ISSN 0968–0470

Bulletin of The Natural History Museum

Zoology Series

THE
NATURAL
HISTORY
MUSEUM

VOLUME 67 NUMBER 1 28 JUNE 2001

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World List abbreviation: *Bull. nat. Hist. Mus. Lond.* (Zool.)

Zoology Series
ISSN 0968–0470 Vol. 67, No. 1, pp. 1–107

The Natural History Museum
Cromwell Road
London SW7 5BD

Issued 28th June 2001

Typeset by Ann Buchan (Typesetters), Middlesex
Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Bull. nat. Hist. Mus. Lond. (Zool.) **67**(1): 1–24 Issued 28 June 2001

Freshwater nematodes from Loch Ness, Scotland Part I. The orders Tylenchida Thorne, 1949 and Rhabditida Chitwood, 1933 (Nematoda, Secernentea).

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CONTENTS

SYNOPSIS. During a survey of the nematodes of Loch Ness, Scotland (Project Urquhart 1993–94) 94 nematode species were identified from benthic core samples collected from the profundal (90–211 m) and from river mouth areas (< 0.5 m). This paper presents a taxonomic review of the nematodes of the two orders Tylenchida Thorne, 1949 and Rhabditida Chitwood, 1933. Thirty five species are described and figured; some morphological features are illustrated by Normarski interference-contrast microscopy.

INTRODUCTION

This study is based on nematodes collected in Loch Ness, Scotland during Project Urquhart (1993–94). The first part presented here deals with species that belong in the orders Tylenchida Thorne, 1949 and Rhabditida Chitwood, 1933. The second part, now in preparation, will cover species of the remaining orders. The results of ecological studies (R. David,1998 – Ph.D. thesis) will be published elsewhere. The following brief profile of Loch Ness is essentially based on the literature Maitland (1981) and Shine & Martin (1987).

Loch Ness is the largest body of freshwater in the United Kingdom. It runs in a north-east/ south-west direction and is 39 km in length, but only 2.4 km at its widest point with an average depth of 132 m. A new maximum depth of 239.5 m was found during a Project Urquhart sonar survey. The loch basin has in most places very steep, sometimes precipitous shelving sides, thus it has a very small shore zone for its surface area Maitland (1981). The flat bed of the loch is divided into two basins of 220 m depth as a result of fluvial deposits of material opposite the entrance to the River Foyers. The floor is extensively covered by black lake sediments which occupies over 50% of the area of Loch Ness greater than 150 m depth. Shine & Martin (1987) found that a 4 m core only just penetrated to clay, suggesting that the organic sediment is at least of that depth. Sediments analysed from a single core obtained from the profundal area of Loch Ness were found to consist of fine size fractions with clay (< 39 µm, 45.8%), fine silt (39–63 µm, 18.1%) and sand (63–125 µm, 36.4%) (Smith B. D. *et al.*, 1981).

Water levels remain relatively constant throughout the year although stream levels vary because of snow melt in spring, but more importantly because of fluctuations in rainfall. The loch has a catchment area of 1775 km^2 providing 84 m^3 s^{-1} mean inflow with the majority of the catchment being rough ground or forest, and only 7.5 km^2 urbanized. Surface water is slightly acidic with an annual mean pH 6.7; it has low conductivity 30 µS cm^{-1} at 20°C and is stained with humics. Low conductivity levels in lake water are often associated with dark colouration and a high concentration of organic compounds because they have been drained through swampy/peaty regions. The total organic carbon concentrations of the surface water is 3 mg C1^{-1} Maitland (1981). In many systems of lake classification, Loch Ness falls within the nutrient-poor Spence (1967) and oligotrophic category Vollenweider (1968). However, Bailey *et al.*, 1981 debate whether Loch Ness along with Loch Awe should be described as dystrophic (acid), a category considered by Jarnefelt (1958) as supplementary to, rather than comparable with oligotropic and eutrophic categories.

The dissolved oxygen content of the Loch Ness water column was, along with other lochs studied, consistently found to be over 80% saturated (often approaching 100%) even during periods of stratification Smith, I. R. *et al.*, (1981)

Under the classification system of Yoshimura (1936), Loch Ness is a warm monomictic lake which means that the temperature never falls below 4°C at any depth, there is one circulation of the water column every year in winter and the loch is stratified during the

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[*] R. Hunter *nee* R. David.

summer Murray & Pullar (1910). From late autumn to the spring the loch is the same temperature throughout, with progressive development of stratified conditions from May to the following autumn. The temperature range in midsummer is typically 14.5°C at the surface to 5.5°C at 220 m (Mackal & Love, 1969; Murray & Pullar, 1910).

Maitland (1981) gives a detailed account of human activities which influence the environmental parameters inherent in scientific studies effecting Loch Ness. The loch is relatively unpolluted despite arable, tourist and urban influences. The Scottish Environmental Protection Agency has supplied details of sewerage inputs to Loch Ness which indicate that there are seven direct septic tank inputs from small communities or hotels and tourist attractions, only two of which have monitored flows. Another septic tank inflow enters Loch Ness indirectly via the River Moriston. There are two activated sludge plants for full biological treatment, one at Drumnadrochit and another at Fort Augustus. When maximum flow is reached, sewerage by-passes the treatment plant and discharges untreated into the water course. Seasonal information on the loading variation was not available. However, Drumnadrochit and Fort Augustus are known to frequently breach their consent limits. The water regime of Loch Ness is affected directly by an hydro-electric pump storage scheme based at Foyers and indirectly by four more in the catchment area. These influences may have an effect on the flora and fauna of Loch Ness.

NEMATODE FAUNA

So far as is known the only study of nematodes from freshwater lakes of the United Kingdom is that of Martin *et al.*, (1993) who published a full listing of macrobenthic and meiofaunal species from profundal sediments of both Loch Ness and Morar. Their list of nematodes from Loch Ness profundal cores ($\geq$ 200 m) although not exhaustive includes *Ironus tenuicaudatus* de Man, *Tripyla glomerans* grp, *Tobrilus gracilis* grp, *Tobrilus cf. pellucidus* and Dorylaimid 'A'. Additional species listed (*Eumonhystera filiformis* grp, *Eumonhystera* cf. *longicaudatula*, *Ethmolaimus pratensis* grp, *Aphanolaimus* sp. and *Dorylaimus* cf. *stagnalis*) were collected at lesser depths such as 50–170 m.

In addition Coles (1996) records *Chromadorita tenuis* Schneider, 1906 and *Aphanolaimus ? aquaticus* Daday, 1894 from 'trickle of freshwater spring from beside footpath from Goyes Hotel, Foyers Harbour, Loch Ness, Scotland'.

MATERIAL AND METHODS

SAMPLING AND FIXATION

Profundal sampling: cores were taken with a Bowers and Connolly Multicorer deployed from the research vessel Seol Mara. This device takes four core tubes (each of 5.9 cm diameter giving a core surface area of 27.34 cm^2), allowing sediments to be recovered without disturbing the sediment water interface.

Sediments were sampled at four stations: Fort Augustus Bay, Deep South Basin, Foyers Plateau and Deep North Basin covering a range of depths between 91 and 211 m (Fig. 1, Table 1). At each station sampling was concentrated within approximately 10–20 m^2 between 10–13th July 1993, allowing for boat drift. Eight cores were collected from each station except for the Deep North Basin where only four cores were taken because of poor weather conditions. Of the eight cores collected six were used for faunal analysis; of these five were sectioned into two, one centimeter layers. One was sectioned into five one centimeter layers i.e. 0–1 cm, 1–2 cm, 2–3 cm, 3–4 and 4–5 cm. The seventh core was used to take redox potential readings immediately on recovery. The top two centimeters of the remaining core was placed in a cold box for carbon content analysis.

River sampling: sediments were collected by hand with a coring tube of the same dimensions as used for collecting profundal samples. The cores were sectioned as above. Three stations i.e. Rivers Oich, Foyers and Moriston were selected by surveying the area for soft sediment similar in grain size to the profundal samples where core tubes could used with ease. Samples were then taken randomly within an area of 10 m^2. All samples were sublittoral ranging from 0.08–0.39 m depth. Eighteen cores, six from each station were collected from 7–8th August 1994.

After slicing, all samples were immediately fixed using 8% formaldehyde, at ambient temperature, giving a final dilution of 4% after mixing. A trace of rose bengal was added to the fixative to temporarily stain the nematodes, thus making them easier to see when counting and sorting.

In addition to the stations listed in Table 1, four sub-littoral qualitative cores were taken from a sandy beach at Borlum Bay, Fort Augustus (NH 085 385) on 22 July 1992 from depths of 0.10–0.38 m. Some of the nematode species found did not reoccur during the 1992–93 surveys, so we have taken this opportunity to include them in this paper. They are identified in the descriptions as Borlum Bay

Table 1 Summary of sampling stations, core depths and sediment characteristics.

Station	Core No's	Position	Date	Depth (m)	Sediment
Fort Augustus Bay (FA)	2–7	57°08.80´ N 4°39.45´ W	10/7/93	91–105	Organic matter (OM) floc, occasionally ferrugineous mixed with grey siliceous sand
Deep South Basin (DSB)	8–13	57°12.55´ N 4°34.55´ W	11+12/7/93	194–210	As above but with slight sulphurous smell
Foyers Plateau (FP)	14–19	57°15.80´ N 4°29.60´ W	12+13/7/93	150–161	As above
Deep North Basin (DNB)	20, 22	57°16.40´ N 4°29.10´ W	13/7/93	211 211	As above
River Oich (RO)	31, 32	NH 094 382	7/8/94	0.31	Sublittoral. River mouth.Algae and OM on surface, coarse sand below
	33, 34	NH 094 382	7/8/94	0.20	Small stones and gravel
	35	NH 094 382	7/8/94	0.33	Coarse sand and small pebbles
	36	NH 094 382	7/8/94	0.17	Coarse sand
River Foyers (RF)	40–45	NH 211 495	7/8/94	0.14–0.39	Stagnant sublittoral. 50 m from river mouth. OM and grey siliceous sand containing black streaks. Strong sulphurous smell
River Moriston (RM)	50	NH 211 495	8/8/94	0.15	100 m from river mouth Sand between boulders
(account of full data set	51,52	NH 211 495	8/8/94	0.10 0.08	Coarse sand small pebbles
in prep.)	53	NH 211 495	8/8/94	0.20	Sand and gravel, some pebbles
	54	NH 211 495	8/8/94	0.15	Coarse sand
	55	NH 211 495	8/8/94	0.16	Sand and gravel

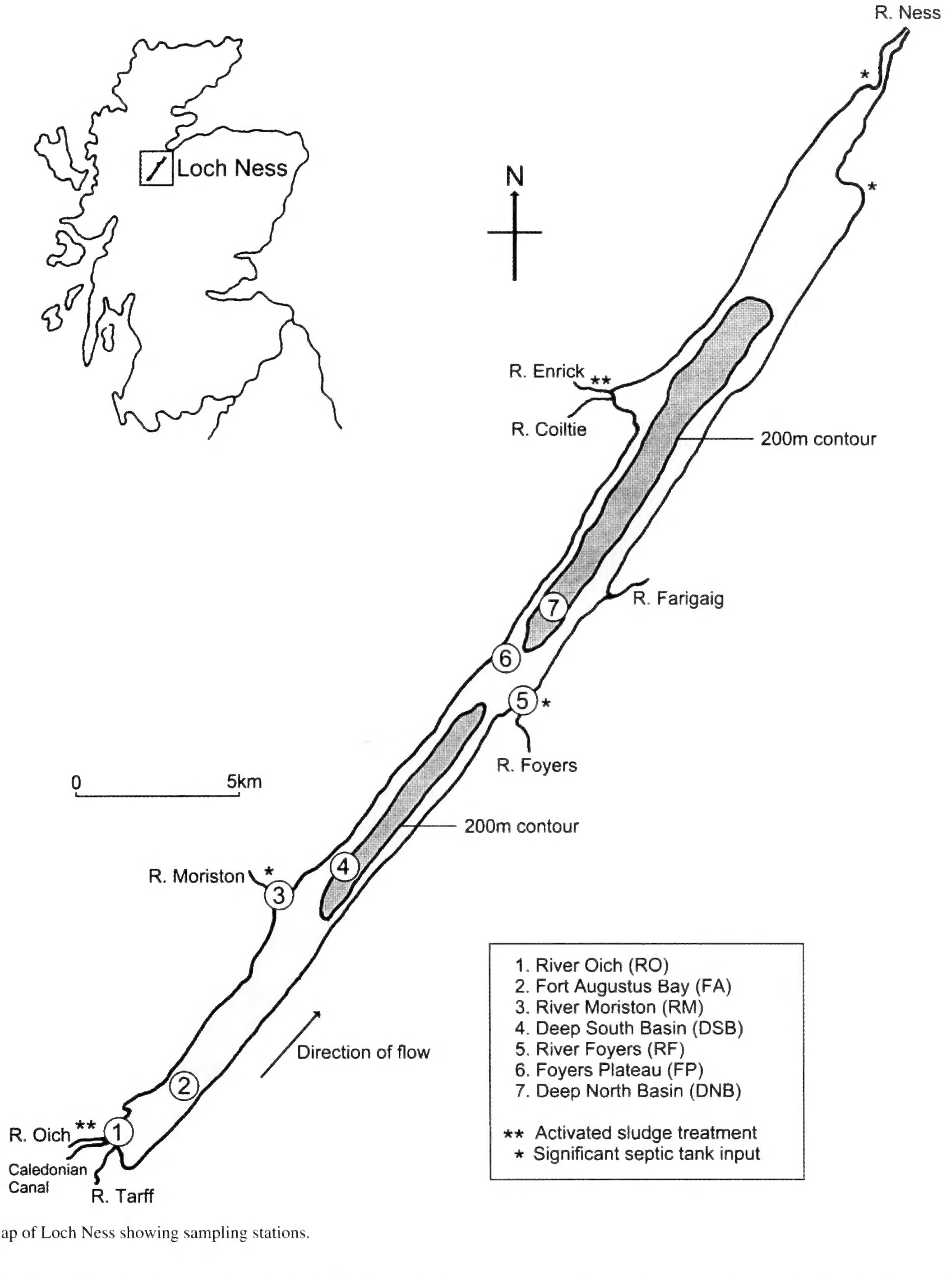

Fig. 1 Map of Loch Ness showing sampling stations.

(1992 collection). Also, they have not been included in the ecological part of this study which is based entirely on the 1992–93 samples.

EXTRACTION AND SLIDE PREPARATION

Nematodes were extracted by the Ludox centrifugation-floatation technique (Persmark *et al.*, 1992). However, after extracting the first core it was found that the nematodes were still obscured by large amounts of organic matter of very similar density to that of the nematodes. In order to reduce sample sorting time, it was decided to subsample the remaining 1 cm core slices using the 'Asko sample splitter' Elmgren (1973). Two hundred nematodes were picked out from each core; if less than 200 nematodes were present in the first subsample, further subsamples were extracted until the required number was found. Extracted nematodes were then dehydrated to glycerine by the Seinhorst method (Seinhorst 1962).

FIGURES, PHOTOGRAPHS AND MEASUREMENTS

Specimens were examined, figured and photographed with an Olympus BH-2 interference contrast microscope fitted with camera lucida. The drawings are original and based entirely on Loch Ness specimens. All absolute measurements of nematodes are given µm.

SEDIMENT HORIZON

This can be taken as 0–1 cm unless a statement is made to the contary in the descriptions.

ABBREVIATIONS USED

a = body length ÷ greatest body width
b = body length ÷ distance from anterior end to junction of esophagus and intestine
b´ = body length ÷ distance from anterior end to posterior end of oesophageal glands
c = body length ÷ tail length
c´ = tail length ÷ body width at anus
L = total body length
MB = distance of median bulb from anterior end ÷ oesophageal length × 100
R = total number of body annules
Roes = number of annules in oesophageal region.
Rex = number of annules between anterior end of body and excretory pore
Rv = number of annules between anterior end and vulva
Rvan = number of annules between vulva and anus
Ran = number of annules on tail
tail/V–a = tail length ÷distance between vulva and anus
V = distance of vulva from anterior end ÷ body length × 100
V´ = distance of vulva from anterior end ÷ distance of anus from anterior end × 100
VL/VB = distance between vulva and posterior end of body ÷ body width at vulva

SPECIES LIST

The systematic classification of the order Tylenchida is based on that of Fortuner, Geraert, Luc, Maggenti and Raski (1987–1988) 'A reappraisal of Tylenchina (Nemata)'. That of the order Rhabditida is after Lorenzen (1981).

Order **TYLENCHIDA** Thorne, 1949	**S***	**P**
Family **TYLENCHIDAE** Örley, 1880		
Aglenchus agricola (de Man, 1884)	+	+
Coslenchus polonicus Brzeski, 1982	+	+
Coslenchus sp. 1	–	+
Coslenchus sp. 2	+	–
Filenchus cf. *discrepans* (Andrássy, 1954)	+	–
Filenchus facultativus (Szczgiel, 1969)	–	+
Filenchus thornei (Andrássy, 1954)	+	+
Filenchus sp. 1	–	+
Filenchus sp. 2	–	+
Filenchus sp. 3	–	+
Lelenchus leptosoma (de Man, 1880)	–	+
Lelenchus sp.	–	+
Malenchus acarayensis Andrássy, 1968	+	+
Malenchus bryophilus (Steiner, 1914)	+	+
Malenchus pachycephalus Andrássy, 1981	–	+
Malenchus pressulus (Kazachenko, 1975)	–	+
Miculenchus salvus Andrássy, 1959	–	+
Tylenchus rex Andrássy, 1979	–	+
Tylenchinae sp.	+	+
Family **ANGUINIDAE** Nicoll, 1935		
Ditylenchus sp.	+	–
Family **BELONOLAIMIDAE** Whitehead, 1960		
Geocenamus cf. *nanus* (Allen, 1955)	+	–
Tylenchorhynchus sp.	–	+
Family **HOPLOLAIMIDAE** Filipjev, 1934		
Helicotylenchus pseudorobustus (Steiner, 1914)	+	+
Family **HETERODERIDAE** Filipjev, 1934		
Meloidogyne ardenensis Santos, 1968	+	–
Meloidogyne kralli Jepson, 1983	–	+
Family **CRICONEMATIDAE** Taylor, 1936		
Criconema annuliferum (de Man, 1921)	–	+
Criconema demani (Micoletzky, 1915)	+	–
Criconema sp.	–	+
Discocriconemella sp.	–	+
Hemicycliophora sp.	–	+
Ogma sp.	+	–
Family **TYLENCHULIDAE** Skarbilovich, 1947		
Paratylenchus sp.	–	+
Family **APHELENCHOIDIDAE** Skarbilovich, 1947		
Aphelenchoides sp. 1	+	–
Aphelenchoides sp. 2	+	–
Aphelenchoides sp. 3	+	–
Order **RHABDITIDA** Chitwood, 1933		
Family **RHABDITIDAE** Chitwood, 1933		
cf. *Caenorhabditis* sp.	+	–
Family **DIPLOGASTERIDAE** Micoletzky, 1922		
Diplogasteritus nudicapitatus (Steiner, 1914)	+	–
Family **CEPHALOBIDAE** Filipjev, 1934		
Eucephalobus oxyuroides (de Man, 1876)	+	+
Eucephalobus sp.	+	–

* S =. Sublittoral, P = Profundal.

DESCRIPTIONS OF SPECIES

Aglenchus agricola (de Man, 1884) Andrássy, 1954

(Fig. 2)

MATERIAL EXAMINED. Fort Augustus Bay: 92, 105 m; cores 2, 3; 2♀♀. Foyers Plateau: 150–161 m; cores 14–17; 2♀♀ 4♂♂. River Foyers: 0.14–0.39 m; cores 40, 43, 45; 2♀♀, 2♂♂.

HORIZON. Core 2 (2–3 cm), core 14 (3–4 cm), core 40 (2–3 cm).

FEMALES. (n = 5). L = 650 μm (625–667); a = 31 (26.4–34.4); b = 6.6 (6.3–6.9); c = 3.3 (3.2–3.4); c′ = 14.5 (12.7–15.8); V = 55.1 (53–56); V′ = 77.6 (76.5–78.4); tail/V–a = 1.9 (1.7–2.0); tail = 194 μm (188–200).

Head continuous, not annulated. Body annules 1.6–1.8 μm wide at mid-body. Lateral fields with three lines; outer lines sometimes appear double, whereas the inner line which is usually weakly expressed, could be interpreted as two lines very closely set as they appear as either gully or ridge-like (dependent on optical settings). Spear moderately robust, 11.0–12.8 μm long, basal knobs distinct about 3.2 μm wide. Oesophagus 92.7–101.7 μm long; median bulb ovoid with usually distinct valves at 44–50% of oesophageal length. Vulva with flaps about 5.0 μm long covering about three annules; vagina curved anteriorly with swollen pyriform walls; anterior genital branch 123–146 μm long; spermatheca partly offset, usually poorly defined, ovoid to elongate-ovoid, sometimes appearing double, length variable 20–25.6 μm; postuterine sac lacking.

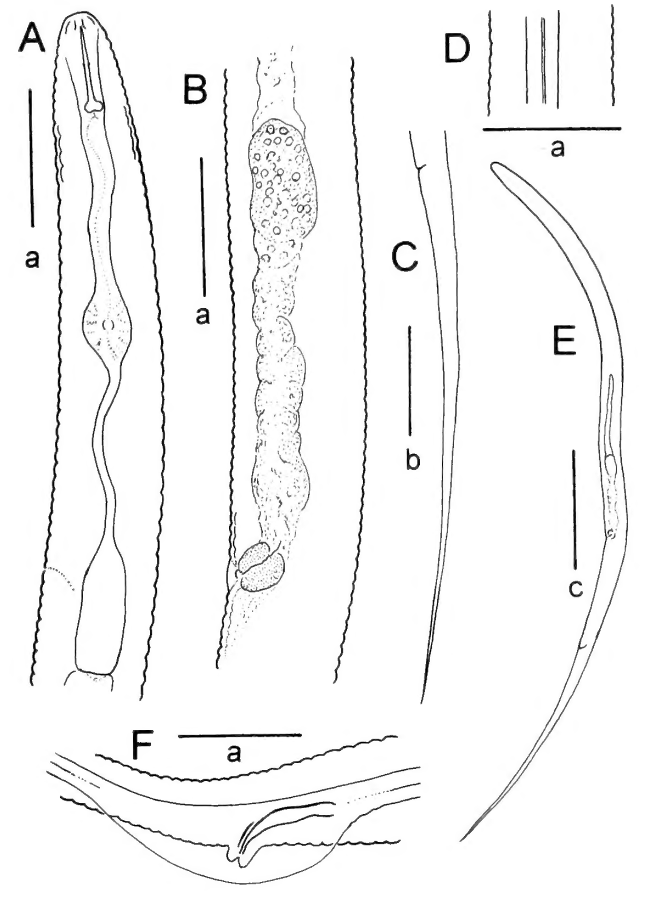

Fig. 2 *Aglenchus agricola* (de Man, 1884). A–E, female. A, oesophageal region; B, posterior end of reproductive system; C, tail; D, lateral field; E, habitus; F, male spicular region. Scale bars a = 20 μm, b = 40 μm, c = 100 μm.

MALES. (n = 6). L = 591.5 μm (469–670); a = 38.9 (33–43); b (n = 4) = 6.2 (5.6–6.7); c = 3.1 (2.9–3.3); c′ = 17.5 (15.3–19); gubernaculum (n = 5) = 6.4 μm (6.3–6.4); spicules (n = 5) = 14.7 μm (14–15.3); tail = 193.8 μm (153–219).

Similar to female. Annules 1.6–1.96 μm wide at mid-body. Spear 12–12.8 μm long, with rounded knobs about 2.6 μm wide. Oesophagus 81.6–101 μm long; median bulb ovoid with usually distinct valves at 46–48% of oesophageal length. Testis 144–153.6 μm long occupying 24–25% of body length; cloacal lips tube-like, somewhat asymmetrical; bursa adanal 32–38.4 μm long with smooth or very finely crenate margins.

DISTRIBUTION AND HABITAT. Cosmopolitan, in various soils, lives on or near plant roots, in mosses and freshwater.

REMARKS. Morphometric measurements of this population fall midway between those of two very similar species, *A. agricola* and *A. muktii* Phukan & Sanwal, 1980. *A. muktii*, according to the original authors, is distinguished from *A. agricola* 'in having a non-annulated lip region, 3 incisures in the lateral field, and a very long filiform tail. (*A. agricola* has 3 annules in the lip region, 1 lateral incisures and a tail which is not as filiform as in *A. muktii*).' Of these characters the first two are mistaken because in *A. agricola* the head is not annulated and the lateral field is comprised of three lines. In practice *A. muktii* is distinguished from *A. agricola* by its very long filiform tail. Tail length in *A. agricola* ranges from 134 to 179 μm, whereas in *A. muktii* the range is 178–276 μm (Geraert & Raski, 1988). Female tail length of this population varies between 153–197 μm. Brzeski (pers. comm.) notes tail lengths of *A. agricola* varying from 134–208 μm. In males of both species there would appear to be a distinction between tail lengths and ratio c'. Tail length 140–169 μm in *A. agricola vs* 178–330 μm in *A. muktii*; ratio c′ 13–15 *vs* 22–25 in *A. muktii*. However the Loch Ness males bridge the gap in respect of tail length 153–219 μm and fall between the range of values in the case of ratio c′, c′ = 15.3–19.

The overlap in tail lengths and other morphometric measurements suggest that the specific status of *A. muktii* is doubtful. This population is therefore identified as *A. agricola*.

Coslenchus polonicus Brzeski, 1982

(Fig. 3)

MATERIAL EXAMINED. Deep South Basin: 204 m; core 9; 1♀. River Foyers: 0.22 m; core 40; 1♀.

HORIZON. Core 40, (1–2 cm)

FEMALES. (n = 2). L = 635, 744 μm; a = 41.5, 46.5; b = 5.4, 6.2; c = 5.8, 5.4; c′ = 11, 12; V = 65.8, 64; V′ = 79.6, 80; Rex = 47, 52; Roes = 62, 63; Rv = 203; Rvan = 44, 49; Ran = 55, 65; tail/V–a = 1.0; tail = 110, 137.6 μm.

Head more or less continuous with body contour, 6.4–6.7 μm wide with 4 very fine annules. Annules 2.3, 2.8 μm at mid-body. Lateral fields with 4 lines, the two inner lines closely spaced, thus sometimes appearing as a single line. Cuticle with 18–20 longitudinal ridges (difficult to count) excluding lateral fields. Spear robust 15, 13.4 μm long; knobs rounded, 3.8, 3.2 μm wide. Oesophagus 118, 120 μm long; median bulb ovoid, valve at about 45% of oesophageal length. Vulva, with lateral vulval membranes, 6.4 μm long or about 3 annules wide; vagina inclined anteriorly with thick, somewhat pyriform, walls; postuterine sac small; spermatheca

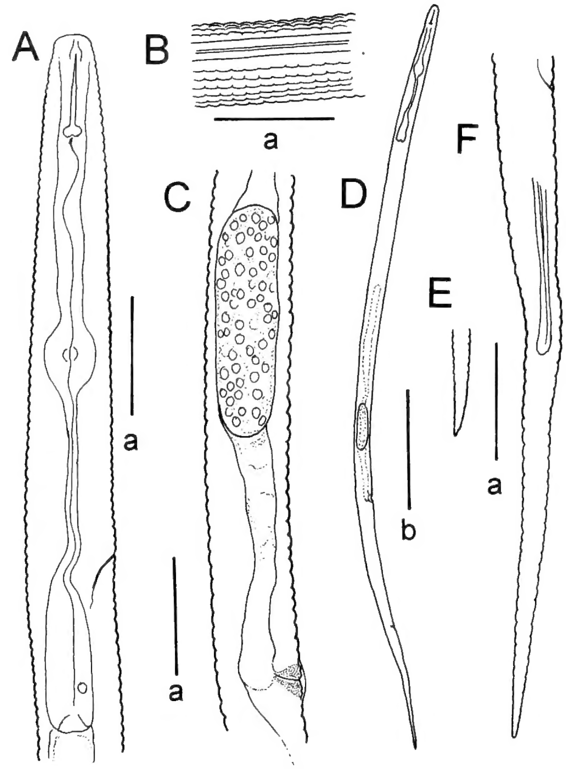

Fig. 3 *Coslenchus polonicus* Brzeski, 1982. A–F, female. A, oesophageal region; B, lateral field; C, posterior end of reproductive system; D, habitus; E, tail tip; F, tail. Scale bars a = 20 μm, b = 100 μm.

elongate, 38, 41 μm long, packed with sperms about 2.0 μm in diameter. Distance from vulva to anus 107–128 μm. Tail tip finely rounded with annules in one specimen; rounded without discernible annules in other.

DISTRIBUTION AND HABITAT. 'Collected in several places in Poland and in Andreevskoe, Karelia, USSR, always in low peat soil, in small number of specimens' (Brzeski, 1987).

REMARKS. These nematodes were not originally identified as *C. polonicus* because they have fewer cuticular ridges (18–20 *vs* 26 in *C. polonicus*). However, Brzeski (pers. comm.) recognized these females, and suggested they appeared to be *C. polonicus*. As there are no other significant differences between these females and descriptions of *C. polonicus* (Brzeski, 1982, 1987) it is assumed that the lower number of cuticular ridges lies within the range of variation that might be expected in this species.

Coslenchus sp. 1

(Fig. 4)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 4; 1♀. Foyers Plateau: 157 m; core 16; 1♀.

FEMALES. (n = 2). L = 520, 527 μm; a = 23.2, 24.7; b = 5.5, 5.4; c = 5.6, 6.1; c´ = 7.2, 6.9; V = 64, 65; V´ = 77, 79; Rex = 37, 42; Roes = 42, 46; Rv = 136, 138; Rvan = 40, 37; Ran = 59, 53; tail/V–a = 0.92, 0.93; tail = 93.4, 86.4 μm.

Head offset in one specimen; 7.0, 7.5 μm wide with 4 annules. Annules about 2.6, 2.7 μm at mid-body. Lateral fields with four lines. Cuticle with 14 longitudinal ridges (excluding lateral fields). Spear moderately robust 11.5, 12.8 μm long, knobs rounded, slightly sloping posteriorly, 2.6, 3.0 μm wide. Oesophagus 96.3, 94.7 μm long; median bulb ovoid; valve well developed at about 46% of oesophageal length. Vulva with lateral vulval membranes 7.0, 7.6 μm or 3 adjacent annules long; vagina perpendicular or slightly inclined anteriorly, with thick walls; postuterine sac not evident; spermatheca without sperm. Distance from vulva to anus 100, 120 μm. Tail tip finely rounded.

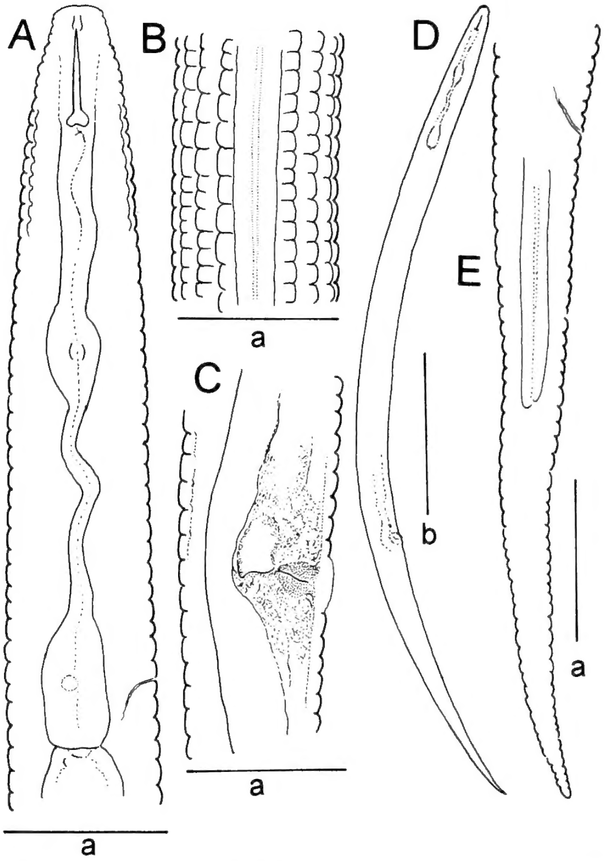

Fig. 4 *Coslenchus* sp. 1. A–E, female. A, oesophageal region; B, lateral field; C, vulval region; D, habitus; E, tail. Scale bars a = 20 μm, b = 100 μm.

REMARKS. Using Brzeski's (1987) and Geraert & Raski's (1988) keys, these nematodes come close to *C. andrassyi* Brzeski, 1987, but the mid-body annules are marginally too wide 2.6, 2.7 *vs* 2.1–2.5 μm in *C. andrassyi*, also the number of annules between the vulva and the anterior end of the body are too low, 136, 138 *vs* 157–186 in *C. andrassyi.*

Coslenchus sp. 2

(Fig. 5)

MATERIAL EXAMINED. River Foyers: 0.22 m; core 40; 1♀.

HORIZON. Core 40, (1–2 cm).

FEMALE. (n = 1). L = 546 μm; a = 24; b = 4; c = 5.4; c´ = 7; V = 65; V´ = 79.5; Rex = 40; Roes = 63; Rv = 152; Rvan = 41; Ran = 66; tail/V–a = 1.1; tail = 102 μm.

