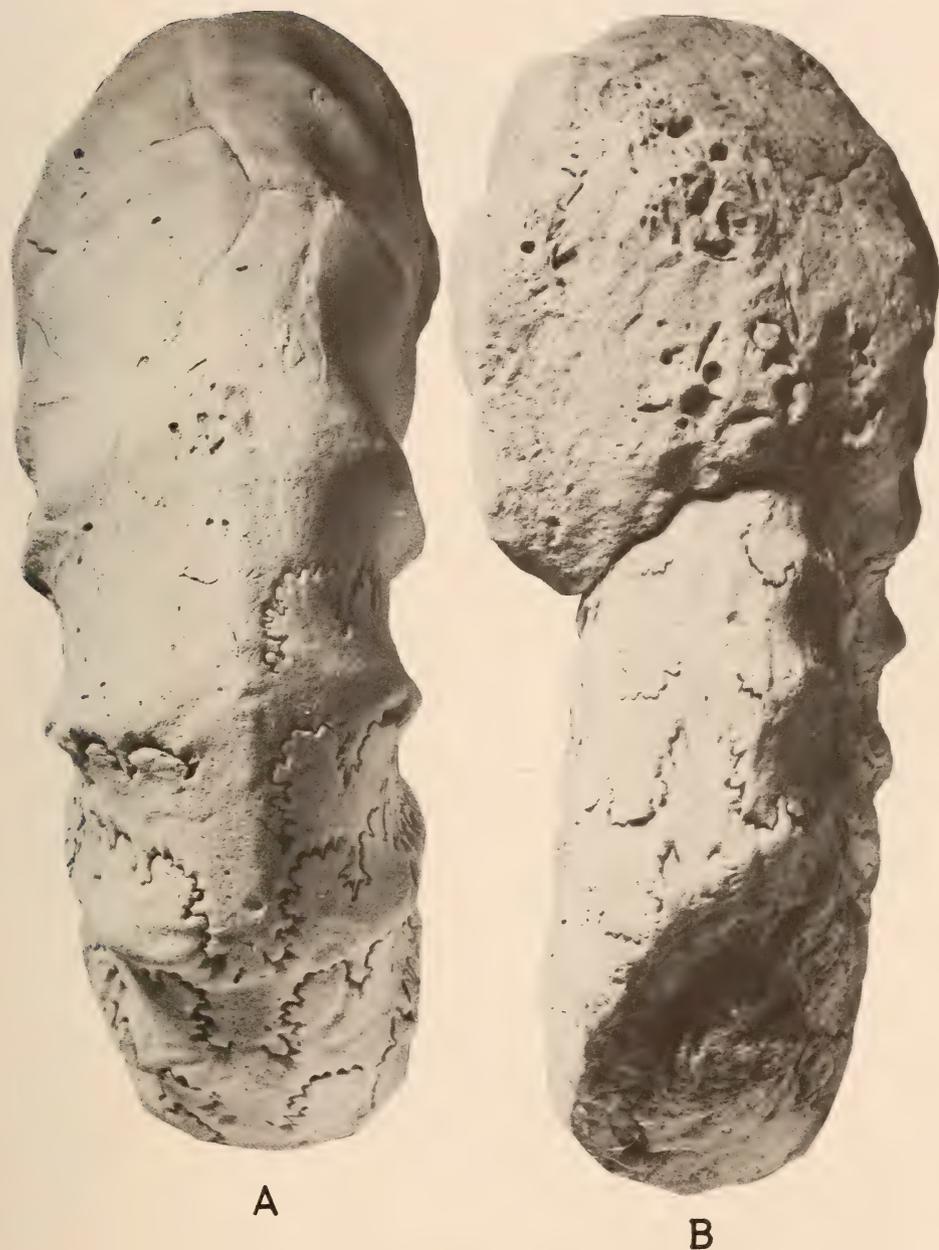


Fig. 126. *Gauthiericeras album* (van Hoepen, 1965). SAS Z871. $\times 0.65$.

Description

Coiling is moderately involute, with an umbilical diameter of 35 per cent in the only complete specimen available. The whorl section is ovoid throughout ontogeny, compressed, with little-inflated flanks (the maximum width at mid-flank), and a broadly rounded venter. The umbilical wall is gently rounded.

Ornament on the inner whorls of the holotype is very weak, consisting of umbilical bullae, prorsiradiate ribs and ventrolateral clavi. The venter appears tricarinate, but this is a result of the strong development of depressions on either side of the keel. On the outer whorls ornament strengthens considerably. The ribs become sharp-crested and widely spaced, whereas the umbilical tubercles become progressively radially elongated and eventually merge with the ribs. The ventrolateral tubercles similarly merge with the ribs, giving the latter a club-like appearance. Part of the body chamber is preserved in SAS Z871 (Fig. 125) and here adult ornament is fully developed.

Discussion

Unfortunately this species is poorly represented in numbers, so that the range of intraspecific variation cannot be established. It is easily distinguished from *G. obesum* by the ovoid, rather than quadrate to rectangular whorl section of the latter. The outer whorls of *G. listeri* are remarkably similar to those of *G. album*, but, again, the whorl section of the former is more quadrate.

Occurrence

Coniacian IV of Zululand.

Gauthiericeras albiforme sp. nov

Figs 127–129

Type specimens

The holotype is SAS 92/4 (Figs 127–128) from between localities 83 and 84, near Picnic Point, False Bay, Zululand, St. Lucia Formation, Coniacian V. Paratypes are SAS 92/2–3, from the same locality and horizon as the holotype.

Dimensions

	D	Wb	Wh	Wb/Wh	U	R
92/3	113,0	36,0(31,9)	48,0(42,5)	0,75	30,0(26,6)	—
92/2	160,0	48,0(30,0)	58,0(36,2)	0,83	55,0(34,4)	—
92/4	181,0	61,0(33,7)	72,0(39,8)	0,85	62,0(34,2)	19:20

Description

The umbilicus is narrow in the early growth stages, comprising only 27 per cent of the diameter, but increases to about 34 per cent in larger individuals. In adults the whorl section is distinctly subtrigonal, with an overhanging umbilical wall and little-inflated flanks converging to a narrow, unicarinate venter.



Fig. 127. *Gauthiericeras albiforme* sp. nov. Holotype SAS 92/4. $\times 0,86$.

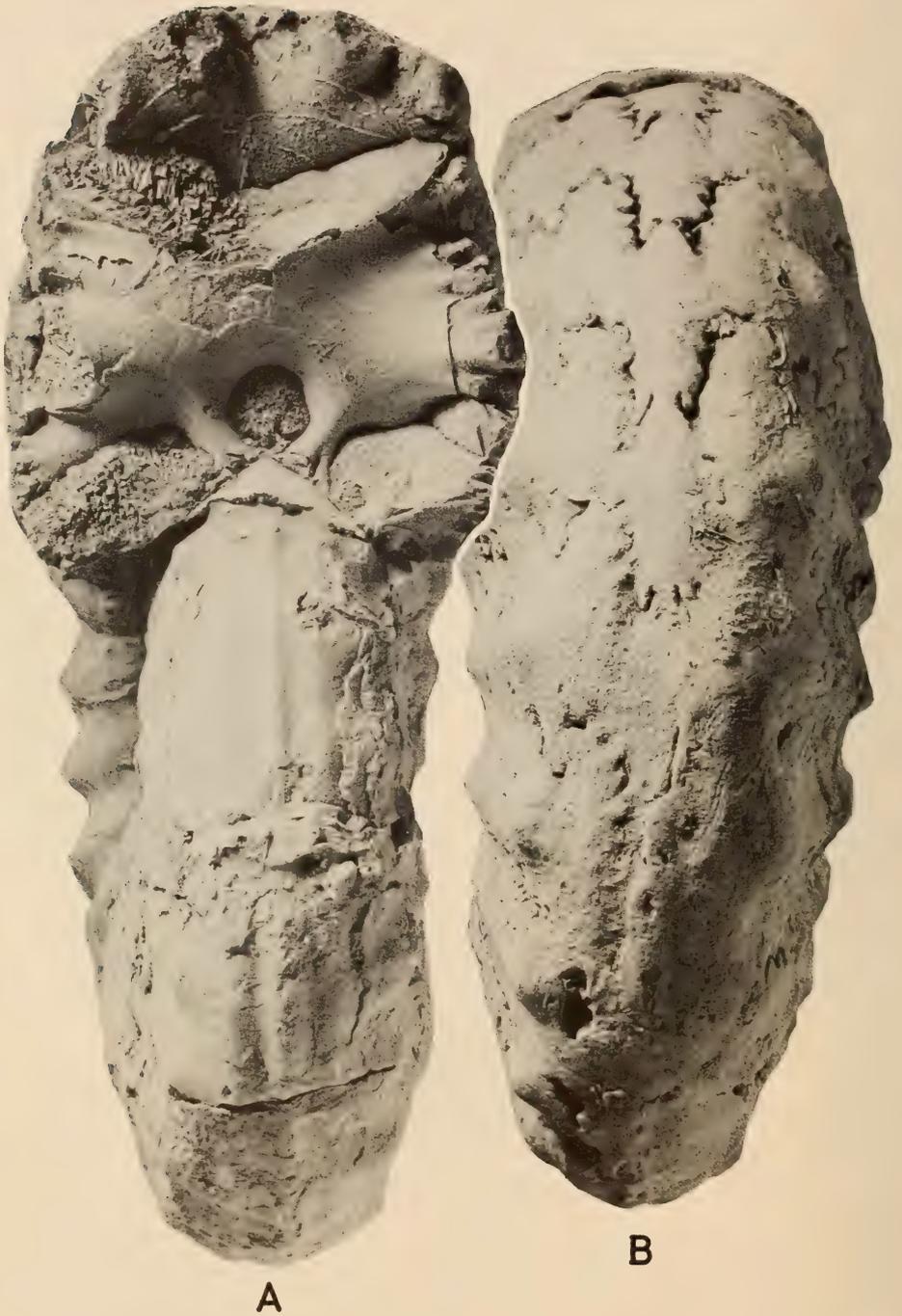


Fig. 128. *Gauthiericeras albiforme* sp. nov. Holotype SAS 92/4. $\times 0.96$.

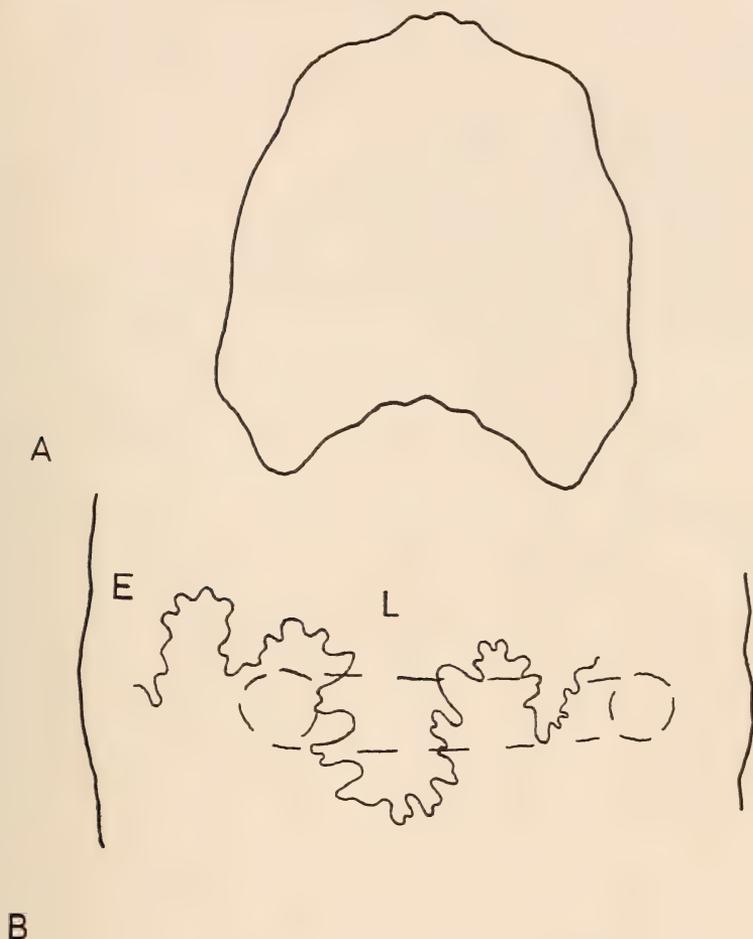


Fig. 129. *Gauthiericeras albiforme* sp. nov. Whorl section and suture-line. $\times 0,5$.

Ornament throughout consists of distinctly pinched, auricular umbilical bul-
lae that merge into strong, more or less radial or slightly prorsiradiate concave
ribs. These terminate in indistinct ventrolateral tubercles. On the outer whorls
ribbing is generally single, but on the inner ones bifurcations may occur at the
umbilical tubercle. Rib density is 19 to 20 on the outer whorls.

The venter is distinctly uncarinate, with only shallow spiral depressions on
either side of the keel.

Discussion

Distinguishing features of this species are the narrow umbilicus and the sub-
trigonal whorl section with an overhanging umbilical wall. As far as ornament is
concerned, there is great similarity to *G. album*, described above. Although the

material is limited, it may be possible to derive *G. albiforme* from *G. album* through slight decrease in umbilical diameter and increasing rate of whorl expansion. Given enough material connecting the two species, separation at sub-specific level would probably be sufficient.

The subtriangular whorl section serves to distinguish the species from *G. obesum* and *G. listeri*.

Occurrence

Upper Coniacian of Zululand. This appears to be the last surviving species of *Gauthiericeras*.

Gauthiericeras libertae van Hoepen, 1955

Figs 130–134

Gauthiericeras libertae van Hoepen, 1955: 372, figs 23–25.

Gauthiericeras planulatum van Hoepen, 1955: 374, figs 29–31.

Type specimens

The holotype of *Gauthiericeras libertae* is SAS Z4 (Figs 132–134), it was found by Van Hoepen in a pile of rubble probably at locality 91 or 92 of Kennedy & Klinger (1975) near the Hluhluwe estuary, Zululand, St. Lucia Formation, probably Coniacian IV. The holotype of *G. planulatum* is SAS Z3, also from near the Hluhluwe estuary close to locality 89 or 90 of Kennedy & Klinger, St. Lucia Formation, probably Coniacian IV.

Material

SAS Z1136, from locality 73, degraded river cliffs and stream exposures on the Mzinene River downstream from the junction with the Munywana, Zululand, St. Lucia Formation, Coniacian IV or V. SAS H205/22 is from locality 90, SAS H205/1 from locality 90 or 91, both near the Hluhluwe estuary, Zululand, Coniacian IV or V. SAS Z2018 and BMNH C83797–C83799 from locality 83, foreshore exposures at Mason's Camp, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>R</i>
Z2018	131,0	41,0(31,3)	52,0(39,7)	0,79	48,0(36,6)	22:22
Z3	134,0	37,0(27,6)	51,0(38,1)	0,72	46,0(34,3)	18:21
H205/22	135,0	37,0(27,2)	49,0(36,0)	0,75	53,0(38,9)	—
Z1136	137,0	43,0(31,4)	50,0(36,5)	0,86	50,0(36,5)	—
H205/1	148,0	41,0(27,7)	53,0(35,8)	0,77	54,0(36,5)	16:16
Z4	150,0	40,0(26,7)	54,0(36,0)	0,74	55,0(36,7)	17:30



Fig. 130. *Gauthiericeras libertae* van Hoepen, 1955. SAS Z3 holotype of *G. planulatum* van Hoepen, 1955. $\times 0.96$.

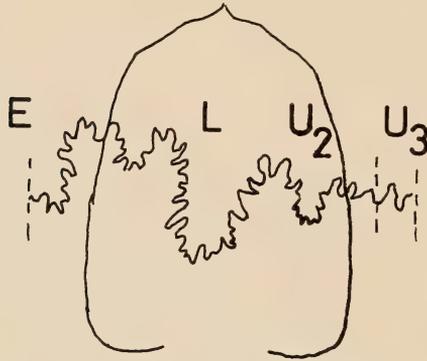


Fig. 131. *Gauthiericeras libertae* van Hoepen, 1955. Whorl section and suture-line of the holotype of *G. planulatum*. $\times 1$. (After Van Hoepen 1955, figs 30–31.)

Description

Coiling is evolute, the umbilical diameter varying between 34 and 38 per cent of the total diameter, with successive whorls overlapping to the ventral tubercle or a little beyond, so that about 25 per cent of the previous whorl is covered. The whorl section is compressed throughout, with whorl breadth to height ratios that vary between 0,72 and 0,86. The inner flanks are gently rounded, the outer flanks flattened and subparallel or slightly convergent, the venter narrow and fastigate.

There are 16 to 22 weak to prominent umbilical bullae per whorl. These give rise to either single ribs or pairs of ribs that vary from weak to strong between individuals but are straight and prorsiradate to mid-flank and curve slightly forward to terminate in weak ventral clavi. The ribs are prolonged forward to the edge of a shallow groove that flanks a blunt undulating siphonal keel. The outer edges of the grooves are also undulose, giving an appearance of incipient lateral keels.

Suture simple, as in other members of the genus (Figs 131, 134).

Discussion

Van Hoepen separated *Gauthiericeras libertae* and *G. planulatum* on the basis of the predominance of single ribs in *libertae* and the predominance of paired ribs in *planulatum*, as well as sutural details. New material shows that there is variation in this respect, and the common features of overall shell form and the distinctive ventral ornament with crenulate siphonal keel and crenulate edges to the flanking grooves suggest that only a single species is present.

Ribbing style, evolute coiling combined with compressed whorls and the distinctive venter distinguish this species from all others.

Occurrence

Coniacian IV of Zululand.



Fig. 132. *Gauthiericeras libertae* van Hoepen, 1955. Holotype SAS Z4. $\times 0,85$.



Fig. 133. *Gauthiericeras libertae* van Hoepen, 1955. Holotype SAS Z4. $\times 1$.

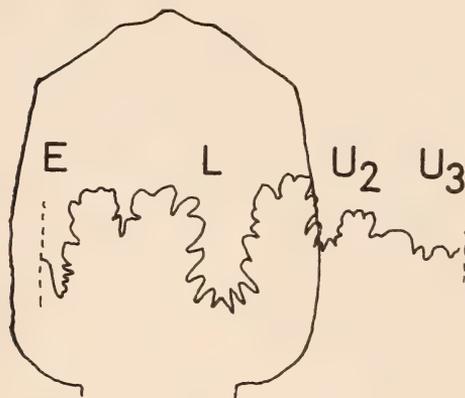


Fig. 134. *Gauthiericeras libertae* van Hoepen, 1955.
Whorl section and suture-line of holotype. $\times 1$.
(After Van Hoepen 1955, figs 24–25.)

CONCLUSIONS

A general reappraisal of Coniacian stratigraphy and revision of the very rich peroniceratid faunas found in Zululand provide an outline of the evolution of the group that is of some significance for interregional correlation and elucidation of evolutionary patterns among late Cretaceous ammonites (Fig. 135).

The earliest genus of the Peroniceratinae is *Peroniceras* itself. The appearance of *P.* (*Peroniceras*) (of which *Fraudatoroceras* van Hoepen, 1965, *Cobbano-ceras* Matsumoto, 1965, and *Gloriaceras* Etayo-Serna, 1979, are synonyms) marks the base of the Middle Coniacian as that term is used here. There is a hiatus in the record between the first appearance of *Peroniceras* and the Collignoniceratinae, which are believed to be the ancestral stock spanning the Lower Coniacian. Matsumoto (1965: 213) believed that the origin of *Peroniceras* lay in *Prionocyclus*, and the *Prionocyclus* lineage certainly survived to give rise to *Prionocycloceras*, which extends to the Upper Coniacian. Matsumoto suggested that the lateral keels of *Peroniceras* arose by the elevation of the outer edges of the grooves flanking the keel of ancestral *Prionocycloceras*. Independent observations by Etayo-Serna (1979) and the present authors shows that the keels arise by elongation and eventual absorption of outer ventrolateral clavi into a keel, and that both lateral and siphonal keels of several *Peroniceras* (*Peroniceras*) species show undulations at some stage in ontogeny.

The suture of the type species of *Peroniceras* (*Peroniceras*), *P.* (*P.*) *moureti* de Grossouvre, 1894 (a synonym of *P.* (*P.*) *tridorsatum* (Schlüter, 1867)) is relatively simple, like that of ancestral Collignoniceratinae. Other species, such as *P.* (*P.*) *dravidicum* Kossmat, 1895, have a much more complex suture, with long, narrow and finely indented saddles. Evolution must have been from the simple *P. tridorsatum* type to complex *P. dravidicum* type, although there is no

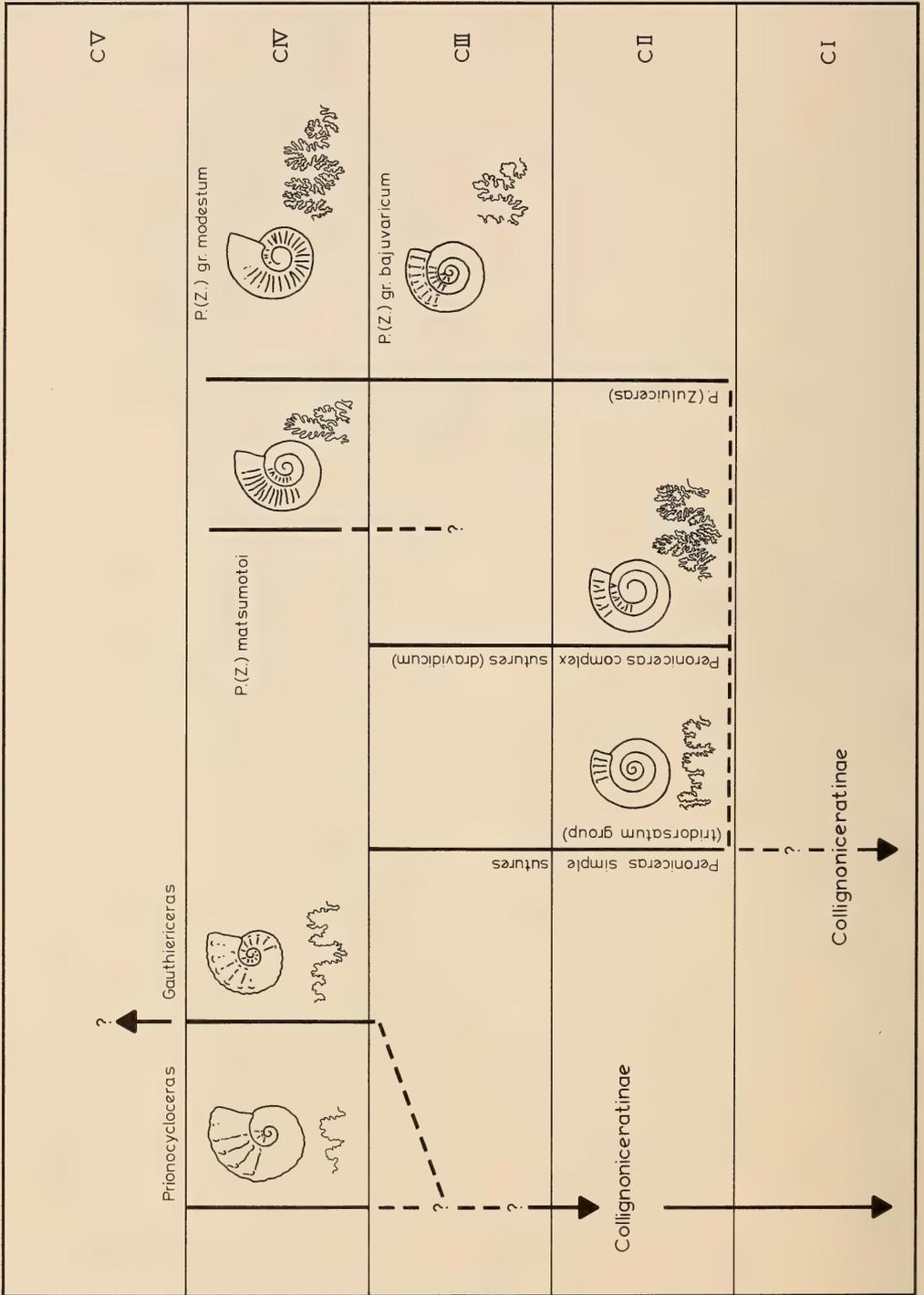


Fig. 135. Suggested phylogenetic relationships within the subfamily Peroniceratinae.

detailed stratigraphy to support this. In Zululand, *P. (Peroniceras)* of both types are confined to the Middle Coniacian. Only in Japan is there a suggestion that *P. (Peroniceras)* extends above this and into the Santonian; however, the supporting evidence is not wholly convincing.