Head narrower than adjacent body; 7.7 μm wide with 5 annules.Annules 2.7 μm wide at mid-body. Lateral fields with 4 lines. Cuticle with longitudinal ridges and additional short ridges distributed irregularly, giving an estimated total of 15–16 ridges excluding lateral fields. Spear slender, 13.5 μm long; knobs small,

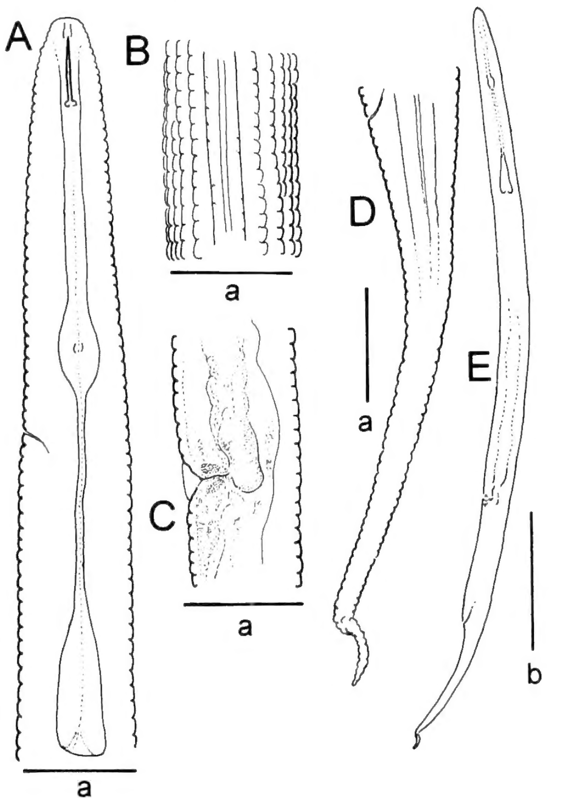

Fig. 5 *Coslenchus* sp. 2. A–E, female. A, oesophageal region; B, lateral field; C, vulval region; D, tail; E, habitus. Scale bars a = 20 µm, b = 100 µm.

rounded about 2.6 µm wide. Oesophagus 136 µm long; median bulb ovoid, valve well developed at 45.5% of oesophageal length. Vulva with lateral vulval membranes, 7.6 µm long or about 3 annules wide; vagina slightly inclined anteriorly with thickened walls; postuterine sac short; spermatheca empty. Distance from vulva to anus 91 µm. Tail damaged, but annules up to finely rounded terminus.

REMARKS. Although the tail of this specimen is damaged, it is clearly different from the other species of *Coslenchus* found in Loch Ness. Ratios effected by this damage are considered to be close to measurements that would have been obtained had the specimen been undamaged. It keys out close to *C. pastor* Andrássy, 1982, but the morphometrics are a poor fit.

***Filenchus* cf. *discrepans* (Andrássy, 1954) Raski & Geraert, 1987**

(Fig. 6)

MATERIAL EXAMINED. Fort Augustus Bay: 98, 102 m; cores 5, 6; 2♀♀. Deep South Basin: 196, 204 m; cores 8, 10; 2♀♀. Foyers Plateau: 158,–160 m; cores 14, 15, 18; 3♀♀. Deep North Basin: cores 20, 22; 211 m, 2♀♀. River Foyers: 0.25–0.39 m; cores 41, 42, 44; 1♂, 3♀♀.

HORIZON. Core 14, (1–2 cm).

FEMALES. (n = 10). L = 429 µm (337–526); a = 35 (27.0–45.8); b = 5.3 (5.0–6.1); c = 3.8 (3.4–4.5); c′ = 14.1 (12.8–17.6); V = 60 (57–64); V′ = 82.3 (80.5–84); tail/V–a = 2.1 (1.7–2.5); tail = 109 µm (91.4–140).

Head 3.8–5.0 µm wide at base. Annules 1.2 µm (0.8–1.6) wide at mid-body. Lateral fields with two lines. Spear slender, 6.0–7.6 µm long with small basal knobs, about 1.2 µm wide. Oesophagus 69–92 µm long; median bulb somewhat fusiform, valve weak at 35–42% of oesophageal length. Anterior genital branch 68–156 µm long. Spermatheca axial, oblong with rounded sperms about 1.3 µm in diameter. Postuterine sac 7.0–13.4 µm long. Vagina more or less perpendicular to body axis.

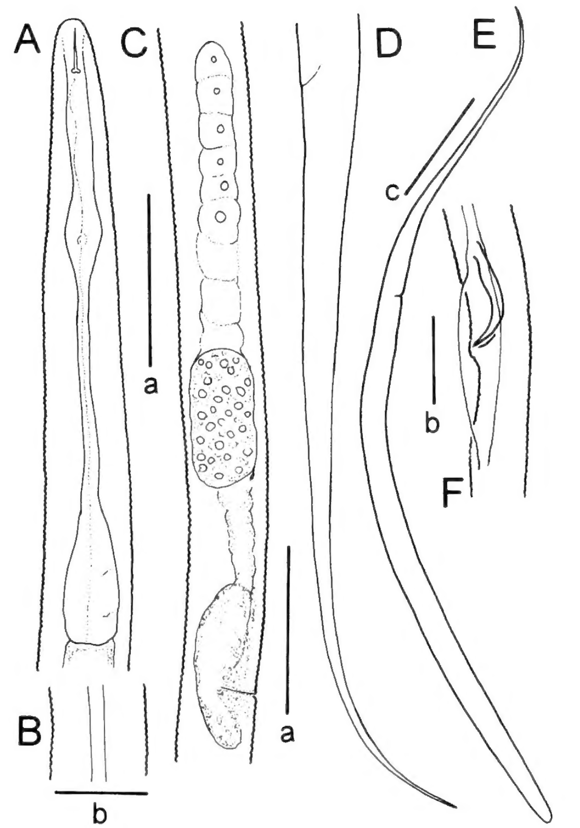

Fig. 6 *Filenchus* cf. *discrepans* (Andrássy, 1954). A–E, female. A, oesophageal region; B, lateral field; C, reproductive system; D, tail; E, habitus. F, male spicular region. Scale bars a = 20 µm, b = 10 µm, c = 50 µm.

MALE. (n = 1). L = 453 µm; a = 47; b = 5.0; c = 4.5; c′ = 14.5; gubernaculum = 3.0 µm; spicules = 13.8 µm; tail = 101 µm.

Similar to female, except body more slender with narrower lateral fields. Testis 152 µm long, occupying 33% of body length. Bursa adanal, 19 µm long.

DISTRIBUTION AND HABITAT. Widely distributed in Europe with additional records from Mexico, Russia, USA (terrestrial soils) and New Guinea (terrestrial and fresh water).

REMARKS. This population keys out to *F. discrepans*. The morphology of the female reproductive system closely resembles that figured for the type specimen, especially in respect of the oblong spermatheca in females. However, the cephalic region is not makedly narrower than the adjacent body region as figured by Andrássy (1954) and described by Troccoli & Geraert (1995). Brzeski (pers. comm.,) suggests that these nematodes show affinities to *F. misellus* (Andrássy, 1958), but in *F. misellus* tail length (28–71 µm) and ratio tail/V–a (0.7–1.6) are different (Brzeski, 1979); tail shape also differs.

Filenchus facultativus (Szczygiel, 1969) Raski & Geraert, 1987

(Fig. 7)

MATERIAL EXAMINED. Fort Augustus Bay: 91, 98 m; cores 2, 5; 3 ♀♀.

HORIZON. Core 2, (2–3 cm).

FEMALES. (n = 3). L = 515 µm (434–557); a = 36 (35–37.8); b = 6.1 (6.0–6.3); c = 4.0 (3.9–4.1); c´ = 13 (11.6–14.5); V = 63.2 (62–64.6); V´ = 84.8.(83.7–85.6); tail/V–a = 2.1 (2.0–2.2); tail = 127 µm (105–142).

Head about 4.6 µm wide at base with 2–3 annules. Amphids sinuous. Annules 1.7 µm (1.5–1.9) at mid body. Lateral fields with two lines. Spear slender 9.0 µm (n = 2) long with small basal knobs, about 1.2µm wide. Oesophagus 83.8 µm (73.6–91) long; median bulb ovoid, valve weak at 39–42% of oesophageal length. Excretory pore 62.4, 68.7 µm (n = 2) from anterior. Anterior genital branch 145 µm (127–159) long. Spermatheca axial or slightly offset, elongate 23, 26 µm long with rounded sperms (n = 2). Postuterine sac 7.7–12 µm long. Vagina 7.0–8.0 µm long, more or less perpendicular to body axis. Tail tip pointed to finely rounded.

DISTRIBUTION AND HABITAT. A widespread species found in terrestrial soils.

REMARKS. *F. facultativus* is a variable species and these nematodes are within the range of measurements of other populations described in the literature. However, the spear at 9.0 µm long is at the extreem range recorded for this species (6.0–9.0 µm.). A range of 6.0–8.0 µm is given by Raski & Geraert (1987) in their key to species of *Filenchus*, the same range is also given by Karegar & Geraert (1988) in their summary of characters distinguishing *F. facultativus* from other very similar species, whereas Torres & Geraert (1996) record spear lengths of 7.5–9.0 µm in a population described from Argentina.

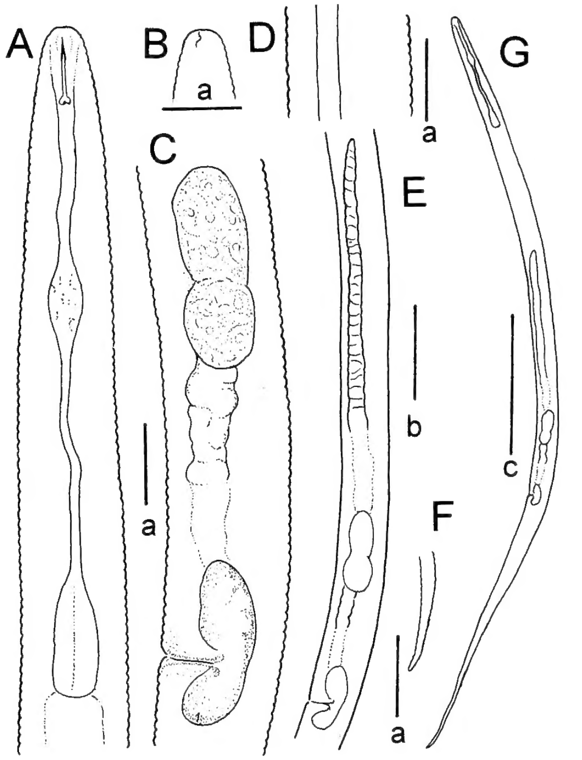

Fig. 7 *Filenchus facultativus* (Szczygiel, 1969). A–G, female. A, oesophageal region; B, head showing amphid; C, posterior end of reproductive system; D, lateral field; E, reproductive system; F, tail terminus; G, habitus. Scale bars a = 10 µm, b = 30 µm, c = 100 µm.

Filenchus thornei (Andrássy, 1954) Andrássy, 1963

(Fig. 8)

MATERIAL EXAMINED. Deep South Basin: 161 m; core 19, 1 ♀. River Foyers: 0.22 m; core 40, 1 ♀. Foyers Plateau: 159 m; core 14, 1 ♂.

HORIZON. Core 14, (2–3 cm); core 19, (1–2 cm); core 40, (2–3 cm).

FEMALES. (n = 2). L = 997, 1003 µm; a = 38, 44.7; b = 6.9, 6.5; c = 5.0, 4.1; c´ = 14.5, 18; V = 59, 56; V´ = 73, 73.5; tail/V–a = 0.95, 1.16; tail = 131.5, 191.5 µm.

Head about 7.6, 8.0 µm wide at base with 3–4 annules; height about 3.5 µm. Amphids not observed. Annules 1.3–1.6 µm wide at mid-body. Lateral fields with four lines, inner lines very faint and not always evident. Spear distinct, moderately slender, 13.4, 12 µm long with small basal knobs about 2.0 µm wide. Oesophagus 144–155 µm long; median bulb more or less ovoid, valves moderately distinct at 39.7, 42% of oesophageal length. Excretory pore sclerotized at 112, 122 µm from anterior. Anterior genital branch 432 µm (n = 1); spermatheca 42 µm long, offset. Vagina perpendicular to body axis about 13.5 µm long. Tail tip finely pointed.

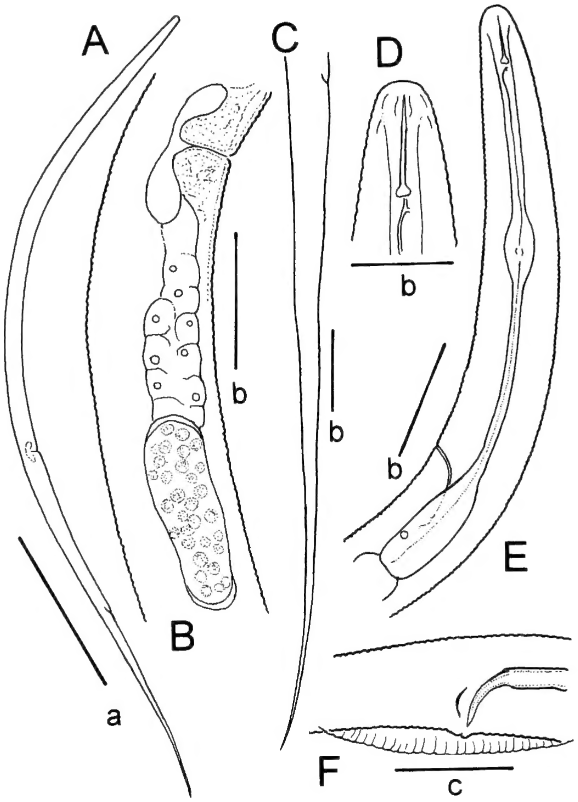

Fig. 8 *Filenchus thornei* (Andrássy, 1954). A–E, female. A, habitus; B, posterior end of reproductive system; C, tail; D, head region; E, oesophageal region. F, male spicular region. Scale bars a = 200 µm, b = 30 µm, c = 20 µm.

MALE. (n = 1). L = 960 µm; a = 44.2; b = 7.1; c = 5.1; c′ = 12.8; gubernaculum = 6.0 µm; spicules = 22.6 µm; tail = 188 µm.

Similar to female; body slightly sinuous and curved distally, also narrowed in region of cloaca – possibly an artefact as the body is slightly twisted in this region. Bursa 38 µm long, with crenate borders; cloacal lips protruding. Tail tip finely rounded.

DISTRIBUTION AND HABITAT. Cosmopolitan, found in damp soils and freshwater habitats.

REMARKS. This species was recently redescribed by Brzeski (1997) and these specimens fall well within the range of measurements presented for *F. thornei*. The height of the head is perhaps slightly lower, but this is not thought to be of any significance.

Filenchus sp. 1

Fig. 9

MATERIAL EXAMINED. Foyers Plateau: 159 m; core 14, 2 ♀♀. Deep North Basin: 211 m; core 22, 1 ♀.

HORIZON. Core 14, (1–2 cm; 3–4 cm).

FEMALES. (n = 3). L = 531 µm (439–615); a = 40.6 (39.7–41.8); b = 6.0 (5.5–6.5); c = 3.4 (3.2–3.6); c′ = 18.5 (15.8–20.2); V = 58.6 (57–60); V′ = 83.3 (82.6–84.5); tail/V–a = 2.5 (2.2–2.7); tail = 157 µm (132–191.5).

Head 5.0–5.7 µm wide at base with two annules. Amphids sinuous. Annules about 1.6 µm wide at mid-body. Lateral field (only evident in two specimens) with four lateral lines, the inner two being very faint and close to outers. Spear indistinct, slender, 9.6 µm long with small rounded knobs about 1.3 µm wide. Excretory pore 64 µm (56–73) from anterior. Oesophagus 85 µm (74–94.2) long; median bulb with poorly developed valves at 40.4% (35–45.6) of oesophageal length. Anterior genital branch 163 µm (115–198) long. Spermatheca offset, 27.7 µm (22.4–32) long. Postuterine sac 8.9 µm (8.3–9.6) long. Vagina 7.0–7.7 µm long, gently inclined anteriorly with thickened walls. Tail terminus pointed to finely rounded.

REMARKS. The specific identity of these females is uncertain. They show affinities with *F. facultativus* described above and may be conspecific. However, in these nematodes the spear is slightly longer and the walls of the vagina are slightly thickened.

Filenchus sp. 2

(Fig. 10)

MATERIAL EXAMINED. Foyers Plateau: 157 m; core 14, 1 ♀.

FEMALE. (n = 1). L = 625 µm; a = 40.1; b = 5.2; c = 5.5; c′ = 9.0; V = 65.8; V′ = 80; tail/V–a = 1.0; tail = 108 µm;

Head 5.7 µm wide at base. Amphids not observed. Annules fine, 1.3 µm wide at mid-body. Lateral field with four lines, inner two faint. Spear indistinct, 9.3 µm long with small basal knobs about 1.3 µm wide. Excretory pore 82.5 µm from anterior. Oesophagus 119 µm long; median bulb ovoid, valves weak at 40.7% of oesophageal length. Anterior genital branch 175 µm long; spermatheca axial, about 22 µm long, with rounded sperms about 1.9 µm in diameter. Postuterine sac 6.4 µm long, occupying 41% of corresponding body diameter. Vagina about 5.8 µm long, perpendicular to body axis. Tail terminus finely rounded.

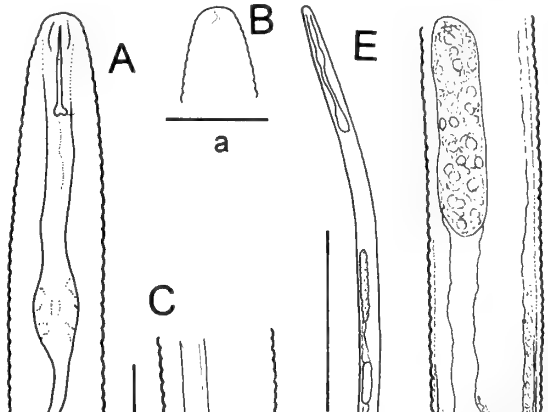

Fig. 9 *Filenchus* sp. 1. A–F, female. A, oesophageal region; B, head showing amphid; C, lateral field; D, tail tip; E, habitus; F, posterior end of reproductive system. Scale bars a = 10 µm, b = 100 µm.

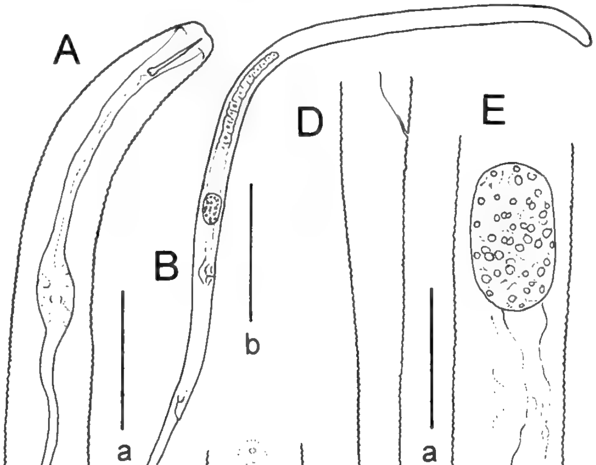

Fig. 10 *Filenchus* sp. 2. A–E, female. A, oesophageal region; B, habitus; C, lateral field; D, tail; E, posterior end of reproductive system. Scale bars a = 20 µm, b = 100 µm.

REMARKS. This nematode is close to *F. butteus* (Thorne & Malek, 1968) Brzeski, 1997, but the tail is longer and differs in shape.

Filenchus sp. 3

(Fig. 11)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 3, 1♂.

MALE. (n = 1). L = 434 µm; a = 35.7; b = 6.4; c = 4.4; c′ = 10.3; gubernaculum = 5.8 µm; spicules = 15 µm; tail = 99 µm.

Head 5.0 µm wide at base with 3–4 annules. Amphids not observed. Annules fine about 0.9 µm at mid-body. Lateral field with four lateral lines, hardly evident. Spear moderately slender, 11.2 µm long with small basal knobs 1.9 µm wide. Excretory pore 61.4 µm from anterior. Oesophagus poorly preserved, about 68 µm long; median bulb ovoid, valves not observed, centre at about 59% of oesophageal length. Testis 138 µm long, occupying 32% of body length, bursa adanal, about 19 µm long, with fine crenated margins. Tail tip pointed.

REMARKS. No conclusion can be reached on the specific identity of this specimen. It is close to *F.thornei*, but differs by its shorter body length, spicules and tail.

Lelenchus leptosoma (de Man, 1880) Raski & Geraert, 1985

(Figs 12, 36B)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 3; 1♀. Deep South Basin: 194 m; core 13; 1♀. Foyers Plateau: 159, 160 m; cores 14, 15; 3♀♀.

FEMALES. (n = 5). L = 546 (487–583) µm; a = 46.6 (40–49.8); b = 5.5 (4.9–6.3); c = 3.1 (2.7–3.35); c′ = 24.8 (22–27.9); V = 52 (48–54.8); V′ = 77.6 (75.5–78); tail/V–a = 2.2 (1.9–2.5); tail = 180 µm (156–215).

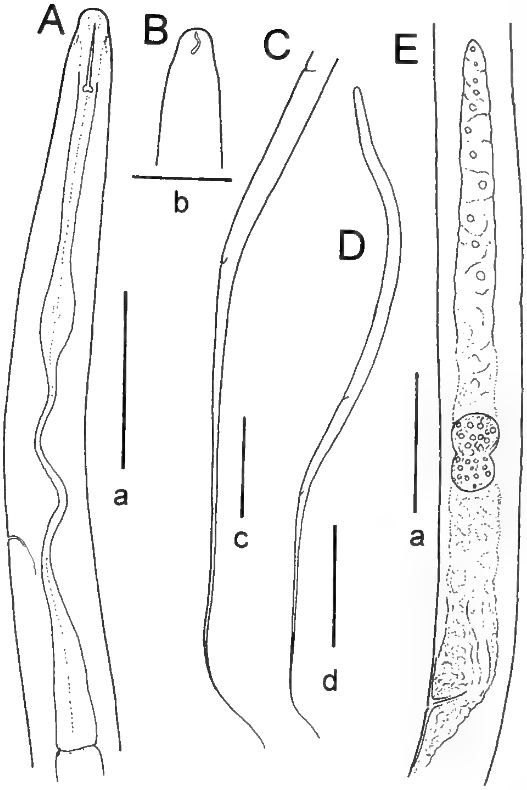

Fig. 12 *Lelenchus leptosoma* (de Man, 1880). A–E, female. A, oesophageal region; B, head showing amphid; C, posterior region; D, habitus; E, reproductive system. Scale bars a = 20 µm, b = 10 µm, c = 60 µm, d = 100 µm.

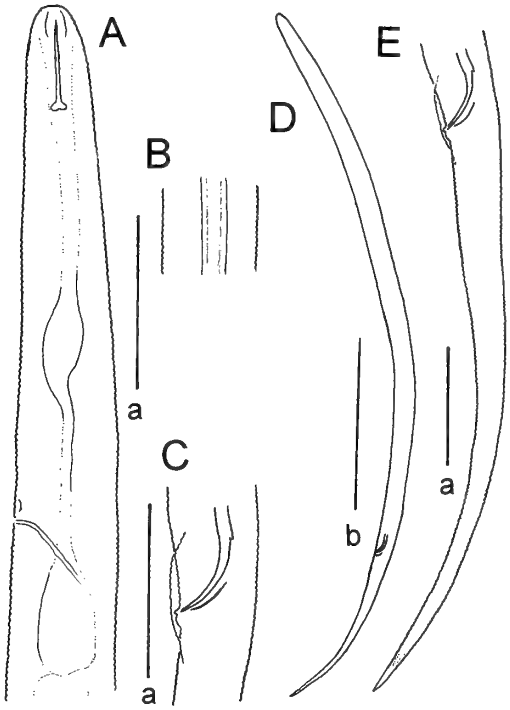

Fig. 11 *Filenchus* sp. 3. A–E, male. A, oesophageal region; B, lateral field; C, spicular region; D, habitus; E, tail and spicular region. Scale bars a = 20 µm, b = 100 µm.

Cephalic region narrowed dorso-ventrally. Cuticle smooth by light microscopy. Amphids sinuous. Lateral field absent. Spear slender, 7.7–9.3 µm long with small rounded knobs about 1.4 µm wide. Oesophagus 88–108 µm long; median bulb spindle-shaped with valves at 41–43% of oesophageal length. Anterior genital branch 96.7–121.5 µm long. Spermatheca more or less bispherical with rounded sperm (absent in one specimen) about 1.3 µm in diameter. Postuterine sac not evident in any specimen, possibly collapsed. Vagina about 5.5 µm long with thin walls, curved anteriorly.

DISTRIBUTION AND HABITAT. Cosmopolitan; soils and freshwater.

REMARKS. These specimens, for the most part, agree with the description and morphometrics presented in the literature (Raski & Geraert, 1985). Minor differences slightly extending the range of several ratios are not considered to be of any significance.

Lelenchus sp.

(Figs 13, 36A)

MATERIAL EXAMINED. Deep South Basin: 195, 204 m; cores 9, 11; 2♀♀. Foyers Plateau: 157, 159 m; cores 14, 16; 1♂, 1♀.

FEMALES. (n = 3). L = 620 (512–763) µm; a = 47.4 (42–54.5); b = 6.0 (5.5–6.5); c = 3.5 (3.3–3.8); c′ = 22.8 (21.4–24); V = 57.6 (57–58); V′ = 81 (80–82); tail/V–a = 2.1 (1.8–2.4); tail = 173 (154–200) µm.

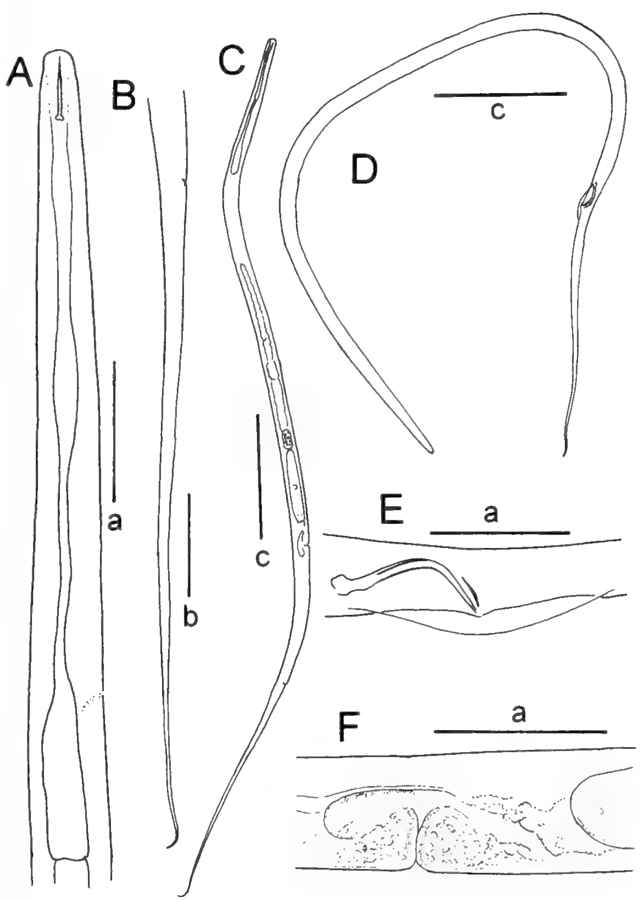

Fig. 13 *Lelenchus* sp. A–C, F, female. A, oesophageal region; B, tail; C, habitus; F, vulval region. D, E, male. D, habitus; E, spicular region. Scale bars a = 20 µm, b = 30 µm, c = 100 µm.

Cephalic region narrowed dorso-ventrally. Cuticle smooth by light microscopy. Lateral field absent. Spear slender, poorly defined, 9.0–9.3 µm long (n = 2) with small rounded knobs about 1.3 µm wide. Oesophagus 92–118 µm long; median bulb spindle-shaped, valves very indistinct, at about 48% of oesophageal length. Anterior genital branch 175–250 µm long. Spermatheca elongate ovoid without sperm. Egg present in two specimens about 62 µm long by 10 µm wide. Postuterine sac about 11.5 µm long or 80% of vulval body width (n = 2). Vagina more or less perpendicular, about 7.7 µm long with slightly thickened walls.

MALE. (n = 1). L = 920 µm; a = 58; b = 6.4; c = 4.5; c′ = 19.5; spicules = 23 µm; gubernaculum = 6.5 µm; tail = 203 µm.

Similar to female except body longer and more slender. Spear indistinct, about 10 µm long, with small, possibly deformed, rounded knobs. Oesophagus 145 µm long; median bulb spindle-shaped with indistinct valves at 40% of oesophageal length. Testis 300µm long, occupying 32.6% of body length; bursa adanal about 38 µm long with smooth margins.

REMARKS. These nematodes are possibly conspecific with *L. leptosoma*, but for the present they are treated as a separate species. In females the vagina walls are thicker and generally more pronounced. The male differs from males of *L. leptosoma* described in the literature by its greater body length and longer, strongly curved, almost bent spicules.

Malenchus acarayensis Andrássy, 1968 Geraert & Raski, 1986.

(Fig. 14)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 3, 1 ♀. Foyers Plateau: 159, 160 m; cores14, 15, 3 ♀♀. River Foyers: 0.39 m; core 42, 1 ♀.

HORIZON. Core 14 (2–3 cm).

FEMALES. (n = 5). L = 352 µm (323–373); a = 24.7 (23–26.6); b (n=3) = 4.4 (4.3–4.6); c = 4.4 (4.0–4.9); c′ = 9.1 (8–10.1); V = 63.3 (61–66.4); V′ = 80.8 (79–82); tail/V–a = 1.5 (1.25–1.73). tail = 78.9 µm (71.7–92).

Head narrow, about 4.0–5.0 µm at base, with very fine annules. Amphids not clear. Annules 1.0–1.3 µm at mid-body. Lateral fields with two lines appearing smooth or crenate, depending on fine focus; originating between 6.4–7.0 µm posterior to spear base, ending at 27–33% of tail length. Spear fine, especially conus, 8.3–9.0 µm long, knobs small, sloping posteriorly, about 1.3 µm wide. Excretory pore 56–66 µm from anterior. Oesophagus 73.6–86 µm (n = 3) long; median bulb ovoid, valve hardly evident, but positioned at 44–47.8% of oesophageal length. Anterior genital branch 101–112 µm long. Spermatheca usually rounded, ovoid in one specimen, 9.6–12.8 µm wide. Postuterine sac 6.4 µm long or 43% of vulval body width (n=1), collapsed in other specimens. Vagina with thickened walls, perpendicular to body axis or slightly tilted anteriorly. Distance from vulva to anus 45–56.9 µm. Tail tip slightly to strongly curved, tapering to a fine point, but not thread-like.

DISTRIBUTION AND HABITAT. Described from N. and S. America,

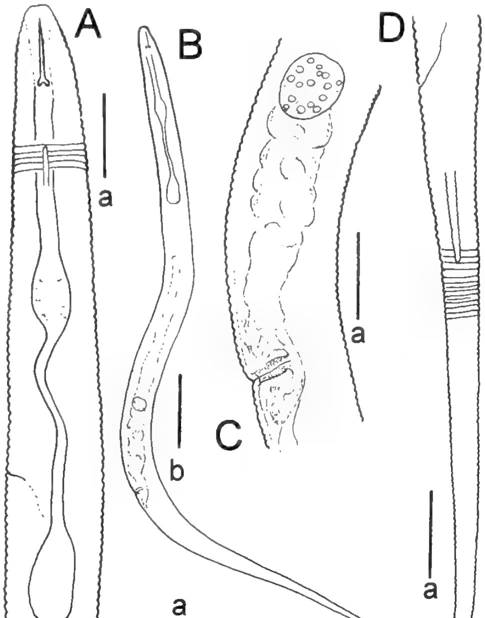

Fig. 14 *Malenchus acarayensis* Andrássy, 1968. A–F, female. A, oesophageal region; B, habitus; C, posterior end of reproductive system; D, tail; E, F, lateral field at different focal levels. Scale bars a = 10 µm, b = 50 µm.

India, Malawi, Holland, Poland and Belgium. Terrestrial, found in various soils, forest litter and sand dunes.

REMARKS. These specimens are all identified as *M. acarayensis* using Geraert & Raski's key (1986); furthermore they compare well with the range of measurements presented for *M. acarayensis*. However, they possibly differ by the more anterior origin of the lateral field, 6.4–7.0 μm behind spear base in these females, compared with 11–15 μm in a Spanish population (Gomez Barcina *et al.*, 1992). Other populations are more difficult to compare in the same manner as the start of the lateral field is given as originating at a level of 1/3 to about middle of the oesophageal procorpus (Geraert & Raski, 1986).

Malenchus bryophilus (Steiner, 1914) Andrássy, 1980

(Fig. 15)

MATERIAL EXAMINED. Fort Augustus Bay: 91, 105 m; cores 2, 7, 1♀, 2♂♂. Foyers Plateau: 158, 160 m; cores 15, 18, 1♀, 1♂. River Oich: 0.31 cm; core 31, 2♀♀.

HORIZON. Core 2 (1–2 cm) Core 31 (3–4 cm).

FEMALES. (n = 4). L = 349.5 μm (334–364); a = 21.3 (18–24.7); b (n = 2) = 4.5 (4.4–4.5); c = 4.9 (4.6–5.1); c´ = 7.9 (7.1–8.6); V = 64.4 (63.8–65.3); V´ = 81.2 (63.8–65.3); tail/V–a = 1.4 (1.2–1.5); tail 72 μm (69.1–73.6).

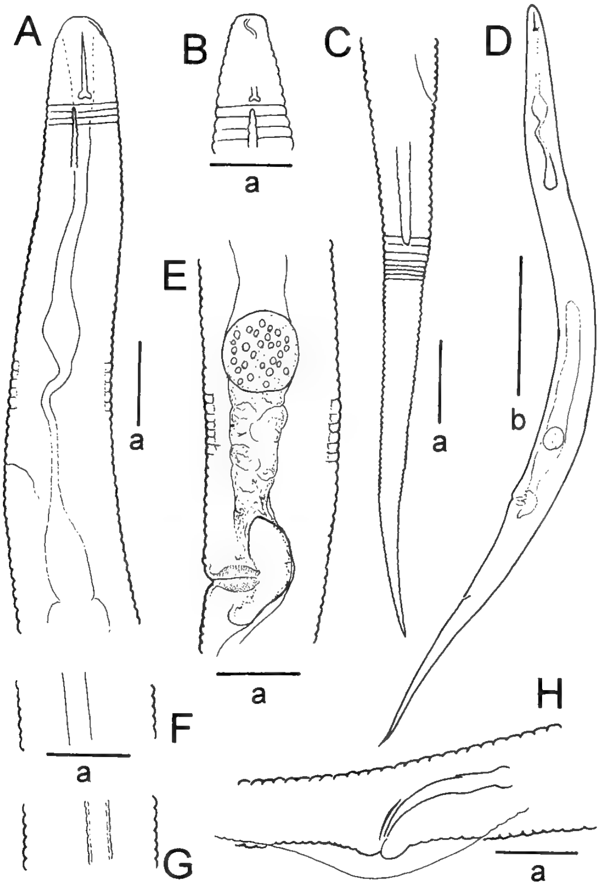

Fig. 15 *Malenchus bryophilus* (Steiner, 1914). A, C–G, female. A, oesophageal region; C, tail; D, habitus; E, posterior end of reproductive system; F, G, lateral field at different focal levels. B, H, male. B, head region showing amphid and origin of lateral field in respect of spear knobs; H, spicular region. Scale bars a = 10 μm, b = 60 μm.

Head slightly narrowed, about 5 μm wide at base with 4–5 annules. Amphids not clear. Annules 1.4–1.5 μm at mid-body. Lateral field with two lines appearing smooth or crenated depending on fine focus; originating at level of spear knobs to two annuli posterior, or 0–2.5 μm from spear knobs, ending between 25–35% of tail length. Spear fine, especially conus, 9–9.6 μm long, knobs small, about 2.56 μm wide. Excretory pore 61–71 μm from anterior. Oesophagus 78.8 μm long (n = 2); median bulb ovoid, valve poorly developed, at 45–50% of oesophageal length (n = 2). Vulva sunken. Vagina perpendicular or slightly tilted anteriorly with thickened walls; anterior genital branch 96–113 μm long; spermatheca rounded to ovoid, packed with sperms. Postuterine sac about 5 μm long (n = 2), possibly collapsed in other females. Distance from vulva to anus 48.6–57 μm. Tail tip finely rounded to pointed.

MALES. (n = 3). L = 362 μm (337–379); a = 21.1 (20.6–21.5); b = 4.7 (4.4–5.0); c = 4.5 (4.1–4.7); c´ = 7.3 (6.6–8.3); gubernaculum = 5.5 μm (5.3–5.76); spicules = 16.5 μm (16–17); tail = 80.6 μm (71.6–91)μm.

Similar to female. Head narrowed, about 5 μm wide at base with 5 fine annules. Amphids sinuous. Body annules 1.4–1.5 μm at mid-body. Spear 9.0–9.6 μm long. Oesophagus 71–85 μm long; median bulb ovoid, valve weak, at 48.6–53.8% of oesophageal length. Testis 189–213 μm long, occupying 41–56% of body length. Cloacal lips pronounced; bursa adanal, 27–32 μm long, with smooth margins.

DISTRIBUTION AND HABITAT. Cosmopolitan, occurs in soil, near or in roots; in humus, forest litter and moss.

REMARKS. The morphometrics and morphology agree for the

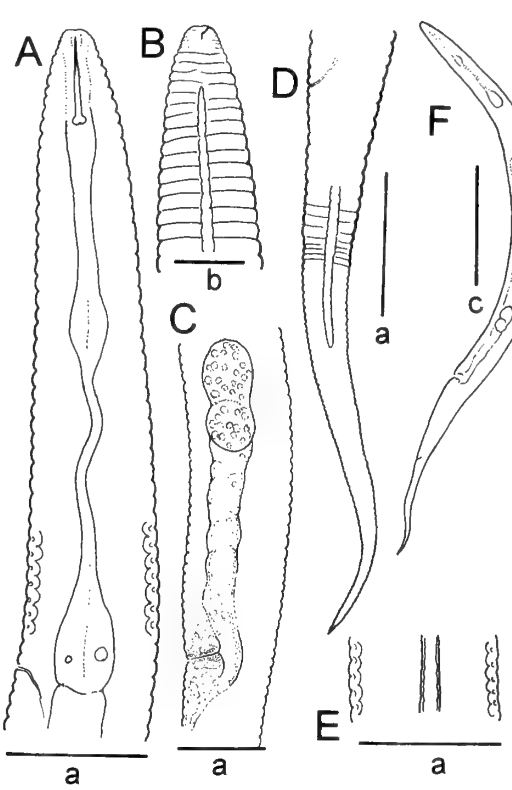

Fig. 16 *Malenchus pachycephalus* Andrássy, 1981. A–F, female. A, oesophageal region; B, anterior region showing amphid and origin of lateral field; C, posterior end of reproductive system; D, tail; E, lateral field; F, habitus. Scale bars a = 20 μm, b = 10 μm, c = 100 μm.

most part with the original description. Minor differences include slightly lower values for tail length, tail/V–a and ratio c´. These measurements however, fall within the range of measurements of females of *M. bryophilus* examined by Brzeski (pers. comm.).

Malenchus pachycephalus Andrássy, 1981

(Fig. 16)

MATERIAL EXAMINED. Foyers Plateau: 157 m; core16, 1 ♀.

FEMALE. (n = 1). L = 497 µm; a = 20; b = 4.9; c = 6.1; c´ = 7.0; V = 69; V´ = 81.6; tail/V–a = 1.0; tail = 81.2 µm.

Head slightly offset, 6.4 µm wide at base with 4–5 fine annules. Amphids not evident. Annules 2.1 µm wide at mid-body. Lateral field with two lines appearing smooth or strongly crenate depending on fine focus; originating at 3 annules or 4.0 µm anterior to spear knobs; terminating at about 46% of tail length. Spear 12 µm long with knobs about 2.4 µm wide. Excretory pore 93 µm from anterior, almost at level of posterior margin of basal bulb. Oesophagus 100 µm long; median bulb slender ovoid; valve hardly evident located at 44% of oesophageal length. Phasmid like structure not seen. Anterior genital branch 170 µm long. Spermatheca bilobed 24 µm long with rounded sperms about 1.3 µm in diameter. Postuterine sac 9.6 µm long. Vagina slightly tilted anteriorly with thickened walls. Vulva – anus distance 76.8 µm. Tail tip tapering to a fine point.

DISTRIBUTION AND HABITAT. Recorded from USA, Spain, Hungary and Bulgaria; occurs in soil around plant roots.

REMARKS. Using the keys of Andrássy (1981) and Geraert & Raski (1986), this specimen can be identified as *M. pachycephalus*, but the anterior part of the oesophagus is not distinctly longer than the posterior as described in the original description, however, this feature is not evident in the accompanying illustration of the anterior end (Andrássy, 1981: Fig. 13c). It also differs in having a longer tail 81 µm *vs* (56–72); this range includes measurements from the original description and a Spanish population (Gomez Barcina *et al.*, 1992).

Malenchus pressulus (Kazachenko, 1975) Andrássy, 1981

(Fig. 17)

MATERIAL EXAMINED. Deep South Basin: 204 m; core 9, 1 ♀.

FEMALE. (n=1). L = 460 µm; a = 25; b = 5.1; c = 5.9; c´ = 8.1; V = 66.9; V´ = 80.5; tail/V–a = 0.95; tail = 77.7.

Head not offset, 7.0 µm wide at base with 3–4 minute annules at focal level of dorso-ventral margin, otherwise appearing smooth by light microscopy. Amphids sinuous. Annules 1.5 µm at mid body. Lateral fields with two lines appearing smooth or crenate depending on fine focus; originating at level of spear knobs, terminating at about 32% of tail length. Spear delicate, 11.8 µm long with spear knobs 2.5 µm wide. Excretory pore 86 µm from anterior at level of posterior margin of basal bulb. Oesophagus 89 µm long; median bulb slender ovoid, valve not evident; centre of median bulb located at about 51% of oesophageal length. Phasmid like structure located at 14 annules anterior to vulva. Anterior genital branch 170 µm long. Spermatheca elongate ovoid, 19 µm long with indistinct rounded sperms about 1.3 µm in diameter. Postuterine sac 12.8 µm long. Vagina slightly tilted anteriorly, with thickened walls. Vulva slightly sunken. Vulva – anus distance 74.5 µm. Tail tip pointed.

DISTRIBUTION AND HABITAT. Originally described from Russia in soil of a coniferous forest with an additional record from soil around grass roots (Andrássy, 1981).

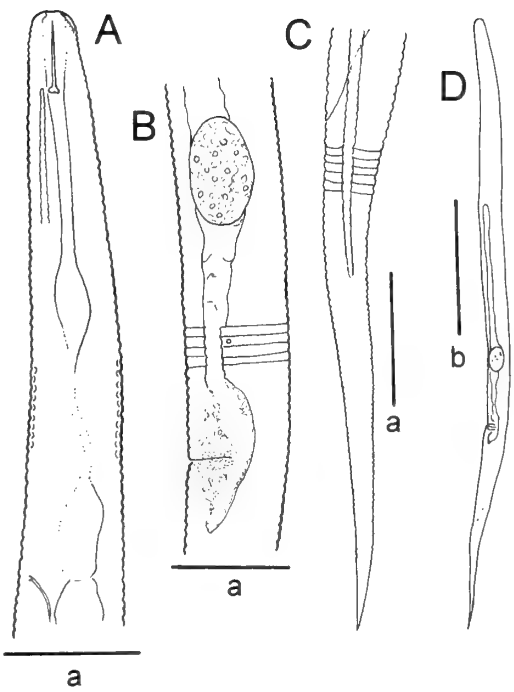

Fig. 17 *Malenchus pressulus* (Kazachenko, 1975). A–D, female. A, oesophageal region; B, posterior end of reproductive system; C, tail; D, habitus. Scale bars a = 20µm, b = 100 µm.

REMARKS. This single female largely agrees with the redescription of *M. pressulus* by Andrássy (1981) minor differences in ratios c, c´ and tail/V–a are not considered to be of specific importance.

Miculenchus salvus Andrássy, 1959

MATERIAL EXAMINED. Fort August Bay: 91, 92, 98 m; cores 2, 4, 5, 3 ♀♀, 1 ♂. Deep South Basin: 197 m; core 12, 2 ♀♀. Foyers Plateau: 157–160 m; cores 14–16, 18, 6 ♀♀, 1 ♂.

REMARKS. These specimens were described and figured by Wanless & David (1997).

Tylenchus rex Andrássy, 1979

(Figs 18, 36D)

MATERIAL EXAMINED. Deep South Basin: 194 m; core 13, 1 ♂.

MALE. (n = 1). L = 974 µm; a = 36.3; b = 6.3; c = 6.1; c´ = 9.0; gubernaculum = 5.9 µm; spicules = 24 µm; tail = 160 µm.

Head 8.5 µm at base with 4–5 annules. Amphid opening a gently curved slit. Annules distinct about 2.1 µm at mid-body. Lateral field with four lines, outers weakly crenate. Spear robust, 20.5 µm long, with large basal knobs 3.5 µm wide. Excretory pore 130 µm from anterior. Oesophagus 154 µm long; median bulb ovoid, valves distinct at 47.5% of oesophageal length. Testis 262 µm long occupying 27% of body length. Bursa adanal about 38 µm long with crenated margins. Anterior margin of cloacal lips with two spicate projections (arrowed, fig.36D). Tail tip rounded.

DISTRIBUTION AND HABITAT. The type population was found in moss, Ben Hedi, Scotland. Also known from Poland and Australia.

REMARKS. This specimen largely agrees with the original description except that the basal bulb is more or less elongate rather than pyriform; the outer lateral lines of the lateral field are weakly crenate

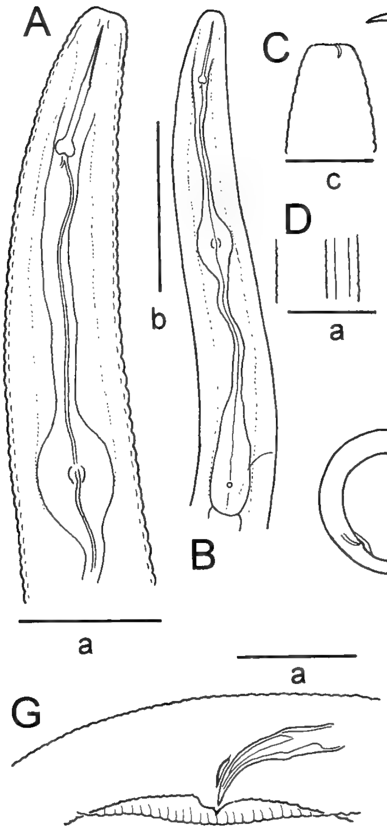

Fig. 18 *Tylenchus rex* Andrássy, 1979. A–F, male. A, anterior region; B, oesophageal region; C, head region showing amphid; D, lateral field; E, tail and spicular region; G, spicular region. Scale bars a = 20 μm, b = 50 μm, c = 10 μm, d = 100 μm.

rather than smooth; the tail is longer (160 μm *vs* 130–140 μm); ratio c is lower (6.1 *vs* 6.3–6.6) whereas c´ is slightly higher (9.0 *vs* 7–8). However, these ratios and tail length fall within the range of measurements given for *T. rex* by Brzeski (1996).

Tylenchinae sp.

(Figs 19, 36C)

MATERIAL EXAMINED. Foyers Plateau: 159 m; core 14; 1♀. River Foyers: 0.39 m; core 42, 1♀.

HORIZON. Core 14, (1–2 cm).

FEMALES. (n = 2). L = 468, 520 μm; a = 43.3, 40.6; b = 4.5, 4.7; c = 4.7, 5.0; c´ = 12, 12.5; V = 65, 62; V´ = 80; tail/V–a = 74.8, 94; tail = 99.2, 104 μm.

Head not set off, about 6.6 μm wide at base. Amphid apertures not seen. Annules fine about 0.8 μm at mid-body. Lateral fields narrow with two lines. Spear moderately robust, 11.5 μm long with rounded basal knobs 2.5 μm wide; shaft slightly longer than conus. Oesophagus 103, 110 μm long; median bulb ovate, valve at about 45% of oesophageal length. Excretory pore 71.4, 78.7 μm from anterior. Anterior genital branch 115, 109 μm long. Spermatheca empty. Postuterine sac not seen, possibly collapsed. Vagina about 6.0 μm long, slightly inclined or curved anteriorly. Tail elongate, not filiform; tip rounded.

REMARKS. The generic position of these nematodes is uncertain. They are placed in Tylenchinae because they are close to *Tylenchus* Bastian, 1865 in which the anterior conus and posterior shaft of the spear are about equal in length. However, the presence of two lines in the lateral fields is not compatible with the generic definition of *Tylenchus*, which is characterized by the presence of four lines Additional material and SEM studies are required in order to resolve the status of these interesting nematodes.

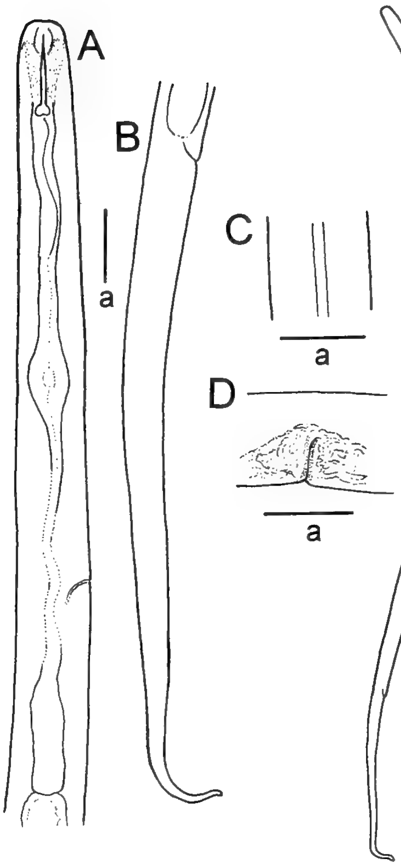

Fig. 19 Tylenchinae sp. A–E, female. A, oesophageal region; B, tail; C, lateral field; D, vulval region; E, habitus. Scale bars a = 10 μm, b = 100 μm.

Ditylenchus sp.

(Fig. 20)

MATERIAL EXAMINED. River Foyers; 0.39 m; core 44, 1♂.

MALE. (n = 1). L = 754 μm; a = 58.9; b = 5.7; c = 7.4; c´ = 9.5; spicule = 16 μm; gubernaculum = 5.2 μm; tail = 102 μm.

Head 4.2 μm wide, annuli not seen. Cephalic framework weak. Lateral fields with five lines at mid-body, apparently four lines on anterior and posterior regions, but for the most part difficult to observe. Body annuli fine, less than 1.0 μm wide. Spear delicate, 7.6 μm long; cone shorter than shaft; knobs rounded about 2.0 μm wide. Excretory pore 91 μm from anterior. Oesophagus 131 μm long; median bulb oval with distinct valve at 39.6% of oesophageal length; basal bulb and isthmus indistinct. Caudal alae about 30.7 μm long, 30% of tail length. Tail terminus finely rounded.

REMARKS. *Ditylenchus* species are rather uniform and do not show many characters helpful for identification (Brzeski, 1991b). This single male cannot be named with any confidence and additional specimens, particularly females, are required for proper identification.

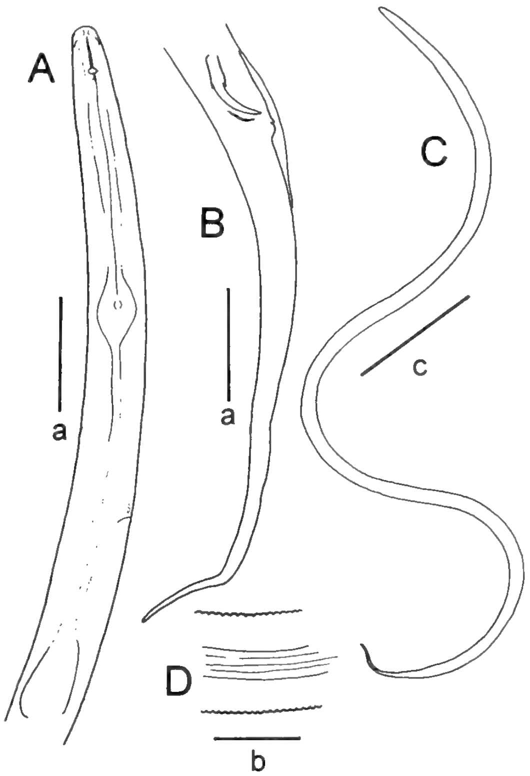

Fig. 20 *Ditylenchus* sp. A–D, male. A, oesophageal region; B, spicular region; C, habitus; D, lateral field. Scale bars a = 20 μm, b = 10 μm, c = 100 μm.

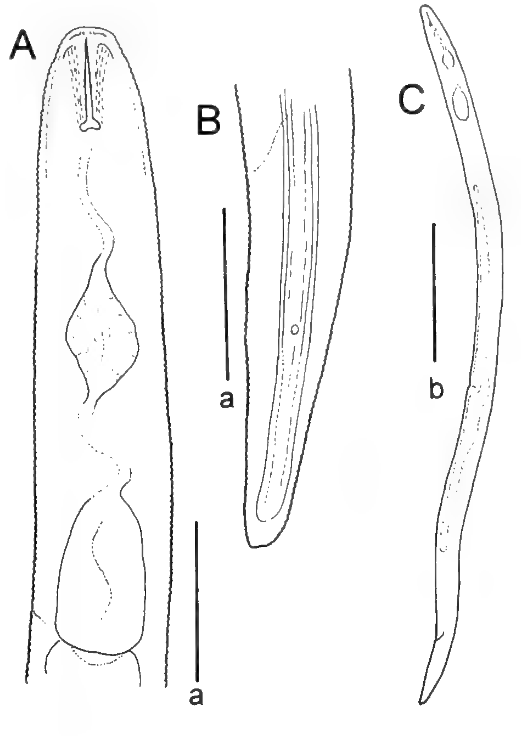

Fig. 21 *Geocenamus* cf. *nanus* (Allen, 1955). A–C, female. A, oesophageal region; B, tail; C, habitus. Scale bars a = 20 μm, b = 100 μm.

Geocenamus cf. ***nanus*** (Allen, 1955) Brzeski, 1991

(Fig. 21)

MATERIAL EXAMINED. River Oich: 0.31 m; core 31, 1 ♀.

FEMALE. (n = 1). L = 510 μm; a = 26.5; b = 6.3; c = 11; c´ = 3.5; V = 54; tail/ V–a = 0.24; tail annules 54; tail = 44.8 μm.

Head slightly narrower than adjacent body with 5 or 6 fine annules; labial frame work weak. Spear 12 μm long with backward-sloping knobs, 2.5 μm wide. Cuticle annules fine and moderately distinct, about 0.9 μm wide at mid-body. Lateral fields with 6 lines at mid-body, inner lines faint and not always evident throughout the entire length of the lateral fields. Deirid at level of excretory pore. Excretory pore 77 μm from anterior. Oesophagus (possibly contracted) 80 μm long; median bulb ovoid, valve weak at 49.5% of oesophageal length. Vulva and vaginal structures poorly defined. Genital branches stretched out; anterior and posterior branches do not extend into the oesophageal or anal regions respectively. Phasmids at 40% of tail length. Tail annules continue almost to terminus.

DISTRIBUTION AND HABITAT. Originally described from the Netherlands with further records from Iran, Turkey, Belgium, and Poland. Terrestrial, in soils around roots of various plants (Saltukoglu *et al.,* 1976); also in meadow and peat soils (Brzeski, 1991a).

REMARKS. Provisionally identified as *G. nanus* on account of the number of tail annuli and the value of ratio c´. Other very similar species have fewer tail annules and ratio c´ is generally lower, but observed values overlap. For a discussion on relationships between *G. nanus* (Allen, 1955), *G. alboranensis* (Tobar Jimenéz, 1970) and *G. microdorus* (Geraert, 1966) see Brzeski (1991a).

Tylenchorhynchus sp.

MATERIAL EXAMINED. Fort Augustus Bay: 105 m; Core 7, 1 juvenile. Foyers Plateau: 157 μm; core 16, 1 juvenile.

Helicotylenchus pseudorobustus (Steiner, 1914) Golden, 1956

(Fig. 22)

MATERIAL EXAMINED. Fort Augustus Bay: 91 m; core 2, 1 ♀. River Oich: 0.33 m; core 35, 1 ♀.

FEMALES. (n = 2). L = 800, 830 μm; a = 26.6, 34; b = 6.8, 6.9; b´ = 5.0, 5.1; c = 43.2, 37; c´ = 1.3, 1.4; V = 60, 62; tail = 18.5, 22.4 μm.

Head hemispherical 6.4, 7.0 μm wide with 4–5 annules. Spear 27.5, 26.8 μm long, with distinct knobs about 6.0 μm wide. Cuticle annules about 1.6 μm wide at mid-body. Lateral field with 4 lines, outers weakly crenate. Dorsal oesophageal gland opening 9.6, 10.0 μm behind spear knobs. Excretory pore 110 μm from anterior. Oesophagus 160, 162 μm long. Spermathecae offset without sperm. Phasmid 6–8 annules before anus. Tail with 12 ventral annules, dorsally convex and terminating in a long projection that has a fine irregular outline.

DISTRIBUTION AND HABITAT. Cosmopolitain; found in soils and also fresh water.

REMARKS. These females are in close agreement with descriptions of *H. pseudorobustus* by Sher (1966) and Siddiqi (1972).

Meloidogyne ardenensis Santos, 1968

(Fig. 23)

MATERIAL EXAMINED. Borlum Bay (1992 collection): 0.18 m; core 4, second-stage juvenile.

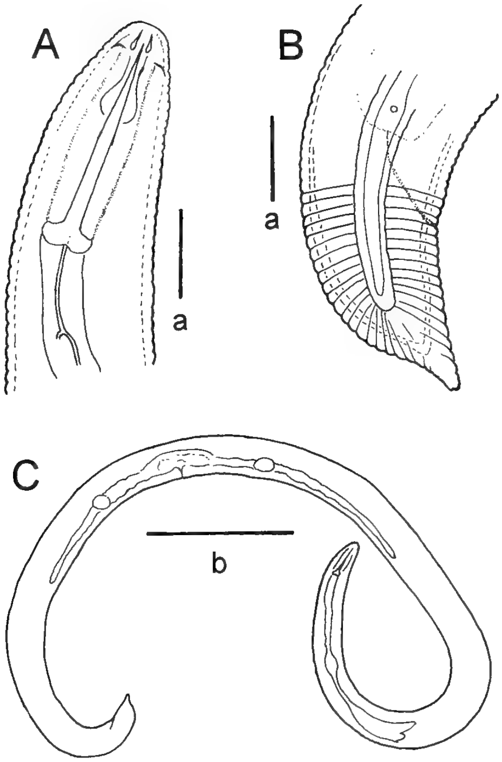

Fig. 22 *Helicotylenchus pseudorobustus* (Steiner, 1914). A–C, female. A, anterior region; B, tail; C, habitus. Scale bars a = 10 µm, b = 100 µm.

SECOND-STAGE JUVENILE. (n = 1). L = 403 µm; a = 26.8; b = 6.1; c = 9.8; c´ = 4.0; tail 40.9 µm..

Head not offset from body with two faint post labial annules. Cuticular annulation distinct but fine, about 0.9 µm at mid-body. Lateral field with four lines, the outer ones finely crenate and giving the impression of two vague additional lines in the post oesophageal region. Spear slender, 11.5 µm long with small backward-sloping knobs. Dorsal gland opening 2.5 µm behind spear knobs. Length of oesophagus (from anterior to base of median bulb) 65.3 µm; median bulb ovoid. Excretory pore 75.8 µm from anterior. Hemizonid not seen. Tail with rounded tip; phasmid not seen; Length of hyaline tail terminus 12.1 µm.

DISTRIBUTION AND HABITAT. Reported from Belgium, France, Germany, Poland, Russia and the United Kingdom (Karssen & Van Hoenselaar, 1998). Infective, migratory second-stage juveniles have been found in a wide variety of soils including dunes; adults are commonly associated with roots of vegetable and herbaceous crops (Jepson, 1987).

REMARKS. Although the hemizonid and phasmids could not be seen, this second-stage juvenile is otherwise in close agreement with descriptions of *M. ardenensis.*

Meloidogyne kralli Jepson, 1983

(Fig. 24)

MATERIAL EXAMINED. Foyers Plateau: 159 m; core 14, second-stage juvenile.

SECOND-STAGE JUVENILE. (n = 1). L = 435 µm; a = 31.7; b = 7; c = 6.7; c´ = 6.8; tail 64.6 µm.

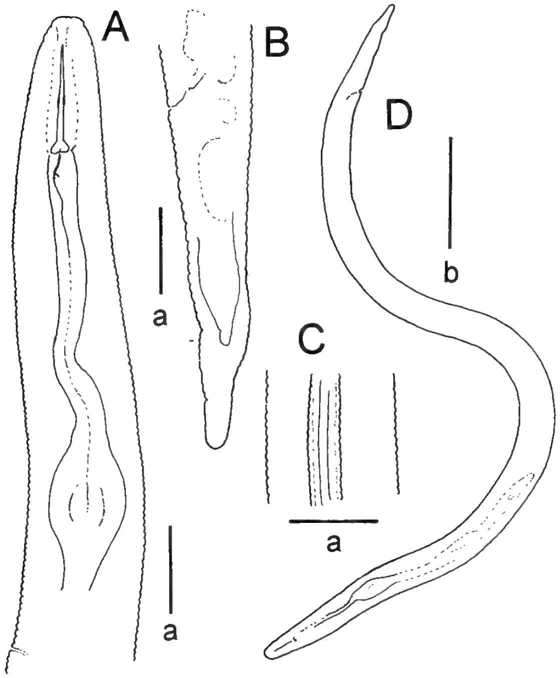

Fig. 23 *Meloidogyne ardenensis* Santos, 1968. A–D, second stage juvenile. A, anterior region; B, tail; C, lateral field; D, habitus. Scale bars a = 10 µm, b = 50 µm.

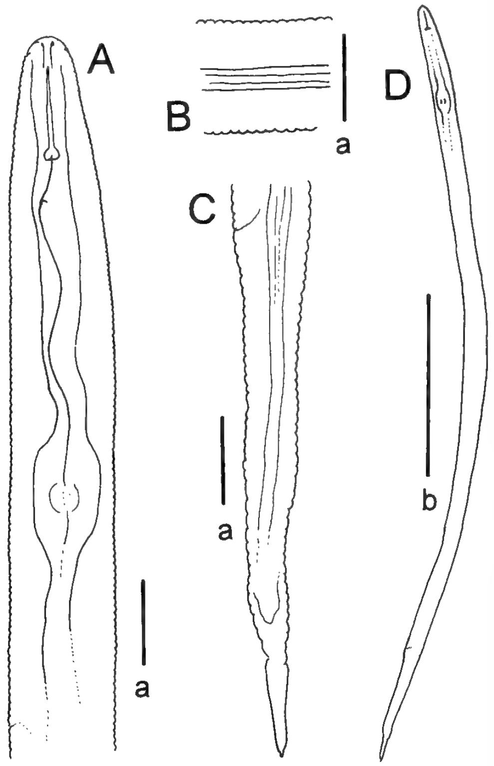

Fig. 24 *Meloidogyne kralli* Jepson, 1983. A–D, second stage juvenile. A, anterior region; B, lateral field; C, tail; D, habitus. Scale bars a = 10 µm, b = 100 µm.

Head not offset from body, with labial cap and one postlabial annule. Cuticular annulation distinct but fine, about 0.9 µm wide at mid-body. Lateral fields with four lines. Spear slender, 11.5 µm long with small backward-sloping knobs. Dorsal gland opens 5.0 µm behind spear knobs. Length of oesophagus (from anterior to median bulb) 61.4 µm; median bulb more or less ovoid; excretory pore 81.2 µm from anterior. Hemizonid immediately anterior to excretory pore. Phasmid not seen. Tail terminus tapers sharply with a short terminal portion ending in a finely rounded tip. Length of hyaline tail terminus 16.5 µm.

DISTRIBUTION AND HABITAT. Recorded from Estonia, Russia, Poland and the United Kingdom, all in wet sandy, peat and silt soils (Karssen & Van Hoenselaar, 1998).

REMARKS. The present second-stage juvenile agrees well with descriptions of the species.

Criconema annuliferum (de Man, 1921) Raski & Luc, 1984

(Fig. 25)

MATERIAL EXAMINED. Foyers Plateau: 160 m; core 15, 1 ♀.

FEMALE. (n = 1). L = 598 µm; a = 11.2; b = 3.9; c = 25; V = 88; R = 60; Rex = 20; Rvan = 5; Ran = 4; VL/VB = 1.4; tail = 22.4 µm.

Labial disc low. Head region offset, collar-like. Annule two slightly smaller and narrower than annule three, both distinctly smaller than annules one and four. Annules 10.8 µm wide at mid-body, outer edges smooth, rounded or slightly retrorse; interspaces sometimes filled with fine detritus. Spear straight, 101 µm long; knobs 11.5 µm wide, anterior surfaces indented. Vulva closed, anterior lip well developed, overlapping entire posterior lip. Ovary not reflexed, oocytes arranged in two rows. Spermatheca not observed. Anus inconspicuous. Tail terminus peg-like.

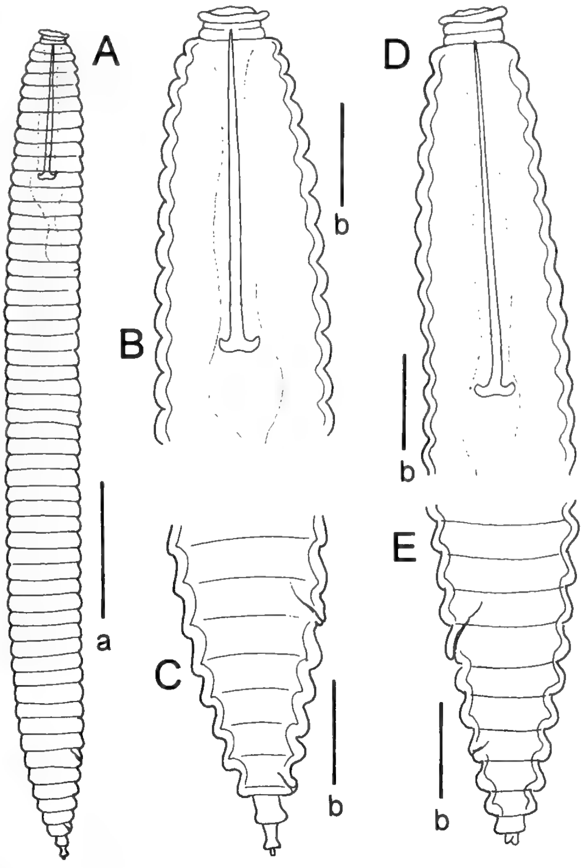

Fig. 25 *Criconema annuliferum* (de Man, 1921) A–C, female. A, habitus; B, anterior region; C, posterior region. *Criconema* sp. D, E, female. D, anterior region; E, posterior region. Scale bars a = 100 µm, b = 30 µm.