Peroniceras (Zuluiceras) van Hoepen, 1965 (of which *Zuluites* van Hoepen, 1965, and *Sornayceras* Matsumoto, 1965, are synonyms) also appears in the Middle Coniacian, with some slight evidence (in Zululand at least) that it slightly post-dates the nominate subgenus. It has a relatively complex suture of *P. dravidicum* type. The earliest species are relatively evolute, but through the higher Middle and lower Upper Coniacian there is a trend towards increasing involution, compression of the whorls, and loss of ornament.

Gauthiericeras (of which *Ciryella* Wiedmann, 1960, *Fluminites* van Hoepen, 1965, *Andersonites* van Hoepen, 1965, *Hluhluweoceras* van Hoepen, 1965, and *Falsebayites* van Hoepen, 1965, are synonyms) appears at the base of the Upper Coniacian in Zululand. Only the cryptic diminutive '*Schloenbachia boreau*' de Grossouvre, 1894, which may appear in the Middle Coniacian in France, points to a possible slightly earlier appearance. The genus shows much stronger similarities to *Prionocycloceras* than to other, earlier Peroniceratinae, and this is believed to be its origin. Both evolute and involute species occur in the fourth division of the Zululand Coniacian, but there is insufficient evidence to allow interpretation of this in terms of an evolutionary trend as has been demonstrated in the *Peroniceras* → *Zuluiceras* series through the Middle and Upper Coniacian. *Ishikariceras* Matsumoto, 1965, with its evolute strongly ornamented inner whorls with strong umbilical and ventral tubercles, a strong siphonal keel flanked by weak grooves, and an almost smooth body chamber, appears to be a distinct genus. Its precise horizon within the Coniacian is unknown. If, as appears likely, the two known specimens are adult, it is a micromorph.

Neogauthiericeras Collignon, 1969, described from the Santonian–Campanian boundary of Madagascar, is, by virtue of its stratigraphic isolation from other Peroniceratinae, more likely to be a *Gauthiericeras* homoeomorph of texanite affinities analogous to *Reginaites*, a texanite homoeomorph of *Peroniceras*.

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

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

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii 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

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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.:

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

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

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

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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.

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&

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CRETACEOUS FAUNAS FROM
ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE SUBFAMILY
PERONICERATINAE HYATT, 1900

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ANNALS

OF THE SOUTH AFRICAN
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(continued inside back cover)

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MORPHOLOGICAL AND BIOLOGICAL NOTES
ON SOME SOUTH AFRICAN ARTHROPODS
ASSOCIATED WITH DECAYING
ORGANIC MATTER

PART 2

THE PREDATORY FAMILIES CARABIDAE,
HYDROPHILIDAE, HISTERIDAE,
STAPHYLINIDAE AND
SILPHIDAE (COLEOPTERA)

By

A. J. PRINS

Cape Town Kaapstad

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HYDROPHILIDAE, HISTERIDAE, STAPHYLINIDAE AND
SILPHIDAE (COLEOPTERA)

By

A. J. PRINS

South African Museum, Cape Town

(With 16 figures)

[MS accepted 16 June 1983]

ABSTRACT

The morphology of the immature stages of fourteen species of beetles belonging to the families Carabidae, Hydrophilidae, Histeridae, Staphylinidae, and Silphidae, as collected along a narrow strip between Mossel Bay and Elands Bay and in a small area around Laingsburg and Tulbagh, is illustrated. Available data on their biology and ecology are given and their association with decaying organic matter is noted. These insects play an important part in the predation of the arthropods attracted to carcasses and cadavers and other decaying organic matter.

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INTRODUCTION

In the first part of this series of papers some specimens belonging to the myriapods, arachnids, crustaceans, and hemimetabolous hexapods are dealt with; in this second part the immature stages of the first group of the holometabolous families are considered.

This group comprises one species of the adepagous Coleoptera and thirteen species of the polyphagous series Staphyliniformia, which includes the superfamilies Hydrophiloidea, Histeroidea, and Staphylinoidea.

The surveys covered the beach, the dune system and the adjacent inland area along a narrow strip of the southern and western coastal regions of South Africa; a small strip between Laingsburg and Beaufort West, as well as between Worcester and Tulbagh, was also included.

Nearly half of all known insects are beetles and, although they are of such diverse form and habits and include some of the largest and also some of the smallest of insects, only a very few of them have developed a tendency to sociality. Of the some 150 known families only about nine show some signs of sub-social behaviour and these include the Staphylinidae, Silphidae, Hydrophilidae, and also the Scarabaeidae. However, none of the South African species or, at least, those that have been collected during the surveys, can be regarded as sub-social, except perhaps hydrophilids belonging to the genus *Spercheus*; some may well be described as gregarious as in the case of *Harpalus capicola* Dejean and *H. agilis* Péringuey (Carabidae); *Gonocephalum arenarium* (Fabricius), *G. simplex* (Fabricius), *Zophosis boei* Solier, and *Stenocara longipes* (Olivier) (Tenebrionidae), and various other species often collected in very large numbers under semi-dry to dry cow-pats, such as the vegetable weevil, *Listroderes costirostris* Schönherr (Curculionidae).

All the species discussed in this paper are geophiles and all are predacious both in the adult and larval stage, except the hydrophilids, the adults of which are coprophages. All are attracted to decaying organic matter in which other arthropods are breeding, and therefore play an important part in reducing the number of coprophagous species. Nevertheless, they will feed on the colloids oozing from the decaying matter if circumstances necessitate this, particularly the hydrophilids and silphids and, to a certain extent, the staphylinids.

The larvae of most species are campodeiform, and in the case of the Sphaeridiinae the legs are reduced and they resemble the scarabaeoid forms.

As the amount of food available plays an important part in the development of these insects, and as this food source is often limited, dwarfed individuals are common in nature, sometimes differing markedly from the normal forms. This is clearly demonstrated by some specimens of an unidentified species of *Philonthus* (Fig. 1B) collected in various localities during the survey and included here in the discussion on the Staphylinidae. To the naked eye the adults appeared to be two different species; however, there were no morphological

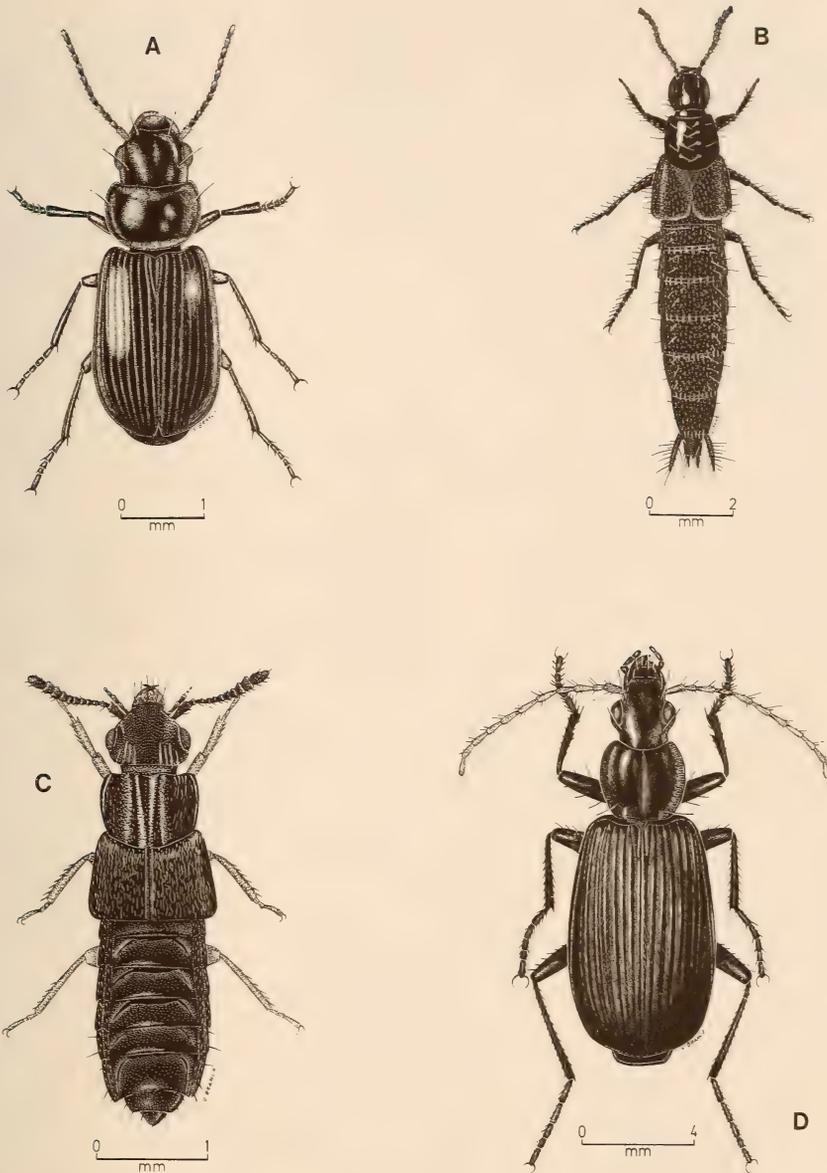


Fig. 1. Families Carabidae, Staphylinidae.
 A. *Amblystomus capensis* (adult). B. *Philonthus* sp. (adult). C. *Oxytelus caffer* (adult).
 D. *Liamegalonychus* sp. (adult).

differences when the larvae were examined under the microscope and it is therefore assumed that they are variants of the same species.

The morphological terms used in this paper in the descriptions of the immature stages are those of Richmond (1920), Böving & Craighead (1931), Hafez (1939a-d), Dorsey (1940), Van Emden (1942), and Kasule (1968).

MORPHOLOGICAL AND BIOLOGICAL NOTES

Family Carabidae

Flat to oval, usually dark-coloured beetles with the thorax generally narrower than the elytra, except in certain groups such as the tribe Scaritini. Head narrower than pronotum and tarsi five-segmented. Antennae eleven-segmented. Wings well developed or absent.

The ground beetles can be divided into species that live near or in water, on the ground and in trees; of these groups the geophiles are the most abundant, the vast majority of which belongs to the subfamilies Carabinae and Harpalinae. The eggs of the different species are laid either in the soil or in little mud packets and there are three larval stages. Pupation usually occurs in the soil in a pupal cell.

Certain species are commonly found under kelp strings and flakes just above the highwater mark, such as the black *Acanthoscelis ruficornis* (Fabricius) (Fig. 2B), which was on various occasions excavated from the burrows of the isopod *Tylos capensis* Krauss and was also observed to feed on beach-fleas (*Orchestia* and *Talorchestia* spp.), fly maggots, and even on the ladybird *Lioadalia flavomaculata* de Geer, which is often found on the kelp. It was now and then collected from dead sea-birds. When feeding, the prey is held between the fore-legs, and in the case of maggots almost everything is consumed except the mouth-hooks and a few pieces of the skin. Its food included the smaller, pale, straw-coloured cicindelid, *Platychila pallida* (Fabricius) (Fig. 2G), which occurred under similar conditions. This tiger beetle seems to favour the more arid parts of the north-western Cape Province.

Scarites rugosus Wiedemann (Fig. 2A) closely resembles *A. ruficornis*, but is much larger (30 mm) and has a wider distribution in South Africa, both along the coast and inland. Péringuey's (1896) note that it is generally found on the sea-shore, or at no great distance inland, is therefore not entirely correct. It was often found in the sand under shore plants; otherwise its habits are unknown.

Various other carabids have been collected in decaying and dry kelp, mostly of the flake and string types, of which *Harpalodes xanthorhaphus* (Wiedemann), *Harpalus fuscoaeneus* Dejean, *Tetragonoderus immaculatus* LaFerté, *Agonum rufipes* (Dejean), and *Liamegalonychus* spp. (Fig. 1D) were the most common. The first two species are widely distributed in South Africa and, together with *Liamegalonychus* (which also feeds on the flesh-fly *Sarcophaga maritima* Engel) have often been collected under cow-pats. *Hystrichopus vigilans* (Sturm), which resembles *Liamegalonychus* spp. and sometimes occurs in manure in the western Cape Province, has been found by the author to cause mild

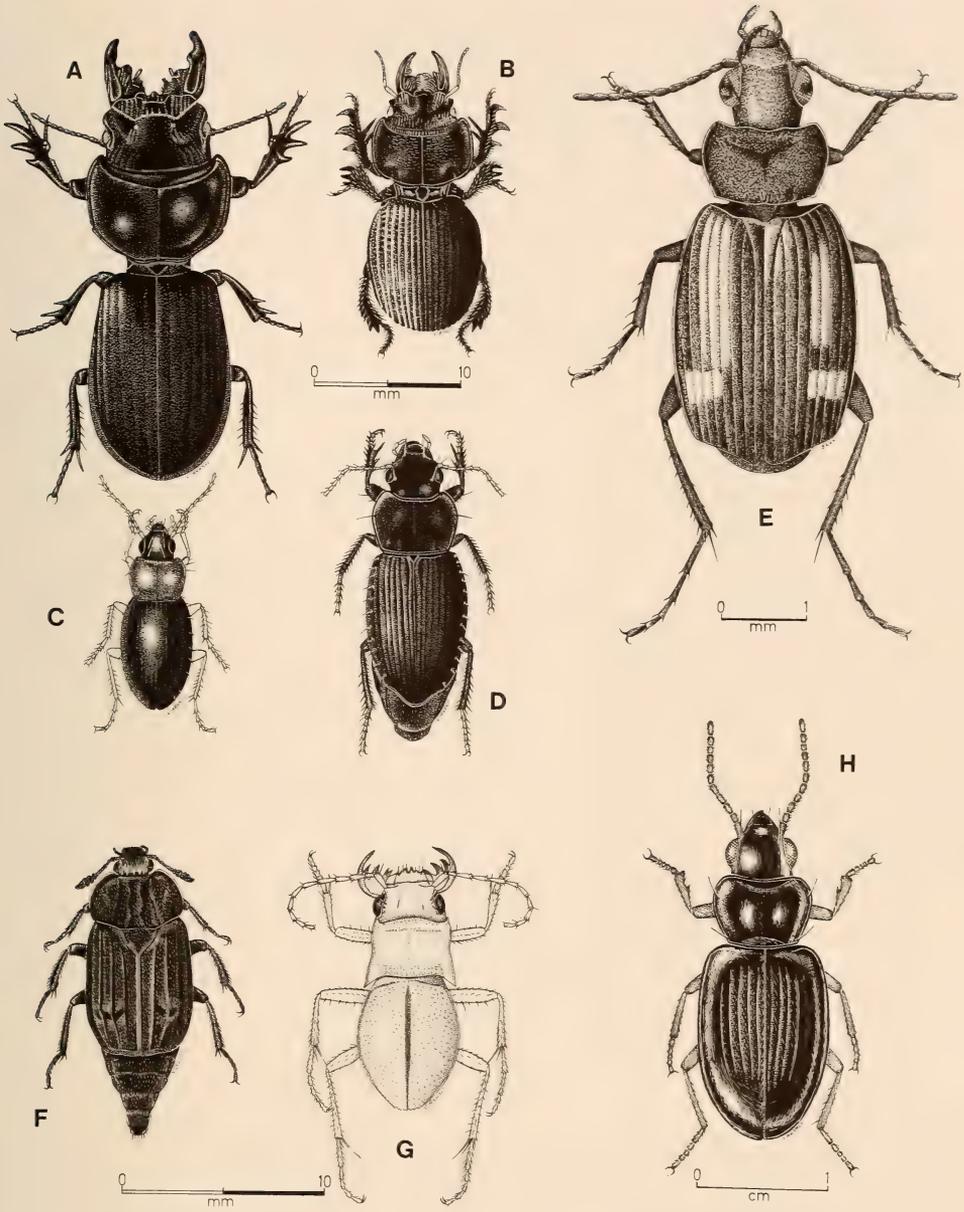


Fig. 2. Families Carabidae, Cicindelidae, Silphidae.

A. *Scarites rugosus* (adult). B. *Acanthoscelis ruficornis* (adult). C. *Geobaenus lateralis* (adult). D. *Harpalus capicola* (adult). E. *Tetrasonoderus thunbergi* (adult). F. *Silpha mutilata* (adult). G. *Platychila pallida* (adult). H. *Thachys capicola* (adult).

irritation of the skin in hypersensitive people when carelessly handled. All these species are black, except the first named, which is brown. *Agonum rufipes* has light-reddish legs.

Tetragonoderus immaculatus is rather similar to *T. thunbergi* (Crotch) (Fig. 2E), which occurred together with *Harpalus agilis* Péringuey and *H. fuscoaeus* in soils rich in organic matter such as fish-meal and compost, but it is somewhat bigger and lacks the two pale-yellowish patches on the apical parts of the elytra.

At least twelve carabids were collected under dry cow-pats, the largest being the previously mentioned *Liamegalonychus* sp. (14–15 mm). *Harpalomorphus capicola* Péringuey, *Harpalus capicola* Dejean (Fig. 2D), *H. agilis* Péringuey, *H. fulvicornis* Thunberg, *H. fuscoaeus* Dejean, and *Cratognathus mandibularis* Dejean are all medium-sized species (7–12 mm) and often occurred in large numbers under pats along the west coast, particularly during the winter. *Harpalomorphus capicola*, which was not as abundant, was collected only in the north-western parts. *Harpalodes xanthorhaphus*, common under kelp, and *Geobaenus lateralis* Dejean (Fig. 2C) are both widely distributed and occurred under dry pats in fair numbers in almost all the areas surveyed.

Some carabids are generally attracted to fresh dung, particularly *Amblystomus capensis* (Motschulsky) (Fig. 1A), but only very small numbers were observed. On the other hand the shiny, reddish-black *Tachys capicola* Péringuey (Fig. 2H), which is about the same size as *A. capensis*, is a common species in leaf litter in the Cape Peninsula and also occurs in soil rich in compost.

A small, oval, pale straw-coloured carabid, *Omophron capicola* Chaudoir (about 6,9 mm long), is often encountered in sandy areas along the western parts of the southern coastal region. It resembles the tenebrionid, *Pachyphaleria capensis* (Castelnau), but can easily be distinguished by the metallic green patches on the head, median area of the prothorax and elytra, and by the sickle-shaped mandibles, the large eyes and longer antennae. It was observed to stalk *Machilinus* sp. (Order Microcoryphia) common on the debris in these regions, and probably feeds on this machilid.

Laemostenus complanatus Dejean

DESCRIPTION

Adult (Fig. 3J).

Previously described by Péringuey (1896) and Hinton (1945). Black to dark brownish black in colour, head and thorax fairly shiny, elytra duller, with somewhat silky sheen. Antennae, palpi and tarsi reddish brown; first three antennal segments devoid of pubescence, segments 4–11 pubescent. Elytral striae fine but clearly indicated.

This is a cosmopolitan species and, according to Hinton (1945), apparently a native of Europe or north Africa. According to collection data found only around Cape Town, on the Cape Flats, Robben Island, and near Stellenbosch.

In Britain it appears in granaries and in glue and chemical works (Hinton 1945) and, according to Pescott & Miller (1937), the adults were observed to prey on the larvae of the codling-moth, *Cydia pomonella* (Linnaeus) in Australia. Around Cape Town it is commonly attracted to decaying carcasses and compost heaps.

Larva (Fig. 3A–B)

A general description of carabid larvae is given by Van Emden (1942). Elongate, subcylindrical and 16.6–17 mm long when full grown.

Body creamy white, with tergites and sternites pale piceous brown. Head directed slightly upwards. Pronotal tergite largest and also more strongly sclerotized, all tergites divided by a thin, pale, longitudinal median line. Mesothoracic spiracle largest and oval; abdominal spiracles (of which one on first segment is larger than rest) annular (Fig. 3P). Two lateral abdominal sclerites present, of which upper one bears five and lower one six setae, except in eighth segment where both have five setae in all specimens examined. Ninth segment with only one lateral sclerite bearing only two setae, and also with two long cerci, each with nine long setae. Tenth segment tubular and functioning as a proleg. Sternal region (Fig. 3L) of abdominal segments 1–7 each with single large anterior ventrite bearing eight to ten setae and four posterior postventrites, of which inner pair bears two and outer pair four setae. One pair of minute praeventrites also present. Sterna 8 and 9 with sclerites fused into a single plate, which is divided posteriorly on eighth segment. Sternal plate on eighth segment with thirteen to fourteen setae, that on ninth segment with ten to twelve. Each tergum with nineteen to twenty setae, except that of eighth segment, which has ten to twelve only, and ninth segment, which has four, one of which is situated on base of each cercus.

Legs (Fig. 3D) with some scattered setae on coxae, each trochanter with two posterior and about four anterior spine-like setae, as well as two long ventral setae. Femur with a double ventral row of four to five spine-like setae and single short seta dorsally near apex. Tibia with about six spine-like setae around apex. Tarsus slightly longer than tibia, bearing two spine-like apical setae dorsally and two simple, acute claws, which are only slightly shorter than tarsus. Compare with Staphylinidae where legs are four-segmented (Figs 9E, 10F, 11E, 13F, 14E).

Young larvae collected during September resemble mature specimens in form, shape, and number of setae present on head and thorax, but middle tooth-like process in mandibles is much more acute, and (in the few specimens examined) third seta on cercus is branched (Fig. 3O). Abdominal sterna are not fully differentiated into various sclerites present in later instars.

Head capsule (Fig. 3C, F–G)

Dark reddish brown, finely reticulate, somewhat shiny. Frontal and epicranial sutures distinct; neck absent. Cervical keels well indicated. Nasale

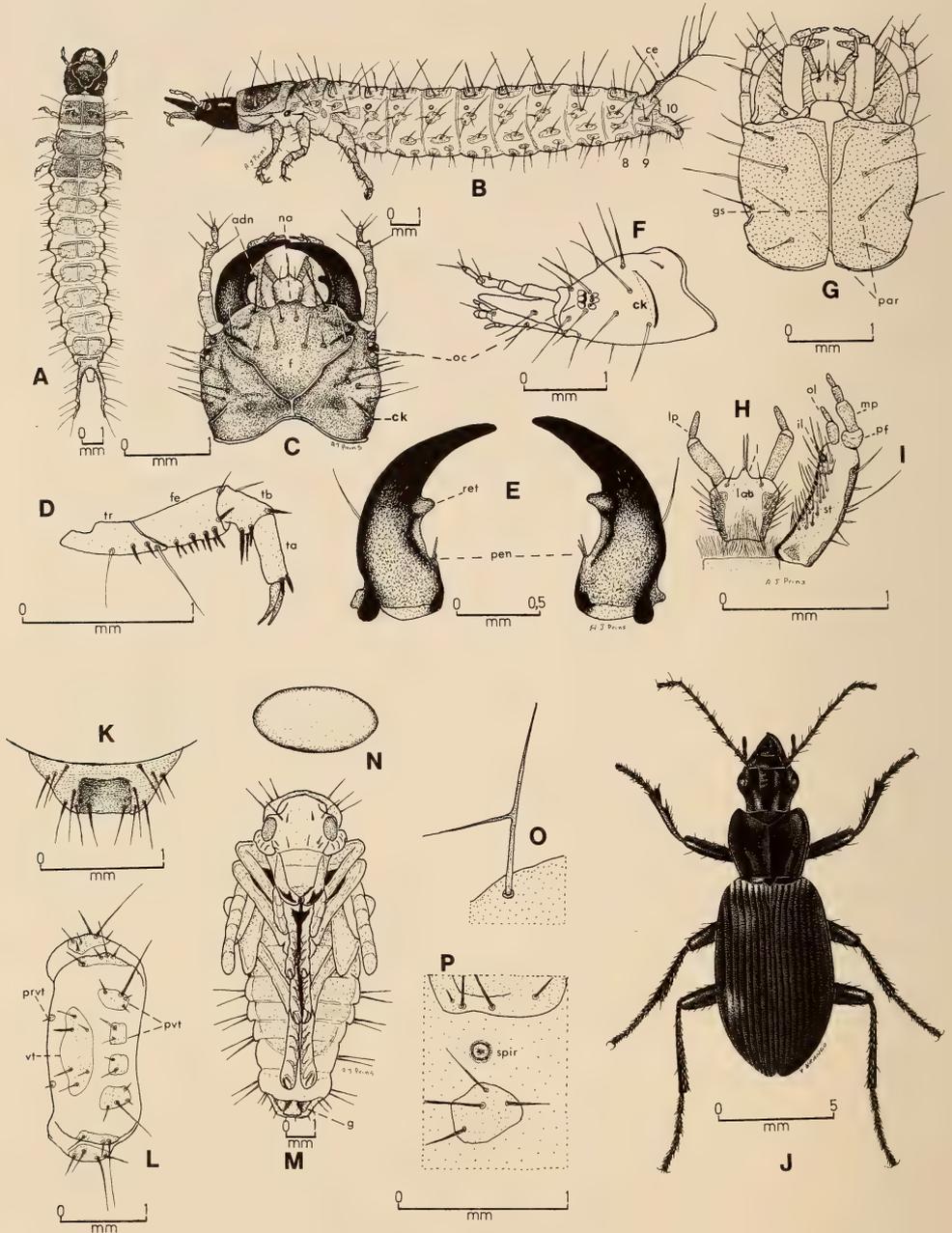


Fig. 3. Family Carabidae.