DISTRIBUTION AND HABITAT. Throughout Europe, associated with plant roots in both dry and wet soils.

REMARKS. This nematode agrees with descriptions and morphometrics presented for *C. annuliferum*.

Criconema sp.

(Fig. 25)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 3, 1 ♀.

FEMALE. (n = 1). L = 670 µm; a = 12.3; b = 4.1; c = 21.8; V = 90; R = 65; Rex = 21; Rvan = 3; Ran = 5; VL/VB = 1.5; tail = 30.7.µm.

Labial disc low. Head region offset, collar-like; annules two and three of equal size, distinctly smaller than annules one and four. Body annules 10.2 µm wide at mid-body, outer edges smooth, rounded or slightly retrorse; interspaces with fine scattering of detritus. Spear 120 µm long; shaft gently curved, conus straight; knobs 12.2 µm wide, anterior surfaces indented. Vulva closed, anterior lip well developed, overlapping entire posterior lip. Ovary poorly preserved; oocytes arranged in two rows. Spermatheca not evident. Anus conspicuous. Tail terminus bifurcate.

REMARKS. Similar to *C. annuliferum* and keys out to that species (de Grisse & Loof, 1965) but the spear is longer with a gently curved shaft, possibly an artefact; the tail terminus is bifurcate, also the 2nd and 3rd head annules are equal in size.

Criconema demani (Micoletzky, 1915) Raski & Luc, 1984

(Fig. 26)

MATERIAL EXAMINED. River Oich: 0.31, 0.18 m; cores 31, 33, 2 ♀ ♀.

FEMALES. (n = 2). L = 401, 417 µm; a = 8.3, 8.7; b = 3.8, 4.0; c = 10.6, 10; V = 84.5, 82.2; R = 73, 71; Rex (n = 1) = 20; Rvan = 5; Ran = 9; VL/VB = 1.7; tail = 37.7, 42.2 µm.

Labial disc low. Head region offset with second annule broader than first. Annules 5.8, 6.4 µm wide at mid-body; outer edges smooth, rounded or moderately retrorse; with fine, scattered, foreign detritus but nevertheless margins apparently minutely crenate. Spear 70.4, 71.6 µm long; knobs 8.3, 8.6 µm wide, anterior surfaces indented. Vulva closed; anterior lip well developed, overlapping entire posterior lip. Ovary reflexed distally. Spermatheca poorly preserved, without sperms. Anus inconspicuous. Tail with terminus straight or curved dorsally.

DISTRIBUTION AND HABITAT. Belgium, Denmark, Netherlands and North America. Terrestrial, in moist soils and alongside riverbanks, ditches and lake margins.

REMARKS. Keys out to *C. demani* and generally fits in well with descriptions of the species (Taylor, 1936), (Bongers, 1988), (de Grisse & Loof, 1965); except that ratio a is slightly lower, as is V in one specimen. Differences between the tail termini are not considered in this instance to be of specific importance.

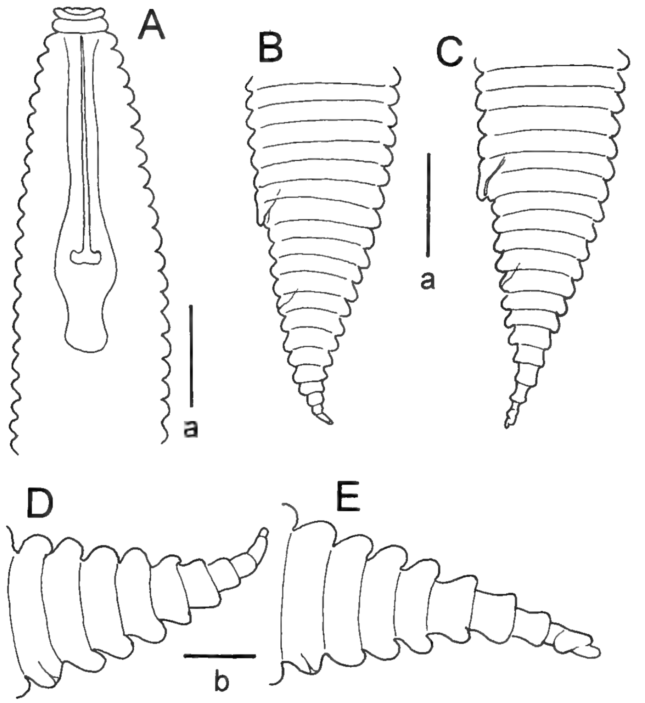

Fig. 26 *Criconema demani* (Micoletzky, 1915). A, B, D, female 1. A, anterior region; B, posterior region; D, tail. C, E, female 2. C, posterior region; E, tail. Scale bars a = 30 µm, b = 10 µm.

Discocriconemella sp.

(Fig. 27)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 4, 1 ♀.

FEMALE. (n = 1). L = 257 µm; a = 6.2; b = 3.1; c = 18.2; V = 89; R = 98 (ventral side); Rex = 38; RV = 13; Ran = 8; VL/VB = 1.0; tail = 14.1 µm.

Labial annule discoid, offset from body. Body annules retrorse except fifth to twelfth which are anteriorly directed on ventral side; annules with anastomoses and finely crenate posterior edges; outline somewhat angular. Spear 54 µm long, knobs 7.4 µm wide with anterior surfaces indented. Oesophagus about 82 µm long. Vulva apparently closed. Anterior genital branch poorly preserved. Spermatheca filled with sperms. Tail terminus bluntly rounded.

REMARKS. This female closely agrees with the description of *D. limitanea* Luc, 1959 by Rashid *et al.,* (1987) but differs by having fewer anteriorly directed annules (5th to 12th in this female *vs* 4th to 23rd annules in their population). Possibly this is the first record of this tropical genus in Europe.

Hemicycliophora sp.

MATERIAL EXAMINED. Foyers Plateau: 159 m; core 14, 1 ♀.

REMARKS. Specimen in very poor condition and not worth describing.

Ogma sp.

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 3, 1 ♀. River Oich: 0.31 m; core 31, 1 ♀.

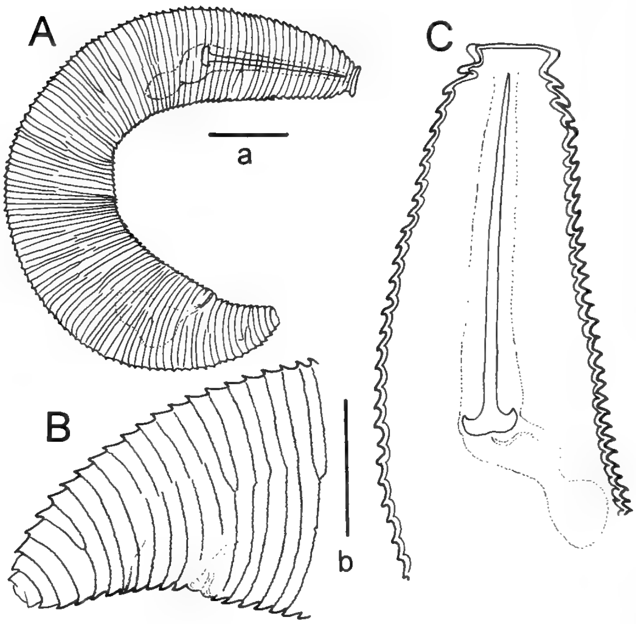

Fig. 27 *Discocriconemella* sp. A–C, female. A, habitus; B, posterior region; C, anterior region. Scale bars a = 30 µm, b = 20 µm.

REMARKS. Neither specimen is in good condition, the spear knobs are missing; the oesophagus and genital structures are poorly preserved.

Paratylenchus sp.

(Fig. 28)

MATERIAL EXAMINED. Fort Augustus Bay: 92 m; core 4, 1 ♀.

FEMALE. (n = 1). L = 318 µm; a = 23.7; b = 4.6; c = 9.3; c′ = 4.1; V = 77; tail = 34.2 µm.

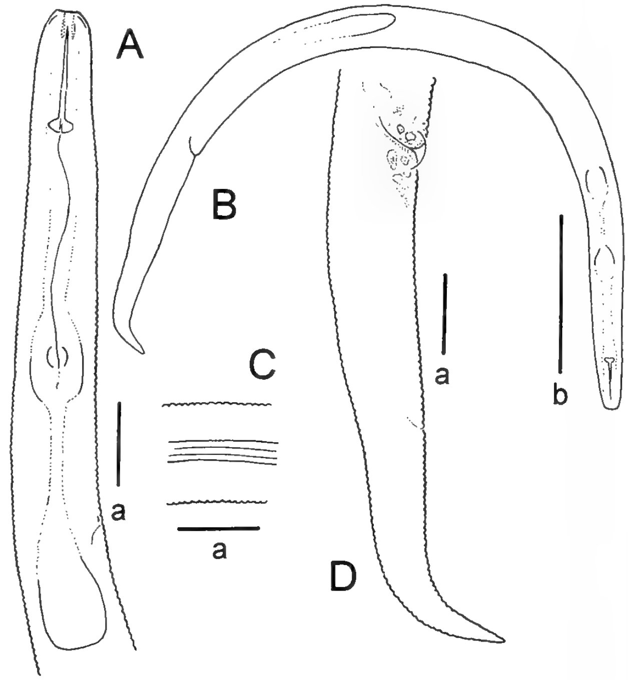

Fig. 28 *Paratylenchus* sp. A–D, female. A, oesophageal region; B, habitus; C, lateral field; D, tail. Scale bars a = 10 µm, b = 50 µm.

Head rounded with truncate anterior end, and minute protrusions at margins of lip region Annules 1.0 µm at mid-body. Lateral field with four lines. Spear 14 µm long with laterally directed knobs 3.2µm wide. Dorsal oesophageal opening about 5.0 µm behind spear knobs. Excretory pore 69 µm from anterior. Hemizonid just anterior to excretory pore. Oesophagus 84 µm long, poorly preserved. Vulva flaps prominent about 5.0 µm long. Vagina curved anteriorly. Anterior genital branch outstretched. Spermatheca not seen. Vulva-anus distance 36.5 µm. Tail tip finely rounded.

REMARKS. Using Raski's (1975) key to, *Paratylenchus* spp with a spear < 38 µm long, this female comes to either *P. italiensis* Raski, 1975 or *P. tateae* Wu and Townshend, 1973. Unfortunately these species are difficult to separate from one another because of overlap or continuous sequences in respect of their measurements. Head structures are also remarkably similar. The present female differs slightly in respect of ratios c, V and spear length, also the head is not offset. More specimens are required to assess variation and identify this female with any confidence.

Aphelenchoides sp. 1

(Fig. 29)

MATERIAL EXAMINED. River Oich: 0.31 m; core 31, 1 ♀. River Foyers: 0.22 m; core 40, 1 ♀.

HORIZON. Core 40, (1–2 cm); Core 31, (2–3 cm).

FEMALES. (n = 2). L = 387, 492 µm; a = 35, 33.4; b = 6.7, 8.2; c = 12.2, 13.9; c′ = 4.5, 4.0; V = 67.7, 69; tail = 31.5, 35.4 µm.

Head region smooth, slightly offset. Cuticle with fine striations about 0.9 µm wide. Lateral fields with four lateral lines, inner pair faint. Spear 10.2, 10.8 µm long with small basal thickenings. Procorpus of oesophagus narrow; median bulb ovoid, valve well developed, located posterior to middle of bulb. Excretory pore less than one body width posterior to median bulb. Vagina slightly inclined anteriorly. Ovary outstretched anteriorly 116, 152 µm long. Spermatheca not seen. Postvulval uterine sac apparently absent. Anus distinct, anterior lip slightly raised. Tail conical, terminating in a pointed ventral mucro.

REMARKS. Using Sanwal (1960) these females key out as *A. goeldi* Steiner, 1941 primarily because the postvulval uterine sac is absent. However, these females clearly differ from *A. goeldi* in both head and tail shape.

Aphelenchoides sp. 2

(Fig. 30)

MATERIAL EXAMINED. River Oich: 0.31 m; core 31, 1 ♀.

HORIZON. Core 31, (1–2 cm).

FEMALE. (n = 1). L = 470 µm; a = 33; b = 8.1; c = 16.2; c′ = 3.5; V = 72; tail = 29 µm.

Head region smooth, offset by constriction. Cuticle with fine annules about 0.9 µm wide. Lateral fields with four lines, inners very faint. Spear 10.2 µm long with small basal thickenings. Procorpus of oesophagus moderately wide; median bulb ovoid, valve well developed, located slightly posterior to middle of bulb. Excretory pore opening slightly anterior to base of median bulb. Vagina slightly tilted anteriorly. Anterior genital branch outstretched 204 µm long; spermatheca 177 µm long with disc-like sperms. Postvulval uterine sac 43.5 µm long without sperm. Anus moderately distinct.

REMARKS. Additional specimens are needed in order to identify this nematode with confidence. Morphometric measurements and the anterior position of the excretory pore suggests that it may be

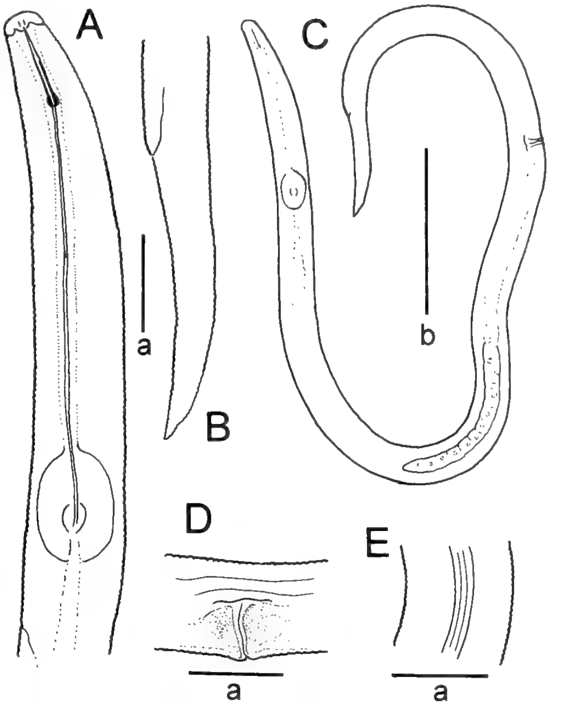

Fig. 29 *Aphelenchoides* sp. 1. A–E, female. A, anterior region; B, tail; C, habitus; D, vulval region; E, lateral field. Scale bars a = 10 µm, b = 50 µm.

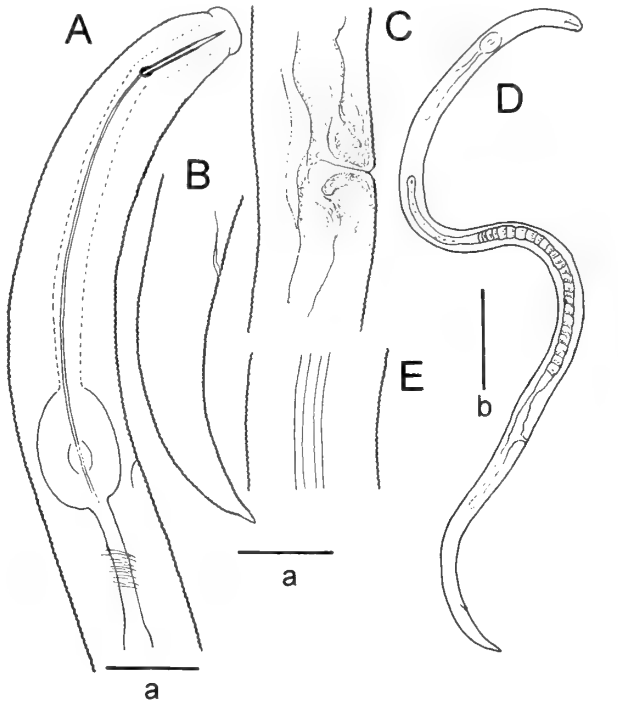

Fig. 30 *Aphelenchoides* sp. 2. A–E, female. A, anterior region; B, tail; C, vulval region; D, habitus; E, lateral field. Scale bars a = 10 µm, b = 50 µm.

close to *A. cyrtus* Paesler, 1957 originally described from mushroom-beds of the Champignonzuchtinstitut Dieskau near Halle, Germany.

Aphelenchoides sp. 3

(Fig. 31)

MATERIAL EXAMINED. River Foyers: 0.22 m; core 40, 1♀.

FEMALE. (n = 1). L = 813 µm; a = 52; b = 13.4; c = 17.3; c´ = 5.2; V = 68; tail = 50 µm

Head region smooth and slightly offset. Cuticle with fine striations about 0.9 µm wide. Lateral fields with four lines, the inner pair indistinct and fading away in some regions. Spear 10.8 µm long with pronounced basal thickenings. Procorpus of oesophagus hardly visible; median bulb more or less ovoid with well developed valve located slightly posterior to middle of bulb. Excretory pore about 1.5 body widths posterior to median bulb. Vagina directed anteriorly. Anterior genital branch outstretched, about 290 µm long. Spermatheca 58 µm long with globular sperms. Postvulval uterine sac 123 µm also with globular sperms. Anus distinct. Tail concoid with terminal mucro.

REMARKS. This female is very similar to *A. fragariae* (Ritzema Bos, 1890), but differs by having more robust basal spear thickenings; described as minute but distinct in *A. fragariae*, Siddiqi (1975).

cf. ***Caenorhabditis*** sp.

(Fig. 32)

MATERIAL EXAMINED. River Oich: 0.31 m; core 31, 1♀.

HORIZON. Core 31 (1–2 cm).

FEMALE. (n = 1). L = 625 µm; a = 30; b = 3.9; c = 5.9; c´ = 8.6; V = 50; tail = 105 µm.

Head not offset, 7.0 µm wide with minute labial papillae. Amphids not seen. Cuticle finely annulated; annules about 0.9µm wide at mid-body. Stoma 14.1 µm long; cheilostome distinct, lightly sclerotised, barely setoff from long prorhabdions; metastome with two small denticles. Oesophageal collar not observed. Oesophagus 159 µm long with swollen midbulb. Excretory pore not seen. Ovaries paired, anterior branch reflexed. Spermatheca filled with more or less rounded sperms about 2.2 µm.in diameter. Tail straight, tapering to fine tip. Phasmids inconspicuous.

REMARKS. Additional specimens, especially males, are required in order to properly identify this nematode.

Diplogasteritus nudicapitatus (Steiner, 1914)

(Figs 33, 36H)

MATERIAL EXAMINED. Borlum Bay (1992 collection): 0.38 m; core 4, 1♂.

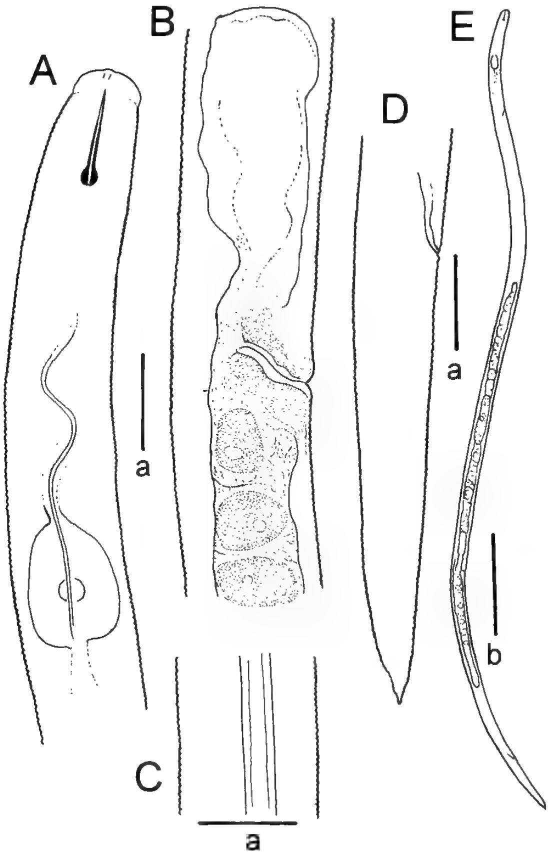

Fig. 31 *Aphelenchoides* sp. 3. A–E, female. A, anterior region; B, vulval region; C, lateral field; D, tail; E, habitus. Scale bars a = 10 µm, b = 100 µm.

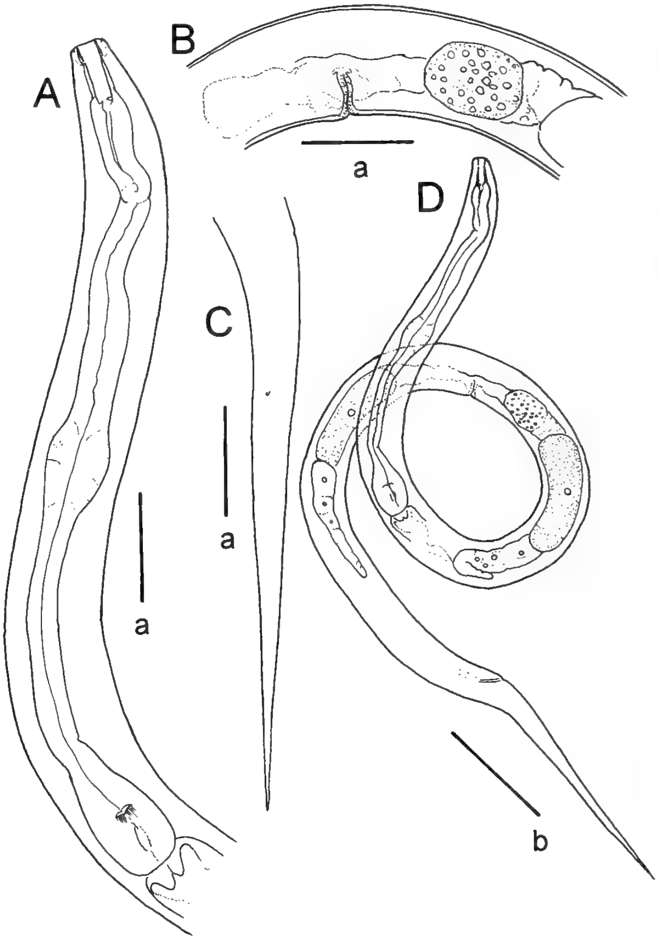

Fig. 32 cf. *Caenorhabditis* sp. A–D, female. A, oesophageal region; B, vulval region; C, tail; D, habitus. Scale bars a = 20 µm, b = 50 µm.

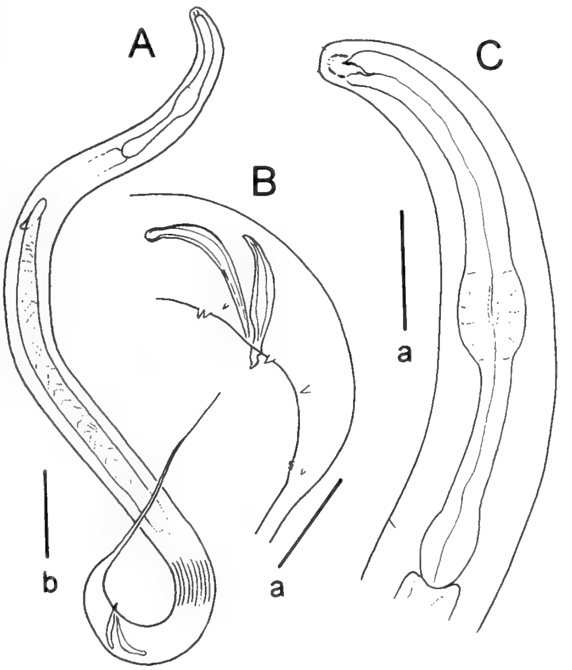

Fig. 33 *Diplogasteritus nudicapitatus* (Steiner, 1914). A–C, male. A, habitus; B, spicular region; C, oesophageal region. Scale bars a = 20 µm, b = 50 µm.

MALE. (N =1). L = 637 µm; a = 25; b = 6.3; c = 4.0; c´ = 8.5; gubernaculum = 25.6 µm; spicule = 33 µm; tail = 155 µm.

Head not offset; labial papillae minute. Amphids not seen. Cuticle with ca. 20 prominent longitudinal lines. Annules minute, less than 0.8µm wide. Oesophagus with large median bulb and smaller basal bulb; 105 µm long. Excretory pore 98µm from anterior, at mid-level of basal bulb. Testis anteriorly directed with reflexed tip. Spicula 1.8 times anal body width. Gubernaculum, distally with two pairs of mound-like swellings (arrowed, fig. 36H). Bursa absent. Nine pairs of caudal papillae; three pairs pre-anal and six post-anal.

DISTRIBUTION AND HABITAT. A common species found in Europe and South Africa in terrestrial and aquatic habitats.

REMARKS. Morphology and measurements closely agree with the descriptions of *D. nudicapitatus* provided by Bongers (1988) and Zullini (1982).

Eucephalobus oxyuroides (de Man, 1876) Steiner, 1936.

(Figs 34, 36E–G)

MATERIAL EXAMINED. Foyers Plateau: 161 m; core 19, 1 ♀. River Oich: 0.17 m; core 36, 1 ♀.

FEMALES. (n = 2). L = 558, 615 µm; a = 23.5, 19.6; b = 3.6, 3.9; c = 6.5, 7.7; c´ = 6.6, 4.8; V = 55.5, 61; tail 85, 79.3 um.

Cuticle 1.9 µm thick with annules 1.4, 2.1 µm wide at mid-body. Lips six, pointed. Lateral fields with three lines ending at level of phasmids. Stoma (n = 1) 14.7µm long, rhabdions distinct. Oesophagus cylindrical, 153, 157 µm long, basal bulb ovate. Excretory pore (n=1) 91 µm from anterior end at level of hemizonid. Reproductive system monodelphic, prodelphic. Reflexed at oviduct. Spermatheca and postuterine sac not seen. Vagina length about one half of vulval body width. Vulva not protruding. Rectum 23, 26 µm long or 1.8, 1.6 times anal body width. Tail 80–86µm long. Phasmid at 28, 32% of tail length.

Fig. 34 *Eucephalobus oxyuroides* (de Man, 1876). A, B, E, F, female 1. A, tail; B, anterior region; E, vulval region; F, habitus. C, D, female 2. C, habitus; D, tail. Scale bars a = 20 µm, b = 100 µm.

Fig. 35 *Eucephalobus* sp. A–D, female. A,oesophageal region; B, reproductive system; C, tail; D, habitus. Scale bars a = 20 µm, b = 50 µm.

DISTRIBUTION AND HABITAT. Cosmopolitan, prefers dry ground, but also mentioned from freshwater.

REMARKS. These specimens agree with descriptions of this species by Thorne (1937) and Rashid *et al.,* (1984). Note variation in length of the slender tail terminus and appearance of the lateral field at different focal levels.

Eucephalobus sp.

(Fig. 35)

MATERIAL EXAMINED. River Oich: 0.31 cm; core 31, 1♀.

FEMALE. (n = 1). L = 430 µm; a = 19.8; b = 3.5; c = 10.2; c′ = 3.4; V = 63. tail 42 µm.

Cuticle 1.2 µm thick. Annules 1.6 µm wide at mid-body. Lips six, pointed. Lateral field with three lines in region of oesophageal basal bulb, not evident elsewhere. Stoma 12.8 µm long, rhabdions indistinct. Oesophagus cylindrical, 122 µm long. Excretory pore 73.6 µm from anterior end, hemizonid not seen. Reproduction system monodelphic, prodelphic. Ovary with double flexure. Egg 38 µm long by 16 µm wide. Spermatheca not seen. Postuterine sac 9.6 µm long. Vulva protruding. Length of vagina about one quarter of vulval body width. Rectum 10.2 µm long, or 0.8 times anal body width. Tail terminus without distinct annules, broadly spear-shaped. Phasmid not evident.

REMARKS. The distinctive spear-like tail terminus of this female is not known to occur in other species of *Eucephalobus* and this specimen may represent a new taxon. It cannot however, be described until additional material becomes available for study.

ACKNOWLEDGEMENTS. This work was made possible by the financial support of The Natural History Museum, London and by sponsorship of the all-documentory television station The Discovery Channel under the auspices of Project Urquhart. Additional support was provided by Simrad, the electronics company which was the main sponsor of the hydrological survey of the loch. Special thanks are due to Mr Nicholas Witchell, the founder and Chairman of Project Urquhart. We also thank the crew of the research vessel Soel Mara who's skills contributed greatly to the success of the profundal coring programme. The late Professor M. W. Brzeski, Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland kindly read through early descriptions of these nematodes and his comments are greatly appreciated. Several of our colleagues also deserve many thanks; Nicola Mitchell gave invaluable help assisting with field and laboratory work; Dr T, J Ferrero produced the map of Loch Ness and 'sorted' many of the word processing problems encountered by the first author. Translation of various German and Dutch texts by Dr R. Huys is also gratefully acknowledged.

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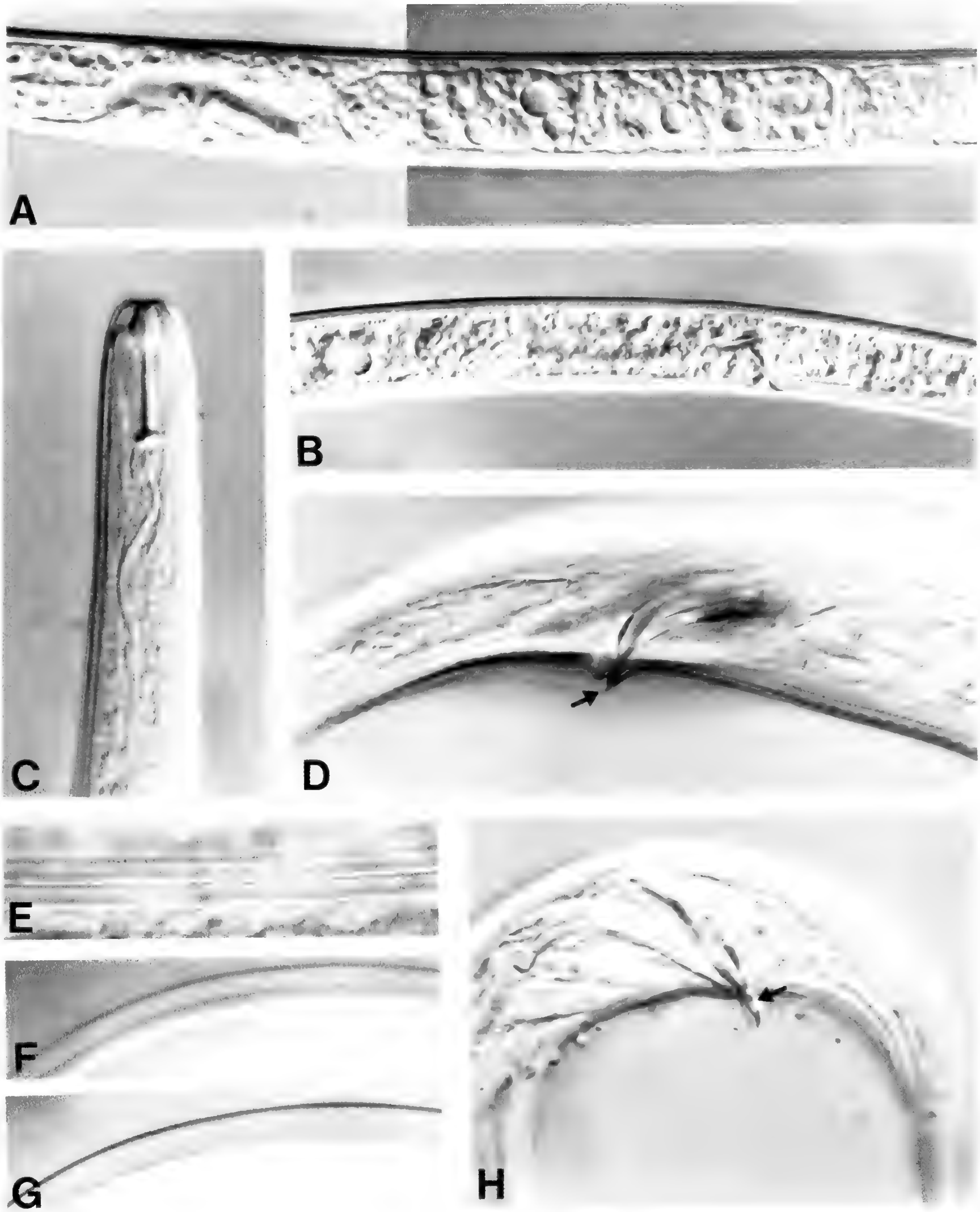

Fig. 36 A, *Lelenchus* sp. female, posterior region of reproductive system. B, *Lelenchus leptosoma* (de Man, 1880) female, posterior region of reproductive system. C, Tylenchinae sp. female, head region. D, *Tylenchus rex* Andrássy 1979 male, spicular region showing spicate projection, arrowed. E–G, *Eucephalobus oxyuroides* (de Man, 1876). E, female 1, lateral field showing three lines. F, G, female 2, lateral field showing variation in number of lines depending on fine focus using light microscopy. H. *Diplogasteritus nudicapitatus* (Steiner, 1914) male, spicular region showing mound–like swellings on gubernaculum, arrowed. Magnifications A, B, D, H ×1360. C, ×1900. E–G, ×1600.

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Bull. nat. Hist. Mus. Lond. (Zool.) **67**(1):25–84

Issued 28 June 2001

Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s.str.

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SYNOPSIS. Seven species of Oncaeidae (one of which is new to science) are described from the Red Sea, including a description of the hitherto unknown male of *Oncaea clevei* Früchtl. They all belong to *Oncaea sensu stricto* as defined in a phylogenetic study of oncaeid species by Böttger-Schnack and Huys in 1998. The genus is defined by a combination of characters including the absence of a conical process on the distal margin of the endopod of swimming leg 4, ornamentation of the labrum and mandibular blade and sexual dimorphism in antennary setae and in endopods of swimming legs. *Oncaea* s. str. includes two subgroups, the *venusta*-subgroup and the *clevei*-subgroup, females of which can be separated by the absence or presence of a dorso-posterior projection on the P2-bearing somite. Species of the *venusta*-subgroup in the Red Sea include *O. venusta* Philippi, *O. mediterranea* (Claus), *O. media* Giesbrecht, *O. scottodicarloi* Heron & Bradford-Grieve and *O. waldemari* Bersano & Boxshall; the *clevei*-subgroup consists of *O. clevei* Früchtl and *O. paraclevei* sp. nov. *Oncaea praeclara* Humes is a junior subjective synonym of *O. venusta*. *O. philippinensis* (Kazatchenko & Avdeev) as well as *Oncaea* sp. 1 and sp. 2 sensu Ferrari are regarded as *species inquirendae* in *Oncaea* s.str. The type species of the genus, *O. venusta*, has two form variants, forma *typica* and forma *venella* Farran, which can be distinguished by differences in size and in a few minor morphological characters. Their spatio-temporal distribution differs considerably in the Red Sea, which may indicate reproductive isolation. The world-wide records of *O. venusta* forms are reviewed and discussed.

CONTENTS

INTRODUCTION

Small copepod species of the family Oncaeidae are widely distributed in marine pelagic areas, extending from the epipelagic zone (e.g. Boxshall, 1977a; Dessier & Donguy, 1985; Cowles *et al.*, 1987) to the deep-sea (Wishner, 1979; Humes, 1988) and from tropical (Tsalkina, 1970; Deevey & Brooks, 1977) to polar regions (Hopkins, 1985; Richter, 1994; Metz, 1995). Due to their small size, oncaeid copepods are often neglected or under represented in marine plankton investigations, which are usually conducted with conventional nets of 0.3 or 0.5 mm mesh sizes. In recent years, increasing attention has been paid to the study of smaller mesozooplankton organisms sampled with fine mesh nets of 0.1 mm mesh size or less. In particular, small oncaeid copepods were sampled in high abundance by these nets (e.g. Böttger, 1982; Paffenhöfer, 1983; Schnack *et al.*, 1985; Cowles *et al.*, 1987; Böttger-Schnack, 1987) and subsequent research topics have focussed on their community structure and biology [see Böttger-Schnack (1999) for a review of the literature], thereby providing new insights into the largely unknown ecological importance of this copepod group.

Apart from ecological issues, the taxonomy of oncaeid species has been the subject of increasingly detailed studies over the past two decades (e.g. Boxshall, 1977b; Heron, 1977; Malt, 1982a, b, 1983a, b, c, d; Heron *et al.*, 1984; Kršinić & Malt, 1985; Boxshall & Böttger, 1987; Kršinić, 1988; Böttger-Schnack & Boxshall, 1990; Heron & Bradford-Grieve, 1995; Böttger-Schnack & Huys, 1997a, b, in press; Itoh [in: Chihara & Murano (1997)]). Despite these efforts, however, the taxonomy of many oncaeid species is still inadequate and particularly those species that are smaller than 0.5 mm have not been described in sufficient detail. Moreover, many oncaeid species are morphologically very similar, and thus can be distinguished only by a few characters, including microstructure of the mouthparts and on the exoskeleton, which require a level of detail not generally adopted in most taxonomic descriptions. Such integumental microstructures have been used to differentiate between closely related species of cyclopoid (Ueda *et al.*, 1996; Rocha, 1998) and oncaeid (Böttger-Schnack, 1999; Böttger-Schnack & Huys, in press) copepods.

The phylogenetic relationships of the Oncaeidae are not well understood. The diphyletic status of the family has recently been recognized by Huys & Böttger-Schnack (1996/97), who proposed the new family Lubbockiidae to accommodate *Lubbockia* Claus, 1862 and related genera, retaining only *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891 and *Epicalymma* Heron, 1977 in the Oncaeidae. The large type genus *Oncaea sensu lato*, which currently contains over 70 validly described species (Heron & Bradford-Grieve, 1995), has been recognized as a paraphyletic assemblage (Huys & Böttger-Schnack, 1996/97). A detailed phylogenetic analysis of the three oncaeid genera at the species level is currently in progress and will result in the recognition of numerous new genera. Some preliminary results of the phylogenetic study were briefly presented by Böttger-Schnack & Huys (1998).

The Red Sea is an extreme environment, with constant and unusually high deep-sea temperatures (21.7°C) and salinities (40.5 PSU) (Edwards, 1987). Due to these unique environmental conditions an impoverished zooplankton fauna is found in the Red Sea, which is characterized by the absence of true deep sea species (Weikert, 1982, 1987). This phenomenon was also reported for oncaeid copepods (Böttger-Schnack, 1994, 1999) and their estimated species number in the Red Sea (about 26) appears to be low in comparison to the adjacent Arabian Sea, where the vast majority of the about 70 recorded oncaeid species and forms is made up by deep-living representatives (Böttger-Schnack, 1994). The surface waters in the Red Sea show a considerable increase in salinity from the southern entrance to the central-northern areas (Morcos, 1970). Due to the less favourable environmental conditions in the north, species numbers of planktonic taxa generally decrease from south to north (e.g. Halim, 1969; Kimor, 1973; Almeida Prado-Por, 1983; Böttger-Schnack, 1995). For oncaeid copepods, however, a corresponding regional decrease in species number from south to north is less pronounced (Böttger-Schnack, 1995). This unexpected result was assumed to be at least partly attributable to the taxonomic difficulties encountered in the identification of oncaeids, since the proportion of unidentified form variants recorded in the south was much higher than in the north. In a subsequent taxonomic study five new species of oncaeids were described, four of which occurred mainly or exclusively in the southern area (Böttger-Schnack, 1999), thereby indicating some latitudinal difference in species numbers for this copepod group.

The ecology of oncaeid copepods in the Red Sea has been investigated intensively during the past years within the framework of multidisciplinary environmental research programmes (Thiel *et al.*, 1986; Weikert, 1988). The species diversity, vertical distribution and diurnal vertical migration, as well as some biological parameters, such as variation in body length and breeding activity or feeding of oncaeid copepods were studied on the basis of routine sampling with fine nets of 0.1 mm or 0.05 mm mesh size in the upper 500 m or 1000 m of the water column during different seasons and in various regions [see Böttger-Schnack (1999) for a review of the literature]. The taxonomy of Red Sea Oncaeidae is less well known, however. Boxshall & Böttger (1987) and Böttger-Schnack & Boxshall (1990) described four new oncaeid species from the central Red Sea, and provided a redescription of *Oncaea atlantica* Shmeleva. More recently, *O. mediterranea* (Claus) was redescribed from this area, including a thorough review of the taxonomic history of this allegedly cosmopolitan species (Böttger-Schnack & Huys, 1997). In a recent taxonomic study, 11 species of Oncaeidae were described or redescribed from the Red Sea, which belong to the *conifera/similis*-group as defined in the phylogenetic study of Böttger-Schnack & Huys (1998). A new genus, *Triconia*, was proposed to accommodate all oncaeid species belonging to this group (Böttger-Schnack, 1999).

As part of an ongoing taxonomic study of Red Sea Oncaeidae, the present paper describes seven species, which belong to the *venusta*-group as defined by Böttger-Schnack & Huys (1998). In their cladogram of oncaeid species it is equivalent to species group 2. This core-group includes *Oncaea venusta* Philippi, the type species of the genus, and is considered here as *Oncaea sensu stricto*. *Oncaea* s.str. is defined by a combination of characters including the absence of a conical projection on the distal margin of P4 endopod, ornamentation of the labrum and of the dorsal blade of the mandible, sexual dimorphism in the antenna and in the endopods of the swimming legs. *Oncaea* s. str. is considered as the sister-group of *Triconia* Böttger-Schnack, 1999, and the establishment of the revised genus is briefly substantiated in the present paper. A detailed discussion of phylogenetic relationships of *Oncaea* s.str. within the Oncaeidae will be published separately (Huys & Böttger-Schnack, in prep.).

Oncaea s.str. currently includes 8 species, 6 of which had previously been reported from the Red Sea (Böttger-Schnack, 1994) and are redescribed in the present account. For *O. mediterranea*, redescribed recently by Böttger-Schnack & Huys (1997b), some short corrective notes will be given. A new species similar to *O. clevei* Früchtl will be described. The taxonomic status of *O. curta* Sars, for which no material was available, will be discussed on the basis of literature data.

The type species of *Oncaea* s.str., *O. venusta*, was recently redescribed in detail by Heron & Bradford-Grieve (1995), based on specimens collected in the Gulf of Naples, near the type locality in the Mediterranean Sea. Their account does not contain information about the two size variants of the species, forma *typica* and forma *venella* (Farran, 1929), which are generally known to occur in tropical and temperate areas (Malt, 1983b), but are poorly documented morphologically. Apart from a distinct size difference, only few minor differences in body morphology have been reported for the two forms so far (Farran, 1929; Sewell, 1947; Ferrari, 1975; Boxshall, 1977a). In the Red Sea, both size variants of *O. venusta* occur. They differ considerably in spatio-temporal distribution (Böttger-Schnack, 1990b, 1995), which may indicate reproductive isolation. Both forms of *O. venusta* will be redescribed in detail in the present account, including observations with scanning electron microscope (SEM). Particular attention is paid to microstructures in the mouthparts and on the exoskeleton, which might provide new and helpful information for the separation of the two forms. The relationship of the two Red Sea forms with the species occurring in the Mediterranean Sea is defined upon re-examination of specimens from Heron & Bradford-Grieve's material. The present knowledge on the world-wide distribution of the two *venusta* forms is reviewed.

The two size variants of *O. media* as defined by Sewell (1947) have recently been recognized as distinct species by Heron & Bradford-Grieve (1995). They assigned forma *major* to *O. media* Giesbrecht (except for his Plate 47, Fig. 11), and described forma *minor* as a new species, *O. scottodicarloi*. Both species occur in the Red Sea and are briefly redescribed in the present paper, including some important morphological details not noted by these authors. *O. waldemari*, which is very similar to *O. media* and *O. scottodicarloi*, had recently been described from Brazilian waters by Bersano & Boxshall (1994). Due to some descriptive errors, however, the authors did not notice the close relationship of *O. waldemari* with species of *Oncaea* s.str. and erroneously placed it in a group containing *O. petila* Heron, *O. ovalis* Shmeleva and others. In the present account, *O. waldemari* is completely redescribed based on Red Sea specimens (figures) and the type material from Brazilian waters, with additional comparisons on specimens from different localities in the Atlantic and Pacific Ocean.

MATERIAL AND METHODS

Oncaeids were collected using a multiple opening-closing net with a mesh size of 0.05 mm during cruise 5/5 of R/V *Meteor* (Weikert, 1988) in various locations of the Red Sea (Fig. 1). Samples collected during cruise 29 of R/V *Valdivia* with the same sampling gear, but equipped with nets of 0.1 mm mesh, were also examined. A station list and sampling data are given in Table I. The plankton was initially fixed in a 4% formaldehyde-seawater solution buffered with hexamethylene tetramine and transferred after ca 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976). Specimens were dissected in lactic acid, mounted on slides in lactophenol and sealed with transparent nail-varnish. All figures have been prepared using a camera lucida on a Leitz Dialux differential interference contrast microscope.

Total body length and the ratio of prosome to urosome (excluding caudal rami) were calculated as the sum of the middorsal lengths of individual somites measured in lateral view. In the case of telescoping somites these lengths are measured from the anterior to the

Table 1 Sampling data of multiple opening-closing net in the Red Sea and adjacent areas (D = Day, N = Night).

Stn. No.	Date	Time	Total water depth (m)	Mesh size (mm)	Geographic position (°N, °E)
Red Sea + Gulf of Aden					
R/V Valdivia Cruise 29					
130	28.10.1980	D	1960	0.1	21°25.5', 38°01.9'
664	21. 2.1981	D	2000	0.1	21°22.1', 38°05.1'
R/V Meteor Cruise 5/5					
631a	11.7.1987	N	1400	0.05	11°55.5', 43°37.9'
663	20.7.1987	D	1200	0.05	22°58.4', 37°19.4'
703	3.8.1987	D	970	0.05	15°34.8', 41°54.9'
708	5.8.1987	D	190	0.05	13°40.0', 42°37.4'
Northern Arabian Sea					
R/V Meteor Cruise 32/3					
247	14. 5.1995	D	3000	0.05	ca 19°, ca 65°
Eastern Mediterranean Sea					
R/V Meteor Cruise 5/1					
35	20. 1.1987	N	3400	0.05	34°25.3', 26°14.8'

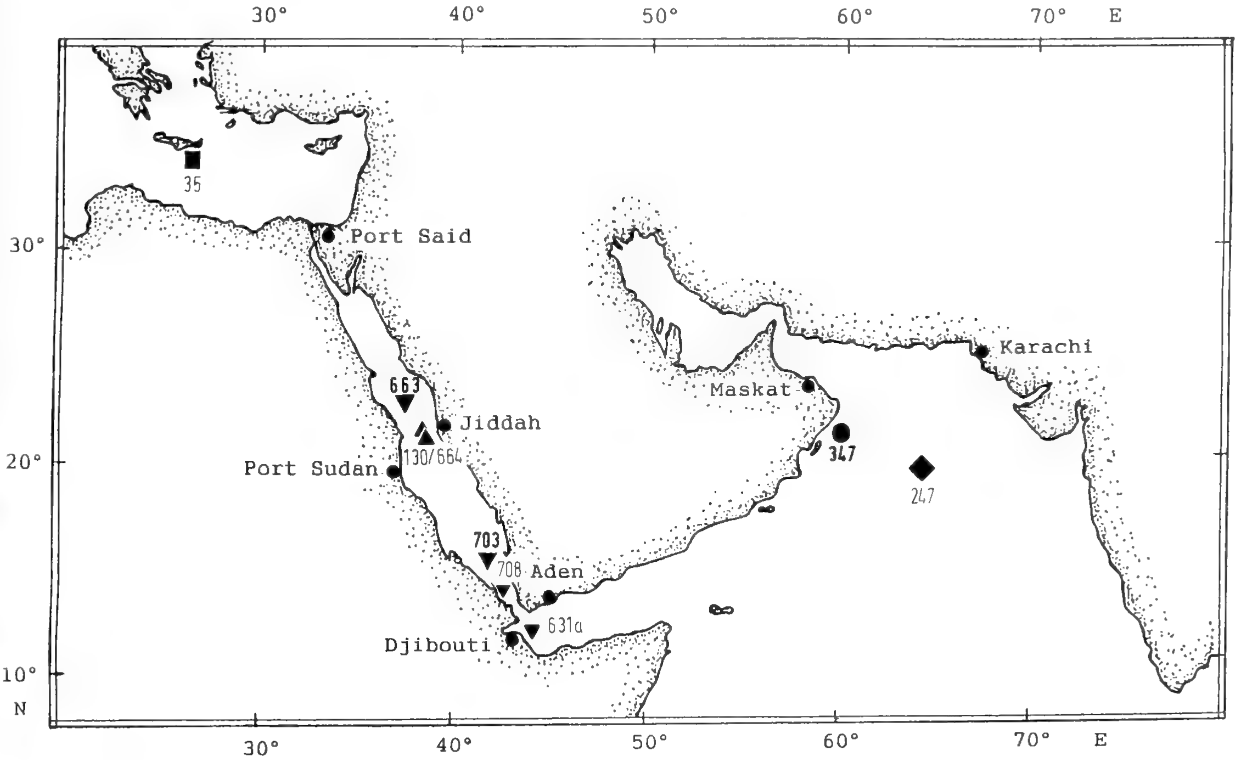

Fig. 1 Location of stations in the Red Sea and adjacent areas. ▲ = *Valdivia*-Cruise 29, October 1980, February 1981; ■ = *Meteor*-Cruise 5/1, January 1987; ● = *Meteor*-Cruise 5/3a, April 1987; ▼ = *Meteor*-Cruise 5/5, July/August 1987; ◆ = *Meteor*-Cruise 32/3, May 1995.

posterior margin. This approach differs from that traditionally used in oncaeid taxonomy, where the telescoping of somites is not considered in length measurements. Traditional length data of Red Sea oncaeids as given by Böttger-Schnack *et al.* (1989) are only up to 70% of the sizes presented in this paper, due to the excessive telescoping of somites in the sorting medium. In order to make sizes of the species in this paper comparable to those of previous taxonomic descriptions (e.g. Heron & Bradford-Grieve, 1995; Bersano & Boxshall, 1994), length data of each species were obtained by the traditional method as well (i.e. measured dorsally from the tip of prosome to the distal end of caudal ramus) and are given in square brackets.

Descriptive terminology for body and appendages follows that of Huys and Boxshall (1991). Abbreviations used in the text are: ae = aesthetasc; CR = caudal rami; enp = endopod; exp = exopod; exp(enp)-1(-2, -3) = to denote the proximal (middle, distal) segment of a ramus; P1–P4 = swimming legs 1–4. Species of Oncaeidae have a number of pores and other integumental structures (e.g. pits, scales) on body surfaces, but only those discernible with a light microscope were figured or mentioned.

O. venusta was examined with a Philips XL30 scanning electron miscroscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter-coated with palladium.

Type and other material is deposited in the collections of The Natural History Museum, London (BMNH), Smithsonian Institution (USNM) and the Zoologisches Institut und Museum der Universität Hamburg (ZMH). Paratypes or other material retained in personal collection, R. Böttger-Schnack designated (RBS).

GENERIC DIAGNOSIS

Order **POECILOSTOMATOIDA** Thorell, 1859
Family **ONCAEIDAE** Giesbrecht, 1892

Oncaea sensu stricto

DIAGNOSIS. *Body* cyclopiform, prosome stout or broad-oval. P2-bearing somite with (*clevei*-subgroup) or without (*venusta*-subgroup) dorsoposterior projection in female. Cephalosome without lateral lobate extensions. Genital double-somite female slightly flask-shaped, not particularly swollen dorsally. First and second postgenital somites shorter than anal one. Anal somite with wide anal opening; operculum with small spinules.

Exoskeleton well or heavily chitinized, usually ornamented with numerous pores, ridges and scales.

Sexual dimorphism in antennule segmentation and armature, antennary setae, maxilliped, genital segmentation and ornamentation, endopods of P1–P3 (sometimes also in P4), P5 and P6, and in caudal ramus.

Antennule 6-segmented in female with armature formula 1-[3], 2-[8], 3- [5], 4-[3 + ae], 5-[2 + ae], 6-[6 (1 +ae)]; 4-segmented in male with formula 1-[3], 2-[8], 3-[4], 4-[11 + (1 + ae) + 2ae]. Distalmost seta of female segment 3 absent in male. Aesthetascs slender.

Antenna. Enp-1 with triangular projection on outer margin forming concavity distally; inner margin with 1–2 denticular rows. Enp-2 shorter than enp-1; posterior surface with double row of spinules; lateral armature consisting of 3 well developed, bare or minutely pinnate setae (I, II and IV) and 1 pinnate spine (III) in female; distal armature consisting of 4 pinnate setae, 1 long bare or minutely pinnate seta, and 2 bare setae; posterior seta well developed. Sexual dimorphism in lateral armature of enp-2, with seta III much stouter and seta IV spiniform and curved in male, both elements shorter than in female; often also expressed in coxobasal seta, being short and naked in male.

Labrum distinctly bilobate, forming paired semi-circular posteroventral lobes. Lobes without marginal teeth but with row of minute denticles around outer ventral margin, with row of long fine setules latero-distally (except for *clevei*-subgroup) and dentiform processes converging and decreasing in size medially. Lobes separated by semicircular vertex covered anteriorly by overlapping rows of small hyaline petaloid flaps, flanked by slit-like pores located on proximal part of each lobe; posterior face with median sclerotized teeth and usually with paired patches of long fine setules (absent in *media*). Anterior face with paired spinular patches or denticulate rows (except for *venusta*); paired integumental pockets usually well developed, free margin of pockets serrated or ornamented with denticle row.

Mandible with 2 blades, 2 setae and 1 spine. Dorsal blade with 3 dentiform processes along distal margin and up to 2 additional processes along dorsal margin.

Maxillule weakly bilobate; praecoxal arthrite with innermost element proximally displaced and outermost element spiniform and bearing transverse row of spinules.

Maxilla. Allobasis shorter than syncoxa.

Maxilliped (female). Large, moderately ovoid. Basis without ornamentation on posterior surface; anterior surface with spinular row and spinular fringe along palmar margin half the distance between distal seta and endopod; both palmar elements long, spiniform and spinulose, similar in length. Enp-1 completely separated. Enp-2 with long, minutely pectinate claw, rudimentary outer setule and fused unipinnate inner spine.

Maxilliped (male). Palmar margin forming shallow longitudinal cleft bordered by anterior denticulate fringe and posterior multiple rows of coarse, blunt spinules; not developed into distal flap. Anterior surface of basis with patch of transverse spinular rows. Palmar setae short, smooth. Endopodal claw curved, naked, with hyaline apex.

P1 exopod. Outer and terminal spines with subapical tubular extensions.

P1 endopod. Enp-3 distal spine stout, with broad serrate hyaline flange; base of distal inner seta concealed beneath long anterior spinous outgrowth of segment; length of outgrowth (often) sexually dimorphic, relatively longer in the male.

P2–P4 exopods. Outer spines stout, with broad, serrate hyaline flanges; lateral spines not markedly increasing in size distally.

P2–P4 endopods 3-segmented. Enp-3 twice as long as enp-1 and -2 combined or longer; with large conical processes on P2–P3, not on P4. Enp-3 distal spine short in P2–P3, longer in P4; distal outer spine small in P2–P3, always longer than conical process in female. Sexual dimorphism usually expressed in length of conical processes, being longer in the male, and in spine length of enp-3, being reduced in the male.

Swimming leg armature formula:

Leg	Coxa	Basis	Exopod	Endopod
P1	0–0	1–I	I–0;I–1;III,I,4	0–1;0–1;I,5
P2	0–0	1–0	I–0;I–1;III,I,5	0–1;0–2;I,II,3
P3	0–0	1–0	I–0;I–1;II,I,5	0–1;0–2;I,II,2
P4	0–0	1–0	I–0;I–1;II,I,5	0–1;0-2;I,II,1

P5 small; represented by outer basal seta and small exopod with 2 spiniform setae; exopod delimited at base in females, fused to somite in males; sometimes additional sexual dimorphism in shape and length of exopodal setae. Genital apertures of female large; located near midregion of dorsal surface of genital double-somite but usually in proximal half; each operculum with small spine and 2 minute spinules or spinous processes.

Male P6 membranous flaps produced posterolaterally into spinous process; without armature.

Caudal ramus about 3–4 times as long as wide or shorter, without conspicuous dorsal expansion surrounding base of seta VII. Seta I absent; setae II and III unipinnate; setae IV and V not resilient, relatively rigid and bipinnate; seta VII plumose and distinctly shorter than V; seta VI spiniform and sparsely pinnate. None of setae displaced. Sexual dimorphism expressed in length to width ratio of CR, being smaller in male, and in proportional lengths of caudal setae.

TYPE SPECIES. *Oncaea venusta* Philippi, 1843 (by monotypy)

OTHER SPECIES

O. mediterranea (Claus, 1863)
O. media Giesbrecht, 1891
O. curta Sars, 1916 [not *O. curta* sensu Boxshall, 1977b]
**O. clevei* Früchtl, 1923
[*O. praeclara* Humes, 1988] syn. of *O. venusta*
O. waldemari Bersano & Boxshall, 1994
O. scottodicarloi Heron & Bradford-Grieve, 1995
**O. paraclevei* sp. nov.

SPECIES INQUIRENDAE

Oncaea sp. 1 Ferrari, 1975
Oncaea sp. 2 Ferrari, 1975
O. philippinensis (Kazatchenko & Avdeev, 1977)

[Species marked with an asterisk (*) belong to the *clevei*-subgroup, remaining species belong to *venusta*-subgroup.]

REMARKS

Within the Oncaeidae *Oncaea* s.str. belongs to a lineage comprising the *conifera/similis*-group (*Triconia* Böttger-Schnack, 1999), the *notopus*-group and the *brocha*-group (including *O. brocha* Heron and *O. olsoni* Heron). These four groups correspond with species groups 2, 3+4, 6 and 7 recognized by Böttger-Schnack & Huys (1998) and together are considered to form a monophyletic lineage on account of the structure of the labrum (median concavity with 4 posterior dentiform processes) and the male maxilliped (palmar margin with multiple overlapping rows of blunt spinules). *Oncaea* s.str. is considered here as the sistergroup of *Triconia* on the basis of the presence of integumental pockets on the anterior surface of the labrum and the formation of the dorsoposterior projection on the second pedigerous somite. The fact that the latter character is not expressed in all members of both genera is interpreted as the result of secondary loss which happended convergently in each genus. *Oncaea* s.str. differs from *Triconia* in the sexual dimorphism of the antenna (seta II and IV modified in the male), the presence of paired slit-like pores on the anterior surface of the labrum and the absence of a conical process on the distal endopod segment of P4. A more detailed discussion of the phylogenetic relationships of *Oncaea* s.str. within the Oncaeidae is beyond the scope of this paper and will be published separately (Huys & Böttger-Schnack, in prep.).

The revised genus includes two subgroups of species, the *venusta*-subgroup and the *clevei*-subgroup. Females of the *clevei*-subgroup are characterized by a dorso-posterior projection on the P2-bearing somite, which is lacking in the *venusta*-subgroup. The dorsal projection on the prosome ('hump') is a sexually dimorphic character, which is absent in males. Thus males of both subgroups are very hard to distinguish. A further morphological character separating the 2 subgroups is found in the ornamentation of the labrum, the row of long setules on the latero-distal margin of the lobes being absent in the *clevei*-subgroup.

Oncaea curta Sars, 1916 (p. 228, Plate IV, as *Oncæa curta*) was originally described from the western Mediterranean, near the Moroccoan coast. The species has also been widely recorded at low latitudes in the Atlantic and Pacific [as compiled by Malt (1983a) and Razouls (1996)]. Recently, Heron & Bradford-Grieve (1995, p.41) recorded the species from the Gulf of Naples, but at the same time noted in their samples several as yet undescribed species close to *O. media*, *O. scottodicarloi* and *O. curta* indicating that a complex of species close to *O. curta* exists within *Oncaea* s.str. Thus, a number of different species might have been recorded in the literature under the wrong name *curta* (e.g. Boxshall 1977b, see remarks below) and the geographical records of *O. curta* appear to be doubtful. Due to the identification problems, the species had erroneously been placed into the *bowmani*-group in the preliminary cladogram of Böttger-Schnack & Huys (1998). The species could not be re-examined during the present study, since no material was available. Therefore, Sars' description was taken as a basis to compare the morphology of *O. curta* with the closely related *O. media*, *O. scottodicarloi* and *O. waldemari* (see under *O. scottodicarloi*, Remarks). A thorough revision of *O. curta* is needed to clarify the taxonomic confusion surrounding this species.

Oncaea curta sensu Boxshall (1977b: p.141–143, Table 1–2, Fig. 21a–k) does not belong to *Oncaea* s. str. Malt (1983a) has already pointed out the similarity of the species with *O. illgi* Heron, which belongs to the *bowmani*-group as defined in the phylogenetic study of Böttger-Schnack & Huys (1998; their species group 5). Common characteristics of this group are very elongate conical processes on the distal endopod margins in P2–P3 and a very robust maxillipedal basis, armed with 2 relatively short setae. Boxshall (1977b) synonymized *O. curta* with *O. ovalis* Shmeleva, *O. longiseta* Shmeleva and *O. latimana* Gordeyeva, as well as with *Oncaea* sp. 1 and 2 of Ferrari (1975), but his opinion was not followed by Malt (1983a) nor in the present account.

Oncaea sp. 1 and sp. 2 described by Ferrari (1975; *Oncaea* sp. 1: p. 228, Figs. 6E, F, 7A–D; *Oncaea* sp.2: p.228, Figs. 6G, H, 7E–H) are placed in *Oncaea* s.str. on the basis of the swimming leg armature, the lack of a conical process on the distal margin of P4 endopod, and the size and position of the maxillipedal setae. Malt (1983a) tentatively assigned *Oncaea* sp. 1 to *O. media* Giesbrecht forma *minor* and *Oncaea* sp. 2 to both *O. curta* Sars and *O. venusta* Giesbrecht f. *venella*, reflecting the author's undecisiveness on this matter. Since the original description of both species lacks sufficient detail necessary for unequivocal identification, they are regarded here as *species inquirendae* in *Oncaea* s.str.

Myspictosum philippinensis Kazatchenko & Avdeev, 1977 (p. 44–47, Fig. 9a–i, 10a–g) has been synonymized with *Oncaea* s.l. by Malt (1982a; erroneously spelled *Myctospictosum* by Malt) and her opinion was followed by Huys & Böttger-Schnack (1996/97). The single male of *O. philippinensis* was found on the gills of the deep-sea fish *Myctophum spinosum* collected in the Philippine Trench at 7255 m, which is the deepest record of an oncaeid species so far. The unusually deep record has been regarded as accidental rather than real (Huys & Böttger-Schnack, 1996/97). *O. philippinensis* might well belong to *Oncaea* s.str., based on the modified seta IV on the antenna, which is hook-like as in most other species of the genus. However, the leg armature in Kazatchenko & Avdeev's description is incomplete in P2 (endopod missing) and very unusual in P1, the endopod showing 4 inner setae and 3 outer and distal spines, with a conical process at the distal margin. This combination of armature elements is not found in any oncaeid species known thus far and the species is regarded here as *species inquirenda* in *Oncaea* s.str.

Oncaea praeclara Humes is regarded as a synonym of *O. venusta*, on grounds that will be discussed below under *O. venusta*, Remarks.

DESCRIPTION OF SPECIES

Oncaea venusta Philippi, 1843

Oncaea venusta Philippi (1843): 62–63, Tafel III, Fig. 2a–d.

Oncäa venusta Giesbrecht, 1892
Oncœa venusta Farran, 1929
Oncaea praeclara Humes, 1988

RELIABLE DESCRIPTIONS. Giesbrecht (1892): 590–604, 755, 756, 774, 789, Plate 2, Fig. 5, Plate 3, Fig. 7, Plate 47, Fig. 2,5,13,19,39,44,48,50,54,58 [as *Oncäa venusta*]; Farran (1929): 284–285, Fig. 33 [as *Oncœa venusta*]; Wilson (1932): 353–354, Fig. 213a–d; Mori (1937, reprinted 1964): 119–120, Plate 66 Figs. 1–9; Dakin & Colefax (1940): 116, Fig. 205A a–f; Sewell (1947): 263–264; Olson [MS] (1949): 101–104, Plate XXIV Figs.1–8 (♀), Plate XXV Figs. 11–13 (♂); Tanaka (1960): 71–72; Corral Estrada (1970): 216–217; Chen *et al.* (1974): 40–41, Plate 6 Figs. 1–5; Ferrari (1975): 225–228, Figs. 5I–K, 6A–D; Boxshall (1977b): 124–128 Figs. 11a–k (♀), 12a–d (♂); Ho (1984): 41–44, Figs. 12–14; Humes (1988): 475–485, Figs. 1a,b,d [not Fig. 1c, e], 2a–i, 3a–g (♀), 4a–g (♂) [as *Oncaea praeclara*]; Huys & Boxshall (1991): 286,289,445 Figs. 2.10.8.B, 2.10.10.A, 2.10.21.B, 2.10.21.D, 2.10.24.A; Heron & Bradford-Grieve (1995): 33,36, Figs. 14e–l, 15a–j, 27b, 28; Itoh [in: Chihara & Murano 1997]: 981–982, Plate 223 Figs. 371(left) a–b (f. *venella*), 371(right) a–e (f. *typica*).

DOUBTFUL DESCRIPTIONS. Razouls (1974): 236–237, Figs. 1A–H (♀), 2A–C (♂); Humes (1988): only Fig. 1c, e (as *Oncaea praeclara*).

TYPE LOCALITY. Western Mediterranean Sea, near Palermo.