Laemostenus complanatus. A. Larva (dorsal view). B. Larva (left lateral view). C. Head (dorsal view). D. Right mesothoracic leg (posterior view). E. Mandibles (dorsal view). F. Head (left lateral view). G. Head (ventral view). H. Labium (dorsal view). I. Right maxilla (dorsal view). J. Adult. K. Last abdominal segment of pupa (dorsal view) to show depression. L. Second abdominal sternite. M. Pupa (ventral view) with beetle already fully developed. N. Egg. O. Third seta on cercus to show branch (highly magnified). P. First abdominal segment to show spiracle.

somewhat prolonged, shallowly emarginate in the middle and also very slightly so on each side; adnasalia slightly concave; two parietalia dorsally and laterally with about eight setae each. Chaetotaxy as illustrated. Six ocelli present on each side. Antennae four-segmented, fourth segment small, slightly shorter than third; latter with sensorial appendages on exterior side; penultimate segment with one short dorsal seta and two lateral ones; apical segment (fourth) also with one dorsal seta and two lateral ones, and also bearing short setae at extreme apex. Antennal base not very clearly demarcated and bearing single lateral seta. Hind margin of head deeply excavated medially on dorsal side, ventrally only slightly so. Gular suture distinct and with V-shaped notch nearly half-way between anterior and posterior margins.

Mandibles (Fig. 3E)

Falcate, length slightly more than twice the width at base. Apex fairly acute, colour dark reddish brown, almost black in old specimens. Retinaculum present; subbasal penicillus represented by one or few setae in most specimens examined. Exterior lateral side with depression, bearing single long seta.

Maxillae (Fig. 3I)

With large almost rectangular stipes. Ventrally smooth and with about six setae, of which one is very long, on external margin; dorsally beset with numerous setae on mesal side. Outer lobe of maxilla palpiform and two-segmented, with single ventral seta on first segment. Inner lobe present as small conical process, with single long style-like seta at apex. Cardo ventrally with a single seta. Maxillary palpus three-segmented, with apical segment small, about half the length of first. Palpifer segment-shaped and with single ventral seta. Palpi devoid of setae.

Labium (Fig. 3H)

Trapezoidal, with base narrower than apex. Ventrally divided by shallow longitudinal furrow into two lobes, each bearing single seta apically. Ligula prolonged in front and bisetose. Lateral margin of labium sclerotized and bearing numerous setae. Palpiger with single seta. Labium basally covered with long, fine hairs. Labial palp two-segmented, with apical segment small, about half the length of first.

Pupa (Fig. 3M)

Pupa about 16,6 mm long. Almost pure white soon after pupation, but mandibles gradually become red; 3–4 days before beetle emerges, black eyes begin to show through integument. Head and thorax with some scattered brown setae dorsally. Abdominal terga with about nine long brownish-black setae on each side; laterally also with two setae, except the last two or three terga, which bear only few setae. Developing genital capsule represented by two conical tubercles. Terminal abdominal tergum with almost square depression, the lateral sides of which bear four to six setae (Fig. 3K).

BIOLOGY

Both adults and larvae are predacious and feed on various insects in the soil; those collected from the carcasses fed in the laboratory mainly on fly larvae and the grubs of skin-and-hide beetles. The maggots and pupae of the cheese skipper, *Piophilha megastigmata* McAlpine, also seemed to be a favoured source of nourishment, as well as the caterpillars of tineids.

Beetles with fully developed eggs were collected under carcasses during April and May. These eggs (Fig. 3N) measure 1,6 mm \times 0,88 mm and are oval shaped, almost pure white, with the surface microscopically wrinkled or shagreened and somewhat dull. Some beetles were found hibernating under the bark of trees and under stones; those collected during September survived for at least 6 months and bred larvae during the early winter. Full-grown larvae appeared from September to October and pupae were found from October to November. There was only one generation a year during the survey period; however, overlapping occurs and young larvae measuring 4,5 mm were observed during spring. The fully mature larvae construct clay cells in which they remain dormant for a short period (3–20 days) after which they pupate. Pupal stages varied from 11 to 13 days in the laboratory during the late spring and early summer (21–23 °C).

Newly emerged beetles are pale whitish brown, but after about a day the head and thorax become blackish; some 3 days later they usually assume their normal black colour.

Family **Hydrophilidae**

Small to medium-sized oval beetles, the dorsum smooth and convex, and the head prominent. Maxillary palpi fairly long and antennae seven to ten-segmented. Tarsal formula 5–5–5 or 5–4–4. Wings well developed.

Some seventy species have been described from southern Africa, most of which are aquatic or at least semi-aquatic; those of the subfamily Sphaeridiinae are terrestrial, restricted to wet or damp places and breed in dung and other decaying matter; larval breathing in this case is pseudometapneustic. Very little is known about the habits of one genus, *Coelostoma*; according to Böving & Henriksen (1938) the presence of suckers on the underside of the abdomen of the larvae may indicate that they are adapted for moving over rough or hard surfaces such as rotten leaves, etc. Adults of *Coelostoma punctulatum* (Klug) were collected on the green algae growing in stagnant pools in the vicinity of Laingsburg.

At least six species of water scavenger-beetles belonging to the above-mentioned subfamily are common in fresh cow-pats in the areas surveyed. When the dung starts to dry out, however, some of these beetles, together with some of the histerids and staphylinids, which are attracted, generally leave the pats, except those that prefer the drier media. The mandibles of the adult beetles are much better sclerotized than in the coprophagous *Aphodius* species (Scarabaeidae) and they are thus adapted to feed on much drier and harder dung particles,

and predation may not be entirely excluded. Most of these beetles therefore remain in the dung much longer than the smaller scarabs and are often found in fairly dry pats.

Cercyon maritimus Knisch was the most common species found in dung. In Mamre (south-western Cape) quite a large number of the rather small Palaearctic and Nearctic hydrophilid *Cercyon pygmaeus* (Illiger) occurred in association with *C. maritimus* during the early spring, but its larvae could not be traced. It was fairly abundant along the south coast during the late summer and autumn in both semi-fresh and almost dry cow-dung.

Sphaeridium caffrum Laporte & Castelnau appeared in large numbers during the winter and spring in the western parts of the Cape and was very numerous during the late summer when larvae and pupae were present in fresh dung in almost all areas. The related *S. quinquemaculatum* Fabricius (length about 3 mm), which is similar to, but smaller than, *S. caffrum* occurred during the summer in Montagu. It is widespread, not only in the Cape Province but also in other parts of the world such as Sri Lanka, southern Asia, China, and Taiwan (Knisch 1924b). *Sphaeridium caffrum*, however, is known only from the Sub-saharan and Malagasy regions.

Pachysternum capense (Mulsant), on the other hand, which is also small (2,3–2,5 mm long), occurred in fair numbers together with *Sphaeridium quinquemaculatum* in Montagu and can be distinguished from the latter by having inconspicuous longitudinal striae on the elytra. It was common in the Karoo and along the west coast, often in association with *S. caffrum*. In the Sandveld an unidentified species (2,3–3,1 mm long), with blackish head and pronotum and pale straw-coloured elytra, appeared with *P. capense* in the same cow-pats.

Cercyon maritimus and *C. gigas* d'Orchymont usually also breed in decaying kelp and may even be found in the decaying carcasses of marine animals and birds. According to collection data, the latter species is endemic to the Cape Province, and is mainly dark brown with narrow, longitudinal blackish stripes over its elytra.

A third, peculiar, small hydrophilid *Spercheus cerisyi* Guerin-Méneville (about 4 mm long and pale brownish grey in colour) appeared to be common on kelp during the winter and spring in estuaries around the Cape Peninsula. It was very often associated with the chrysomelid *Monolepta bioculata* (Fabricius) (of about the same size), which has four large, oval white spots surrounded by black margins on the dorsum of its orange body. Both beetles were found to feed on the fluids oozing from the decaying kelp. This hydrophilid (subfamily Spercheinae) is apparently a water-living species.

Cercyon maritimus Knisch

DESCRIPTION

Adult (Fig. 4A)

Previously described by Knisch (1924a). Small, rather variable beetles, varying in colour from brown to almost pitch black; in some cases elytra brownish,

marked with black. Each elytron with about nine shallow punctured striae and densely pitted all over, the pits small and as wide apart as their diameter. Beetles vary from 3,7 to 4,6 mm in length.

Widely distributed along the Cape coasts.

Larva (Fig. 4B)

Resembles larva of histerids, but easily distinguished by the last abdominal segment or stigmatic atrium (Fig. 4M), which consists of the tergal plate of the eighth segment, the median and lateral lobes of the ninth segment (lateral lobes also known as acrocerci), the true cerci or mesocerci, each with a long filament at apex, and the procerci, which are actually processes of the eighth pleurites. All spiracles including those of mesothorax of equal size and of biforous type; seven pairs laterally on abdomen, eighth pair opening in atrium. Pro-, meso- and metathoracic shields well developed, though small on last two thoracic segments. Full-grown larvae measuring 10–11 mm in length and dirty to creamy white in colour, except head, thoracic shields and eighth abdominal plates, which are reddish brown and somewhat shiny. Body integument leathery, tough and covered with microscopic spinules (Fig. 4N). Legs present, with femur and tibia distinguishable although minute (contradicts Richmond's (1920) statement that legs are entirely absent in *Cercyon*).

Head capsule (Fig. 4C–D)

Oval, somewhat upwardly directed in most specimens seen, with small ocellus on each side. Frontal sutures not visible. Antennae three-segmented, with first segment about twice as long as the second; latter with small, apparently two-segmented appendage; third segment smaller than the second and with some sensory pegs apically. Postgenae ventrally separated by gular suture, which is Y-shaped and delimits a pregular area anteriorly between its arms. Arrow-shaped tentorial pit posteriorly, almost in centre. Chaetotaxy as illustrated.

Mandibles (Fig. 4H, L)

About half as long as cranium and nearly one-third longer than wide. Broad basally, cutting edge of left mandible without teeth, that of right mandible with single short tooth (t_1) about half-way between apex and molar area. Teeth very similar to those of *C. quisquilius* (Linnaeus) (Hafez 1939d). Molar area thin and almost trenchant in both mandibles, forming a ridge rather than teeth; that of left mandible somewhat broader than that on right. Penicilli not present in the specimens examined. Ventral side of left mandible with longitudinal, curved median groove visible through dorsal integument for reception of right mandible.

Maxillae (Fig. 4I–J)

With broad cardo and stipes, nearly twice longer than wide and with more or less shiny, oval area dorsolaterally furnished with fine setae; mesal margin bearing eight to nine short setae. Fairly long seta also present apically on lateral

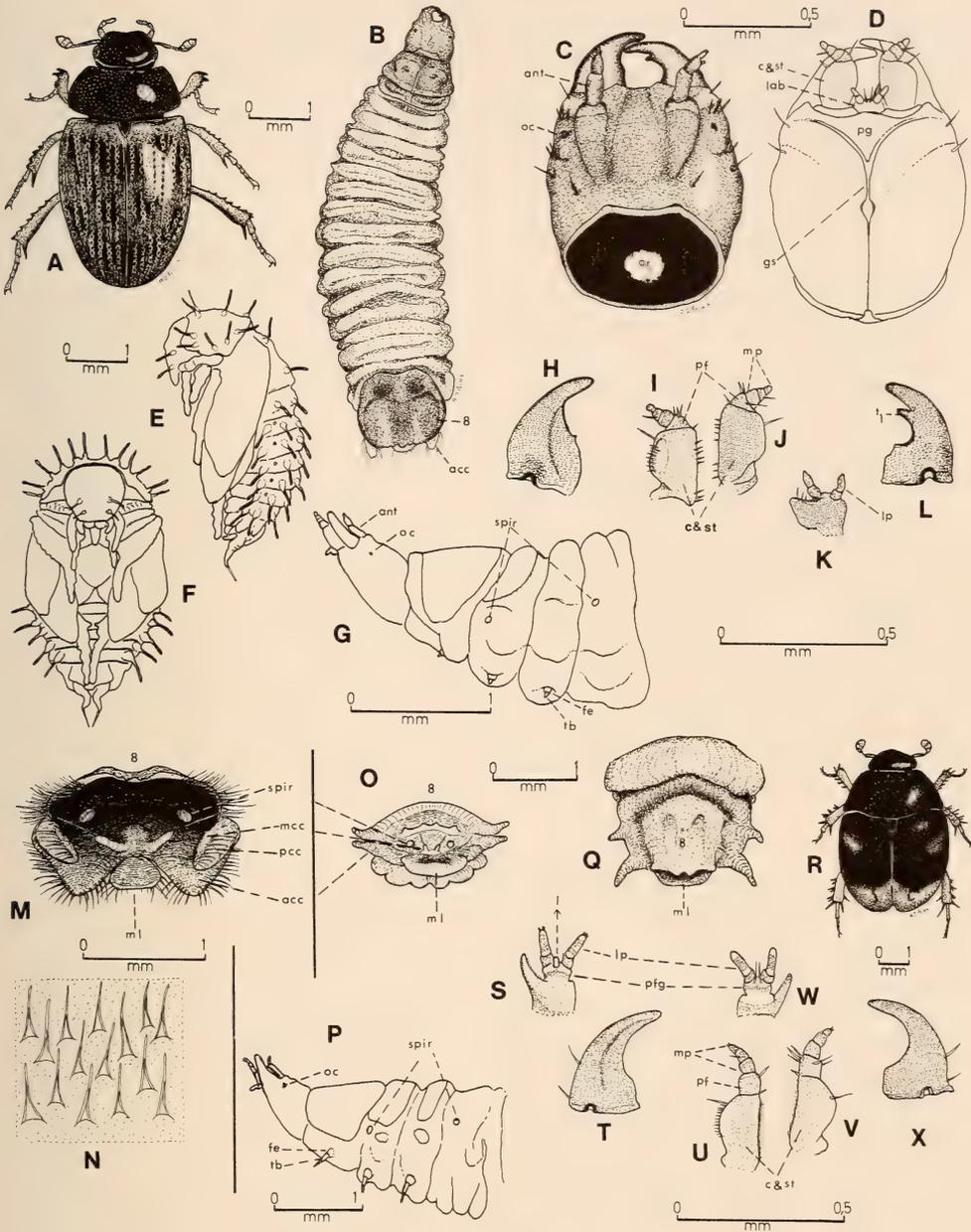


Fig. 4. Family Hydrophilidae.

A-N. *Ceryon maritimus*. A. Adult. B. Larva (dorsal view). C. Head (dorsal view). D. Head (ventral view). E. Pupa (left lateral view). F. Pupa (ventral view). G. First three segments of larva (left lateral view). H. Left mandible (dorsal view). I. Left maxilla (dorsal view). J. Left maxilla (ventral view). K. Labium (dorsal view). L. Right mandible (dorsal view). M. Atrium, straight from behind. N. Integument showing spinules (highly magnified). O-X. *Sphaeridium caffrum*. O. Atrium, straight from behind. P. First three segments of larva (left lateral view). Q. Atrium (dorsal view). R. Adult. S. Labium (dorsal view). T. Left mandible (dorsal view). U. Left maxilla (dorsal view). V. Left maxilla (ventral view). W. Labium (ventral view). X. Right mandible (dorsal view).

side. Ventrally without setae. Maxillary palp three-segmented, with segments tapering towards the apex and of about equal length, the second segment bearing long seta. Apical segment with sensory pegs at apex. Palpifer segment-like and bearing two long setae ventrally; also two to three shorter setae near apical border on mesal side, probably remnant of galea. Short spine-like seta also present basally on mesal margin.

Labium (Fig. 4K)

Small, represented by prementum and two-segmented palpi. Mentum dorsally asymmetrically developed in all specimens seen, forming long, almost triangular projection on left side, which bears some short setae on anterior part. When viewed from below a small part of this projection is visible on mesal side of left cardo-stipes.

Pupa (Fig. 4E-F)

Almost pure white after pupation, but soon changes to straw-yellow with blackish eyes. Head with four tubercles, each bearing long, thick seta or stylus; pronotum with about ten stylus-bearing tubercles on anterior and posterior margin as well as two near middle. Meso- and metathorax with stylus-bearing tubercle on each side of median line. Abdomen on each side with three rows of stylus-bearing tubercles, of which one row is situated laterally. Wings folded down over ventral side of body. Developing genital capsule present as two small, elongate cones situated close together. Fleshy cerci divergent in most specimens studied, each with long filament attached to larval skin. Five pairs of spiracles clearly visible, sixth pair small and inconspicuous. Body length of specimens examined 3,7-5,5 mm.

BIOLOGY

Adults and larvae were observed almost throughout the year, mostly in kelp, but sometimes also in fresh cow-dung. As already stated, the larvae are mainly predacious, but will feed on the colloids oozing from decaying kelp. Larvae collected in this medium along the west coast during spring had a life-span of at least 40 days before pupation occurred. Most pupae were found in the top few centimetres of soil in oval earthen cells constructed by the larvae. Pupal stages varied from 9 to 12 days during August and September, the newly emerged beetles being yellowish white with some orange coloration on pronotum. Those observed assumed their normal dark colour after a few days to about a week.

Sphaeridium caffrum Laporte & Castelnau

DESCRIPTION

Adult (Fig. 4R)

Length 4,3-5,5 mm. Oval, black, only slightly shiny, with fulvous or paler spot near base of each elytron as well as fulvous or paler area on apical third of

elytra. Latter without longitudinal striae but densely punctate, the punctures being small and shallow. External border of elytra also pale fulvous. Legs brownish, furnished with spines.

Widely distributed in South and east Africa and Madagascar (Knish 1924*b*). Specimens studied here were collected mostly in the western parts of the Cape Province.

Larva

Very similar to *Cercyon maritimus*, but easily distinguished by absence of extra tooth on right mandible and by stigmatic atrium, which bears two fleshy projections on each side (the procerci and acrocerci) (Fig. 4Q). Eighth pair of spiracles also opens into atrium. Mesocerci much shorter than in *C. maritimus* and also furnished apically with filament or seta; median lobe broader than in latter species (Fig. 4O), its hind margin almost quadridentate as in *Sphaeridium scarabaeoides* (Linnaeus) (Hafez 1939*b*). Seven pairs of biforous spiracles present laterally on abdomen. Legs much larger than in *C. maritimus* and, apart from femur and tibia (with circle of about nine short setae around apex), third or tarsal segment with one or two setae at tip also present (Fig. 4P). Integument leathery and covered with minute spinules similar to those of *C. maritimus*; also some short setae present. Full-grown larvae measure 8–9,5 mm and are of same colour as those of the latter species.

Head capsule

Very similar to that of *C. maritimus*, including structure of gular suture; also without frontal suture. With two to three ocelli on each side. Integument fairly shiny and brown and cranium wider behind than in front. The antennae three-segmented as in *C. maritimus*, but projection on second segment lacking; second segment also about half the length of first; third segment smallest and with short setae or sensory pegs at tip.

Mandibles (Fig. 4T, X)

Similar to those of *C. maritimus*, including the ventral groove on left mandible, but lacking tooth between apex and molar area on right mandible. Molar areas trenchant. Two small setae usually present on exterior sides, one situated near base.

Maxillae (Fig. 4U–V)

Very similar to those of *C. maritimus*, with cardo-stipes somewhat extended on exterior side and with long seta and also with about four shorter setae ventrally. Mesal margin with numerous very fine setae, otherwise exactly as in *C. maritimus*, including setae on palpifers. Second palpal segment with short seta on both mesal and lateral margin; apical segment with short spine-like seta near base on mesal side, and with sensory pegs at apex.

Labium (Fig. 4S, W)

Very similar to that of *C. maritimus*, but differs from it by longer labial palpi, longer and more pointed projection on left side, which is furnished with fine setae on anterior margin and by presence of a short ligula, which is about three-quarters the length of first segment of palpi. Palpiger about as long as first segment of palpus.

Pupa

Very similar to that of *C. maritimus*, including apical cerci and styli. Number of styli on body and particularly those on head and pronotum also similar to those of latter species, although much longer and thinner in all specimens examined. Cerci somewhat shorter than in *C. maritimus*. Most pupae about 5,4 mm long. Colour of pupae at first more or less creamy white, but eyes become brown after a few days. Whole pupa changes to darker colour just before beetle emerges.

BIOLOGY

Large numbers of beetles were collected in fresh and semi-fresh cow-pats in the western parts of the Cape during the summer and autumn and larvae were observed during the early part of the summer, producing pupae during December and January. The larvae pupate in small cells constructed in the drier parts of the dung and, to judge from their intestinal contents, most of the larvae collected in the pats must have been feeding mostly on the decaying material, particularly the liquids oozing from the wet particles. When crowding occurs they become cannibalistic.

Family **Histeridae**

Very small to medium-sized, oval hard-bodied beetles, head deeply sunk into prothorax, short legs and eleven-segmented antennae capable of being retracted. Tarsal formula 5-5-5 or 5-5-4. Wings well developed; elytra usually not covering last two abdominal segments.

Some 150 species of histerids have already been described from southern Africa, most of which are predacious on coleopterous and dipterous larvae and other smaller arthropods. According to Nuorteva (1970), who experimented with histerids in Finland, there is a very high negative correlation between the occurrence of blow-flies and histerids in fish carcasses. Bornemissza (1968) reported up to 50 per cent kill of fly maggots in cow-pats by *Pachylister chinensis* (Quensel) in Fiji. Some species, however, live in the burrows of small mammals or in the nests of birds (Arnett 1963), particularly species of *Saprinus*, *Gnathonus*, and *Hister*; others again have developed a myrmecophilous or termitophilous life, such as species of *Monoplius* as well as *Hister*. Species of *Teretrius*, which are cylindrical in form, live in the burrows of wood-boring beetles, whereas the flat species of the genera *Hololepta*, *Pachycraerus*, and *Paromalus* are

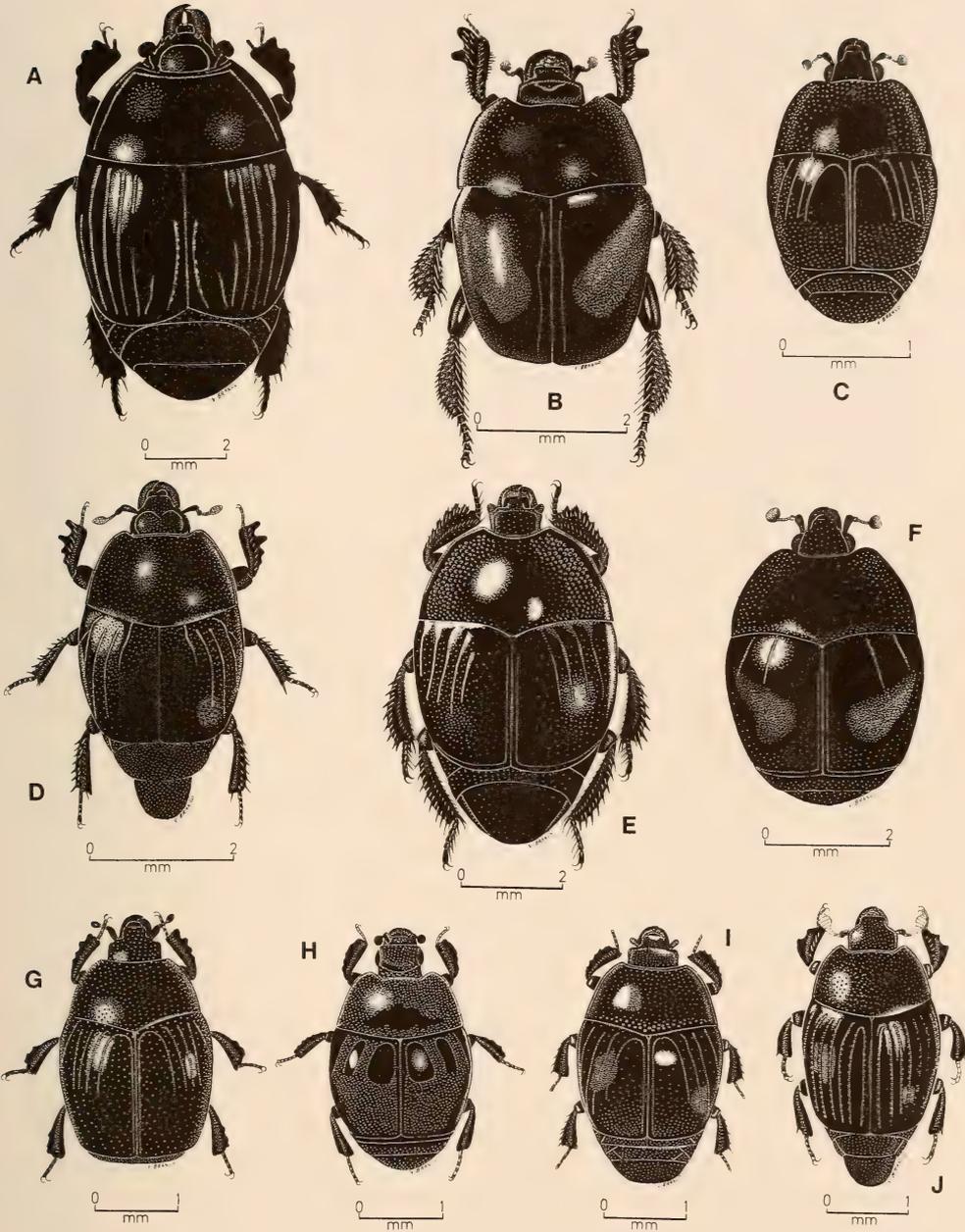


Fig. 5. Family Histeridae.