MATERIAL EXAMINED.
Red Sea: see below under *O. venusta* f. *typica* and f. *venella*
Other areas:

(1) Gulf of Naples, Italy; collected 1 February 1967; depth 0–100 m; leg. B. Scotto di Carlo; identified by G.A. Heron: 1 ♀, 1 ♂ in alcohol (RBS).
(2) Pacific Ocean, off Tanega Islands; R/V *Toyoshio-maru*; collected 5 November 1994 with ORI-plankton net, mesh size 0.33 mm; oblique haul, depth 1600 m; leg. S. Ohtsuka: several ♀♀ and ♂♂ (RBS).
(3) Sea of Japan, Tassha Bay, Sado Island; collected 1978 from colonies of *Solandria secunda* (Inaba), a hydroid; depth 10m; leg. and identified by J.-s. Ho; 4 ♀♀ in alcohol (RBS).
(4) (a) North Pacific Ocean, Galapagos Rift, 00° 48.0'N, 086° 13.0'W; collected 7 December 1979; DSRV *Alvin* dive no. 990; depth 2451 m; 1 specimen in alcohol, labelled *Oncaea praeclara*, Humes, 1988, holotype ♀ (National Museum of Natural History, Smithsonian Institution, Washington, DC, reg. no. USNM 234 109): this vial contains *Oncaea venusta* (1 ♀); parts of the specimen broke off during re-examination and are mounted on slides in lactophenol [right antennule (segment 4–6), left antenna (endopod segments 1 and 2), right maxilliped (claw)].
    (b) North Pacific Ocean, Galapagos Rift; further sampling data not specified; 1 specimen in alcohol labelled: Acc.no. 37 66 47; *O. praeclara*, 13 August 1987 (USNM 234 111): this vial contains *Oncaea venusta* (1 ♀).
    (c) North Pacific Ocean, Galapagos Rift, 00° 48.0'N, 086° 13.0'W; collected 5 December 1979; DSRV *Alvin* dive no. 998; depth 2450 m; 1 specimen in alcohol labelled *Oncaea praeclara*, Humes, 1988, 1 ♂ (USNM 234 112): this vial contains *Oncaea venusta* (1 ♂, possibly f. *typica*).
    (d) North Pacific Ocean, Galapagos Rift, 00° 47'N, 086° 08'W; collected 24 January 1979; DSRV *Alvin* dive no. 883; depth 2493 m; 4 specimens in alcohol labelled *Oncaea praeclara*, 3 ♂♂, 1 ♀(USMN 234114): this vial contains a mixture of *O. venusta* (1 ovigerous ♀, 1 ♂), *Oncaea* sp. (1 ♂, possibly *venusta* f. *venella*), *Triconia* sp. (1 ♂).
    (e) North Pacific Ocean, Galapagos Rift, 00° 48.25'N, 086° 13.48'W; collected 30 November 1979; DSRV *Alvin* dive no. 983; (material donated to R. Böttger-Schnack by A. Humes); 11 specimens in alcohol labelled *Oncaea praeclara*, Humes 1988, 4 ♀♀, 7 ♂♂: this vial contains a mixture of *O. venusta* (2 ♀♀, 3 ♂♂), *O. media* (2 ♀♀), *O. clevei* (1 ♂), Oncaeidae indet. (2 ♂♂), Corycaeidae indet. (1 juvenile); (RBS).
    (f) East Pacific Rise, 12° 48.52'N, 56°48'W; collected 22 November 1987, *Hydronaut* Cruise, *Nautile* dive 221; depth 2630 m (material donated to R. Huys, NHM, by A. Humes); 9 specimens in alcohol labelled *O. praeclara*, Humes, 5 ♀♀, 5 ♂♂: this vial contains 5 ♀♀(1 ♀ovigerous) and 4 ♂♂ of *O. venusta* (all specimens empty exoskeletons with no internal tissue).
(5) Sargasso Sea, near Bermuda, 31° 37.94'N, 64° 09.45'W; collected 9 July 1998 with 1 m net, mesh size 0.15 mm; depth 210 m; leg. D. Steinberg: several ♀♀(ovigerous and non-ovigerous), 3 ♂♂ in alcohol, for molecular analysis (A. Bucklin, Durham, New Hampshire); 2 ♀♀, 2 CV ♀♀ in alcohol (RBS).

Philippi's (1843) description of *O. venusta* was the first account of an oncaeid species. It was based on a single male specimen collected in the western Mediterranean, near Palermo. Unfortunately, the specimen was lost by accident before the author could complete the description. Giesbrecht (1892) redescribed *O. venusta* in more detail from the Gulf of Naples and recently, Heron & Bradford-Grieve (1995) provided an excellent redescription of the species based on material from the Gulf of Naples as well as from other localities in the Atlantic and Pacific Ocean. Both authors do not mention the existence of different size variants among *O. venusta*, although the range of size variation was quite large in Giesbrecht's specimens from the Pacific. In 1929, Farran described two distinct size morphs of *O. venusta*, forma *typica* and forma *venella*, from various Atlantic and Pacific locations, which were separated mainly by their size and some minor morphological characters. The two forms were distinguished in some of the subsequent taxonomic descriptions (e.g. Tanaka, 1960; Ferrari, 1975; Boxshall, 1977b) and a third, 'robust' form was added by Boxshall (1977b). In the Red Sea, both form variants of *O. venusta* sensu Farran occur. They differ considerably in temporal and spatial distribution (Böttger-Schnack, 1990b, 1995), thus indicating the existence of reproductively isolated populations. A detailed morphological examination of both size variants was undertaken during the present study, including microstructures on the appendages and on the exoskeleton (pores, scales), partly by using SEM analyses. The results pointed out several morphological differences between the two forms not noted in the literature before, but these were not regarded as sufficient to warrant recognition of the two forms as separate species. In order to provide the morphological basis required for future taxonomic analyses on *O. venusta*, both forms are redescribed. A further approach to differentiate the two forms using alternative methods, e.g. molecular analysis, is currently in progress.

Oncaea venusta Philippi, 1843 forma *typica* Farran, 1929

Oncaea venusta Farran (1929): 284 [as *Oncæa venusta* forma *typica*]

Oncæa venusta forma *typica* Farran, 1929

TYPE LOCALITY. Not specified, various locations in the temperate and tropical Atlantic, as well as south of New Zealand.

MATERIAL EXAMINED.
Central Red Sea, 21° 22.09'N, 38° 05.09'E: Stn. 664; *R/V Valdivia* leg 29: collected 21 February 1981 with MSN 0.1 mm net (Haul 218/5); depth 0–50 m; total water depth ca 2000 m.
(a) 5 ♀♀, 5 ♂♂ in alcohol (BMNH 1998.2777–2786).
(b) 5 ♀♀, 5 ♂♂ in alcohol (ZMH K-39586).
(c) 2 ♀♀dissected on slides, 1 ♀in alcohol; 3 ♂♂ dissected on slides, 1 ♂ in alcohol; 1 ♀, 1 ♂ in mating position in alcohol (RBS).

DESCRIPTION. Note illustrations are based on (c).

ADULT FEMALE (Figs. 2–5, 8A–E, 9A–F).
Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1615 µm [traditional method 1130 µm, range: 1000–1230 µm, based on 14 specimens (Böttger-Schnack *et al.*, 1989)].

Exoskeleton heavily chitinized, covered with numerous granules, forming long raised structures (lines), especially along lateral part of cephalic shield (Fig. 8A). Prosome 2.1 times length of urosome, excluding caudal rami, 1.7 times urosome length including caudal rami. P2-bearing somite without dorso-posterior projection in lateral aspect (Fig. 2B). P3-bearing somite with conspicuous raised pore protruding laterally (Fig. 2A). Other integumental pores on prosome as indicated in Fig. 2A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 12.2 : 57.7 : 8.5 : 9.1 : 12.5. Proportional lengths (%) of urosomites and caudal rami 10.0 : 47.0 : 6.9 : 7.3 : 10.2 : 18.6.

Genital double-somite 1.5 times as long as maximum width (measured in dorsal aspect) and 1.9 times as long as postgenital somites combined (Fig. 2C); largest width measured at anterior two-thirds, lateral margins of genital double-somite rounded, posterior part tapering gradually. Paired genital apertures located at about 2/5 the distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 8B), only 1 of which discernible under light microscope (Fig. 2G). Double-curved sclerotization between, but slightly anterior to, genital apertures, pore pattern on dorsal surface as indicated in Fig. 2C.

Anal somite 1.6 times wider than long; about half the length of caudal rami (Fig. 2C). Secretory pore discernible on either side of anal opening and additional one near posterior margin. Anterior margin of anal opening (vestigial anal opening) with transverse row of minute denticles. Posterior margin of somite finely serrate ventrally and laterally (Fig. 2D). Ventral face with paired secretory pore near posterior margin (Fig. 2C, cf. also Fig. 6E).

Caudal ramus (Fig. 2F) about 3.5 times as long as wide. Armature consisting of 6 elements: antero- and posterolateral setae (II+III) long, spiniform and unipinnate along medial margin; outer terminal seta (IV) long and plumose; inner terminal seta (V) longest and plumose; terminal accessory seta (VI) more than 2/3 the length of outer terminal seta and 1.4 times longer than caudal ramus; dorsal seta (VII) about same length as posterolateral seta (III) and less than half the length of terminal accessory seta, plumose and bi-articulate at base. Inner margin of somite with fringe of long setules. Dorsal anterior surface (Fig. 2F) with secretory pore near insertion of seta II. Dorsal surface covered with numerous small scales (Fig. 2F).

Antennule 6-segmented (Fig. 2E), relative lengths (%) of segments measured along posterior non-setiferous margin 8.4 : 27.6 : 39.3 : 10.7 : 4.7 : 9.3. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)]. Small element on segment 4 ornamented with row of scales along entire length, tip with tubular extension (SEM observation, not figured). Small element on segment 6 (arrowed in Fig. 2E) with tubular extensions (Fig. 8C), indicating sensory function.

Antenna 3-segmented, distinctly reflexed (Fig. 3A). Coxobasis with row of long, fine spinules or setules near outer margin and with few additional denticles on proximal and distal part of outer (exopodal) margin, curved row of denticles on posterior face; with bipinnate seta at inner distal corner. Endopod segments unequal in length; proximal endopod segment subtriangular forming outer lobate outgrowth bearing patch of branched tubular extensions (Fig. 8D, E), with row of denticles along posterior inner margin. Distal endopod segment distinctly shorter than proximal endopod segment, with narrow cylindrical base articulating; with two patches of branched tubular extensions along outer margin (Fig. 8D); lateral armature with 4 elements, numbered using Roman numerals in Fig. 3A: 1 unipinnate spiniform seta (III) and 3 curved setae (I, II, IV), setae I and II sparsely pinnate, seta I shortest; distal armature consisting of 7 elements: 1 long curved unipinnate seta (E), 4 slightly curved unipinnate setae of graduated length (A–D), seta D being shortest, and 2 slender naked setae (F and G), similar in length and shorter than seta D; none of armature elements spiniform or geniculate.

Labrum (Fig. 3B,C) distinctly bilobed. Each lobe with row of minute denticles around outer ventral margin, row of long fine setules latero-distally and dentiform processes converging and decreasing in size medially. Lobes separated by median concavity covered anteriorly by overlapping rows of broad hyaline petaloid flaps, flanked by paired slit-like pores on proximal part of each lobe (Fig. 9A, B; position of pore arrowed in Fig. 3B). Anterior surface with well developed integumental pockets (Fig. 9C) either side of median swelling, free margin of pockets serrate (Fig. 9D); median swelling with large secretory pore posteriorly. Posterior part of medial incision ornamented with four rounded integumental thickenings (Fig. 3C). Posterior surface with paired patch of very long fine setules and 2 large secretory pores located on proximal part of each lobe.

Paragnaths (Fig. 5, 9C) with small lateral extensions, anterior margin densely covered with several rows of long setules, median bulge unornamented.

Mandible (Fig. 3D) with few minute setules on surface of coxa; gnathobase with 5 elements, indicated by capital letters in Fig. 3D: 1 at subdistal ventral -corner, 2 along distal margin and 2 along subdistal dorsal margin; ventral element (A) shorter than ventral blade, with long, fine setules along dorsal side; ventral blade (B) strong and spiniform, with row of setules on posterior side; dorsal blade (C) strong and broad, with 3 dentiform processes along distal margin; dorsal elements setiform, the shorter (D) hyaline, flat and densely setose, the longer (E) multipinnate.

Maxillule (Fig. 3E) indistinctly bilobed, with numerous spinules on anterior and posterior surfaces. Inner lobe subcylindrical, with 3 elements: outermost one spiniform, swollen at base, fringed with coarse spinules, others setiform and bipinnate; innermost one located along concave inner margin at some distance from other elements. Outer lobe with 4 elements; outermost element spiniform, curved and bipinnate along inner proximal margin, unipinnate along distal margin, longer than the following; other elements bipinnate or naked, element next to the innermost shortest.

Maxilla (Fig. 3F) 2-segmented, comprising syncoxa and allobasis.

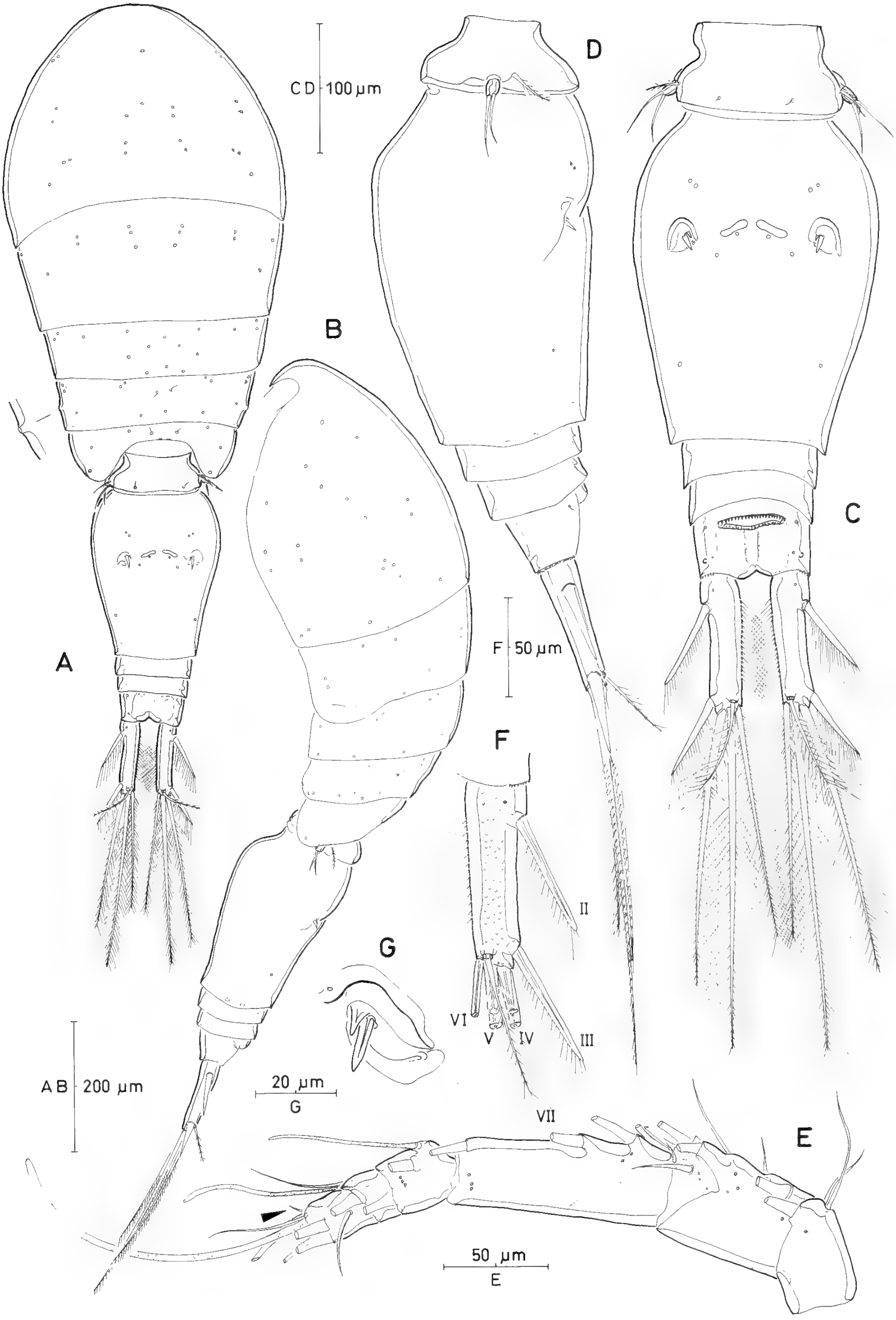

Fig. 2 *Oncaea venusta* f. *typica*, female (Red Sea) (**A**) Habitus, dorsal (lateral raised pore enlarged); (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal; (**D**) urosome, lateral; (**E**) antennule, small sensory element arrowed; (**F**) caudal ramus, dorsal, setae are numbered using Roman numerals; (**G**) P6.

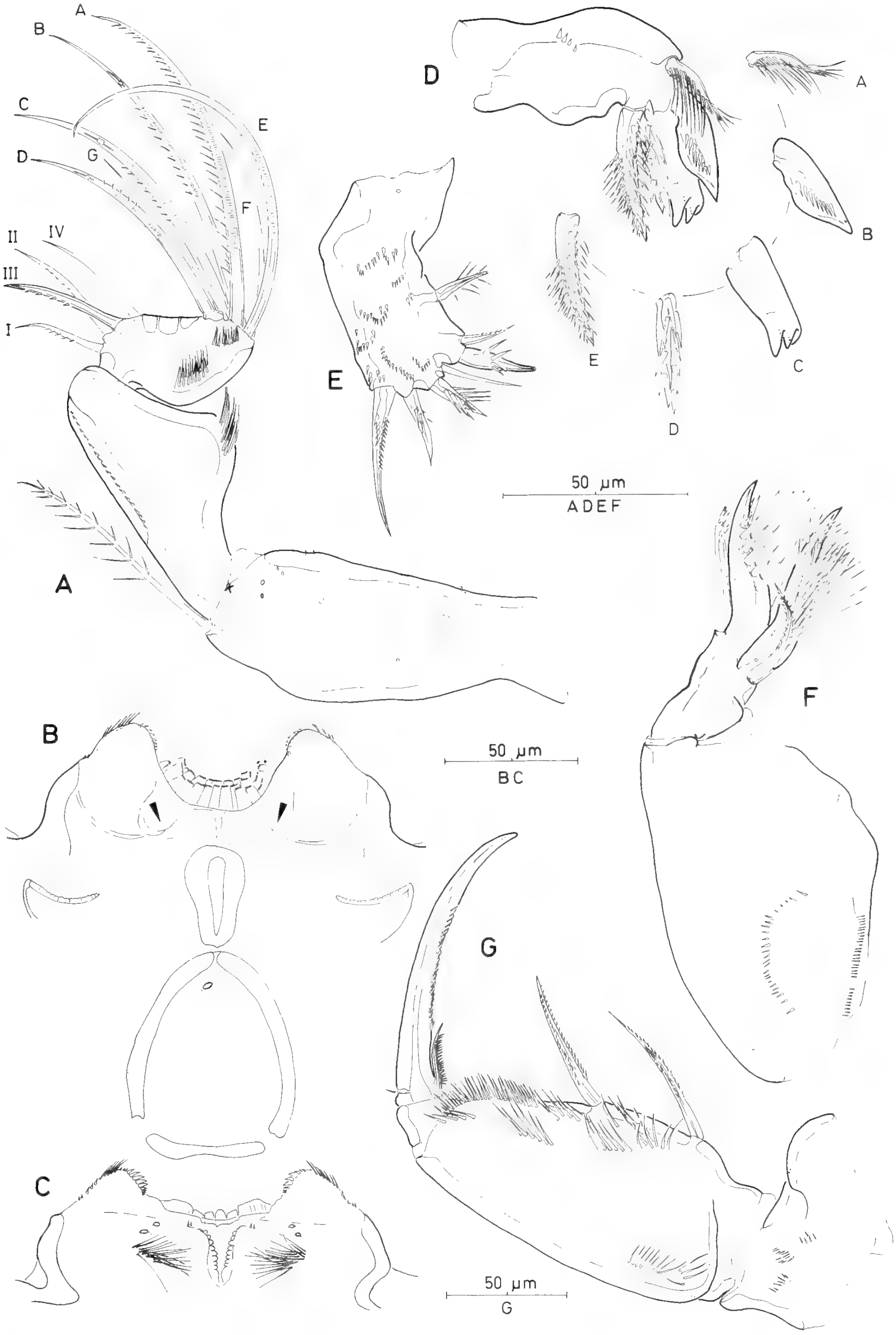

Fig. 3 *Oncaea venusta* f. *typica*, female (Red Sea) (**A**) Antenna, posterior, lateral elements are numbered using Roman numerals, distal elements indicated by capital letters; (**B**) labrum, anterior, slit-like pores arrowed; (**C**) same, posterior; (**D**) mandible, showing individual elements, identified using capital letters; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

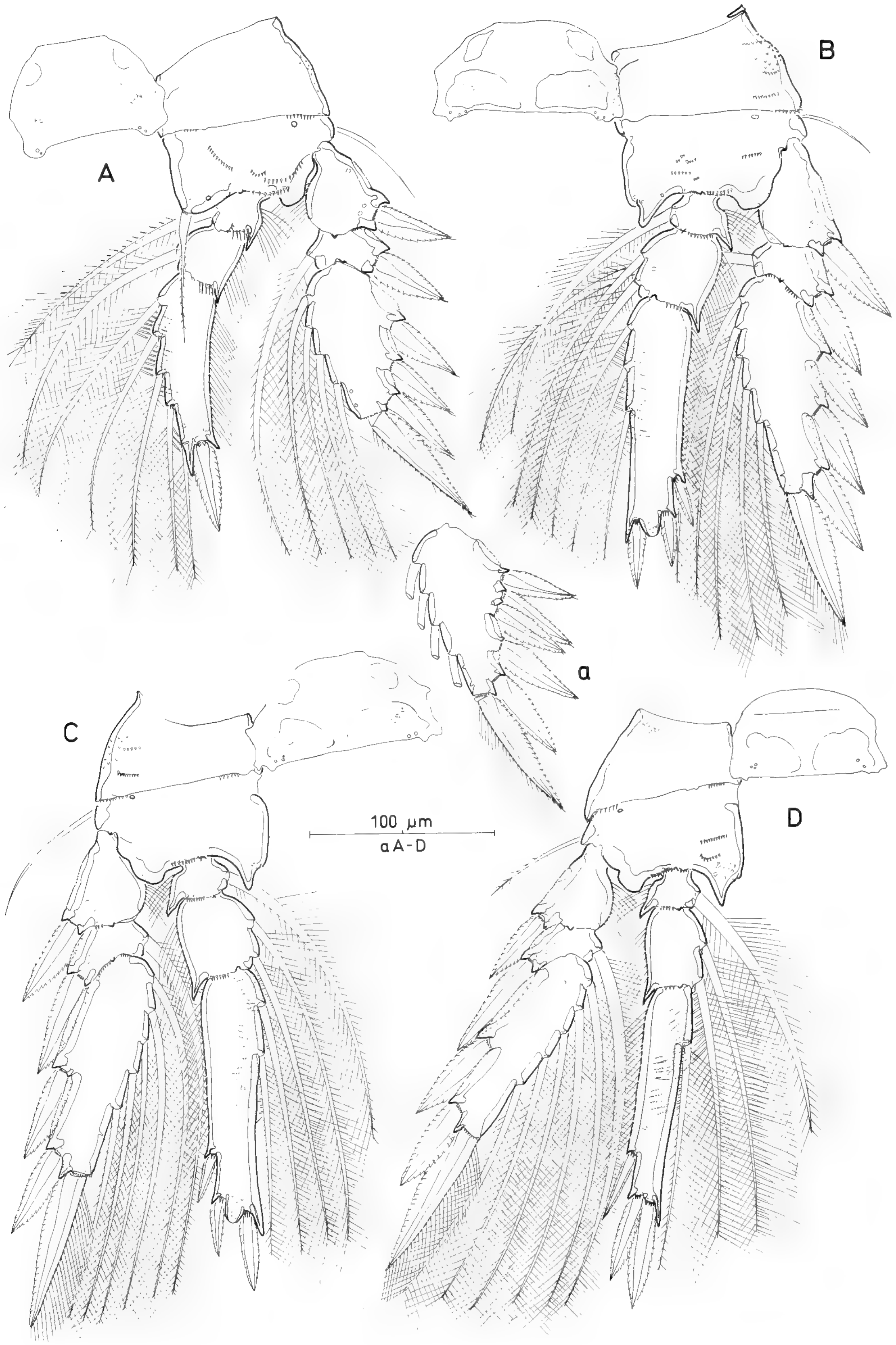

Fig. 4 *Oncaea venusta* f. *typica*, female (Red Sea) (**A**) P1, anterior [**a**, third endopod segment, showing aberrant spine number]; (**B**) P2, anterior; (**C**) P3, anterior; (**D**) P4, anterior.

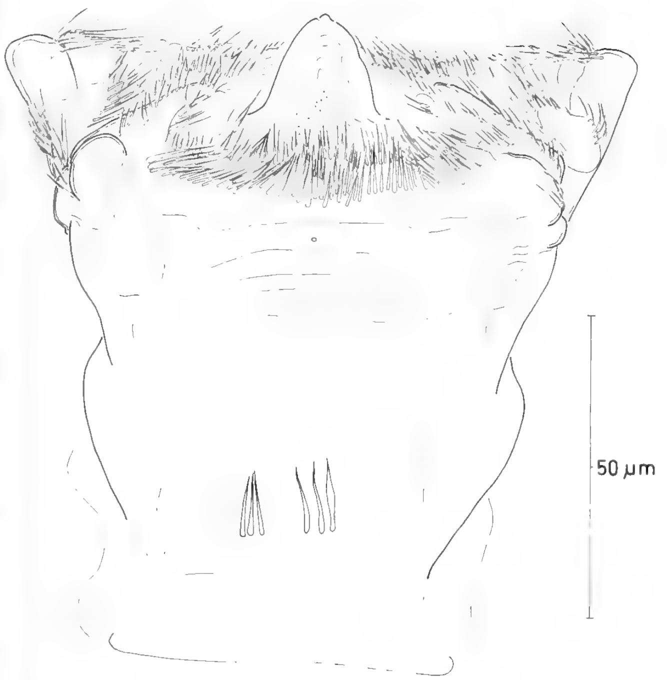

Fig. 5 *Oncaea venusta* f. *typica*, female (Red Sea) Paragnaths, ventral view.

Syncoxa unarmed, surface ornamented with 2 spinular rows and 2 large secretory pores. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta extending almost to tip of allobasal claw, ornamented with few strong spinules distally and a thin hyaline lamella bilaterally, tip of seta with tubular extension; inner margin with slender pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and single row of shorter spinules along outer margin.

Maxilliped (Fig. 3G) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa ornamented with few spinules on anterior surface, unarmed. Basis robust, inner margin with 2 spiniform spinulose elements nearly equal in length; fringe of long setules half the distance between distal seta and articulation with endopod; anterior surface with 2 rows of long spinules along palmar margin, additional longitudinal row of spinules near outer margin as in Fig. 3G. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along proximal two-thirds of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1–4 biramous (Fig. 4A–D), with 3-segmented rami. Spine and setae formula as for genus. Intercoxal sclerites well developed, ornamented with 3 posterior denticles at distal corners in P1–P3. Coxae and bases of legs 1–4 with surface ornamentation as in Fig. 4A–D. Coxae of P1–P4 with posterior raised secretory pore near outer distal corner (not figured, cf. Fig. 13A–D). Bases with short naked (P1–P3) or plumose (P4) outer seta; with anterior secretory pore near outer proximal corner; inner portion slightly produced medially in P2–P4 (Fig. 4B–D). Inner basal seta on P1 spiniform and minutely pinnate. Respective legs without distinct length differences between exopod and endopod (P1) or with endopod slightly longer than exopod (P2–P4). Bases of spines on exopod and endopod segments anteriorly surrounded by small spinules. Anterior face of all segments ornamented with small scales (not figured), similar to those on caudal ramus (Fig. 2F).

Exopods. Outer margin of exopod segments with well developed serrated hyaline lamella, interrupted by small gap at about half the distance, longitudinal concavity below serrated lamellar margin (Fig. 9E); inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments. Hyaline lamellae on outer spines well developed; outer and terminal spines of P1 with subapical tubular extension (Fig. 9F). Terminal spine shorter than distal exopod segment in all legs.

Endopods. Outer margin of endopod segments with fringe of long setules. Inner seta of proximal endopod segment slightly swollen at base. Distal endopod segments with several secretory pores on posterior surface; distal margin of P2 and P3 produced into conical projection ornamented with minute spinules anteriorly (Fig. 4B,C). Outer subdistal spine nearly equal in length to (P2–P3) or shorter than (P4) outer distal spine, always shorter than distal spine. Outer distal spine about 3/4 the length of terminal spine in P4. Outer margin of distal segment of P1 terminating in a long process obscuring insertion of distalmost inner seta (Fig. 4A). Inner setae of distal endopod segments with spinule comb along proximal inner margin; this comb also present on distal inner seta of middle endopod segment in P3–P4.

P5 as figured for *O. venusta* f. *venella* (cf. Fig. 11G), comprising small plumose seta arising from lateral surface of somite, and small free unornamented segment representing exopod. Exopod slightly longer than wide, bearing 2 naked setae nearly equal in length, subapical one spiniform.

P6 (Fig. 2G) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes (Fig. 8B), only 1 of which discernible under light microscope (Fig. 2G).

Egg-sacs paired, oval-shaped; each sac containing appr. 30–40 eggs (diameter 50–60 µm).

ADULT MALE (Figs. 6, 7A–C, 8F, 10).
Body length: 1158 µm [traditional method: 910 µm, range: 880–950 µm, based on 9 specimens (Böttger-Schnack *et al.*, 1989)]. Sexual dimorphism in antennule, antenna, maxilliped, genital segmentation and ornamentation, P1–P3 (endopod), P5–P6, and in caudal ramus.

Prosome 2.0 times the length of urosome, excluding caudal rami, 1.7 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 10.1 : 64.5 : 6.0 : 4.4 : 5.0 : 10.1; proportional lengths (%) of urosomites (caudal rami included) 8.6 : 55.0 : 5.1 : 3.7 : 4.3 : 8.6 : 14.7. Length to width ration of genital somite 1.5 : 1. Caudal rami about 2.5 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 2/3 the length of seta IV and 2.2 times the length of caudal ramus. Dorsal and ventral surface of caudal ramus covered with minute scales as in female. Surface of genital flaps and ventral surface of anal segment ornamented with several rows of small spinules. Ventral face of anal somite with paired secretory pore near posterior margin (Fig. 6E).

Antennule (Fig. 6B) 4-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 8.0 : 27.1 : 43.3 : 23.6. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)].

Antenna (Fig. 6H) with seta on coxobasis naked and shorter than in female. Distal endopod segment with seta III much stouter than in female, seta IV spiniform and curved, both elements shorter than in female (Fig. 8F).

Maxilliped (Fig. 6C) 3-segmented, comprising syncoxa, basis

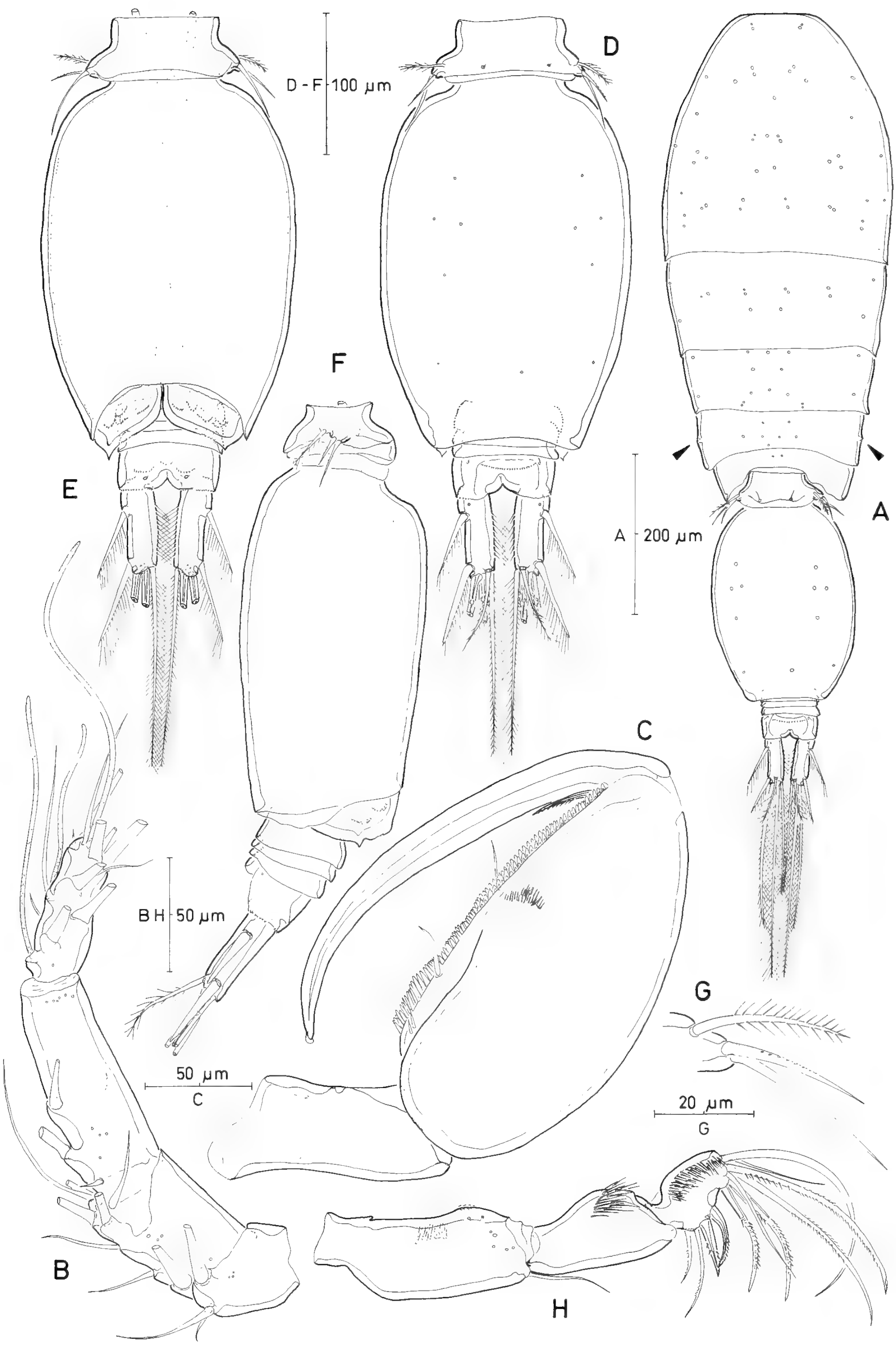

Fig. 6 *Oncaea venusta* f. *typica*, male (Red Sea) (**A**) Habitus, dorsal, arrows indicating position of lateral raised pores; (**B**) antennule; (**C**) maxilliped, anterior; (**D**) urosome, dorsal; (**E**) urosome, ventral; (**F**) same, lateral (spermatophores fully developed); (**G**) P5, dorsal; (**H**) antenna, posterior.