- A. *Hister nomas*. B. *Pachylopus dispar*. C. *Saprinus cupreus*. D. *Rhylochares saprinoides*.
 E. *Saprinus elegans*. F. *Saprinus nitidus*. G. *Gnathoncus rotundatus*. H. *Hypocacculus specillum*. I. *Hypocacculus harmonicus*. J. *Carcinops minuta*.

found under the bark of plants. At least four species of *Pachytraerus* have been collected in Natal under the bark of *Euphorbia* species.

One of the largest histerids found in South Africa is the black, almost smooth *Macrolister maximus* (Olivier) about 25 mm long, widely distributed in the Republic of South Africa, Botswana, Zimbabwe, and west Africa but it is not common. During the recent surveys at least fifteen species have been found in decaying matter, of which *Saprinus bicolor* (Fabricius), *S. cupreus* Erichson, and *S. nitidus* (Wiedemann) were the most abundant. *Saprinus bicolor* occurred mostly in carcasses, both on the beach and inland, whereas *S. cupreus* visited both carcasses and cow-dung. *Saprinus nitidus* was the most common species in fresh dung and was followed by *Hister nomas* Erichson, *H. contemptus* Marseul, *Atholus conformis* (Erichson), the small *Hypocacculus harmonicus* (Marseul), and *Abraeus setulosus* Fahraeus.

Saprinus nitidus (Fig. 5F) is a rather small beetle (2,8–4,2 mm long), shiny black with a fairly large, somewhat diffuse reddish spot as well as two short oblique striae on each elytron. *Saprinus cupreus* (about 3,3 mm long) (Fig. 5C), is a shiny black beetle about the same size as *S. nitidus* (Fig. 5F), but lacks the reddish spots on the elytra. *Hypocacculus harmonicus* (Fig. 5I) is also shiny black but smaller than *Saprinus nitidus* and is only 1,2–1,4 mm long. *Abraeus setulosus* (1,2–1,8 mm long) is almost dull, densely punctate, and characterized by the presence of short club-shaped hairs. These beetles are widely distributed in South Africa and even occur in semi-fresh and almost dry dung.

The shiny black *Hister nomas* (about 8 mm long) (Fig. 5A), with about seven striae on each elytron, was collected mostly in fresh dung in Heidelberg, Cape Province, particularly during the spring; it was accompanied by the smaller and similar *Atholus conformis*. *Hister contemptus* is about the same size as *H. nomas* but has only about five striae on each elytron. None of these beetles seemed to breed in the dung. Species belonging to the genera *Hister* and *Atholus* mentioned here are easily recognized by the stria that runs parallel to the lateral and anterior margins of the pronotum (Fig. 5A).

Three other species, *Rhyphochares saprinoides* (Erichson) (Fig. 5D), *Hypocacculus specillum* (Marseul) (Fig. 5H), and *Tribalus capensis* (Paykull) were found to be prevalent in semi-dry and dry cow-pats and were never collected in fresh dung. All these species are black. *Rhyphochares saprinoides* (about 4,5 mm long), with indistinct striae on the elytra, and *H. specillum* (2,3 mm long), dull black with five shiny patches on its body, are endemic to the Cape Province according to collection data, and are common, but not numerous, in the western parts that were surveyed. The widespread *Tribalus capensis* (about 2,9 mm long) is slightly shiny and oval, the striae on the elytra being almost obsolete. Most of these beetles were observed to feed on the small scarab larvae and on the larvae of any smaller flies that happened to be present.

Soils rich in decaying organic matter, such as compost and fish-meal, attracted the shiny greenish-black *Saprinus elegans* (Paykull) (Fig. 5E), whereas fowl manure, particularly in fowl-pens of the closed type in which the larvae of

the lesser meal-worm, *Alphitobius diaperinus* (Panzer), and those of the skin-and-hide beetle, *Dermestes maculatus* de Geer, were present, produced large numbers of *Carcinops minuta* (Fahraeus) (Fig. 5J) and *Gnathoncus rotundatus* (Kugelann) (Fig. 5G). These two species are common in the Cape Peninsula in decaying carcasses when fly larvae develop, together with the previously mentioned *Saprinus bicolor* and *S. cupreus*. Both *Carcinops minuta* and *Gnathoncus rotundatus* are rather small beetles, the latter more quadrate, with coarser puncturation than the first, the striae covering only a portion of the elytral surface.

In decaying kelp usually two species only of Histeridae were observed, and these fed mainly on the immature stages of the flies that were present. *Pachylopus dispar* Erichson (Fig. 5B), the larger of the two species (3,1–3,5 mm), is dull black in colour without any sculpture on its body and was often found feeding on small maggots in decaying red bait (*Pyura stolonifera* (Heller)). The other species, *Acritus lightfooti* Lewis, is very small (1,4 mm), red-brown in colour and its body is finely rugosopunctate. There is evidence, however, that this species may also feed on Collembola, particularly the purplish *Anurida maritima* (Guerin).

Saprinus bicolor (Fabricius)

DESCRIPTION

Adult (Fig. 6L)

Oval, shiny, 4–6 mm long. Pronotum coppery black. Elytra blackish green to reddish black and finely rugosopunctate, with about five striae on each side near base; central disc of elytra smooth and only shallowly punctate. Pronotum punctate, with punctures larger on sides. Exposed tergites shiny and densely punctate. Legs shiny, brownish black, with all leg segments flattened and tibiae spined on dorsal side. All femora with grooves for receiving tibiae; grooves on front femora situated on anterior side, those on other legs on posterior side.

Widespread in South Africa and Zimbabwe (Thérond 1956).

Larva (Fig. 6B)

Full-grown larva 12–12,5 mm long and dirty creamy white, with head and pronotal shield yellowish brown; subcylindrical. First eight abdominal segments each with four annulets dorsally and lateroventrally with fleshy swellings which, in conjunction with small tenth segment, function as pseudopods. Cerci small, bisegmented, each bearing two terminal setae. Body sparsely covered with golden hairs; integument covered with conical spines (Fig. 6C) visible only under high magnification. All spiracles almost of same size, oval and of biforous type; twin opening clearly visible on ventral side. Mesothoracic spiracle situated ventrally above leg and tilted lengthways, so that long axis is in longitudinal position, with opening pointing forward. Legs (Fig. 6D) small but well developed, tarsungulus long, slightly shorter than tibia, which is nearly twice as long as femur. Both trochanter and femur with ventral seta and tarsungulus with small seta ventrally near base.

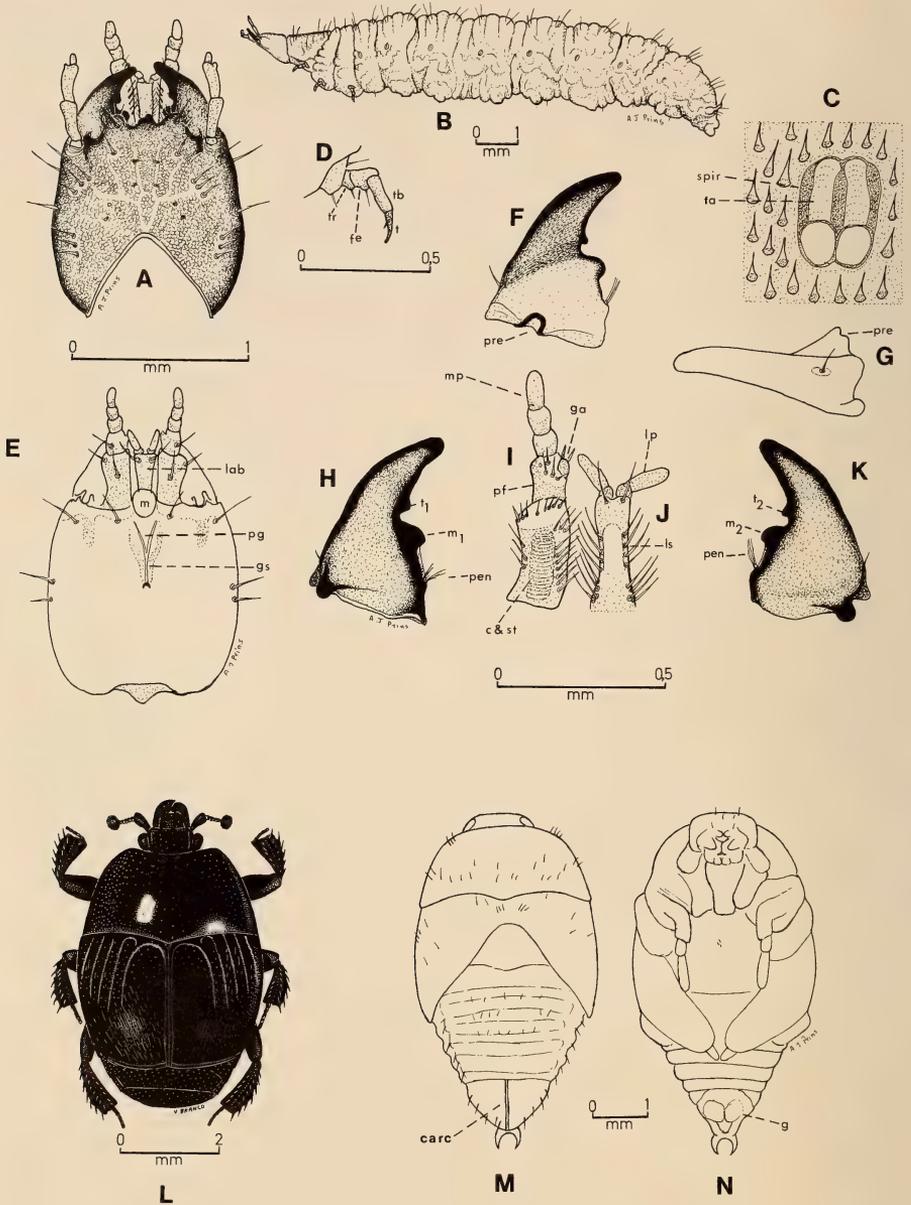


Fig. 6. Family Histeridae.

Saprinus bicolor. A. Head (dorsal view). B. Larva (left lateral view). C. Part of integument highly magnified to show spiracle and spines. D. Right leg (posterior view). E. Head (ventral view). F. Left mandible (dorsal view). G. Left mandible (exterior lateral side). H. Right mandible (ventral view). I. Left maxilla (dorsal view). J. Labium (dorsal view). K. Left mandible (ventral view). L. Adult. M. Pupa (dorsal view). N. Pupa (ventral view).

Head capsule (Fig. 6A, E)

Slightly upwardly inclined, about as long as wide and about as wide behind as in front; posterior margin deeply and angularly emarginate on dorsal side, ventrally only slightly so; dorsally somewhat shiny, microscopically reticulate and light reddish brown. No ocelli visible. Chaetotaxy as illustrated. Nasale extended and emarginate in middle, the two small teeth thus formed asymmetrical in specimens seen; right tooth larger than the left one; sinuate on each side of median extension and forming broad, rounded tooth on each lateral angle, cephalad of the antennae. Frontal and coronal sutures obsolete, but represented by some pale lines as shown in Figure 6A. Small pregula present ventrally between arms of Y-shaped gular suture, of which short stem ends in small posterior tentorial pit at centre of head; postgenae fused posteriorly and gular suture visible only as very shallow longitudinal impression. Antennae about as long as the mandibles; three-segmented, with third segment small, and penultimate one bearing sensory cone; all segments devoid of setae.

Mandibles (Fig. 6F–H, K)

Almost triangular, about half the length of cranium and about a third longer than wide at base. Cutting edge of both mandibles entire, apex rounded and with a small tooth (t_1 and t_2) near molar area, which distally bears a single rounded tooth (m_1 and m_2); proximally with a penicillus. Lateral margin rounded dorsoventrally, without dorsal carina and with small seta near base. Basal portion of mandible raised above the dorsal surface (Fig. 6G) for preartis to join condyle.

Maxillae (Fig. 6I)

Cardo and stipes united; latter dorsally with longitudinal excavation and with three setae on exterior margin and eight to ten setae on mesal; ventrally with only one seta. Apical border with six to eight dorsal setae. Palpifer segment-like, bearing one lateroventral and about four dorsal setae as well as small conical galea on mesal side. Palpus three-segmented, about as long as cardo and stipes and without setae. Galea with two small, palus-like setae.

Labium (Fig. 6J)

Labial stipes (prementum) long, with sides almost parallel and only two ventral setae near apex. Dorsally with row of about ten fairly long setae on each side of basal half and with two setae near apex. Labial palpi two-segmented, with apical segment about twice as long as basal one; both without setae.

Pupa (Fig. 6M–N)

Robust, measuring nearly 6 mm; white in colour with reddish head and mandibles. Body dorsally sparsely covered with short setae. Terminal abdominal segment with a crescent-shaped appendage at apex; dorsum of this segment almost triangular and with longitudinal carina; developing genitalia visible as two swellings on ventral side.

BIOLOGY

Eggs of this species were found in the soil near decaying organic material containing developing fly maggots. The larvae feed mainly on small insects and when mature, construct a soft, silk-lined earthen cell in the soil in which they pupate. Diameter of most of the cells examined was 9,8 mm. The pupal stage lasted for about 13 days during April. The newly emerged beetle is dark brown on the head, with brownish-yellow pronotum. About two-thirds of the pronotal disc in most specimens examined is of a dark brown, the elytra and abdomen pale yellow, with brownish-yellow legs. After a day or two they assume their normal coloration.

Carcinops minuta (Fahraeus)

DESCRIPTION

Adult (Fig. 5J)

Rather small, oval beetle, about 2,5 mm long, reddish black in colour, head black. Fairly shiny all over. Head and pronotum densely and minutely punctured; elytra with seven striae each, striae almost reaching hind margin; spaces between striae also have some fine punctures.

Collection records come from Cape Town and surrounding suburbs, and from Paarl. Also present in Natal, east Africa and Zaire (Thérond 1956).

Larva

Similar to that of *Saprinus bicolor* but smaller, about 6,3 mm long when full grown, and more elongate. Cerci bisegmented and much longer than in latter species, apical segment with two long terminal setae (Fig. 7B). Legs much longer in relation to body than in *S. bicolor* (Fig. 7A). Integument of specimens examined without conical spines, but with rounded tubercles in pseudopodal areas (Fig. 7I).

Head capsule (Fig. 7C–D)

Slightly longer than wide, measuring 0,44 mm wide and 0,50 mm long in most specimens seen, about as wide behind as in front, the sides almost parallel, only slightly convex and somewhat sinuate behind antennae. Almost smooth and shiny, reddish brown to dark brown depending on degree of sclerotization; dorsally with some indistinct sulci as in drawing. Posterior margin dorsally deeply and angularly emarginate, ventrally widely and shallowly so. No ocelli observed. Chaetotaxy as in Figure 7C–D. Pregula very narrow. Nasale (Fig. 7E) in all specimens seen with two asymmetrical lobes in middle, that on left bidentate, right one stronger developed and tridentate. Characteristic of this species is the oblique carina dorsally on posterior one-third of cranium, which is absent in *S. bicolor*. Antennae slightly longer than mandibles, three-segmented; apical segment short, slightly more than half as long as the second, with terminal sensory pegs. First segment longest, about one-quarter longer than penultimate

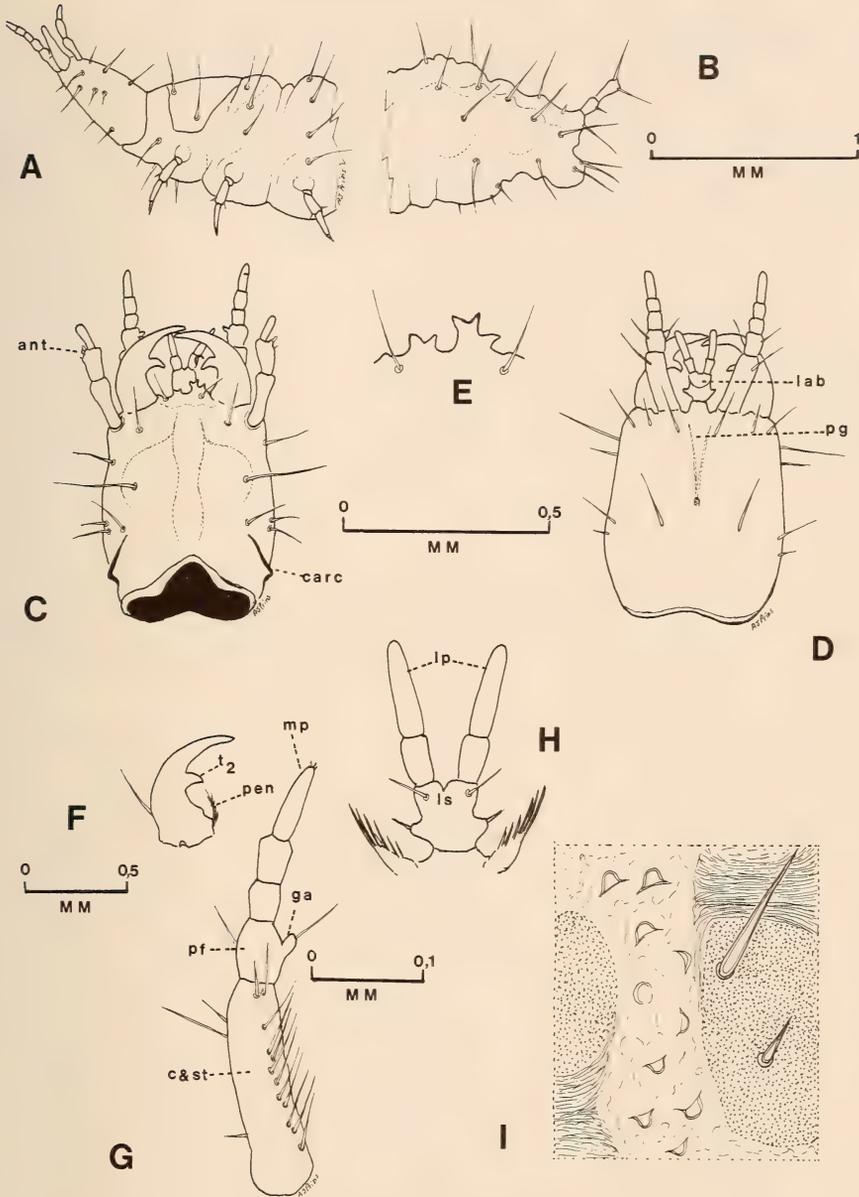


Fig. 7. Family Histeridae.

Carcinops minuta. A. Head and thoracic segments (left lateral view). B. Last two or three abdominal segments (left lateral view). C. Head (dorsal view). D. Head (ventral view). E. Nasale (highly magnified). F. Left mandible (dorsal view). G. Left maxilla (dorsal view). H. Labium (dorsal view) showing lobe-like structures with brush of hairs. I. Part of integument highly magnified to show tubercles.

one, which bears sensory cone and sensory pegs. All segments devoid of setae in the few specimens examined.

Mandibles (Fig. 7F)

Similar to those of *S. bicolor*, but more sickle-shaped, molar area much smaller, tooth t_2 (also t_1 —Fig. 6H) large and acute and situated in about the middle. Mandibles less than half the length of cranium, penicillus fairly long.

Maxillae (Fig. 7G)

Similar to those of *S. bicolor*, but united cardo and stipes much longer, dorsally with single row of about twelve long, fine hairs as well as two setae near apex, inner one the longest. Ventrally with a long seta; also two short setae on external side. Palpifer as in *S. bicolor*, with a ventral seta and conical galea, which is much more developed in this species and bears a long terminal seta. Maxillary palpi three-segmented, apical segment about as long as first and second taken together.

Labium (Fig. 7H)

Labial stipes very short, with two ventral and two dorsal setae, mentum produced on each side in form of a blunt tooth with a terminal spine-like seta. In this species there is dorsally a small lobe-like structure on each side of mentum, bearing a brush of thick hairs. Labial palpi two-segmented, with apical segment nearly twice as long as basal one, both without setae.

Family Staphylinidae

A very large family of elongate, sombre-coloured rove-beetles, with short elytra exposing nearly always about half of the abdomen. They vary from very small to fairly large (about 30 mm or more); antennae usually eleven-segmented (sometimes nine- to ten-segmented), ocelli present in certain forms; hind wings usually well-developed. Tarsal formula 4-5-5, 4-4-4 or even 3-3-3 or 2-2-2.

The beetles abound wherever decaying organic matter accumulates, both along the shore and inland. Many species (subfamily Aleocharinae) live as termitophiles and myrmecophiles, while some species of the genus *Aleochara* are ectoparasitic on fly puparia, such as *A. salsipotens* Bernhauer (Fig. 8A), which were observed to destroy the pupae of the kelp-flies *Fucellia capensis* (Schiner) and *Coelopa africana* Malloch; however, this predation accounts for the destruction of only a very small percentage of the kelp-fly populations.

Some species, particularly those belonging to the subfamily Paederinae, when crushed against the skin, produce a blistering fluid that may cause severe irritation.

The larvae of staphylinids are campodeiform, active, predacious and usually somewhat flattened or depressed. Legs fairly long, four-segmented with a tarsungulus. Ocelli present or absent. Abdomen with ten segments.

Various rove-beetles have been observed in decaying kelp on the beaches, particularly *Cafius xantholoma* (Gravenhorst), which is widespread in Europe (Bernhauer & Schubert 1914) and regarded by Backlund (1945) as eucoenic. Morley (1907) suggests that it may even be omnivorous and will feed on mammal carcasses if necessary. During the present study it was found on carcasses of marine mammals on a few occasions, but appeared to feed on dipterous maggots under these circumstances.

Species of *Aleochara*, including the previously mentioned *A. salsipotens* (Fig. 8A), are some of the most numerous of all the Staphylinidae associated with kelp, together with species of *Omalium*, *Xantholinus* and *Bledius*, particularly *B. alutellus* Bernhauer. Most of them were found all along the coast as well as further inland in the survey area. A tiny, brown, *Omalium*-like *Phyllodrepa hessei* Bernhauer, (about 1,9 mm long) occurred only along the western part of the Cape Peninsula in kelp where the larger species were absent. The large black *Staphylinus hottentotus* Nordman (Fig. 8C), which is distributed throughout South Africa (Scheerpeltz 1973), was as numerous in kelp banks and flakes as in semi-fresh cow-dung and other decaying organic matter such as carcasses of marine and land animals.

The immature stages of *Aleochara* spp., *Bledius* spp., and *Staphylinus hottentotus* were never found in kelp during the surveys and their breeding habits are therefore unknown. However, the larvae and pupae of an unidentified *Aleo-*

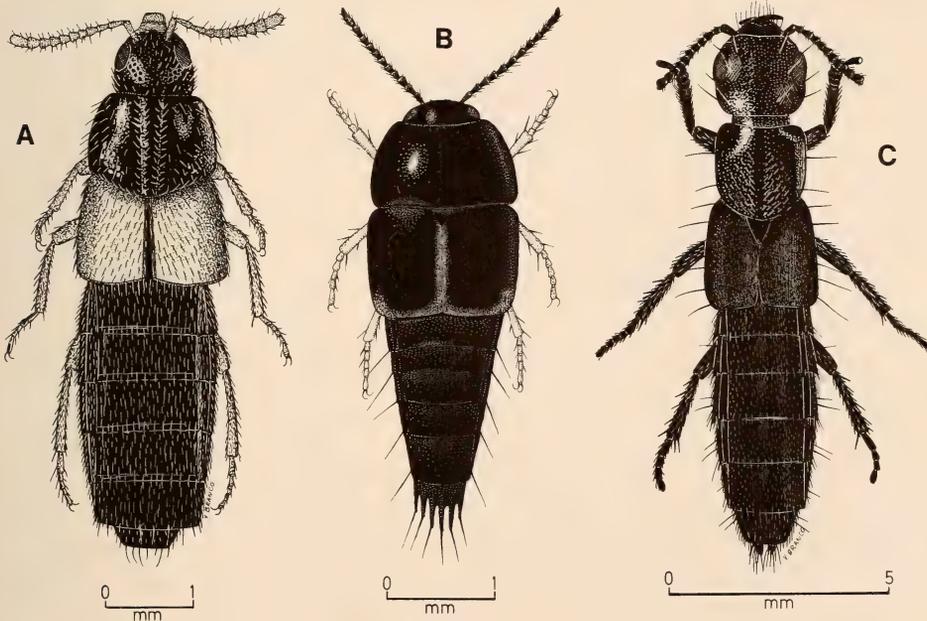


Fig. 8. Family Staphylinidae.