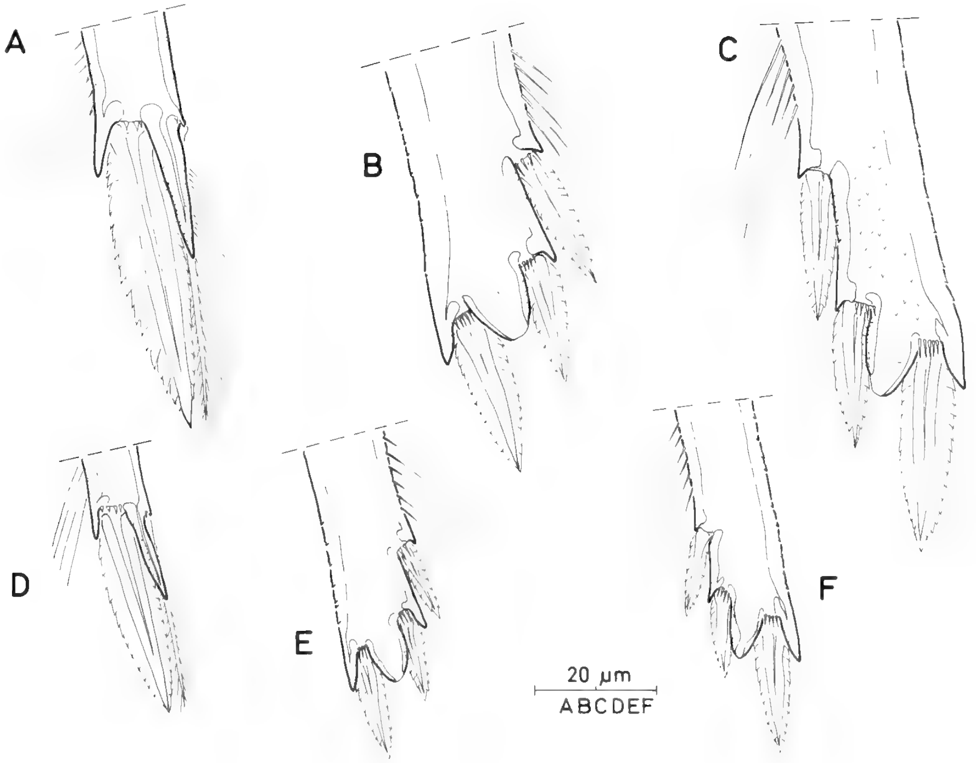

Fig. 7 *Oncaea venusta* f. *typica*, male (Red Sea) (**A**) P1, distal part of endopod; (**B**) P2, distal part of endopod; (**C**) P3, distal part of endopod. – *Oncaea venusta* f. *venella*, male (Red Sea) (**D**) P1, distal part of endopod; (**E**) P2, distal part of endopod; (**F**) P3, distal part of endopod.

and 1-segmented endopod. Syncoxa without surface ornamentation, except for several secretory pores, unarmed. Basis robust, particularly inflated in proximal half forming bulbous swelling; anterior surface with 2–3 transverse spinular rows in addition to row of short flat spinules along inner margin (Fig. 6C); posterior surface with 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 6C); with 2 small naked setae within the longitudinal cleft, nearly equal in length. Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of short, unipectinate spine basally fused to inner proximal corner of claw; tip of claw with minute hyaline apex.

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in terminal process on P1 enp-3, being longer than in female, reaching half the length of distal spine (Fig. 7A) and in conical projections on distal endopod segment of P2–P3, being longer than in female, reaching half the length of outer distal spine (Fig. 7B, C).

P5 (Fig. 6G) exopod not delimited from somite, general shape and armature as in female, except for subapical seta spiniform and shorter than in female, ornamented with row of minute spinules along outer margin.

P6 (Fig. 6E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 6E and 10A; with receptor (pores) at inner edge of posterolateral corners (Fig. 10B); these corners not protruding laterally so that they are hardly discernible in dorsal aspect (Fig. 6D).

Spermatophore oval (Fig. 6F), of variable size according to state of maturity; swelling of spermatophore during development not affecting shape and relative size of genital somite.

Oncaea venusta Philippi, 1843 forma *venella* Farran, 1929

Oncaea venusta Farran (1929): 284–285, Fig. 33 (female only) [as *Oncæa venusta* forma *venella*].

Oncæa venusta forma *venella* Farran, 1929

TYPE LOCALITY. Not specified, various locations in the temperate and tropical Atlantic, as well as south of New Zealand (Farran, 1929).

MATERIAL EXAMINED

(1) Central Red Sea, 21° 22.09'N, 38° 05.09'E: Stn. 664; *R/V Valdivia* leg 29: collected 21 February 1981 with MSN 0.1 mm net (Haul 218/5); depth 0–50 m; total water depth ca 2000 m.
   (a) 5 ♀♀, 5 ♂♂ in alcohol (BMNH 1998.2787–2796)
   (b) 5 ♀♀, 5 ♂♂ in alcohol (ZMH K-39587)
   (c) numerous ♀♀ and ♂♂ (RBS).
(2) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m: 1 ♂ in alcohol (RBS).
(3) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/4); depth 50–100 m; total water depth 970 m: 2 ♀♀, 2 ♂♂ dissected on slides, 1 ♀, 1 ♂ in alcohol (RBS).

DESCRIPTION. Note illustrations are based on (3).

ADULT FEMALE (Figs. 11–13)
Body length (measured in lateral aspect; from anterior margin of

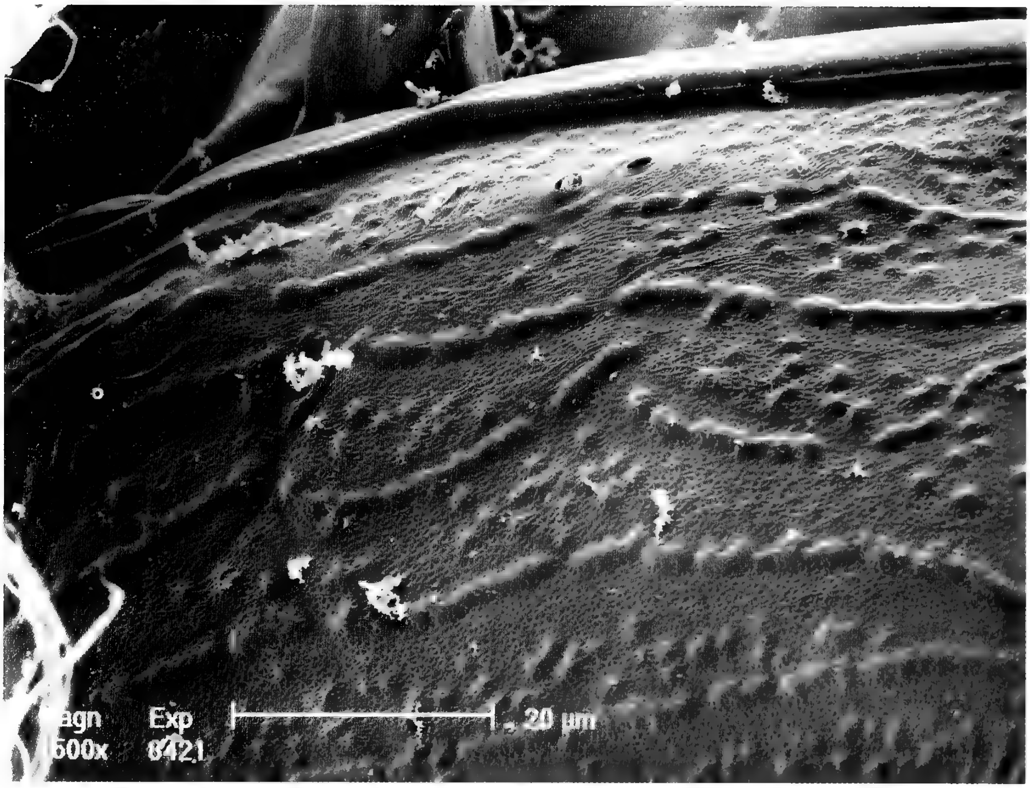

Fig. 8A *Oncaea venusta* f. *typica*, female (Red Sea) Cephalic shield, lateral, showing surface ornamentation.

Fig. 8B *Oncaea venusta* f. *typica*, female (Red Sea) Genital aperture, right;

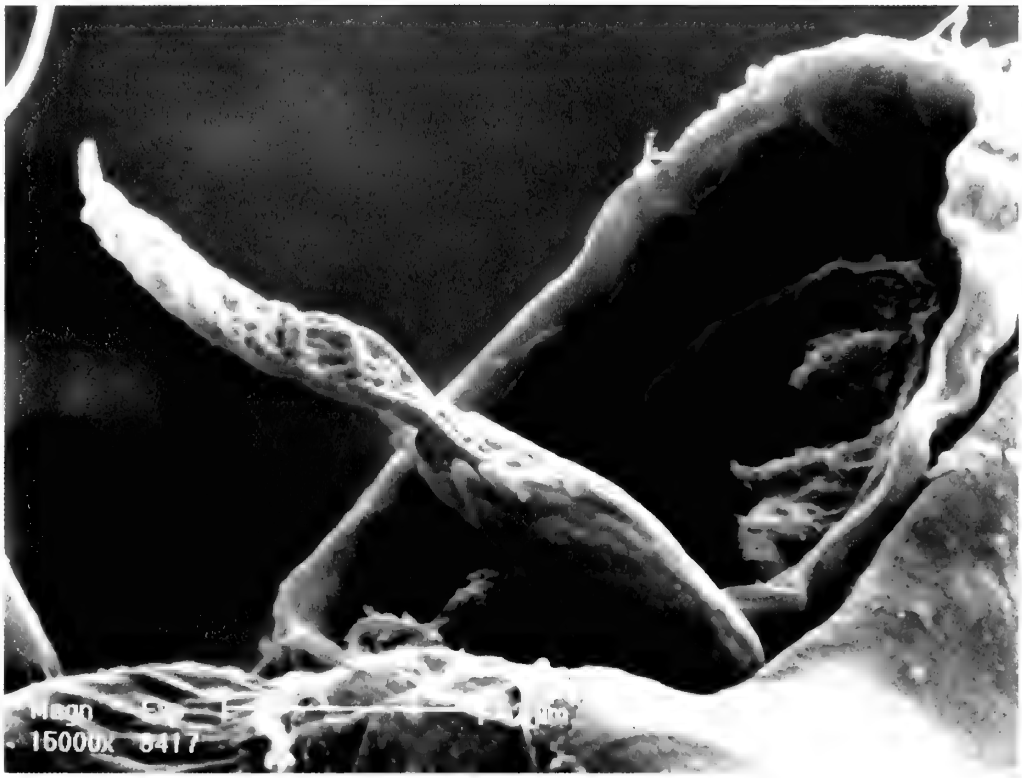

Fig. 8C *Oncaea venusta* f. *typica*, female (Red Sea) Antennule, 6th segment, short sensory element.

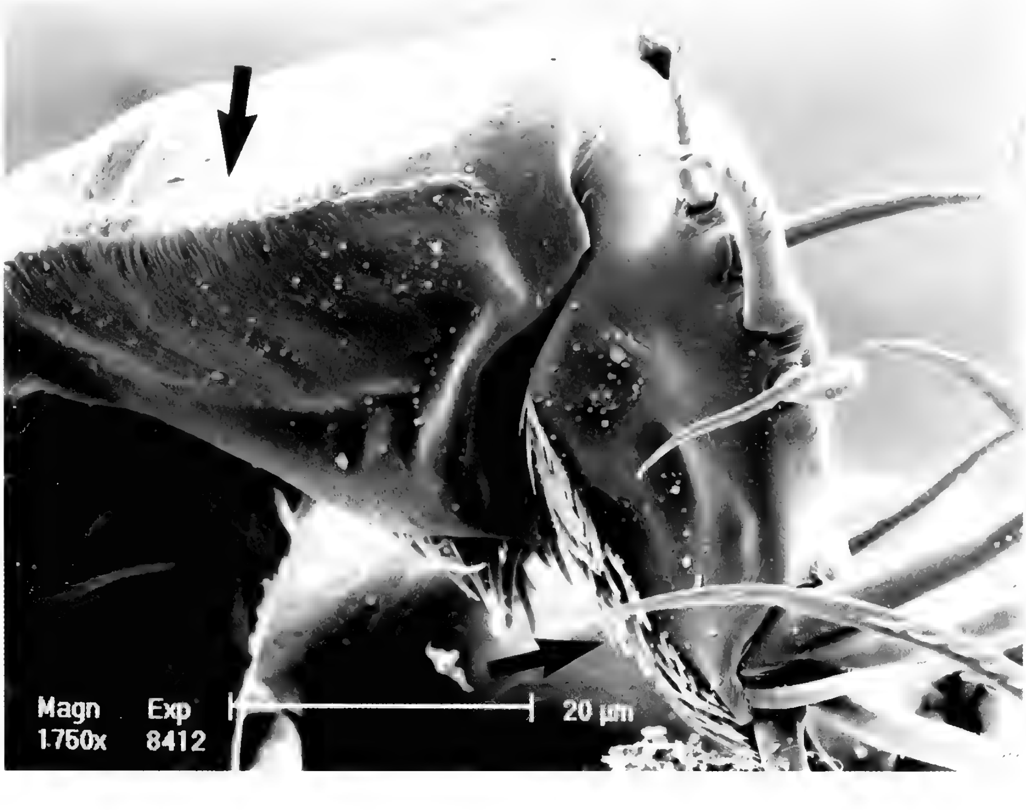

Fig. 8D *Oncaea venusta* f. *typica*, female (Red Sea) Antenna, endopod segment 1 + 2, concavity and patches of tubular extensions arrowed.

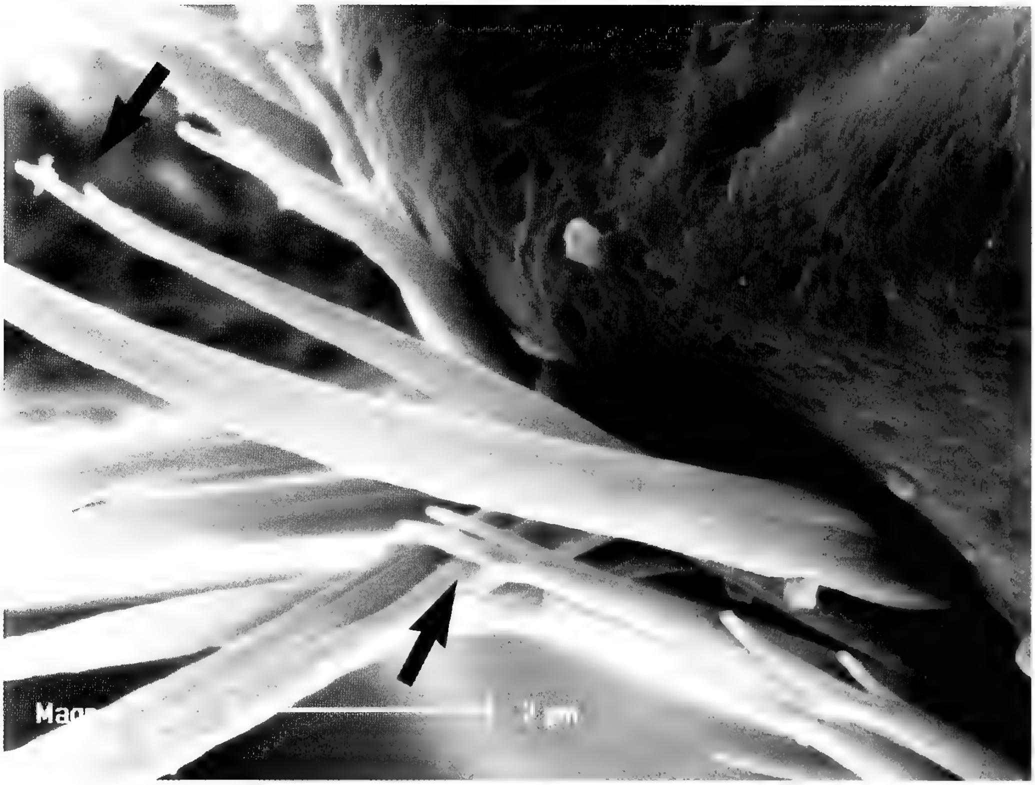

Fig. 8E *Oncaea venusta* f. *typica*, female (Red Sea) Antenna, endopod segment 2, branched tubular extensions (arrowed).

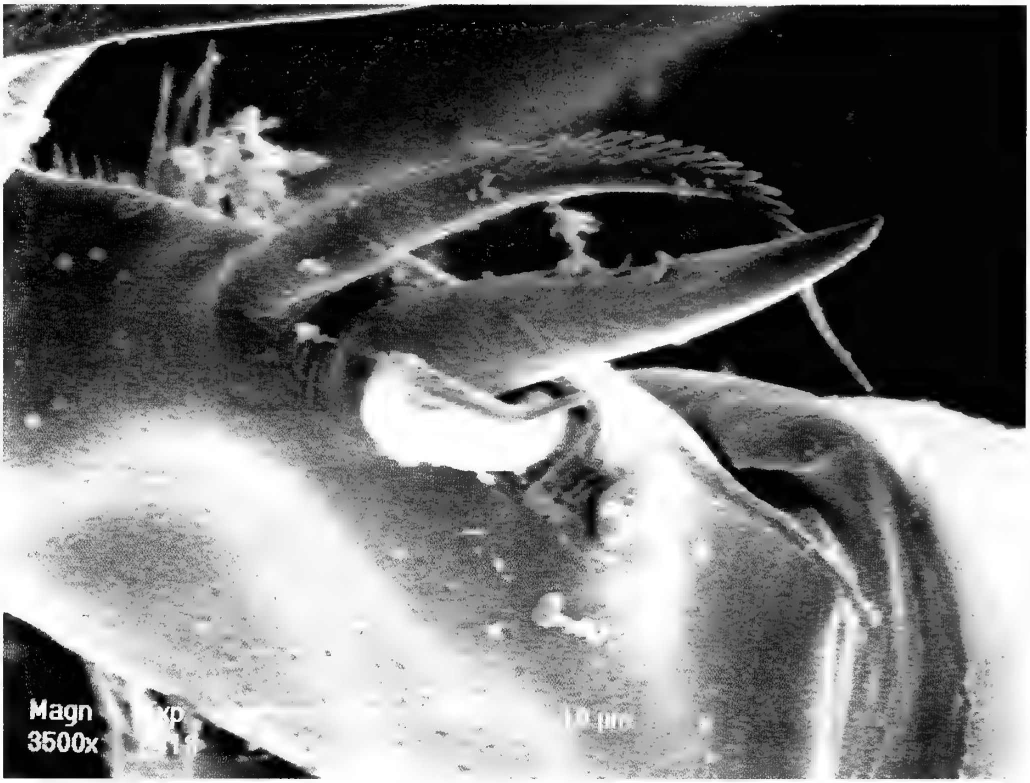

Fig. 8F *Oncaea venusta* f. *typica*, male (Red Sea) Antenna, endopod segment 2, lateral armature.

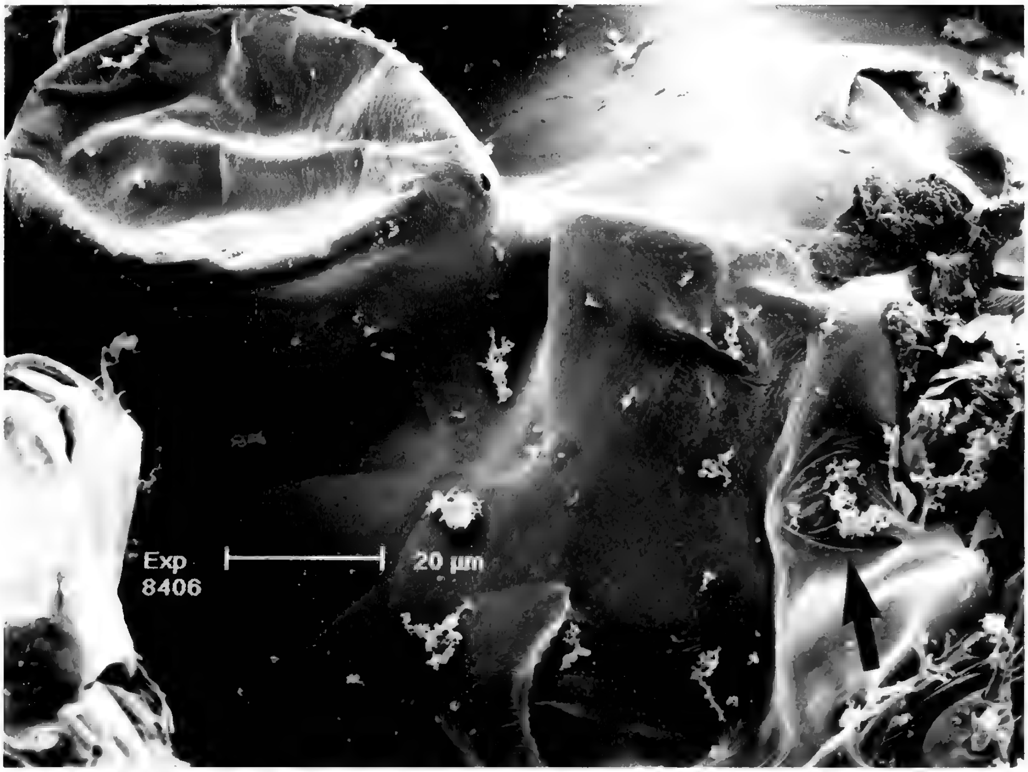

Fig. 9A *Oncaea venusta* f. *typica*, female (Red Sea) Labrum, anterior, showing integumental pockets either side of median swelling and right slit-like pore (arrowed).

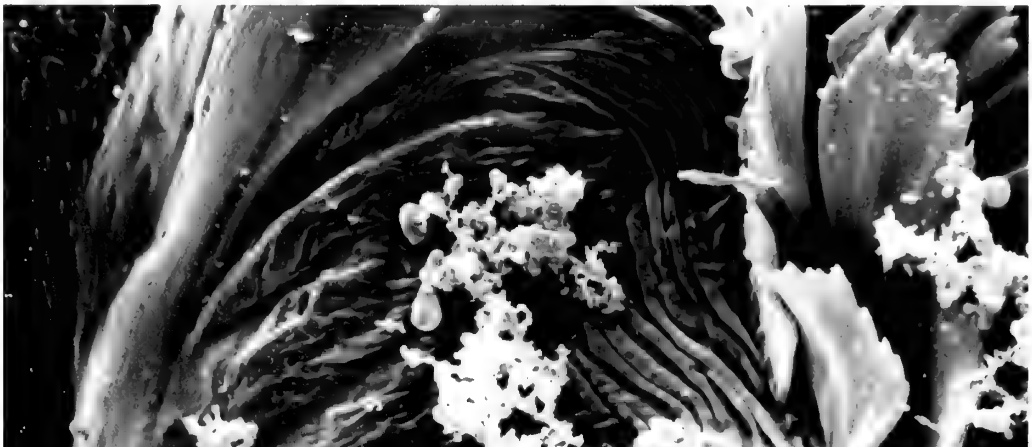

Fig. 9B *Oncaea venusta* f. *typica*, female (Red Sea) Labrum, anterior, slit-like pore, right.

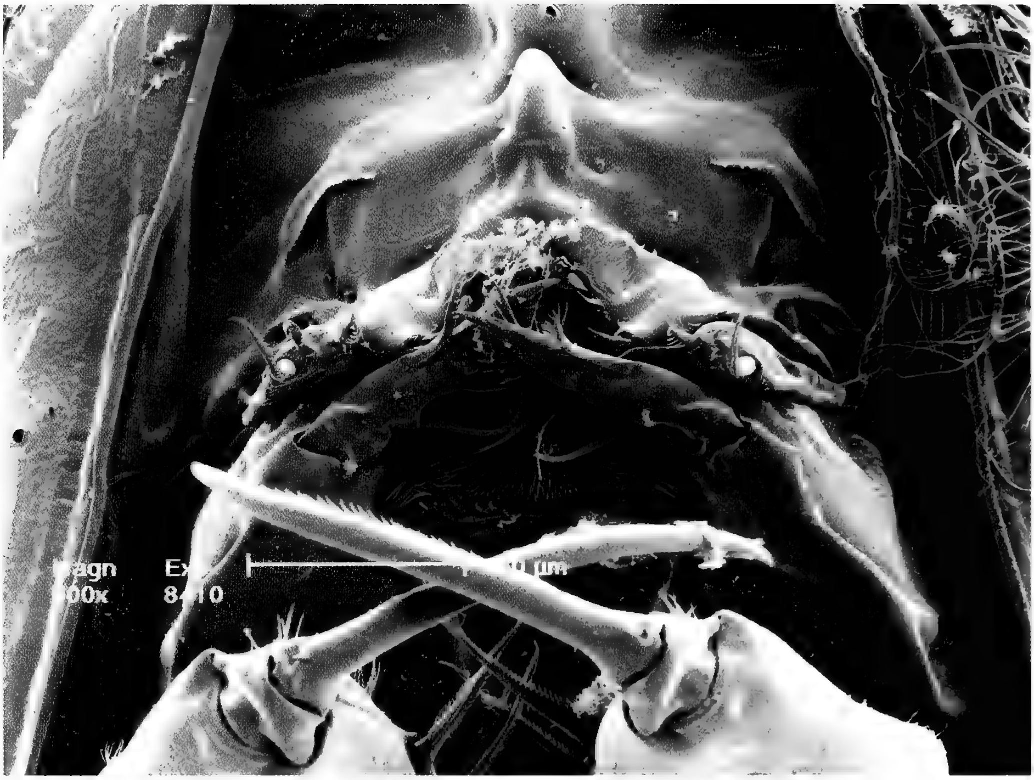

Fig. 9C *Oncaea venusta* f. *typica*, female (Red Sea) Oral area, ventral.

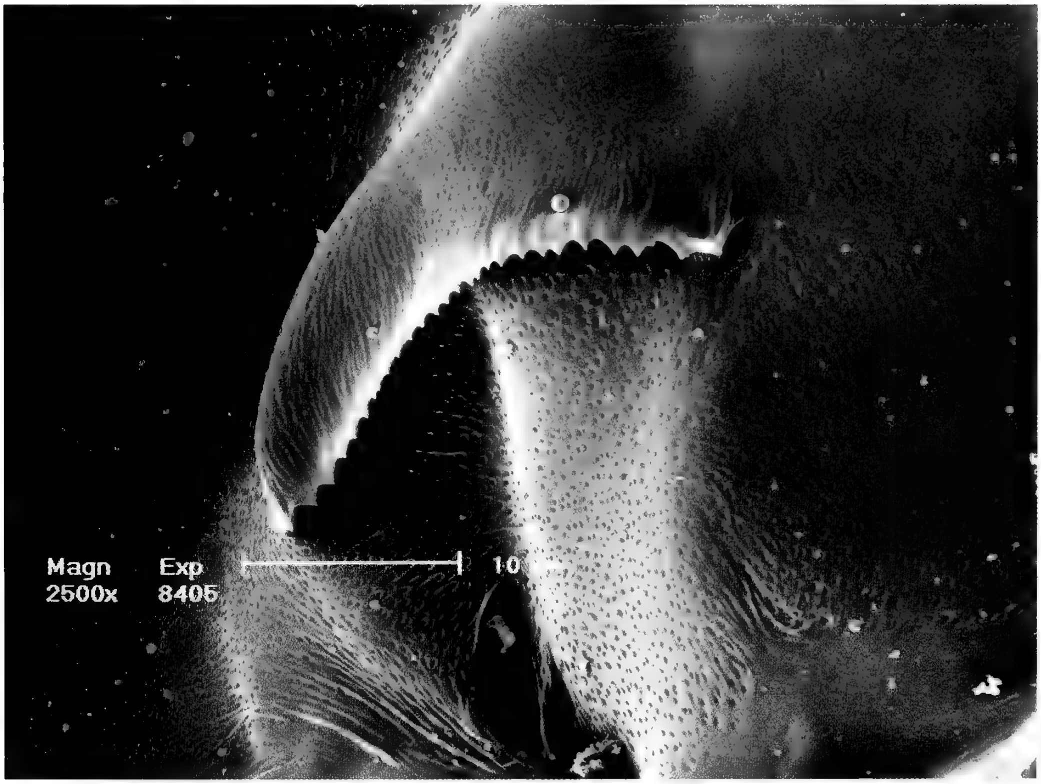

Fig. 9D *Oncaea venusta* f. *typica*, female (Red Sea) Labrum, anterior, integumental pocket, right.

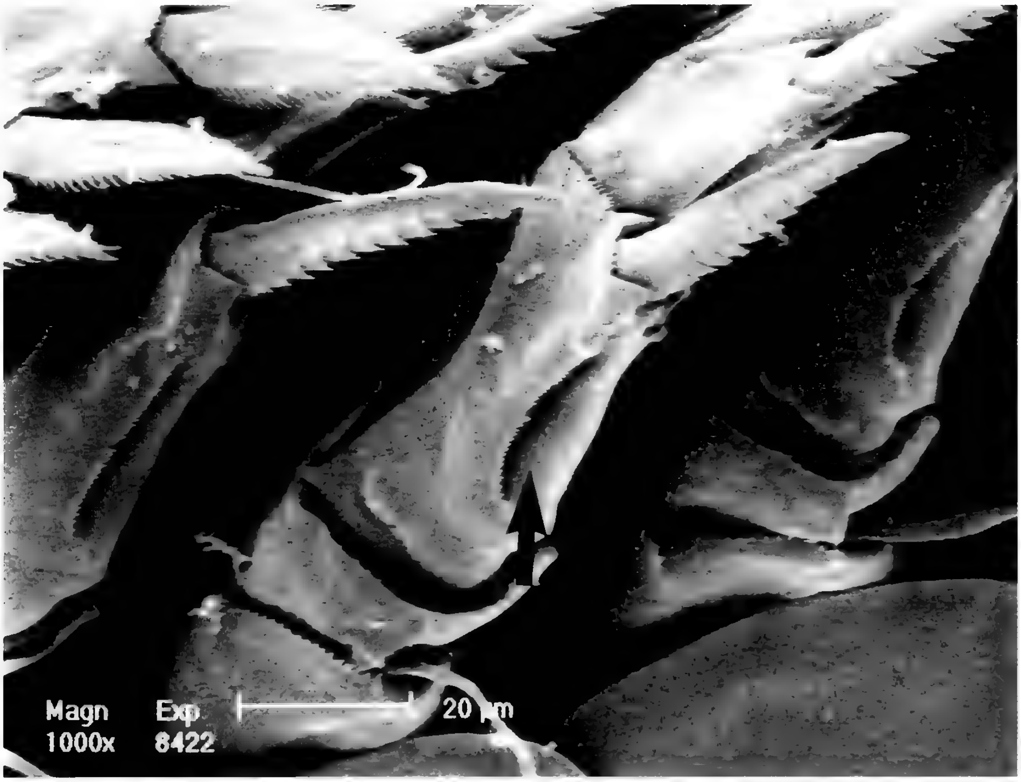

Fig. 9E *Oncaea venusta* f. *typica*, female (Red Sea) P2–P4, exopod-1, showing lateral concavity (arrowed).