A. *Aleochara salsipotens*. B. *Leucoparyphus variipes*. C. *Staphylinus hottentotus*.

chara sp. (Fig. 9) were observed in semi-fresh cow-dung near Elands Bay during the winter, and those of *Omalium arenarium* (Bernhauer) (Fig. 10) in wrack near Kommetjie.

Fresh cow-dung on the beach and in the interior attracted mainly rove-beetles of the genera *Aleochara*, *Philonthus*, *Xantholinus*, and *Leptacinus*, all of them generally feeding on the flies and their larvae present in the dung, particularly the young larvae of the green dung-fly, *Orthellia peronii* (Robineau-Desvoidy), and those of the scarabs. *Oxytelus caffer* (Erichson) (Fig. 1C) and an unidentified species of both *Aleochara* and *Philonthus* (Fig. 1B), were the most numerous. All are black, except the one *Philonthus* sp., which has brownish elytra, and normally they all breed in the dung.

The *Philonthus* sp. (7,5–9 mm long) is fairly shiny, the *Aleochara* sp. (only 4,5–5 mm), on the other hand, is duller due to the presence of body hairs. All the species occurred almost throughout the year and are widely distributed throughout the whole area that was surveyed.

Aleochara bipustulata (Linnaeus) (3,2–3,7 mm long), another widespread species in the Cape Province as well as in the Palaearctic and Nearctic regions, occurred in cow-pats together with various other *Aleochara* and *Leptacinus* spp. and seems to have the same parasitic habits as *A. salsipotens*.

An unidentified *Philonthus* sp., very similar to the black species previously mentioned but more polished, particularly on the elytra, was found mainly in decaying birds in the vicinity of Cape Town. Occasionally the medium-sized, shiny, black *Philonthus natalensis* Boheman (Fig. 11J), occurred in fresh cow-pats near Heidelberg. Its large, oval, white eggs together with immature and mature larvae, which are characterized by the very long urogomphi, were collected occasionally during the late spring.

A black *Xantholinus* sp., (6,6–7,9 mm long), was fairly common in fresh dung throughout the region surveyed and also appeared in decaying kelp along the west coast. It is probably the same species that was found to visit decaying carcasses.

The peculiar *Leucoparyphus variipes* Fauvel (Fig. 8B), a small, shiny, black staphylinid (about 3,7 mm long), is common all along the south coast and was mostly attracted to cow-pats in which large numbers of the smaller flies belonging to the families Mycetophilidae, Sciaridae, and Sepsidae were breeding. It is very agile and distinctly resembles members of the order Thysanura.

When cow-pats have dried out to a certain extent, some of the species disappear to be replaced by others such as *Aleochara maura* Sachse, *Staphylinus hottentotus*, *Philonthus caffer* Boheman, and an elongate, yellowish-brown *Astenus* sp. *Oxytelus caffer*, *Aleochara bipustulata*, and some of the *Xantholinus* spp. were also observed to remain in fairly dry dung for long periods and were even found to continue to breed in pats as long as there was some moisture available.

A fairly large, agile and aggressive, unidentified *Staphylinus* sp. (Fig. 13M), chequered with golden yellow and brown, was found to breed in fairly dry to semi-fresh pats, both along the south and west coasts. When a cow-pat is picked

up, the large brownish larvae of this species are often found with open jaws and trying to escape into the soil. In the laboratory these larvae fed on various insects, but did not accept isopods.

The staphylinids that visited carcasses during the surveys included *Aleochara salsipotens* (mostly on the beach), *A. lateripennis* Bernhauer, *Oxytelus caffer*, *O. grandis* (Eppelsheim), *Staphylinus hottentotus* and at least one undetermined species each of *Aleochara*, *Oxytelus*, *Philonthus*, and *Xantholinus* (Fig. 14A). *Oxytelus grandis* is a shiny brown species that is widely distributed, occurring in Natal, Zimbabwe as well as in west Africa; all the other rove-beetles are black, except *Aleochara lateripennis* and the *Xantholinus* sp., which have light-reddish and brownish elytra respectively.

According to Kaufmann (1937) *Oxytelus* spp. and genera of the tribe Omaiini are absent during the warm weather and prefer the cold. However, in this study *Oxytelus caffer* was found throughout the year in fairly large numbers, both in cow-dung and carrion, and immature stages of this species and those of *O. grandis* were collected in bird carcasses along the west coast throughout the summer and autumn.

Aleochara sp.

DESCRIPTION

Adult (Fig. 9A)

Black and shiny, abundantly covered with medium-long, brownish, adpressed setae, particularly on head and thorax; abdomen more sparsely covered and therefore more shiny. Hairs grow from small pits, which are oval and larger on abdomen. Legs and antennae dark brownish. First three and apical antennal segments longer than wide, others as wide as or wider than long. Length 4.8–5 mm.

Widely distributed, collected in cow-dung almost throughout the areas surveyed.

Larva (Fig. 9B)

More robust than in *Philonthus* and *Staphylinus* spp., and more depressed dorsoventrally. Colour bright yellow to cadmium yellow, with oval brownish patch on each side of all body segments except pronotum. Mature specimens 4.6–5 mm long; sparsely covered with medium-long setae, of which four characteristically arranged medially near posterior border of the pro-, meso- and metanotum. Urogomphi (Fig. 9C) very small, apparently one-segmented, each with one long apical seta and one or two preapical setae. Spiracles circular and those on abdomen of same size and situated laterally; mesothoracic spiracles (Fig. 9K) ventral in position, somewhat larger and without setae (there is, however, a seta anterior to it). Legs (Fig. 9E) similar to those of other species, but with reduced number of setae, lacking especially rows of spines on femur; tarsungulus with one ventral and one dorsal spine. Integument dorsally covered with very fine, almost ultramicroscopic spicules; very few triangular denticles present and body hairs mostly simple.

Head capsule (Fig. 9D, F–G)

Smooth and shiny, pale golden yellow in colour; slightly wider behind than in front. Posterior margin slightly or widely emarginate, anterior margin straight and without teeth. Frontal sutures very indistinct and in some specimens indicated only by Y-shaped depression, but epicranial stem usually clearly demarcated. Setal pattern as illustrated. Neck absent. One ocellus present on each side, in some specimens not pigmented and may easily be overlooked. Hind margin deeply emarginate ventrally. Gula small, but clearly visible. Antennae three-segmented; apical segment small with three long subapical setae of which one is ventral in position, and with about four sensory pegs at apex; first and second segments of about equal length, second segment with two small ventral spines near apex and with sensory cone surrounded by about three long setae. Labrum free, trapezoidal, anterior margin slightly emarginate and bearing four long and two short setae; also transverse row of six setae medially, two of which are situated on oblique lateral face.

Mandibles (Fig. 9L, N)

Broad at base and tapering towards apex, thus appearing falcate; about half the length of cranium. Cutting edge of both mandibles bidentate, subapical tooth smaller than other. Molar area absent. Lateral margin fairly rounded dorsoventrally and with two setae placed far ventrally in specimens examined.

Maxillae (Fig. 9H, J)

Definite division between galea and lacinia (visible only on ventral side) and long seta on lateral margin. Lacinia with five spines and long seta on mesal margin; maxilla dorsally without setae but ventrally with three long setae on stipes and single long seta on cardo. Latter with Y-shaped suture. Maxillary palpi appear four-segmented in specimens examined, first segment short and bearing single seta on ventral side; second and apical segments of about equal length; penultimate segment slightly longer and bearing a single lateral and ventral seta.

Labium (Fig. 9I, M)

Labial stipes (prementum) apically with two-segmented labial palpi; short, broad, almost conical ligula present and two long subapical setae on ventral side. Mentum fairly large and almost conical and bearing four setae on ventral side. Boundary between mentum and prementum more strongly sclerotized and ventrally bearing short seta on each side. Submentum as broad as mentum and also bearing four setae ventrolaterally.

Pupa (Fig. 9O–P)

Pale lemon to cadmium yellow in colour, very pale soon after pupation; length 3.9–4 mm. Head with about eighteen short, brownish setae; pronotum with some short setae on front and hind margins and a parabolic transverse row

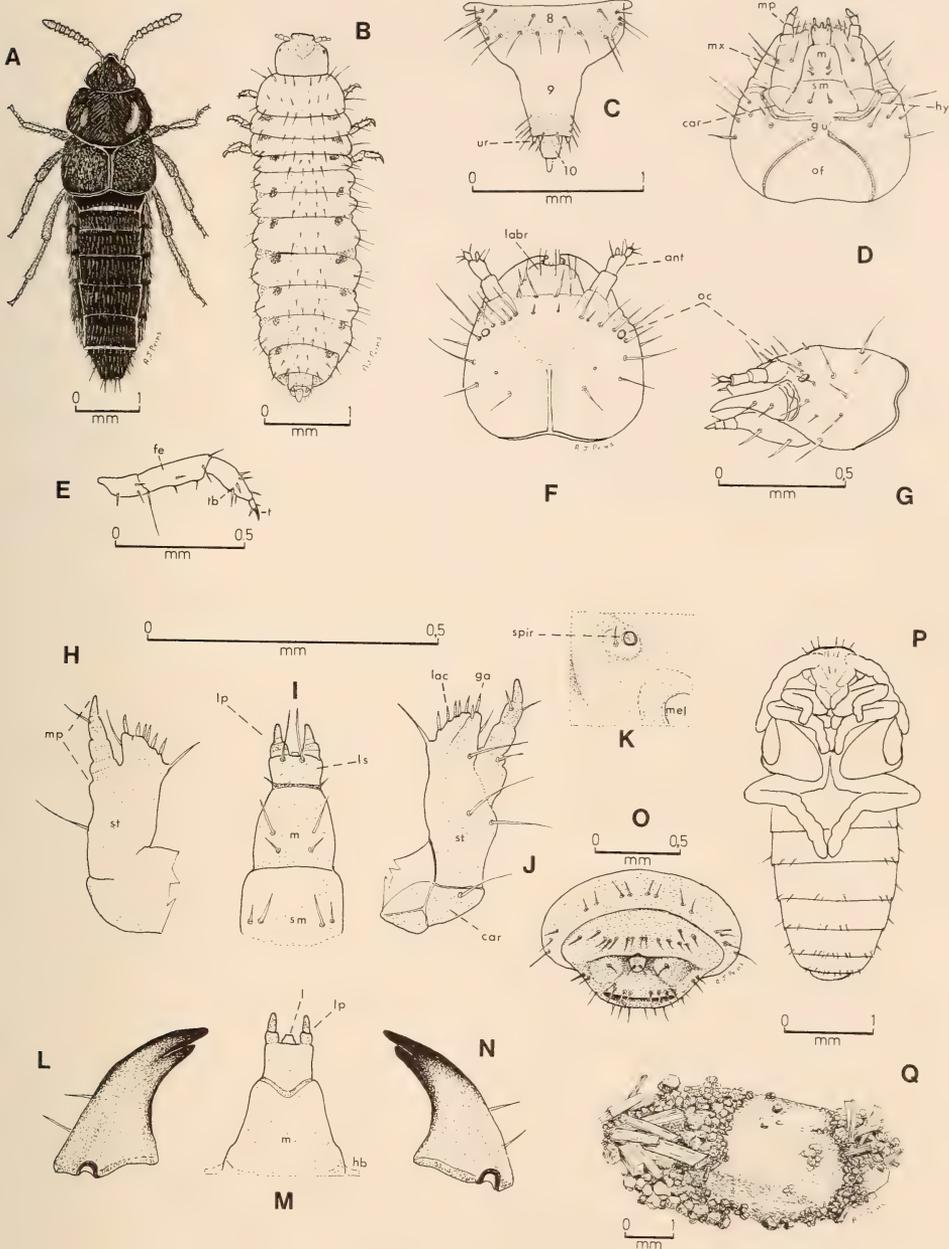


Fig. 9. Family Staphylinidae.

Aleochara sp. A. Adult. B. Larva (dorsal view). C. Abdominal segments 8-10 of mature larva (dorsal view). D. Head (ventral view). E. Right mesothoracic leg. F. Head (dorsal view). G. Head (left lateral view). H. Left maxilla (dorsal view). I. Labium (ventral view). J. Left maxilla (ventral view). K. Left mesothoracic spiracle. L. Left mandible (dorsal view). M. Labium (dorsal view). N. Right mandible (dorsal view). O. Abdominal apex of pupa (ventral view). P. Pupa (ventral view). Q. Pupal cocoon.

of about eight over its middle. Each abdominal tergum with transverse row of about nine short setae near posterior margin. Meso- and metanotum also with few short setae. Abdomen with few short setae ventrally as illustrated; first two sternites medially almost devoid of any setae. Developing genitalia (Fig. 9O) visible as small cone-like structure with two setae flanked on each side by somewhat raised area with centrally placed seta.

BIOLOGY

Larvae of this species were found in association with larvae of *Oxytelus caffer* in the western parts of the Cape during June; they were in semi-fresh cow-pats, which also contained larvae of the scarab, *Aphodius laetus* Wiedemann. Mature larvae construct pale-brownish oval cocoons in the dung (Fig. 9Q), using their saliva and mixing it with dung particles. Pupation occurred after a short prepupal stage; the pupae observed appeared in July and the beetles emerged in August. Although the beetles were attracted to carcasses around Cape Town they did not reproduce under these circumstances.

Omalius arenarium (Bernhauer)

DESCRIPTION

Adult (Fig. 10O)

Light brownish in colour; abdomen somewhat darker, in some specimens piceous; head and scutellum black. Sparsely punctate; elytra also rugulose, shiny. Length 3,3–4,8 mm.

According to collection data it is endemic to the Cape, and during the surveys it was found along the west coast from Paternoster to Kommetjie.

Larva (Fig. 10P)

About 3,8 mm long when full grown and in dorsal view very similar to that of *Oxytelus caffer*, but cerci somewhat longer and, although also dark, they are not piceous; tenth segment also tubular and longer in relation to body. Sparsely covered with setae most of which are of 'frayed' type (Fig. 11L), particularly those forming transverse row in middle of each abdominal tergite (except last two tergites), which are stronger developed than others. As in *O. caffer* a thin, longitudinal, median line traverses thoracic segments and joins epicranial suture. Abdominal shields entire. Legs also similar to those of *O. caffer* and sparsely covered with spines; the tarsungulus long, acute and simple and with short posterodorsal and longer ventral spine some distance from base. Spiracles similar to those of *O. caffer* and similarly situated. Cerci (Fig. 10U) undivided and bearing two 'frayed' type setae on basal half, one on external margin and one dorsal, as well as two long ventrally situated setae, of which one is situated near apex; also two small spine-like setae, one just below exterior 'frayed' seta and one on internal margin, between the two long setae. Apex of cercus conical with single short

seta at base of cone. Integument of dorsal shields lacking triangular denticles found in *O. caffer*.

Head capsule (Fig. 10Q, T, V)

Sides slightly convex and frontal and epicranial sutures fairly distinct; neck absent. Five ocelli present on each side as illustrated. Hind margin almost straight or slightly emarginate with clypeofrontal suture obsolete in specimens examined. Labrum free, its anterior margin widely convex and devoid of any setae dorsally in most specimens seen, except two short submedian setae near anterior border. Extreme apical portion somewhat raised and with two longer setae and some spicules ventrally. Chaetotaxy as illustrated; some hairs of 'frayed' type. Antennae three-segmented, with first segment short, second about twice as long as first and bearing three long subapical setae and fairly long finger-shaped sensory cone, which is about as long as third antennal segment. Latter about as long as the first segment, with three long subapical setae and three to five short spines or sensory pegs apically. Postgenae ventrally separated by short gula.

Mandibles (Fig. 10W, Y)

Almost sickle-shaped and about twice as long as width at base; about half as long as cranium. Cutting edge bidentate (with one long apical and one smaller preapical tooth). Molar area without teeth but trenchant and bearing prostheca distally. Dorsal carinae rounded and indication of scrobis present, bearing long seta distally and shorter one some distance from base.

Maxillae (Fig. 10R)

Mala long and tapering with about six spicules or cones ventrally on mesal side near apex; lateral margin with short seta some distance from base and one on mesal side near base. Another short mesal seta situated about half-way between base and apex. Palpifer short and segment-like in some specimens and ventrally bearing short seta. Palpus three-segmented; first two segments of equal length, third longer; second segment with two lateral setae. Stipes ventrally with two setae. Sclerite between cardo and mala, bearing two short setae near base, which is raised and fairly convex dorsoventrally.

Labium (Fig. 10S)

Mentum small, membraneous and bearing four small setae on basal sclerotized area. Prementum bearing two segmented palpus and two setae on ventral side close to finger-shaped ligula, which is nearly as long as palpi. Prementum minutely setose near base of ligula, otherwise devoid of setae.

Pupa (Fig. 10Z)

Yellowish white in colour, becoming dark shortly before beetle emerges. Length 2,5–2,8 mm. Characterized by long setae: two on front, two on hind

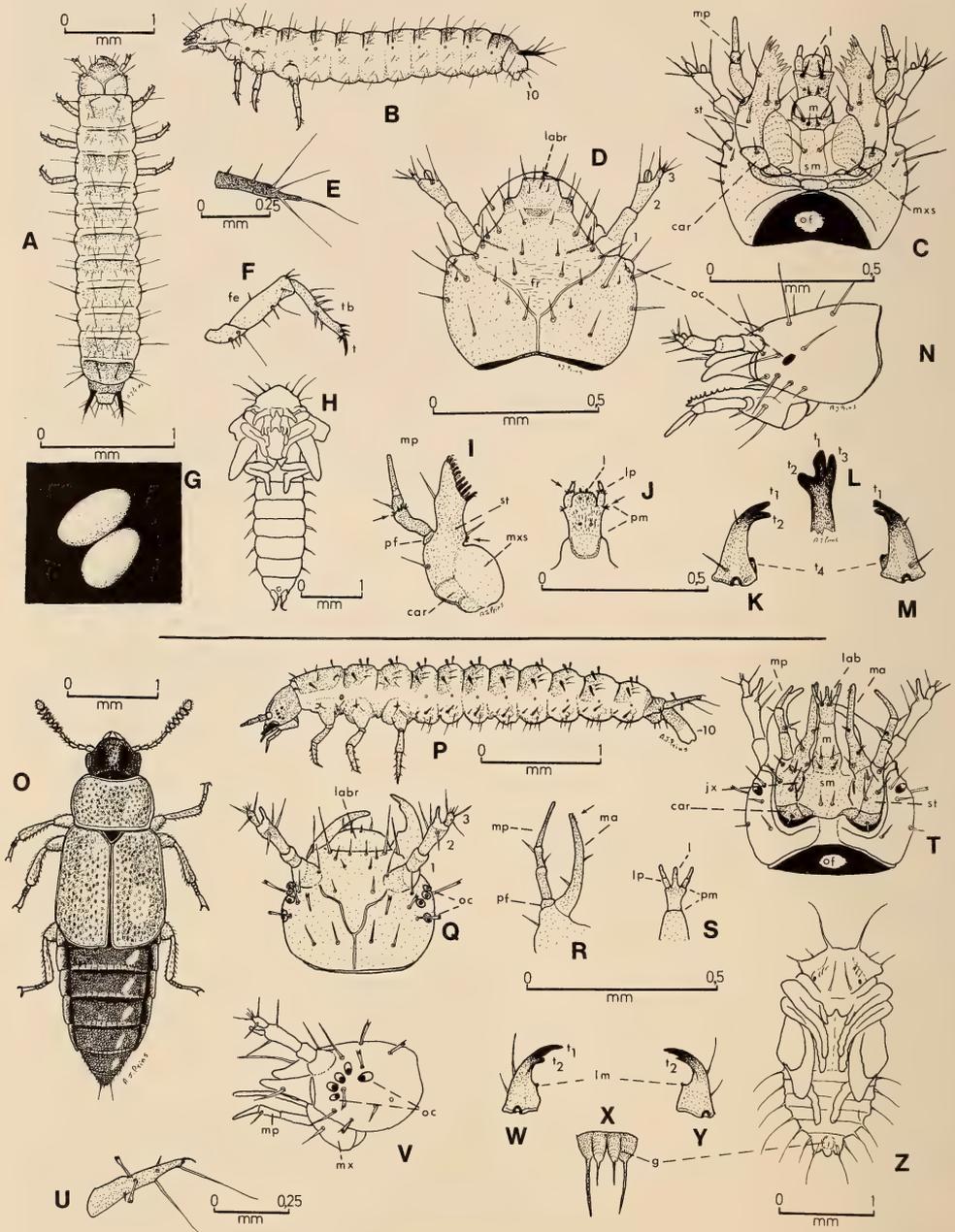


Fig. 10. Family Staphylinidae.

A-N. *Oxytelus caffer*. A. Larva (dorsal view). B. Larva (left lateral view). C. Head (ventral view). D. Head (dorsal view). E. Left urogomphus. F. Right mesothoracic leg. G. Eggs. H. Pupa (ventral view). I. Left maxilla (dorsal view). J. Labium (dorsal view). K. Left mandible (dorsal view). L. Apex of left mandible (lateral view). M. Right mandible (dorsal view). N. Head (left lateral view).

O-Z. *Omalium arenarium*. O. Adult. P. Larva (left lateral view). Q. Head (dorsal view). R. Left maxilla (dorsal view). S. Labium (dorsal view). T. Head (ventral view). U. Left urogomphus. V. Head (left lateral view). W. Left mandible (dorsal view). X. Apex of pupa (ventral view). Y. Right mandible (dorsal view). Z. Pupa (ventral view).

margin of pronotum and seven laterally, two submedially on abdominal terga 1-7. Also two long setae on front margin of head and some smaller ones on both head and pronotum and on abdominal sterna. First three abdominal spiracles circular and clearly visible, the others inconspicuous. Abdominal apex with two fleshy projections, each with a long seta; developing genital capsule either present as a rounded swelling or as two projections, each with short seta apically (Fig. 10X).

BIOLOGY

Larvae of this staphylinid were observed in decaying kelp along the west coast during the winter months. The larval period seems rather short and most larvae collected in June pupated during the same month. Most of the young larvae used for rearing of the adults were kept in decaying kelp from which all other arthropods were removed. These larvae developed to maturity and produced normal adults.

Oxytelus caffer (Erichson)

DESCRIPTION

Adult (Fig. 1C)

Black, matt or slightly shiny, particularly abdomen; strongly punctate and also rugulose, with rugulae more or less longitudinally arranged; areas between rugulae and punctures also minutely reticulate. Legs reddish brown. Easily recognized by presence of four longitudinal, rounded carinae over the middle of the pronotum. Length 3,2-4,2 mm.

One of the most numerous and widely spread staphylinids; according to Scheerpeltz (1973) it is distributed over a large area including South West Africa, South Africa and east Africa.

Larva (Fig. 10A-B)

Whitish yellow to lemon yellow, in some specimens even cadmium yellow in colour. About 7,0 mm long when full grown, subcylindrical and rather similar to that of *Aleochara* sp. Thoracic tergites divided medially by distinct line, but those of abdomen undivided. Anterior borders of all dorsal abdominal shields clearly demarcated by a thin, dark line. Thorax and abdomen sparsely covered with brownish hairs placed more or less in transverse rows; some of these hairs long, particularly those over middle of segments.

Ninth abdominal segment with two short piceous to blackish urogomphi (Fig. 10E), which appear undivided; each urogomphus with long apical seta, three long subapical setae, smaller seta about half-way between base and apex and small seta near base. Tenth segment forming short tube, with anal opening a short Y-shaped slit; stem of the Y pointing downwards and ending in pointed lobe. Abdominal spiracles circular and all more or less of the same size. Meso-

thoracic spiracles also circular, slightly larger than those on abdomen and also situated on side of body between pro- and mesothorax. Dorsal shield without any fine denticles; hairs simple.

Legs (Fig. 10F) as in *Aleochara* sp. with reduced number of spines. Tibia also with three spines around apex, one being dorsal; claws simple, acute and with two small spines placed ventrally near base.

Head capsule (Fig. 10C–D, N)

Pale golden brown with front one-third darker in older specimens; fairly smooth and shiny. Front transversely and finely rugulose; frontal and epicranial sutures rather indistinct in some specimens. Chaetotaxy as illustrated. Sides somewhat convex, hind margin widely and shallowly emarginate on dorsal side. One fairly large ocellus present on each side. Antennae appearing three-segmented; first segment about as long as second; latter with three long sub-apical setae and a large sensory cone on mesal side; third segment small, about as long as sensory cone, with three long preapical setae and about three short setae at apex. Neck absent. Labrum free, trapezoidal, and with rounded lobe on each side at base; also with almost triangular sclerite in middle at junction with clypeus. Frontoclypeal suture only partly developed on each side. Postgenae ventrally separated by small gula. Hind margin of cranium ventrally deeply emarginate.

Mandibles (Fig. 10K–M)

Narrow; broader basally and about twice longer than width at base. Fairly rounded dorsoventrally on external side, without dorsal carina. Long seta present near base (rather dorsally placed) and smaller seta (on external side) near base of apical teeth. Each mandible with three apical teeth although, when viewed from above, mandibles appear bidentate. Molar areas absent, but ventral side with oval, flat area bearing dorsal trenchant ridge which forms broad tooth (t_4) on mesal side.

Maxillae (Fig. 10I)

Rather similar to those of *Aleochara* sp., but galea and lacinia not separated or delineated by suture. Mala oblique, almost trenchant, and furnished with eight to nine strong, palus-like teeth; basal teeth largest and extreme basal one in some specimens accompanied by one or two smaller ones. Basal half of mala ventrally also with three to four smaller teeth and apical part with five to six. Maxilla dorsally without setae, except for one long seta on lateral margin below palpus. Mesal margin of mala with few very small spines (or sensory pegs) near junction with maxillary articulating area. Maxilla ventrally with about four setae of which three are on apical half and one on basal half. Maxillary articulating area ventrally present as large convex lobe on mesal side of stipes. Cardo with one seta only on ventral side and with Y-shaped suture. Palpifer small and

bearing single seta ventrally. Palpus three-segmented, with first and apical segments of about equal length; first is shaped like wide S with a row of very small spine-like setae round its apex; second segment short, about half the length of first and with two ventral setae.

Labium (Fig. 10J)

Rather similar to that of *Aleochara* sp.; submentum fairly large and bearing two setae. Mentum wider than submentum and only partly sclerotized in young larvae; it bears four setae. Prementum with broad, lobe-like ligula and two-segmented palpi. As in maxillary palpi, first segment with row of tiny, spine-like setae or spicules on ventral side of its apex; apical segment with some sensory cones; also few tiny spines at base of first segment on palpiger. Stipes ventrally with two long setae as well as two short ones close to base. Labium dorsally beset with fine setae or spicules and two tiny, spine-like setae at apex of ligula. Four small circular sensory areas, two on ligula and two on stipes, clearly visible dorsally.

Pupa (Fig. 10H)

Oblong and light yellow in colour, but turns almost black just before emergence of beetle. Length 4,9–6,8 mm. Abdominal apex rather similar to that of *Xantholinus* sp. (Fig. 14L), with the developing genital capsule in most specimens visible as small conical tubercle just above two fleshy conical projections. First three abdominal spiracles circular, small and clearly visible; others inconspicuous. First abdominal tergum with two long submedian setae; second to seventh abdominal segments each with lateral setae. Head with three long setae on each side and two on occiput. Pronotum with two long setae on anterior margin and some long setae (about ten) along posterior and lateral margins. Otherwise devoid of setae.

BIOLOGY

Large numbers of the beetles were observed in cow-pats almost throughout the year and occurred in the wet as well as in the drier parts of the dung. Larvae and pupae were collected during autumn and winter and both larvae and beetles were found to feed on dung particles and on colloids oozing from the dung. Eggs (Fig. 10G) of this species are oval, smooth, and shiny, and are whitish yellow to bright lemon yellow in colour; those collected during June along the south coast measure $0,68 \times 0,36$ mm to $0,76 \times 0,46$ mm.

When full-grown, the larvae construct small oval cells in the soil or in the drier parts of the dung, in which the prepupae and pupae are formed. Pupal stages lasted 10–14 days in the laboratory during the winter months. Prepupae are somewhat wrinkled and pale yellow in colour. Newly emerged beetles are black with white wings, which darken after a few hours.

Philonthus natalensis Boheman

DESCRIPTION

Adult (Fig. 11J)

Shiny black beetle, 11–12,5 mm long. Elytra short and covered with medium-long, golden-whitish hairs. Body microscopically striatoreticulate and with silky sheen; abdomen more shiny. Eyes large, oval, slightly less than twice as long as wide. Head smooth, except for row of large punctures around eyes and few postocular punctures, each bearing single long brown seta. Pronotum laterally with some long setae, particularly the transverse row parallel with anterior border on each shoulder; also about eight punctures on each side of the pronotal disc, each with long seta. Antennae brown, legs piceous with spines and hairs on tibiae and tarsi.

Widespread in east, south-east and South Africa (Scheerpeltz 1973).

Larva (Fig. 11A–B)

When mature, about 15,6 mm long. Head and pronotum dark reddish brown, meso- and metathorax yellowish brown with dark spot on each side; mesothorax darker in middle. Underside of thorax and abdomen creamy white; each tergum with two brownish sclerotized plates. Tenth abdominal segment long, tube-like and functioning as pseudopod. Cerci very long, inarticulate and about as long as first seven abdominal segments; basal ninth of each cercus beset with small spines, remainder of cercus with fine hairs; spine-like seta present dorsally near base of each cercus. Head slightly downwardly directed and about as wide as thorax. Pronotum narrower in front than behind and with shallow, oblique, more weakly sclerotized depression on each side near anterior angles. Sclerotized areas fairly smooth and shiny.

Body sparsely covered with long golden brown setae, some of which of 'frayed' type (Fig. 11L) with branched tips. Body integument dorsally with microscopic triangular denticles, visible only under high magnification. Ecdysial suture visible as pale reddish-yellow longitudinal line over the middle of thoracic terga, anteriorly continuous with epicranial stem. Sterna similar to those of *Staphylinus* sp., but most setae of 'frayed' type. Mesonotal spiracle large, oval, and with single seta anteriorly. Abdominal spiracles almost circular, those of first abdominal segment larger.

Only coxae and femora with some short, fine hairs (Fig. 11E), otherwise legs devoid of hairs, but with strong spines or spine-like setae; those on femora arranged in double ventral row; space between rows bare. Each trochanter with six to seven ventral spines, and long slender apical seta. Tibiae with spines distributed over whole surface. Claws as in *Staphylinus* sp. (Fig. 13F), but each one with three short spines, one of which is ventral, the other two situated more or less on posterior side.

The larvae are characteristic of the genus *Philonthus* and easily recognized by their very long cerci.

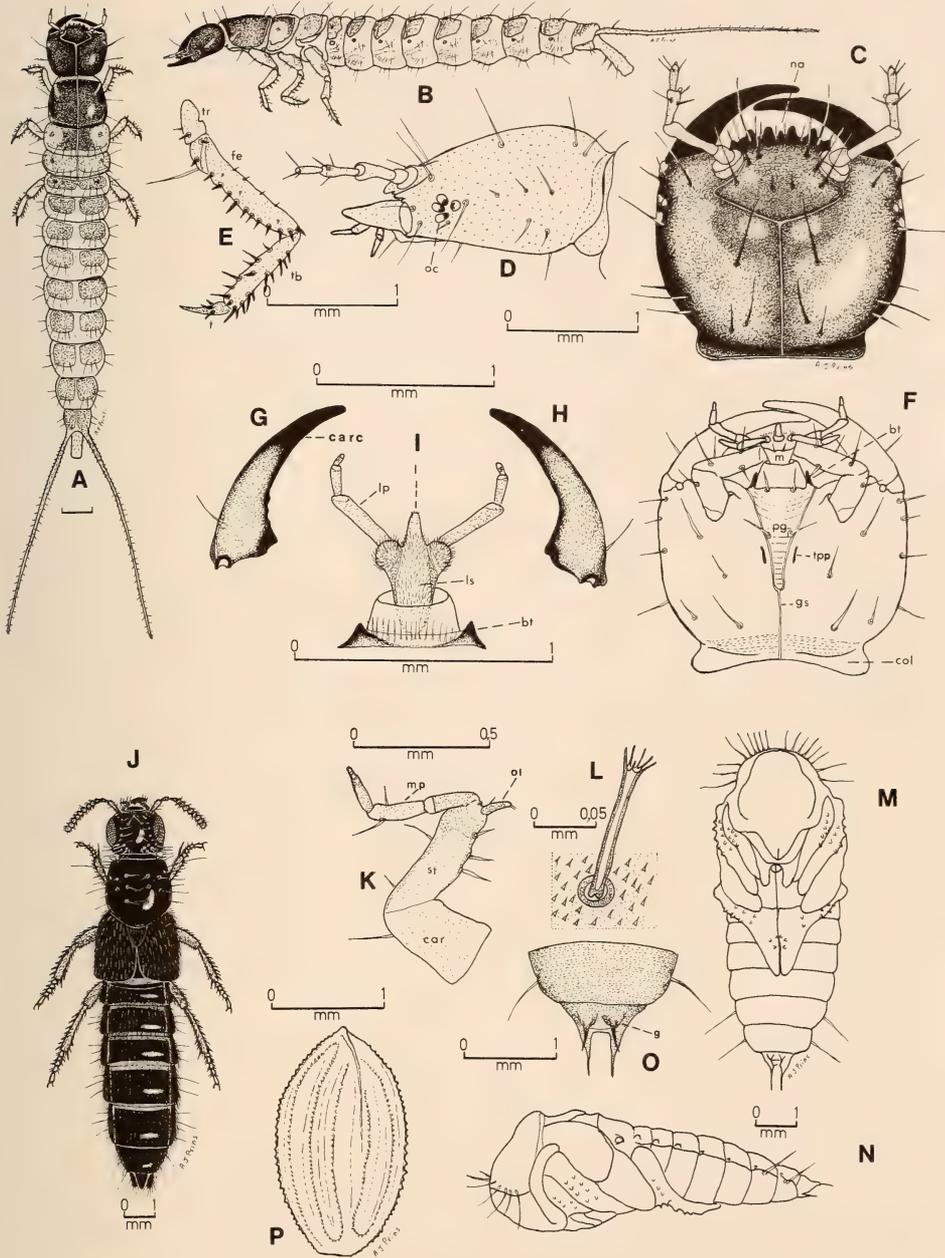


Fig. 11. Family Staphylinidae.

Philonthus natalensis. A. Larva (dorsal view). B. Larva (left lateral view). C. Head (dorsal view). D. Head (left lateral view). E. Right leg (posterior view). F. Head (ventral view). G. Left mandible (dorsal view). H. Right mandible (dorsal view). I. Labium (dorsal view). J. Adult. K. Left maxilla (dorsal view). L. Modified seta and triangular denticles on integument (highly magnified). M. Pupa (ventral view). N. Pupa (left lateral view). O. Ventral view of last two abdominal segments of pupa. P. Egg.

Head capsule (Fig. 11C–D, F)

Dark yellowish brown, fairly smooth and shiny. Sides almost parallel, posterior corners rounded. Long epicranial stem and shorter frontal sutures visible as thin pale-reddish lines. Neck short. Chaetotaxy as illustrated. Four ocelli present. Cheeks rounded dorsoventrally and without carinae. Frons small, with two setae on each side. Each half of epicranium bearing only about eight dorsal setae and only faint indication of paler longitudinal lines. Nasale shaped as in *Staphylinus* sp., septemdentate and with same number of setae.

Ventral aspect of cranium very similar to that of *Staphylinus* sp.; preguila, however, much longer and more acute posteriorly and with same number of setae. Posterior tentorial pits visible as short, elongate black marks laterad to arms of gular suture, not adjacent to stem as in *Staphylinus* sp. Antennae four-segmented, with one sensory cone on apex of fourth segment and one mesally near apex of penultimate segment; latter and apical segment with pre-apical setae.

Mandibles (Fig. 11G–H)

Almost falcate, slightly less than half the length of cranium. Retinaculum absent; each mandible with dorsal carina on cutting edge extending over apical two-thirds of its length. Apices of both mandibles rounded, not pointed as in *Staphylinus* sp. Lateral side of mandible rounded, without carina, and with single fairly long seta near base. Molar areas and penicilli absent.

Maxillae (Fig. 11K)

Similar to those of *Staphylinus* sp. Stipes fairly long, both ventral and dorsal faces devoid of setae, except for single long seta ventrally near base and inconspicuous seta on base of palp; also two setae on lateral margin, one of which is fairly long, and about four setae on mesal side (mala). Inner lobes absent, outer lobes or galea conical and about as long as penultimate segment of labial palp and bearing two setae at apex as well as single short seta near base. Maxillary palps appear three-segmented, with apical and penultimate segments of about equal length, latter with single lateral and mesal seta; terminal segment with apical third narrowed. Palpifer with single seta as in *Staphylinus* sp. Cardo long, about three-quarters length of stipes and bearing single ventral seta.

Labium (Fig. 11I)

Ligula conical as in *Staphylinus* sp. and nearly as long as penultimate segment of palp. Latter three-segmented, with first segment about twice as long as penultimate one, apical segment less than half the length of latter. As in *Staphylinus* sp., prementum can be retracted into mentum and bears ventral seta near each palpal base. Labial stipes, including palpigers, dorsally covered with fine silky hairs as in *Staphylinus* sp. Mentum on each side with tooth, as in latter species.

Pupa (Fig. 11M–O)

Semi-obtect, almost smooth and shiny and very similar to that of *Staphylinus* sp. Light reddish yellow in colour. Length 7,9–8,7 mm. Anterior pronotal margin with sixteen to twenty long barbed setae and lateral margins of abdominal segments 7 and 8 also with fairly long setae. Spiracles as in *Staphylinus* sp. All legs with six to nine pointed tubercles. It differs from pupa of *Staphylinus* in possessing two conical projections at posterior end, each with an elongate seta-like filament. Developing genital capsule (Fig. 11O) also represented by two spine-like projections apically on ventral side.

BIOLOGY

The oval, almost pure-white eggs (Fig. 11P) are fairly large, about 2,2 mm long and about 1,4 mm wide, matt and with indistinct striae and longitudinal tuberculate ridges alternately arranged, as illustrated. They were laid singly in semi-fresh dung during October and hatched in 4 or 5 days. On hatching the chorion splits from the top over one or both sides and just before hatching the mandibles of the larva can be seen in the middle of the egg on one side.

The newly hatched larva looks very much like the mature larva, but is pure white with golden-brown mandibles and four brownish eyes on each side of the head. It measures about 6,1 mm in length shortly after hatching and its long cerci are about as long as the almost transparent body. The spiracles are very conspicuous at this stage and in most of the specimens examined there are only a few setae on the body and most of these, even some of the spines on the legs (except a few on the head, thorax and ventral side of the 8th abdominal segment), are of the 'frayed' type. The claws are conspicuous and bear only two ventral spines. The tenth segment is very large in relation to the rest of the body and is about as long as the head. In the latter the coronal and frontal sutures are obsolete and the two small setae on the middle of the frontal disc, as well as the two posterior setae near the posterior border of the head, are absent. The mandibles are fairly pointed, and the small apical part of the third segment of the maxillary palp is already differentiated. After a few hours the larva becomes greyish in colour, but the first two body segments as well as the head are golden brown.

The lifespan of the larva is short and those reared in the laboratory were mature in about 14 days at 25°–27°C after which they pupated in their larval skins in small clay cells either in the soil or in the remains of the dung. Hafez (1939a) gives the duration of the larval stage of the cosmopolitan *Philonthus quisquiliarius* (Gyllenhal) in Cairo as 6 to 8 days at 30°C. Pupae were recovered during November and the adult beetles emerged after about 9 days. The newly emerged beetles are black with almost pure-white wings and elytra.

This species was very abundant in fresh cow-dung along the south coast. Both larvae and adults are predacious on other insects and also feed on the juices oozing from the dung.

Philonthus spp.
(Fig. 1B)

Two forms of this beetle were collected in cow-dung. The one (sp. A) is somewhat larger than the other (sp. B) and was collected mostly along the south coast; sp. B was found throughout the area surveyed. As a proper identification of the two forms was impossible, they are here treated as two separate species; however, there are no appreciable morphological differences between the larvae.

Philonthus sp. A (large)

DESCRIPTION

Adult

Similar to *P. natalensis* but smaller, only 7.5–7.9 mm long; colour black, head and pronotum very shiny. Head narrower than in latter species and more oval in shape.

This species was found in association with *P. natalensis* and is apparently widely spread along the south coast; it was also observed at Montagu.

Larva (Fig. 12A)

Rather similar to that of *P. natalensis* but smaller, measuring only 10–12 mm in length when mature, and cerci (Fig. 12L) much shorter, consisting of two segments. Second segment of cercus slightly less than half the length of first and with long apical seta, as well as small subapical, spine-like seta; first segment with about six long setae as well as some shorter ones. Tenth abdominal segment tube-like, but shorter than in *P. natalensis*. Whole body sparsely covered with medium-long brownish setae, some of which are of 'frayed' type (Fig. 12B). Otherwise exactly as in *P. natalensis*. The dorsal integument covered with denticles similar to those of *P. natalensis*, but somewhat larger. Spiracles similar to those of *P. natalensis*, including anteriorly situated seta on mesothoracic pair. Legs also similar to those of *P. natalensis*, including tarsal spines and long seta on apical portion of trochanter.

Head capsule (Fig. 12C–D)

Light brown to yellowish brown in colour; very finely reticulate and with some rugae; smooth and shiny, about as long as wide, with sides parallel and hind margin almost straight. Neck as in *P. natalensis*, posterior angles rounded. Nasale, ocelli antennae and ecdysial sutures as in *P. natalensis*. Ventral aspect of cranium also very similar. Chaetotaxy as in Figure 12C–D.

Mandibles

Similar to those of *P. natalensis* and much shorter than cranium; also bearing seta close to base.

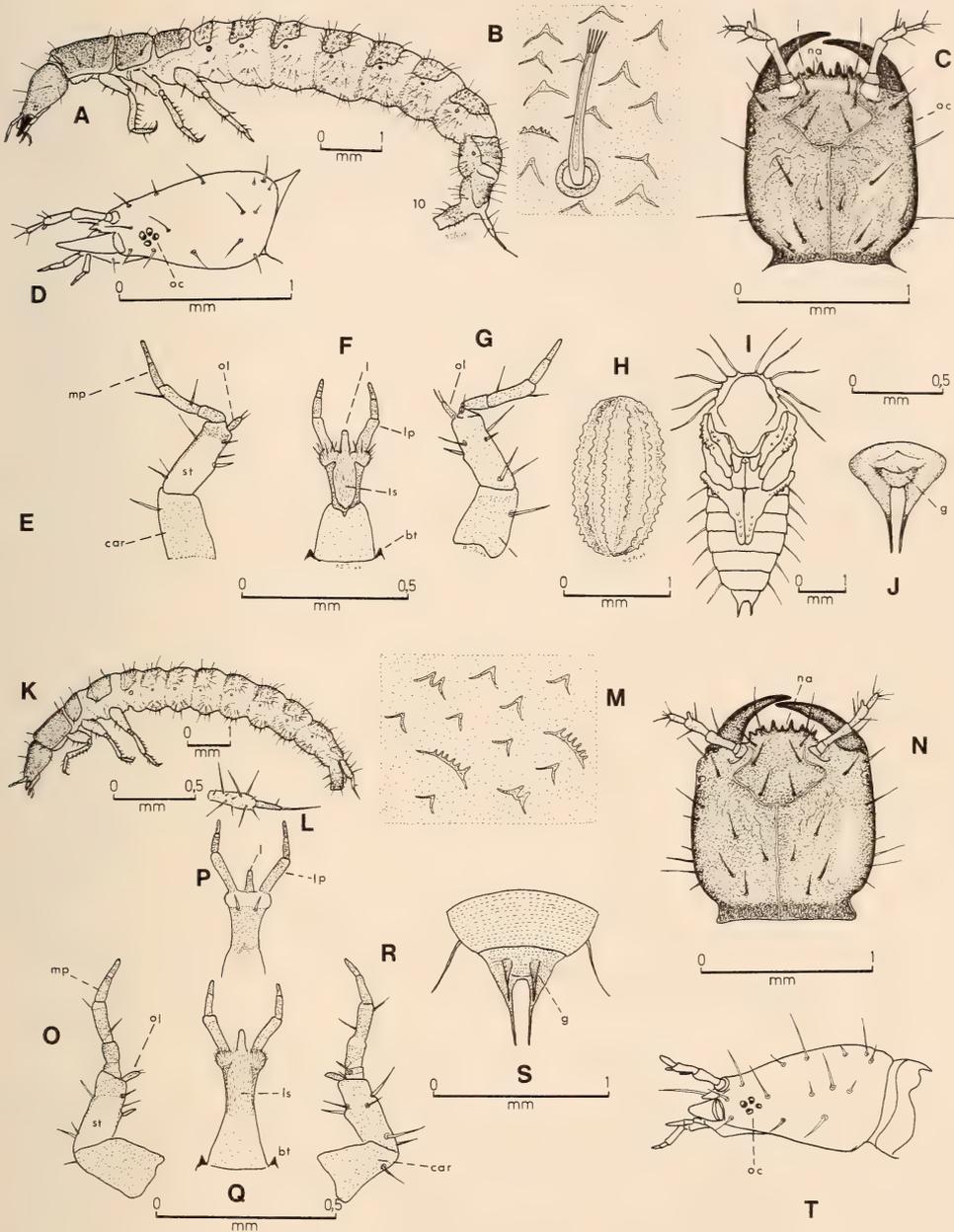


Fig. 12. Family Staphylinidae.

A-J. *Philonthus* sp. A (large). A. Larva (left lateral view). B. Integument of dorsal shield, showing hair and denticles (highly magnified). C. Head (dorsal view). D. Head (left lateral view). E. Left maxilla (dorsal view). F. Labium (dorsal view). G. Left maxilla (ventral view). H. Egg. I. Pupa (ventral view). J. Abdominal apex of pupa (ventral view).

K-T. *Philonthus* sp. B (small). K. Larva (left lateral view). L. Urogomphus. M. Integument of dorsal shield (highly magnified). N. Head (dorsal view). O. Left maxilla (dorsal view). P. Labium (ventral view). Q. Labium (dorsal view). R. Left maxilla (ventral view). S. Abdominal apex of pupa (ventral view). T. Head (left lateral view).

Maxillae (Fig. 12E, G)

Very similar to those of *P. natalensis*. However, maxillary palpi clearly four-segmented, tapering towards apex, with apical and first segments of about equal size; second segment slightly less than twice as long as first, and third segment slightly longer than apical one; only second segment with two setae. Inner lobes absent, outer lobes present as finger-like structure, about as long as first palpal segment and bearing two to three setae at apex. Otherwise as in *P. natalensis*. Stipes with only one spine-like seta mesally and two on lateral side; ventrally with three setae and dorsally either with one near mesal margin or without any setae. Cardo as in *P. natalensis*. Palpifer also with single seta.

Labium (Fig. 12F)

Ligula finger-shaped and conical, almost as in *P. natalensis*, and about as long as penultimate segment of three-segmented palp. First segment of palpus long, about twice as long as the second. Sides of ligular stipes (prementum) sclerotized, median area beset with fine hairs dorsally, as in *P. natalensis*; palpigers not as convex as in latter. Labium ventrally with two submedian setae on posterior boundary of palpigers (Fig. 12P), exactly as in *P. natalensis*; also with tooth on each side of mentum.

Pupa (Fig. 12I-J)

Very similar to that of *P. natalensis* but smaller, only 4,8-5 mm in length. Colour pale whitish yellow, but becoming piceous just before beetle emerges. Differs from pupa of *P. natalensis* in that setae on anterior margin of pronotum are much longer in relation to body; there are furthermore only five to six setae on each side, compared with eight to eleven in *P. natalensis*. In most specimens examined, developing genital capsule (Fig. 12J) appeared as a flat lobe flush with body wall and, except in few cases, the two spine-like projections were absent. Every abdominal segment with medium-long seta laterally, whereas in *P. natalensis* only segments 7 and 8 bear lateral setae.

BIOLOGY

The eggs (Fig. 12H) of this species are very similar to those of *P. natalensis* but are smaller, measuring about 1,5 mm by 0,96 mm and the tubercles or dentations on the ridges are larger; the colour of most of the eggs was dirty white. They were laid singly in fresh dung at the same time as those of *P. natalensis*. The larval lifespan is more or less the same as in *P. natalensis* and pupae appeared during November. As in the latter species, the larvae construct clay cells in the soil in which they pupate. Most of the larvae were reared in fresh dung that did not contain any arthropods, except for mites and a few sciarid larvae; when crowded they became cannibalistic.

Philonthus sp. B (small)

DESCRIPTION

Adult

Black, head and pronotum smooth and very shiny. Elytra brownish black and densely setose. Abdomen shiny and densely covered with setae. Similar to sp. A except for size: most specimens collected measure only 3,7–5,3 mm.

This is one of the most common rove-beetles in cow-dung and was observed in all the areas surveyed.

Larva (Fig. 12K)

Very similar to sp. A in general form, setal pattern and colour, but somewhat smaller, mature larvae measuring 9–10 mm. Spiracles and legs similar to those of sp. A, including long seta on apical portion of trochanters and anteriorly situated seta on mesothoracic spiracles. Dorsal shields with triangular teeth as in sp. A; some of the teeth broad and tri- or multidentate as in sp. A (Fig. 12M) and to some extent also in *P. natalensis*. Body setae of 'frayed' type as in other species.

Head capsule (Fig. 12N, T)

Very similar to that of sp. A; however, nasale somewhat more produced in front. Colour golden brown. Almost smooth and shiny, very finely reticulate and with some rugae, particularly near the frons. About as long as wide or slightly wider than long in some specimens. Chaetotaxy as in Figure 12N, T. Ventral aspect similar to that of sp. A. Antennae as in latter and also four-segmented.

Mandibles, maxillae (Fig. 12O, R), and *labium* (Fig. 12P, Q)

Exactly as in sp. A.

Pupa

Similar to sp. A but smaller, varying from 3,8 to 4,5 mm in length and most specimens collected have the two spine-like projections present (Fig. 12S).

BIOLOGY

Beetles and larvae were found breeding in semi-fresh cow-dung throughout the summer and autumn and the larval lifespan seems to be the same as for sp. A. In both cases the larvae construct loose cells in the soil in which they remain dormant for a short while; the pupal stage in sp. B lasts about 6 days in January.

Staphylinus sp.

DESCRIPTION

Adult (Fig. 13M)

Large, beautiful, and aggressive species, 15,8–17 mm long, densely covered with fine, silky, golden-brown hairs, which give it a chequered appearance. True

colour of body dark brown, except elytra, borders of prothorax and apical margins of segments, which are brownish red. Densely punctate and dull all over, except for a narrow longitudinal, smooth and shiny line over middle of pronotum. Coloration of anterior border of cranium, including a V-shaped area in middle of anterior border and basal part of labrum, reddish yellow. A narrow area around the eyes, extending nearly to the posterior border of the head as well as the clypeus, also reddish yellow. Labrum deeply cleft in middle. Antennae and legs pale yellowish brown.

Distributed throughout the interior of the southern and south-western parts of South Africa where the surveys were made.

Larva (Fig. 13A–B)

Length 23–24 mm when mature. In general shape very similar to the larva of *Laemostenus complanatus*, but head is carried horizontally, with mandibles directed slightly downward. Head and pronotal shield dark reddish brown, head almost piceous in old larvae; meso-, and metathoracic and first abdominal tergum light brown. Thoracic terga with thin, white median line (ecdysial suture), which is anteriorly continuous with epicranial stem. Head as wide as, or slightly wider than, pronotum and in mature specimens examined it measured 4 mm long, including closed mandibles. Legs and antennae pale brownish yellow.

Abdomen creamy white and tergal plates only slightly demarcated on segments 3–9. Second abdominal segment with tergum almost as strongly sclerotized as first. Each abdominal sternum with two sclerotized plates bearing setae, of which at least some are of 'frayed' type; plates rather obscure, except on first abdominal segment, which has two smaller, clearly demarcated plates with about five setae each. Body integument dorsally with microscopic, triangular denticles similar to those of *Philonthus natalensis*. Cerci same colour as abdomen and fairly long. Tenth segment tubular, almost as long as eighth and functions as proleg. Spiracles oval, with mesothoracic pair (Fig. 13D) largest and with strong seta anteriorly; those on first abdominal segment (Fig. 13E) larger than other abdominal spiracles. Inner surface of each spiracle lined with fine, microscopic hairs. Some setae on abdomen with branched tips. Each cercus (Fig. 13H) with six long setae, of which one is situated apically; also six to eight short 'frayed' setae at base of each cercus. Latter appears two-segmented, with apical segment thin, nearly half the length of first, and situated on short segment-like extension of first.

Legs (Fig. 13F) yellowish brown. Tarsungulus simple, acute and about half the length of tibia, bearing two small setae on ventral side, about half-way between its base and apex. All segments except the coxae with strong, almost palus-like setae or spines. Femur on each side with lateroventral row of spines, which meet at apex; ventral area between rows with short basal row of three spines; laterally also with row of finer setae above the spines and with few small scattered dorsal setae; otherwise its dorsum devoid of hairs. Spines on tibia

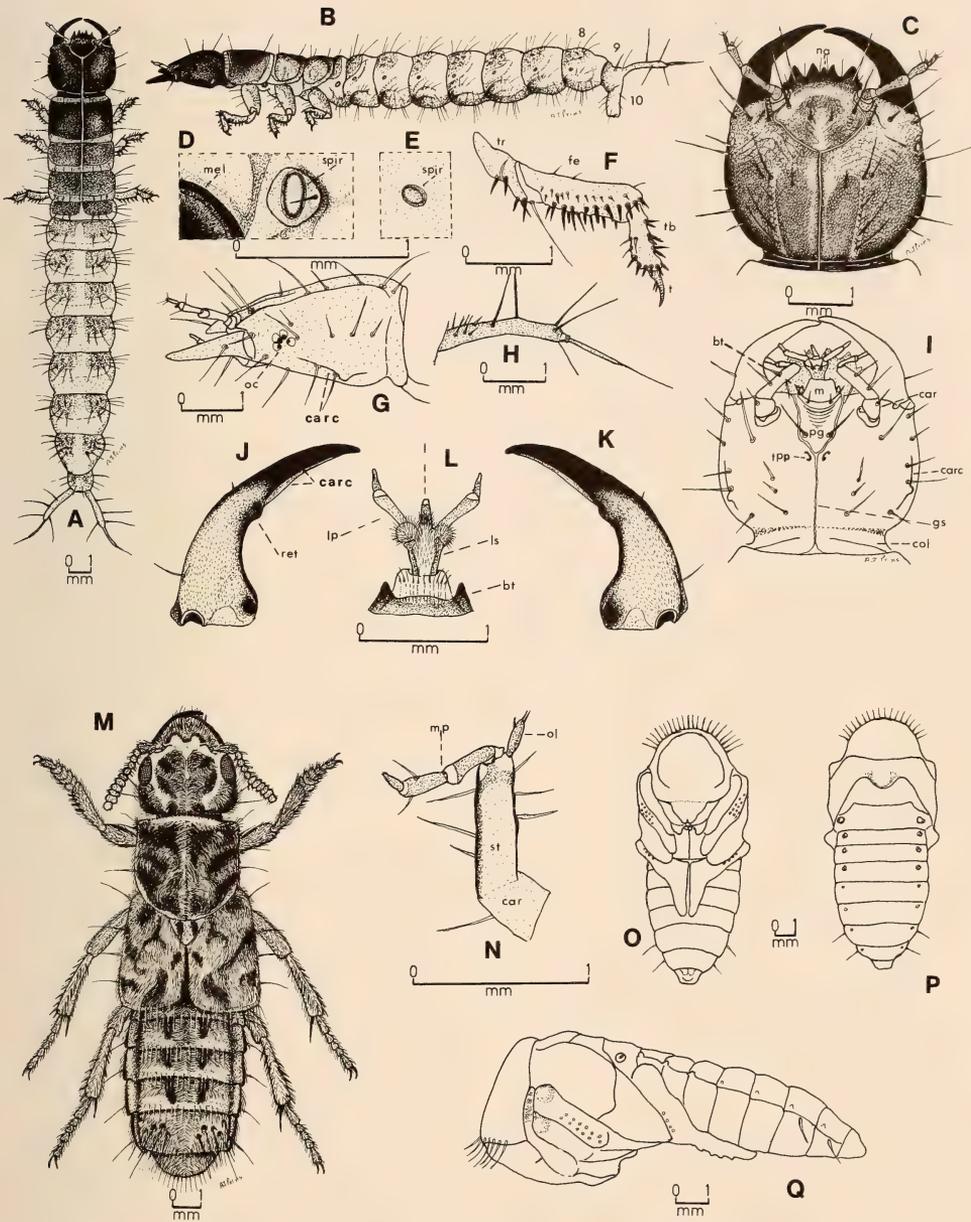


Fig. 13. Family Staphylinidae.

Staphylinus sp. A. Larva (dorsal view). B. Larva (left lateral view). C. Head (dorsal view). D. Right mesothoracic spiracle. E. Right abdominal spiracle. F. Right mesothoracic leg. G. Head (left lateral view). H. Urogomphus. I. Head (ventral view). J. Left mandible (dorsal view). K. Right mandible (dorsal view). L. Labium (dorsal view). M. Adult. N. Left maxilla (dorsal view). O. Pupa (ventral view). P. Pupa (dorsal view). Q. Pupa (left lateral view).

similarly arranged, but with only two spines on ventral area between rows. Trochanters with about twelve strong setae, situated ventrally and laterally; apical one very long.

Head capsule (Fig. 13C, G, I)

About as long as wide, or slightly wider than long. Sutures distinct; epicranial stem long, frontal sutures enclosing small frons. Dark reddish brown in colour. Distal half of cranium and largest part of frons microscopically reticulate; basal half more or less smooth, very superficially reticulate and also with some rugulosity. Whole head somewhat shiny, particularly front half. Chaetotaxy as in illustration. Epicranium on each side with narrow, smooth longitudinal area divided by fine, branched stria; each area with about four setae. Nasale septemdentate, median and lateral teeth small. Intervening spaces between teeth each with short seta; long seta present on each large lateral tooth, and shorter one posteromesad of latter.

Four-segmented antennae situated on each side of nasale. Second antennal segment largest, more than twice as long as first; fourth segment small and about half the length of third; latter with sensory cone on the mesal side; fourth segment with sensory cone at apex. Both penultimate and apical segments with three setae, two on mesal side in penultimate segment and one on mesal side in apical segment.

Four ocelli on each side. Gular suture distinct and Y-shaped, enclosing a narrow pregula; tentorial pits situated just behind latter. Collum short, but distinct. Cranium on each side with weak carina, which ends posteriorly in tooth-like tubercle.

Mandibles (Fig. 13J-K)

Falcate, about half the length of cranium and almost symmetrical. Cutting edge with uninterrupted dorsal and ventral carina and with indication of dorsal tooth or retinaculum half-way between apex and base. Molar areas and penicilli absent. Single, medium-long seta present near base on external margin and minute one opposite dorsal tooth.

Maxillae (Fig. 13N)

Stipes long and devoid of setae ventrally and dorsally, except for two short setae, one on inconspicuous base of three-segmented palp and one on apex of stipes. Mesal and lateral margins both with four setae. Cardo with a single long seta on lateral margin. Inner lobes of maxillae absent; outer lobes one-segmented, conical and slightly less than twice as long as apical segment of palp, and with two apical setae; also with small seta on apical half of lateral margin. First two segments of palp about equal in length, apical one about half the length of penultimate one; latter with single lateral seta on each side. Palpifer segment-like and small, less than half the length of first palpal segment.

Labium (Fig. 13L)

Ligula conical, elongate and one-segmented. Palpi two-segmented; apical segment shorter than ligula and nearly half the length of basal segment. Labial stipes (prementum, with ventral seta near palpal bases) can be retracted into mentum. Pointed tooth present on hypopharyngeal bracon on each side of mentum at base of which is short ventral seta. Mentum basally also with two ventral setae. Labium dorsally with fine, silky hairs on its base and on stipes, extending forward to base of ligula and also covering bases of palpi.

Pupa (Fig. 13O–Q)

Semi-obtect, almost smooth and shiny, heavily sclerotized, orange-brown, and about 12,5 mm long. Body devoid of setae, except for row of about twenty-one barbed setae on anterior margin of pronotum and single barbed seta on lateral sides of segments 7 and 8. Each mesothoracic leg with about sixteen small tubercles and each metathoracic leg with about five. Median area of mesonotum immediately anterior to M-shaped suture and upper boundaries of legs swollen and somewhat conical. First four spiracles on each side conical and conspicuous, last four small and inconspicuous. Labrum narrowly but acutely excised in middle, with short suture extending from emargination. Developing genital capsule indicated only by two almost flat areas (each with tiny depression) on ventral side of apical segment. Pupa darkens after a few days and four small black spots (eyes) become visible on each side of head.

BIOLOGY

Young larvae were collected under semi-fresh cow-pats from April to August and pupation took place from July to September. The larval stages lasted for 100–140 days and the pupal stages at least 35 days. Most of the pupae were found in small clay cells in the soil, but a few were found in cells hollowed out in cow-pats lying on fairly dry and hard soil. The larvae collected fed mostly on larvae of the dung fly, *Orthellia peronii* (Robineau-Desvoidy).

Large, oval, creamy-white eggs measuring about 2,9 mm by 2,5 mm, with the surface densely covered with microscopic spinules or tubercles, and found in dung containing its larvae, apparently belong to this species. The eggs very closely resemble those of some of the larger scarabs.

Xantholinus sp.

DESCRIPTION

Adult (Fig. 14A)

Dark blackish brown to almost black in colour, with apical part of elytra brownish. Very finely reticulate-rugulose, fairly shiny and sparsely punctured with fairly large oblong punctures on head, thorax, and elytra. Covered with medium-long golden hairs. Eyes large, situated near anterior margin of head. Mandibles, legs, and antennal flagellum reddish brown. Length 6,3–7,5 mm.

Widely distributed in the southern Cape Province, having been observed in carcasses around Cape Town and in semi-fresh to fresh cow-pats along the south coast.

Larva (Fig. 14B)

Mature larvae measure about 7,8 mm and are creamy white, except for head and pronotum, which are light reddish brown or brownish red, and meso- and metanotum and legs, which are pale yellowish red. Sparsely covered with medium-long brownish hairs more or less arranged in two transverse rows on tergites. Urogomphi (Fig. 14D) shorter than the tubular tenth segment and two-segmented; the terminal segment thin and with long apical seta. Spiracles oval; meso-thoracic one transverse (Fig. 14F) and with seta anterior to it; those on abdominal segments obliquely arranged; first abdominal and mesothoracic spiracle of about equal size and larger than rest. Legs (Fig. 14E) similar to those of *Philonthus* spp., but spines somewhat longer; trochanter also with a long seta anteriorly; claws acute and with only two spines more or less on ventral side. Median longitudinal line (ecdysial suture) over thorax distinct, anteriorly continuous with epicranial stem. Tergites on abdominal segments divided medially by fairly broad longitudinal line. Dorsal integument without triangular denticles, but in some places with long rows of fine spicules (Fig. 14G). Setae and spines simple.

Head capsule (Fig. 14C, H-I)

About as wide as pronotum, sides almost parallel and somewhat sinuate; posterior corners rounded and posterior margin almost straight. Golden brown to light brownish red in colour, almost smooth and shiny; anterior half rugose in middle and also finely reticulate between rugae; posterior half faintly rugulose. Nasale prolonged in front and consisting of median lobe with three teeth, of which middle one is smallest, and two lateral lobes, each with four teeth of about equal size. Chaetotaxy as illustrated. Frontal and epicranial sutures as in *Philonthus* spp. Neck fairly wide. Antennae appear four-segmented, with basal segment small, much shorter than second; the latter and third antennal segments of about equal size; apical segment with three long subapical setae and about three smaller setae at apex; slightly shorter than third segment, the latter with three long subapical setae and a long sensory cone on the ventral side close to apical border. Single ocellus present on each side. Gular suture Y-shaped and anteriorly enclosing fairly wide pregula, beset with numerous small, rounded tubercles.

Mandibles (Fig. 14N)

Falcate and much shorter than cranium; lateral side rounded, without dorsal carina and with three lateral setae, of which basal one is smallest. Molar area absent but small denticle, reminiscent of prostheca, is present. Cutting edge pointed apically and with dorsal trenchant ridge running from apex to about half the length of mandible.

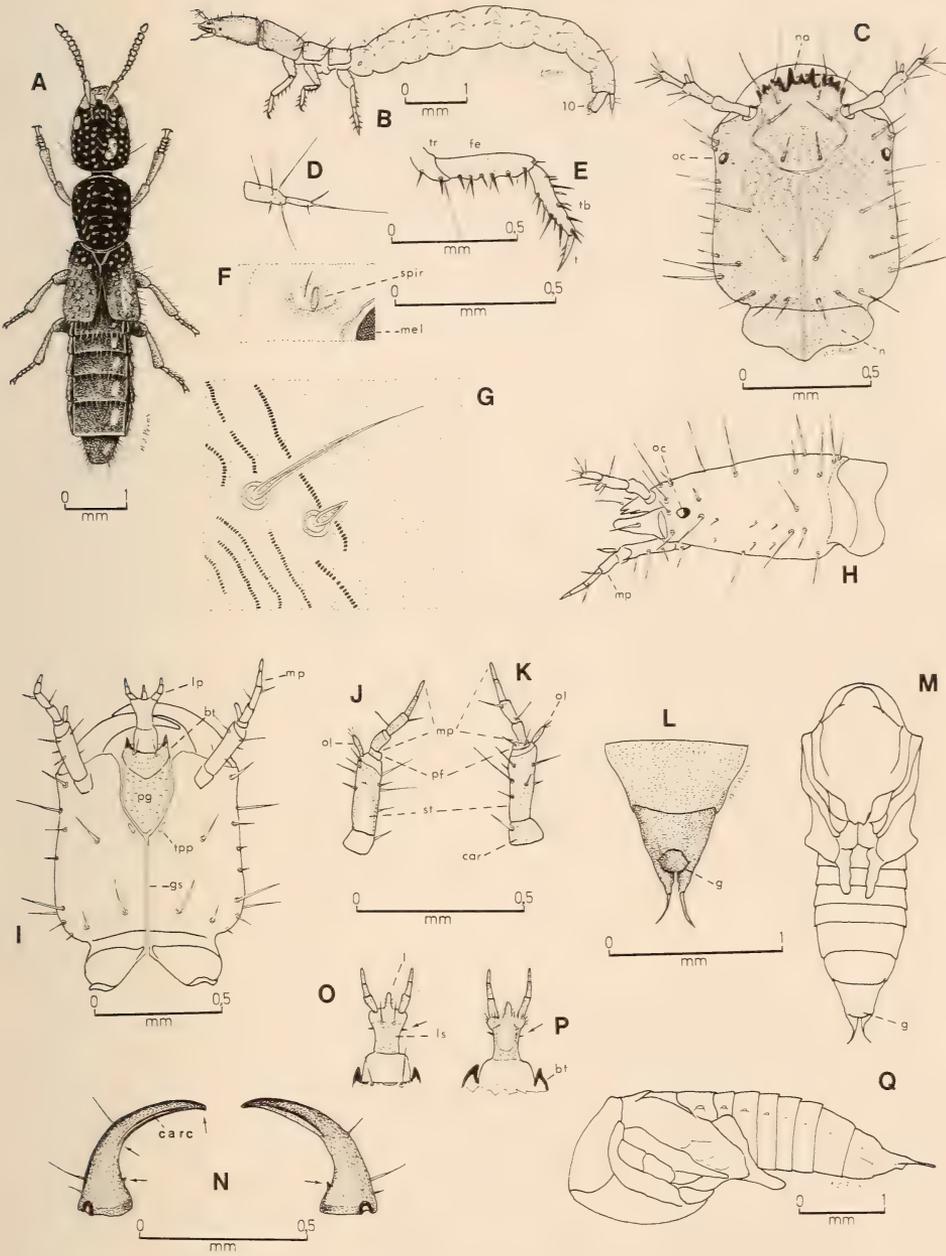


Fig. 14. Family Staphylinidae.

Xantholinus sp. A. Adult. B. Larva (left lateral view). C. Head (dorsal view). D. Left urogomphus. E. Right mesothoracic leg. F. Light mesothoracic spiracle. G. Integument of dorsal shield of abdomen (highly magnified). H. Head (left lateral view). I. Head (ventral view). J. Left maxilla (dorsal view). K. Left maxilla (ventral view). L. Last two abdominal segments of pupa (ventral view). M. Pupa (ventral view). N. Left and right mandible (dorsal view). O. Labium (ventral view). P. Labium (dorsal view). Q. Pupa (left lateral view).

Maxillae (Fig. 14J-K)

Similar to that of *Philonthus natalensis*, but maxillary palp clearly four-segmented, with segments tapering towards apex; second segment with two lateral setae of which one is mesal. Palpifer segment-like and bearing two setae ventrally. Stipes long, ventrolaterally with about six setae and with another seta almost in middle of stipes. Cardo ventrally also with one long seta situated more to mesal side. Stipes and cardo dorsally without setae, except for short one situated laterally just below outer lobe and in some specimens second one just below first. Outer lobe finger-like, nearly as long as second palpal segment and bearing about three apical setae.

Labium (Fig. 14O-P)

Very similar to that of *P. natalensis* and with three-segmented palpi. Ligula conical and beset with fine hairs dorsally (including also the palpigers and median area). Palps tapering towards apex; first segment longest and apical one shortest; tiny spine present laterally just below palpiger.

Pupa (Fig. 14L-M, Q)

Semi-obtect. Newly formed pupae are white but soon turn to a whitish yellow with the posterior projections brownish red and mandibles red-brown. Length 3,9-4,8 mm. Very finely reticulate-punctate, shiny and without any setae, except two diverging, seta-like filaments borne on two conical caudal projections.

Pupae rather similar to those of *Philonthus natalensis* except for absence of hairs. Developing genital capsule (Fig. 14L) appears as a raised or somewhat conical area ventrally on abdominal apex. First four abdominal spiracles fairly large and clearly demarcated, diminishing in size posteriorly; remainder very indistinct.

BIOLOGY

Larvae of this species were found in carcasses in Cape Town from September to October; they were feeding mainly on fly larvae, especially those of the cheese-skipper, *Piophilha megastigmata* McAlpine. The duration of the larval period was approximately 19 days. Mature larvae construct oval clay cells, measuring 7-7,5 mm in length, in the soil for pupation. In most cases there was a prepupal stage of 3-4 days, during which time the larvae became almost pure white, except for the reddish head. The pupal stage lasted 11-14 days in November. Larvae collected in decaying cow-dung from June to August had a somewhat longer lifespan, the pupal period being 20-22 days.

Newly emerged beetles are blackish with pure white wings, which usually become blackish within 4-6 days. Some of the beetles were found to feed on cheese-skipper maggots, but small grubs of skin-and-hide beetles were also attacked; in the laboratory even some of the large white collembolans were devoured.

Family Silphidae

Small to moderately large (about 40 mm) flattened beetles, usually sombre coloured, often with metallic blue sheen; some with red or orange markings. Apical abdominal segments often exposed. Antennae ten- to eleven-segmented. Tarsal formula 5-5-5. Most of them are carrion feeders, both in the adult and larval form; some feed on snails and lepidopterous larvae and a few are phytophagous (not present in South Africa). Species of the genus *Nicrophorus* (not occurring in southern Africa) have the habit of burying the carrion to ensure an adequate food-supply for the larvae; they are therefore known as burying beetles.

Only about ten species have been described from the Sub-Saharan region, of which the endemic *Silpha mutilata* Laporte & Castelnau and the more widespread *S. micans* Fabricius have been introduced into Europe. The latter, together with *S. caeruleoviridans* Dohrn (also widely distributed in the Cape Province, South West Africa and Zimbabwe), were described under the subgenus *Chalcosilpha*; however, according to Arrow (1909) these two species are conspecific. The largest species found in the Cape Province are *S. capicola* Péringuey, *S. peringueyi* Portevin, and *S. punctulata* Olivier (which is common in fynbos along the western parts of the southern Cape), all measuring 17 to 20 mm in length.

Both *S. micans* and *S. mutilata* (which differs from the first-mentioned species by the small elevated area or ridge in the middle of each elytron) (Fig. 2F) were found to be common on carcasses of mammals and birds both on the coast and inland, and were also attracted to soil containing decomposing fish-meal. However, only the one species, *S. micans*, was observed to breed in this medium and in the carcasses examined.

Silpha micans Fabricius

DESCRIPTION

Adult (Fig. 15A)

Elytra blackish to blackish brown with rest of body, including legs and antennae, blackish blue, in some cases even iridescent blue; legs perhaps more bluish brown; eyes black. Integument leathery, elytra not covering three to four terminal abdominal segments. Each elytron with three almost indistinct longitudinal rugae, of which the exterior one is the most prominent and reaches only to about the posterior one-third of the wing cover. Tibiae with numerous spines. Wings well developed. Antennae with three-segmented club. All tarsi five-segmented. Length 12,6-13,8 mm.

Widely spread in the Sub-Saharan region (Jeannel & Hatch 1928).

Larva (Fig. 15C)

General description of the larva of a *Silpha* sp. is given by Dorsey (1940). Depressed dorsoventrally and wider in front than behind. Thoracic terga rounded laterally. Abdominal terga, except ninth and tenth, with anterolateral angles

rounded, posterolateral angles acute, and lateral and posterior borders furnished with setae, some of which (particularly lateral ones) are more strongly developed. Head narrower in front than behind; nearly cordiform. Nine pairs of spiracles situated ventrally, with mesothoracic one largest; first abdominal pair somewhat larger than the other abdominal spiracles; all oval or annular; mesothoracic pair (Fig. 15P) furnished with two setae each, situated on internal side. Colour dark brown to blackish brown, particularly posterior third of each segment. Integument leathery and covered with small tubercles and medium-long setae (Fig. 15S) most of which are cleft at tip, or even cleft two or three times. Sculpture on thoracic terga present as wide, irregular reticulation, particularly on the anterior part of the pronotum. Ecdysial suture distinct in most segments, except perhaps last two or three. Tenth abdominal segment almost tubular, about as long as ninth and tapering towards apex; ninth fringed with fine setae.

Legs (Fig. 15H) well developed, slightly increasing in size from hind legs to forelegs; coxae large, with longitudinal groove on exterior face distinct; strong spine-like setae present, both ventrally and dorsally on tibiae, ventrally only on femora; dorsal setae on latter short but slender; tarsungulus acute and with one ventral and one posterior spine about half-way between base and apex. Urogomphi borne on ninth abdominal segment; fairly long, appearing two-segmented, with first segment much longer than terminal one and furnished with spine-like setae; latter segment subdivided into a smaller proximal and larger distal part in some specimens; with one or two pre-apical setae and with a medium-long seta apically. Mature larvae measure about 14 mm in length.

Head capsule (Fig. 15E-G)

Slightly less than twice as wide as long. Sides very convex, epistomal and frontal sutures clearly indicated. Distal ends of dorsal tentorial arms, although contiguous with frontal sutures, are not in line with antennal sockets as stated by Dorsey (1940) but further back, more or less in line with dorsal ocelli. Latter four in number and situated on lateral margin, about half-way between base and apex. Ventral ocelli two in number, with anterior one situated just below antennal socket. Frontoclypeal suture indicated only laterally, obsolete over middle portion. Posterior margin of head widely and shallowly emarginate dorsally. Antennae three-segmented, with first and apical segments of about equal length, second one somewhat longer and bearing projection on mesal part of its apex. Last two segments with setae. Chaetotaxy of head in most cases as illustrated. Sculpture consisting of small tubercles arranged in form of a wide reticulation, areas between striae minutely reticulate and shiny. Frons more rugulose, with reduced number of tubercles. Head divided ventrally into two halves by deep, emarginate hind border; gula short.

Labrum and clypeus

Labrum and clypeus united, almost triangular; boundary between them indicated by more weakly sclerotized cuticle. Labrum more or less smooth, with

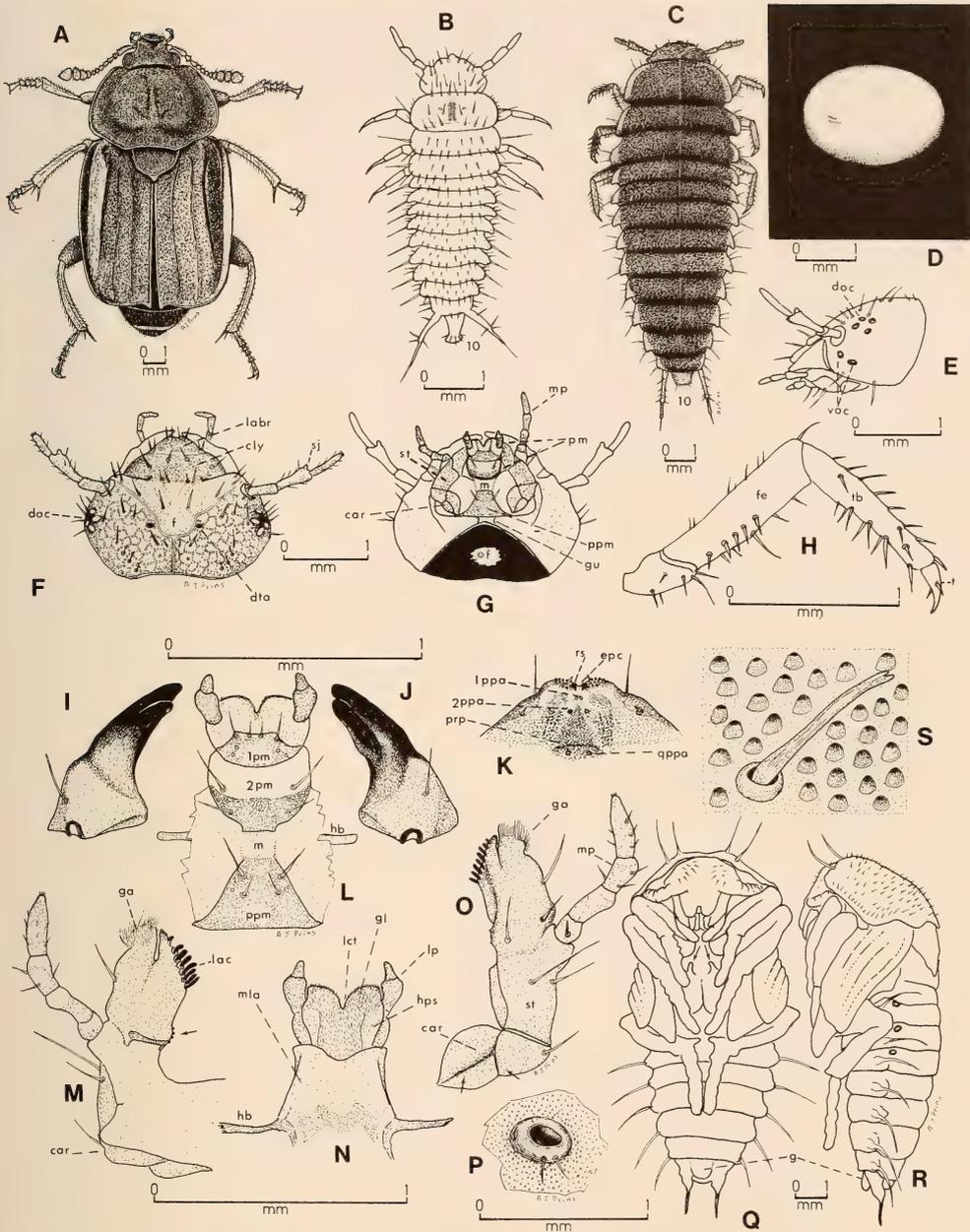


Fig. 15. Family Silphidae.

Silpha micans. A. Adult. B. Newly hatched larva (dorsal view). C. Adult larva (dorsal view). D. Egg. E. Head (left lateral view). F. Head (dorsal view). G. Head (ventral view). H. Right mesothoracic leg. I. Left mandible (dorsal view). J. Right mandible (dorsal view). K. Epipharynx. L. Labium (ventral view). M. Left maxilla (dorsal view). N. Labium (ventral view). O. Left maxilla (ventral view). P. Left mesothoracic spiracle. Q. Pupa (ventral view). R. Pupa (left lateral view). S. Dorsal integument showing tubercles and hair (highly magnified).

few superficial rugae and minute reticulation between rugae; anteriorly bilobed due to presence of short medial cleft; lateral margins sinuate just behind cleft. Labrum with four strong setae on each side of which posterior one is situated on small, lateral, triangular sclerotized area in front of clypeal border; tiny seta also present on each side of labral cleft. Clypeus more or less rugoso-reticulate, about as long as, or slightly longer than, labrum; trapezoidal and bearing transverse row of about six setae behind anterior margin.

Epipharynx (Fig. 15K). Bilobed in front, anterior and lateral margins sclerotized, each lobe in front with rounded denticles, as well as triangular tooth (Dorsey's (1940) rectangular tooth), lateral margins each with short spine situated in line with second porous area. Median area concave, forming more or less a lobe on each side, bearing an oval area beset with spiculi; the two quinqueporous areas clearly indicated in most specimens with anterior parabolic row of fine pores. First porous area visible as two small circles just behind triangular teeth. Anterior to each spiculum-bearing area and just behind anterior lobes in line with first porous area is a small transverse area with fine setae.

Mandibles (Fig. 15I-J)

Slightly shorter than cranium, fairly narrow, with broad subtriangular base and nearly twice as long as width at base. Each mandible with an oblique, transverse dorsal depression separating cutting edge from base. Molar areas absent, cutting edge on each side comprised of two rounded teeth of which apical one is largest. Dorsal carinae absent; mandibles rounded on lateral face, each with single seta.

Maxillae (Fig. 15M, O)

Elongate, mala and stipes fused, lacinia and galea free only at extreme apex; latter with tuft of very fine hairs. Lacinia with eight to nine broad palus-like spines giving it a comb-like oblique anterior margin; mesal area of lacinia with some minute denticles at base. Maxilla dorsally without setae, ventrally with about five, of which one is situated half-way between galea and palpifer and one just below palpifer. Cardo somewhat oval, with Y-shaped suture (arms of Y pointing posteriorly) and with only one seta laterally on apex. Maxillary palpus appearing four-segmented, with apical segment the longest; third segment shorter than the second; first segment very small and with single seta ventrally; both apical and penultimate segments with setae. In his study of six American species, Dorsey (1940) gives the number of palpal segments as three.

Labium (Fig. 15L, N)

Different sclerites fairly easily recognizable; postmentum large and triangular or trapezoidal, usually bearing four setae near anterior margin. Mentum small and less sclerotized. Prementum large, consisting of basal sclerite, ventrally with four setae of which two are situated on its anterior, less sclerotized half. Apical sclerite with two-segmented palpi; this sclerite ventrally also with four setae.

Hypopharynx (Fig. 15N). Glossa deeply cleft in the middle, the two lobes densely covered with fine hairs; hypopharyngeal scleromes (= paraglossae, Böving & Craighead 1931) distinct; hypopharyngeal bracon well developed and symmetrical. Superlinguae united as one broad structure.

Pupa (Fig. 15Q-R)

Exarate, clearly showing broad pronotum of the adult. Anterior margin of pronotum with four long setae and some smaller hairs on disc; small hairs also present on posterior part of head. Abdominal segments each with long lateral setae; apex of abdomen with two strong setae or styli. Developing genital capsule visible as broad lobe between caudal styli. Anterior border of metathorax ventrally with two fleshy spines. Only first four pairs of abdominal spiracles large and clearly visible. Length 11-12 mm.

Newly formed pupae are almost pure white with golden brown hairs; as they develop they become darker, and just before emergence of beetles they are piceous.

BIOLOGY

Beetles were collected during midsummer and midwinter and usually appear wherever carcasses and skins are found. They feed on the latter or on other arthropods present, particularly on fly and blow-fly larvae. They are attracted to fish-meal in large numbers and eggs were often found during January and February in soil containing this medium.

Most of the eggs (Fig. 15D) collected in Claremont, Cape Town, vary from 2,20 by 1,4 mm to 2,4 by 1,6 mm and are oval, yellowish white and almost smooth and shiny. Most eggs were laid singly in the upper few millimetres of soil that contained fish-meal and hatched after 2-3 days during January. Shortly before hatching, two narrow dark lines separated by a thin pale line are visible near the anterior pole of the egg.

Newly hatched larvae (Fig. 15B) are similar to the mature larvae except in colour and size, and are almost pure white with reddish eyes, golden-coloured setae, and two dark or piceous parallel lines on the pronotum (already visible through the chorion in the embryo). These two black lines are visible only in the newly hatched specimens; after the first moult the lines disappear. The newly hatched larvae measure 4-4,2 mm in length and within 2-3 hours they turn to almost pitch black, with reddish eyes. In the laboratory the first instar lasted for about a day. After each moult the larvae are nearly white; second and third instar larvae usually assume their black colour after 2-4 hours, as in the first instar.

The second moult occurs 2-5 days after the first and the larvae then measure 9-10 mm. Within 3-4 days after the second moult they are 13-14 mm long and usually enter the soil, where they construct thin-walled clay cells in which they remain dormant for another 3-4 days before pupation occurs. The total lifespan of the third instar larvae varies from 6 to almost 8 days and the pupal

stages also last for 6–7 days, the adult beetles emerging 17–24 days after oviposition.

Newly emerged beetles are almost white with yellowish-brown pro- and mesonotum; the head is darker and the eyes dark brown; the last abdominal segment, legs, and antennae are pale yellowish brown. After a day or so they assume their normal dark coloration.

Silpha punctulata Olivier

DESCRIPTION

Adult

Dull, brownish black, about 19 mm long, somewhat more oval in outline than *S. micans*, the elytra covering the abdomen. Head and prothorax fairly densely punctate, the punctures coarser on the lateral areas of pronotum than on its disc. The six elytral rugae very prominent, areas between them punctate, the punctures coarser than on pronotum. Legs microscopically reticulate-punctate or rugulose, tibiae spined as in *S. micans*. Antennal club not very prominent, the three segments clearly demarcated by presence of fine, short hairs causing pruinescence, rest of antennae slightly shiny as in the other species. It differs from *S. micans* by absence of hairs on dorsal surface of pronotum and elytra.

This species is widespread in the Sub-Saharan region (Jeannel & Hatch 1928); collection records also come from the western Cape Province.

Larva (Fig. 16A)

When mature about 25 mm long and brownish black in colour. Very similar to that of *S. micans*, but somewhat more elongate; abdominal terga lobe-like on each side, these lobes acuminate or pointed posteriorly. Meso- and metathoracic segments with posterior angles less acute than those of abdomen; prothoracic angles rounded; all posterior angles of body segments each with a short spine-like seta; anterior angles, except those of pronotum, each with three to four short setae. Ecdysial suture fairly distinct in most segments except probably last three or four. Urogomphi shorter in relation to body length than in *S. micans*, appearing two-segmented, with second segment also subdivided in most specimens examined and the setation similar to that of the latter species.

Legs similar to those of *S. micans* with somewhat more spine-like setae present on both femur and tibia. Body integument (Fig. 16C) dorsally covered with short scale-like setae forming a single row along posterior border of segments, except that of abdominal segment nine, which is without such a row. Setae on posterior border of tenth segment longer and spine-like. The integument differs from that of *S. micans* by the distinct reticulation and by the smaller and less obvious tubercles that are present; apices of scale-like setae entire, not cleft. Spiracles similar to those of the latter species, but lacking the two setae on internal side of the mesothoracic pair.

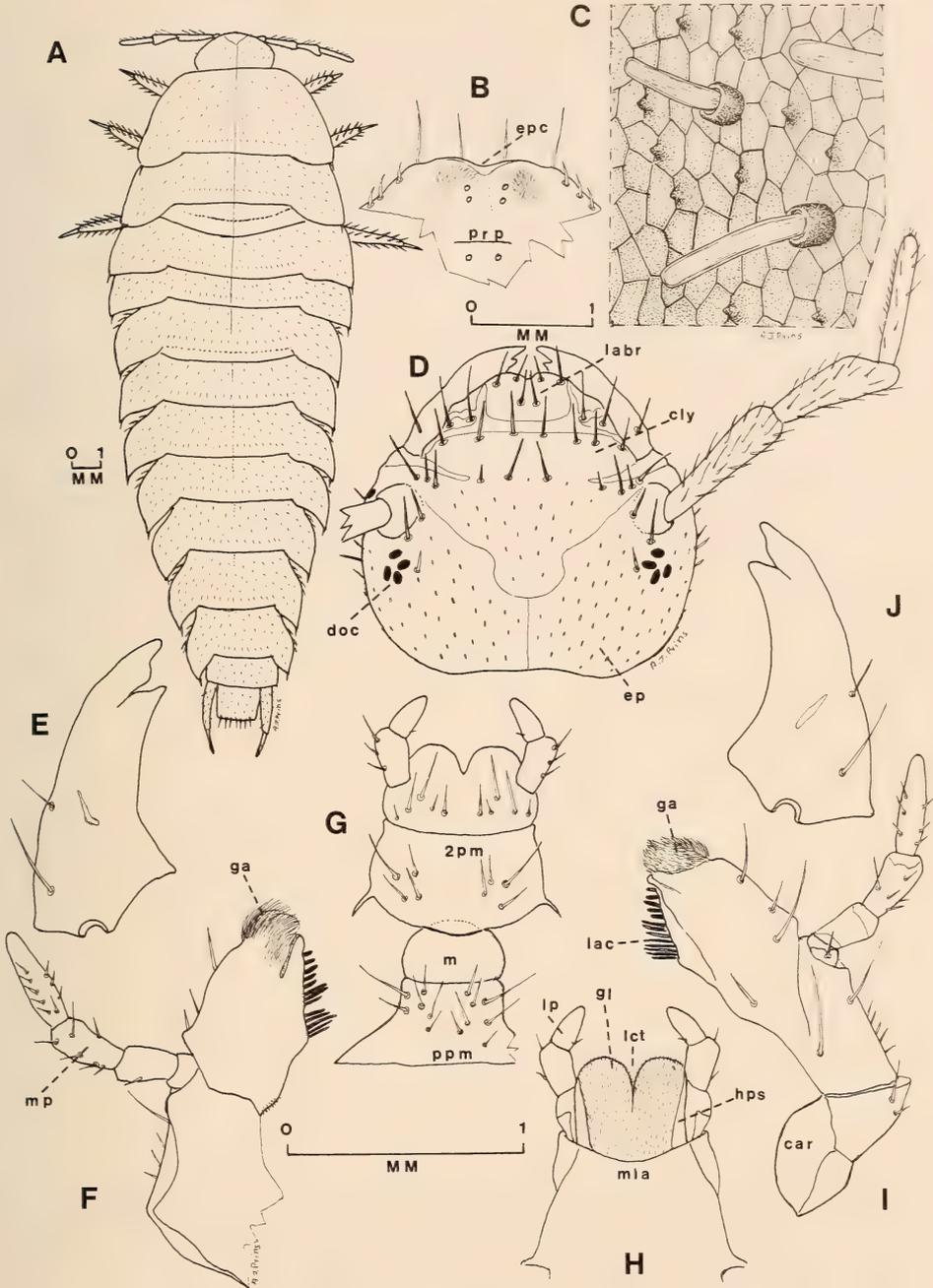


Fig. 16. Family Silphidae.

Silpha punctulata. A. Adult larva (dorsal view). B. Epipharynx. C. Dorsal integument showing tubercles and hair (highly magnified). D. Head (dorsal view). E. Left mandible (dorsal view). F. Left maxilla (dorsal view). G. Labium (ventral view). H. Labium (dorsal view). I. Left maxilla (ventral view). J. Right mandible (dorsal view).

In small larvae measuring about 10,5 mm long that were collected during January, all the antennal segments are about of equal length. In most of the specimens examined there are only about six long setae on the sternal plate just behind the head (about twenty-four in the mature specimens) and there is an extra-long seta on each lateral margin of the central disc of the labrum. There are also only two long setae ventrally on apical segment of labium, the other setae present are short and almost spine-like. Otherwise exactly as in the mature larva.

Head capsule (Fig. 16D)

Dark brown to blackish brown, about as long as wide or only slightly wider than long; minutely, or rather microscopically, reticulate-punctate and somewhat shagreened: cranial chaetotaxy as illustrated, similar to that of *S. micans* but differing from it by presence of short scale-like setae and absence of long setae on dorsal surface of epicranium, except two long setae in front of the four dorsal ocelli just behind antennal base, and one short spine-like seta dorsolaterad of median ocellus. Antenna three-segmented, first segment slightly longer than third (of about equal length in *S. micans*); second segment about as long as apical one (as in the case of the latter species) and without a conical projection. All segments with setae (in *S. micans* the first segment is without hairs).

Ventral side of head similar to that of *S. micans*, including two ventral ocelli, but postmentum with more setae.

Labrum and clypeus (Fig. 16D)

Labrum and clypeus united as in *S. micans* and similar in shape; labrum fairly deeply emarginate on anterior border, lateral margins sinuate behind cleft; dorsal surface with ten long setae, of which two are situated on each side on the sclerotized triangle, just in front of clypeal border. There is no demarcation line between clypeus and frons, except the sulcus on each side as in other species.

Epipharynx (Fig. 16B). Rather similar to that of *S. micans*; however, triangular teeth at apex are absent. Oval area with fine hairs present just behind anterior margin on each side of median concavity. Lateral margins with three short almost sickle-shaped setae (absent in *S. micans*) and denticles present on anterior margin of the latter species absent in this case.

Mandibles (Fig. 16E, J)

Slightly shorter than cranium, fairly narrow and more elongate than in *S. micans* due to narrow bases. As in latter species, a fairly prominent oblique depression present on each mandible separating cutting edge from base. Lateral faces fairly rounded, each mandible with two setae of which proximal one is longest. Two teeth of cutting edge distinct, apical one usually bilobed and larger than the other.

Maxillae (Fig. 16F, I)

Similar to those of *S. micans*, but in this species the lacinia and galea entirely fused, the demarcation line still visible, particularly on dorsal side. Galea forming a lobe with fine golden setae as in latter species; lacinia with twelve to thirteen palus-like spines, of which distal five are shorter with rounded apices, the other eight or nine longer. Mesal area of lacinia also with minute spines at base. Maxilla dorsally without setae, ventrally with about six setae as indicated in Figure 16I; exterior margin below palp with five short setae. Cardo as in *S. micans*, but with one long and one short seta near apex.

Maxillary palpi four-segmented as in *S. micans*, first segment small with one ventral seta, third segment longer than second (shorter than second in *S. micans*), apical one the longest. Both apical and penultimate segments with setae, second with only a single dorsolateral seta.

Labium (Fig. 16G-H)

Also similar to that of *S. micans*, postmentum triangular with about fourteen setae. Mentum smaller, less sclerotized and without setae. Prementum large and with about four setae ventrally on each side of its median area. Apical sclerite ventrally with about ten setae and with two-segmented palpi of which basal segment is slightly longer than apical one and bearing about four setae on exterior margin; apical segment with only a single short seta on its mesal margin in most specimens examined. Glossa deeply cleft in middle, the two lobes densely covered dorsally with fine hairs; hypopharyngeal sclerites clearly demarcated.

BIOLOGY

Nothing is known about the life history of these beetles. Larvae were observed wandering about on the ground covered with fynbos.

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ABBREVIATIONS

acc	acrocerci
adn	adnasale
ant	antenna
bt	teeth on base of labium
car	cardo
carc	carina (see also ck)
ce	cercus (see also ur)
ck	cervical keel (see also carc)
cly	clypeus
col	collum
c & st	cardo and stipes
doc	dorsal ocelli
dta	dorsal spot of distal tentorial arms
ep	epicranium
epe	epipharyngeal cleft

f	frons
fa	finger-shaped air-tube of biforous spiracle
fe	femur
g	developing genital capsule
ga	galea
gl	glossa
gs	gular suture
gu	gula
hb	hypopharyngeal bracon
hps	hypopharyngeal sclerome
hy	hypostomal margin
il	inner lobe
jx	juxta
l	ligula
lab	labium
labr	labrum
lac	lacinia
lct	ligular cleft
lm	prostheca
lp	labial palp
ls	labial stipes
m	mentum
m ₁ , m ₂	molar area
ma	mala
mcc	mesocercus
mel	mesothoracic leg
ml	median lobe
m _{la}	superlinguae/maxillulae
mp	maxillary palp
mx	maxilla
mxs	maxillary articulating area
n	neck
na	nasale
oc	ocellus
of	occipital foramen
ol	outer lobe
par	parietalia
pcc	procercus
pen	penicillus
pf	palpifer
pfg	palpiger
pg	pregula
pm (1 pm, 2 pm)	prementum
1 ppa	first porous area
2 ppa	second porous area
ppm	postmentum
pre	preartis
prp	parabolic row of pores
prvt	praeventrite
pvt	postventrite
qppa	quinque porous area
ret	retinaculum
rs	triangular tooth
sj	sensory appendix
sm	submentum
spir	spiracle
st	maxillary stipes
t	tarsungulus

t ₁ -t ₃	scissorial teeth
ta	tarsus and claw
tb	tibia
tpp	tentorial pit
tr	trochanter
ur	urogomphus (see also ce)
voc	ventral ocellus
vt	ventrite

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.

Laeula bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

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

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

Holotype

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

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

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

A. J. PRINS

MORPHOLOGICAL AND BIOLOGICAL
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PART 2
THE PREDATORY FAMILIES CARABIDAE,
HYDROPHILIDAE, HISTERIDAE, STAPHYLINIDAE
AND SILPHIDAE (COLEOPTERA)

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