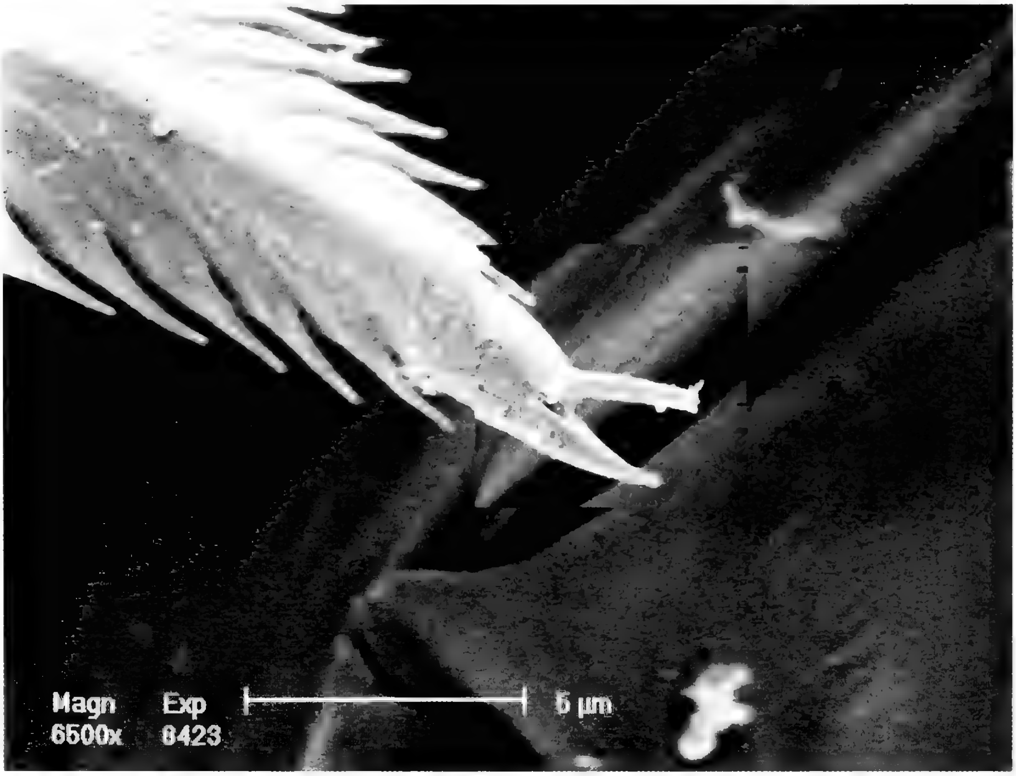

Fig. 9F *Oncaea venusta* f. *typica*, female (Red Sea) P1, exopod-1, tip of spine, showing tubular extension.

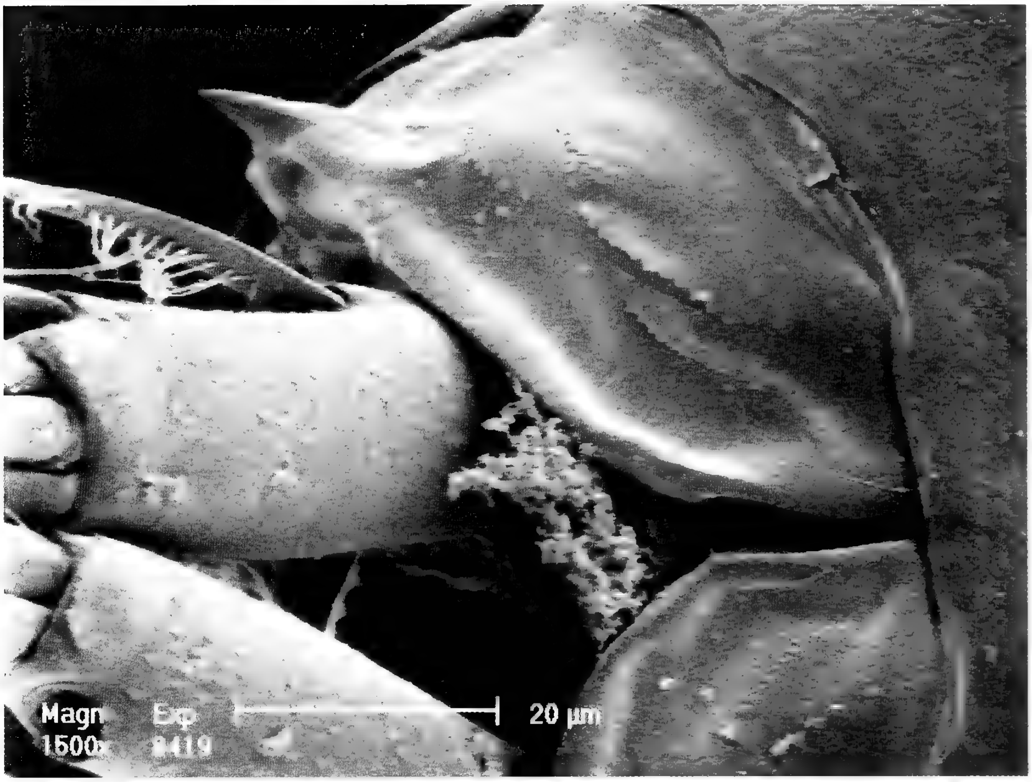

Fig. 10A *Oncaea venusta* f. *typica*, male (Red Sea) Caudal ramus and P6, ventral.

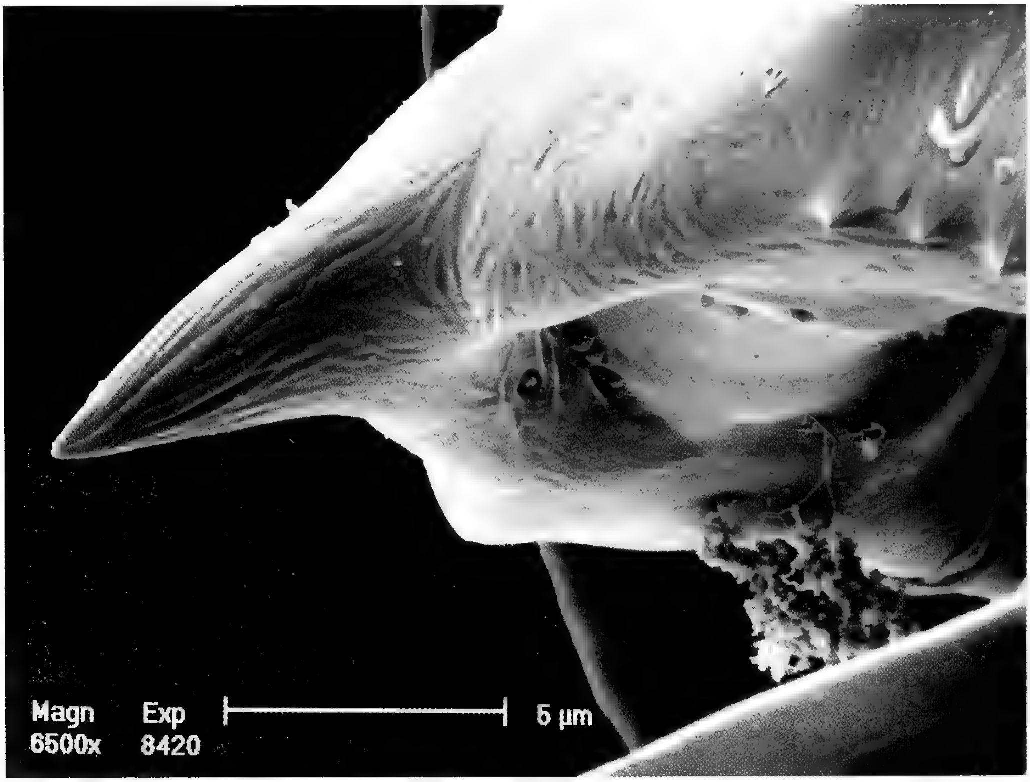

Fig. 10B *Oncaea venusta* f. *typica*, male (Red Sea) P6, posterolateral corners, showing receptor pores at inner edge.

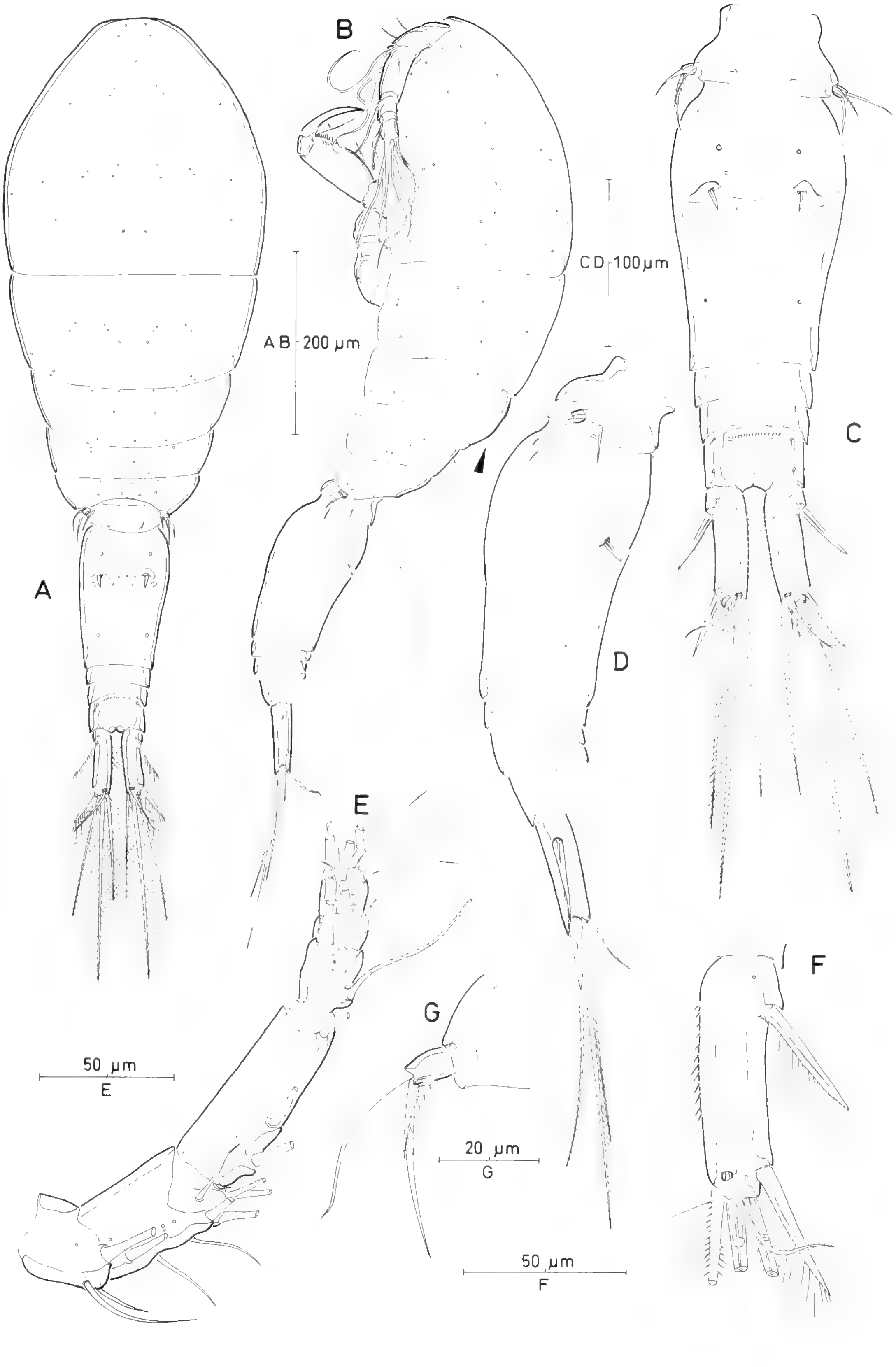

Fig. 11 *Oncaea venusta* f. *venella*, female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted; dorsoposterior swelling on P2-bearing somite arrowed); (**C**) urosome, dorsal; (**D**) urosome, lateral; (**E**) antennule; (**F**) caudal ramus, dorsal; (**G**) P5, dorsal.

rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1096 µm [traditional method: 800 µm, range: 750–880 µm, based on 36 specimens (Böttger-Schnack *et al.* 1989)].

Body proportions different from f. *typica*, with prosome 2.5 times length of urosome, excluding caudal rami, 2.0 times urosome length including caudal rami. P2-bearing somite with insignificant dorsoposterior swelling in lateral aspect (arrowed in Fig. 11B). Integumental pores on prosome as indicated in Fig. 11A, B. Granules and raised structures on exoskeleton less pronounced than in f. *typica*.

Proportional lengths of urosomites similar to f. *typica*. Genital double-somite 1.8 times as long as maximum width (measured in dorsal aspect); largest width measured at anterior third, lateral margins of genital double-somite weakly rounded at anterior third, posterior part nearly straight. Double-scalloped sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 11C.

Anal somite (Fig. 11C) as in f. *typica*.

Caudal ramus (Fig. 11F) about 2.8 times as long as wide, shorter than in f. *typica*. Proportional length of caudal setae as in f. *typica*, except for seta VI 1.6 times longer than caudal ramus.

Antennule (Fig. 11E) and antenna (Fig. 12A) as in f. *typica*, except for slight differences in the ornamentation of setae on second endopod segment in the antenna (seta I; setae C and D).

Labrum (Fig. 12B, C) similar to f. *typica*, except for integumental pockets with free margin serrate along half the distance only (Fig. 12B).

Mandible (Fig. 12D), maxillule (Fig. 12E), maxilla (Fig. 12F) and maxilliped (Fig. 12G) as in f. *typica*.

Swimming legs 1–4 (Fig. 13A–D) as in f. *typica*, except for P4 enp-3 outer distal spine only 2/3 the length of distal spine. Distal spines on endopods of P1–P4 somewhat longer than in f. *typica*.

P5 (Fig. 11G) and P6 as in f. *typica*.

Egg-sacs paired, containing appr. 30–35 eggs each (diameter 40–50 µm).

ADULT MALE (Fig. 7D–F, 14).
Body length: 985 µm [traditional method: 590 µm, range: 550–650 µm (single extreme value 730 µm), based on 17 specimens (Böttger-Schnack *et al.* 1989)]. Sexual dimorphism in antennule, antenna, maxilliped, P1–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.3 times length of urosome, excluding caudal rami, 2.0 times urosome length including caudal rami. Proportional lengths (%) of urosomites similar to f. *typica*. Length to width ratio of genital somite 1.7 : 1, longer than in f. *typica*. Ornamentation of genital flaps as in Fig. 14E. Caudal rami about 1.9 times longer than wide, shorter than in f. *typica*. Caudal setae with proportional lengths as in f. *typica*, except for seta VI less than 2/3 the length of seta IV and 2.4 times longer than caudal ramus.

Sexual dimorphism in antennule (Fig. 14B), antenna (Fig. 14G), maxilliped (Fig. 14C) and in P5–P6 (Fig. 14D, E), as well as in enp-3 of P1–P3 (Fig. 7C, D) similar to f. *typica*. Seta on body near P5 naked.

TAXONOMY

The original description of *O. venusta* by Philippi (1843) was rather poor and the single male specimen was lost by accident before the mouthparts could be documented. Dana's subsequent (1849, 1852) records of *Antaria obtusa* and *A. crassimana* were included under the synonymies of both *O. venusta* and *O. mediterranea* by Giesbrecht (1892), reflecting the author's undecisiveness on this matter. Lubbock (1860) described the species (as *Oncœa pyriformis*) from the equatorial Atlantic and the southern Indian Ocean, and synonymized it with Dana's *A. obtusa*. He was the first to record male-female pairs ('couples') of the species and erroneously believed that he had also been the first author to report the males; however, as the original account of *O. venusta* by Philippi was based on a male specimen, Lubbock's opinion was erroneous. Claus' (1866) description of *Antaria coerulescens* from Nice has been synonymized with *O. venusta* by Giesbrecht (1892). Claus described several characters, such as the heavily sclerotized exoskeleton and its surface ornamentation, which are typical for the species, but at the same time recorded the P4-bearing somite as being heart-shaped and pointed, which is not the case in *O. venusta*. Brady's (1883) illustrations [Challenger Expedition] of *Antaria obtusa* (Dana), were also synonymized with *O. venusta* by Giesbrecht (1892), but he suspected that Brady's specimens might include *O. mediterranea* as well. According to Brady's illustration (Fig. 11), the P4 endopod exhibits a length ratio of distal spine to outer distal spine (1.2 : 1) more similar to *O. venusta* (1.3 : 1) than to *O. mediterranea* (1.55 : 1). His illustration of the male urosome (Fig. 3), however, shows laterally produced genital flaps, which is not typical for *O. venusta*, but can be observed in *O. mediterranea* (Böttger-Schnack & Huys, 1997, their Fig. 4A, D).

Giesbrecht (1892) redescribed *O. venusta* on the basis of material from Naples, reviewed the earlier literature on *Antaria* and *Oncaea* and summarized the synonymies of the respective species known at that time (see above). He stated that, judging from its general habitus, Dana's form variety of *A. gracilis* would also resemble *O. venusta*. However, as the P4-bearing somite of Dana's specimen is pointed in lateral view (Plate 86, Fig. 12) as in *O. mediterranea*, and not rounded as in *O. venusta*, Giesbrecht's opinion is not followed here. [Dana's typical *A. gracilis* (Plate 86, Fig. 11b) is figured with egg-sacs attached, which conceal great parts of the urosome. Thus its unusual, narrow form cannot be used as a specific character for identification as was proposed by Giesbrecht.]

Recently, an excellent redescription of *O. venusta* was provided by Heron & Bradford-Grieve (1995), based on material from the Gulf of Naples and from various locations in the Atlantic and Pacific. The authors did not figure the minute element on the 6th segment of the antennule, and did not report on the sexual dimorphism in the coxobasal seta on the antenna and in the endopodal spines of P1–P3. Re-examination of their material (1 ♀and 1 ♂ from Naples, kindly put at my disposal by G.Heron) showed, however, that these characters are also present in *O. venusta* from Naples and that the specimens from the Red Sea are conspecific. A further discussion of their material will be given below under *Form variants*.

FORM VARIANTS

Farran (1929) distinguished two form variants of *O. venusta*, f. *typica* and f. *venella*, which differed mainly in size: the typical form measured 1.08–1.16 mm (♀) and 0.78–0.81 mm (♂) in total body length, while females of the *venella* form measured 0.91–1.07 mm. No males of the *venella* form were recorded by Farran (1929). Females of the two forms differed furthermore in general habitus, f. *typica* being more 'pear-shaped' than f. *venella*, and in the length ratio of prosome : urosome, which was smaller in f. *typica* (1.3:1) than in f. *venella* (1.5:1).

Sewell (1947) recorded two size variants among female *O. venusta* in the northern Arabian Sea and found no overlap in size between the two groups (1.18–1.25 mm and 0.85–0.91 mm, respectively). He described some morphological differences other than size, which included (1) length to width ratio of prosome, which was larger in f. *venella* than in f. *typica*, (2) length to width ratio of caudal ramus, which was larger in f. *typica* than in f. *venella* and (3) slight differences in the proportions of urosomites and caudal ramus between the two forms.

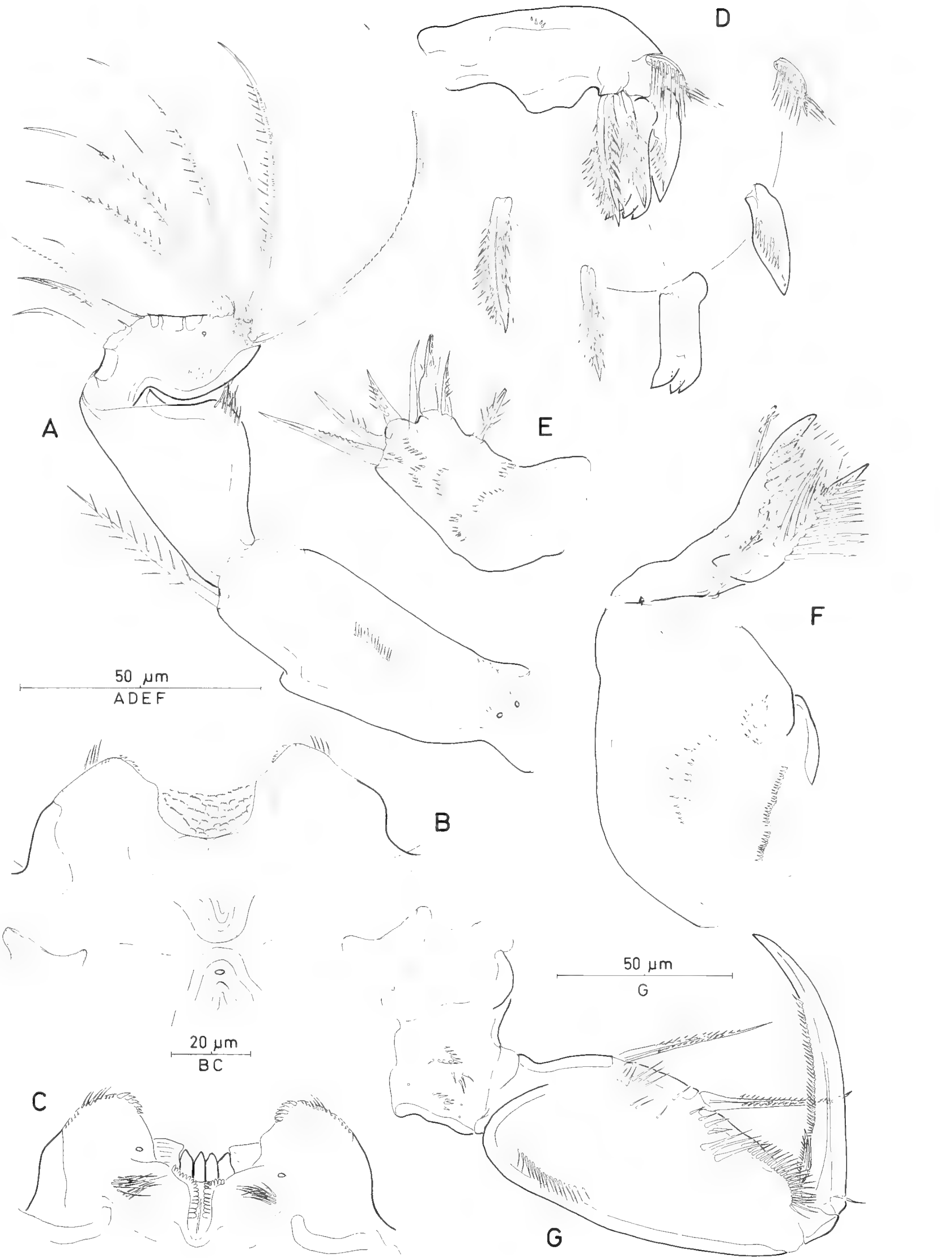

Fig. 12 *Oncaea venusta* f. *venella*, female (Red Sea) (**A**) Antenna, anterior; (**B**) labrum, anterior; (**C**) same, posterior; (**D**) mandible, showing individual elements; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

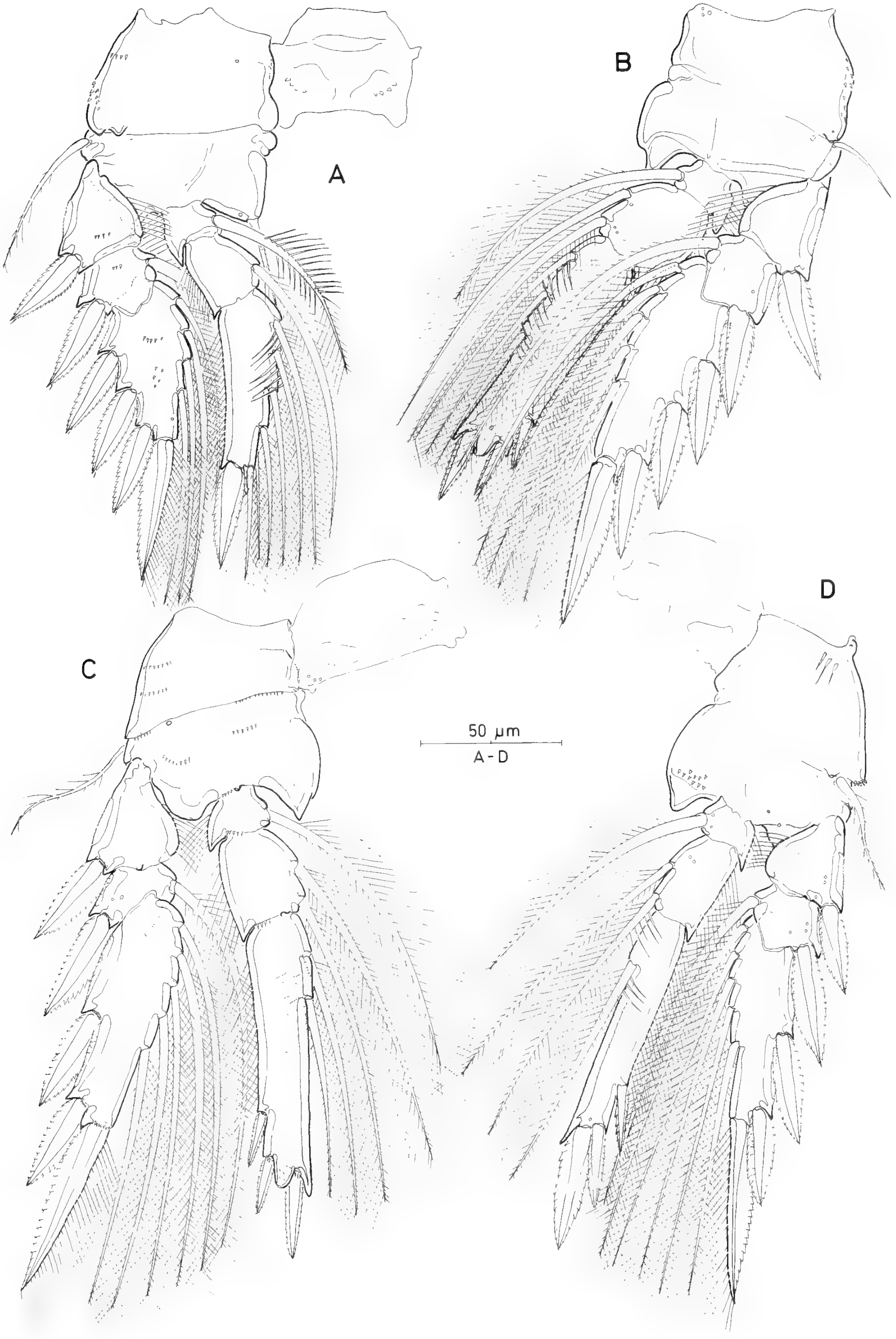

Fig. 13 *Oncaea venusta* f. *venella*, female (Red Sea) (**A**) P1, posterior; (**B**) P2, posterior, intercoxal sclerite omitted; (**C**) P3, anterior; (**D**) P4, posterior.

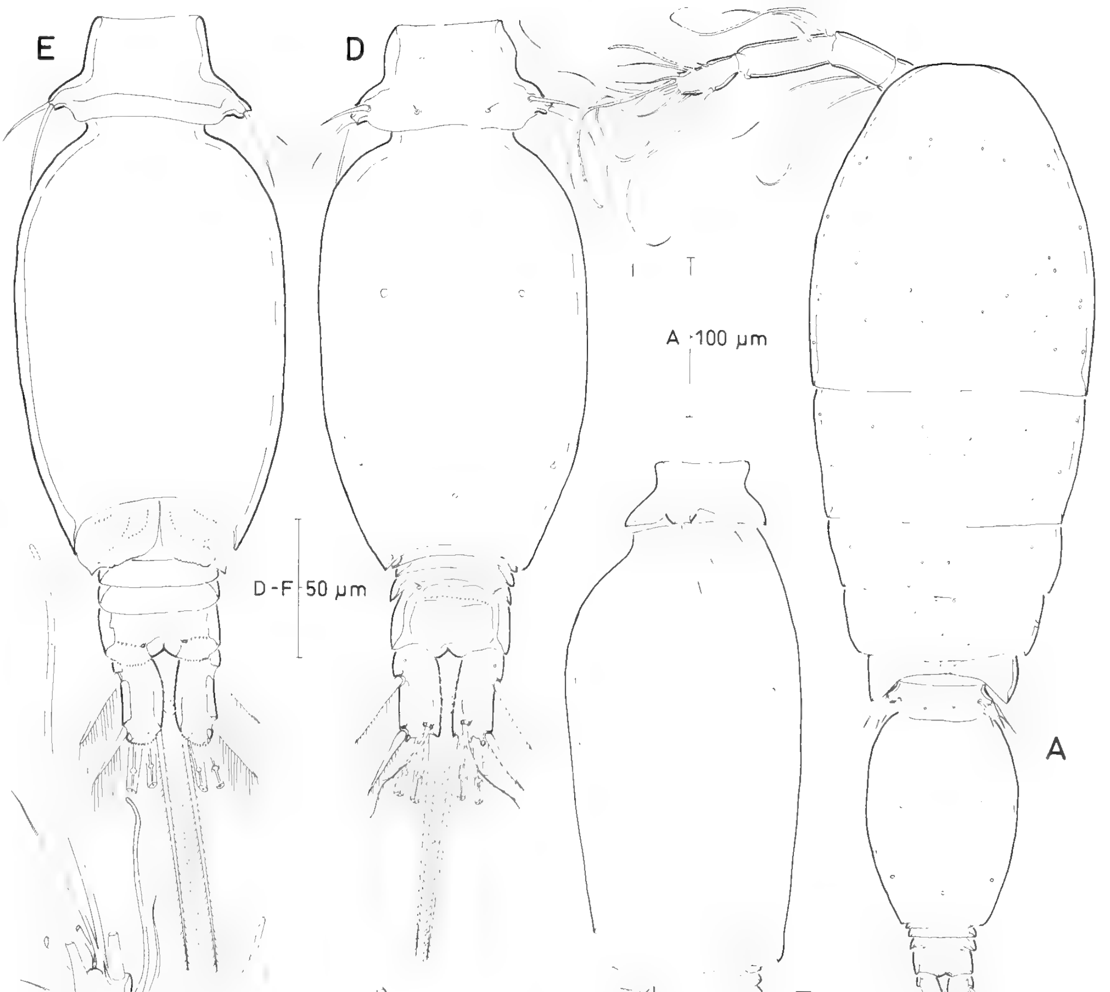

Fig. 14 *Oncaea venusta* f. *venella*, male (Red Sea) (**A**) Habitus, dorsal; (**B**) antennule; (**C**) maxilliped, anterior; (**D**) urosome, dorsal (spermatophores not fully developed); (**E**) urosome, ventral; (**F**) same, lateral; (**G**) antenna, posterior.

Specimens of *O. venusta* from the Red Sea exhibited a corresponding difference in size (Table 2) with no overlap between the two groups. No distinct regional or seasonal differences in the lengths of the two forms were observed, although specimens of f. *venella* in the central Red Sea tended to be smaller in summer as compared to autumn and winter (Table 2). Generally, Red Sea specimens of f. *venella* are smaller than elsewhere, which might be related to the extreme environmental conditions in this basin (Böttger-Schnack *et al.*, 1989). Sizes of f. *typica*, on the other hand, correspond well to those reported from other regions (Böttger-Schnack *et al.*, 1989). A possible explanation for this may be that the large morph penetrates the Red Sea during a limited period only (see below under *Ecological notes*) and does not survive as an indigenous population in this area.

Alternative explanation could be that smaller individuals of f. *venella* may not have been collected during earlier investigations, because nets with fairly large mesh sizes of about 0.3 mm were used (e.g Boxshall, 1977b). However, this would not explain the absence of intermediate sizes, measuring between 0.9–1.0 mm (♀) and 0.75–0.85 mm (♂) in length, in *O. venusta* from the Red Sea.

Morphological differences other than size between the two forms of *O. venusta* females from the Red Sea were similar to those recorded by Farran (1929) and Sewell (1947). Additional differences in body morphology found in the present study include (1) the length to width ratio of female genital double-somite, which is smaller in f. *typica* (1.5:1) than in f. *venella* (1.8:1), (2) the small dorso-posterior protrusion of the P2-bearing somite in female f. *venella*, which is not found in f. *typica*, (3) small differences in the relative lengths of distal spines on P4 endopod, which are likewise found in both sexes, and (4) the length to width ratio of male genital somite, which is smaller in f. *typica* (1.5 : 1) than in f. *venella* (1.7 : 1). The latter two characters are the only differences other than size, by which males of the two forms can be separated. The dorsoposterior swelling on the P2-bearing somite in f. *venella* was consistent for all specimens from the Red Sea and was also found in f. *venella* from the northern Arabian Sea. Altogether, the results pointed to several additional morphological differences between the two forms, which had not been noted in the literature before, but these were not regarded as sufficient to warrant distinction of the two forms as separate species.

Identification of *O. venusta* f. *typica* males during routine counts in plankton samples is facilitated by their great size and overall robust appearance. Males of f. *venella*, on the other hand, are very similar to males of *O. clevei*, which are described in the present account for the first time (see below).

Table 2 Body length (mm) of *O. venusta* in the Red Sea.

Form variant	Sex	n	X	R
AUTUMN *Northern Red Sea*				
f. *venella*	F	15	0.80	0.75–0.85
	M	6	0.58	0.57–0.59
Central Red Sea				
f. *venella*	F	24	0.80	0.75–0.85
	M	4	0.61	0.57–0.73
WINTER *Central Red Sea*				
f. *venella*	F	12	0.80	0.75–0.88
	M	16	0.59	0.55–0.65
f. *typica*	F	14	1.11	1.00–1.23
	M	7	0.92	0.88–0.95
SUMMER *Central Red Sea*				
f. *venella*	F	10	0.76	0.70–0.80
	M	1	0.56	
Gulf of Aden + Strait of Bab al Mandab				
f. *venella*	F	14	0.83	0.74–0.92
	M	3	0.60	0.58–0.63
f. *typica*	F	5	1.15	1.10–1.22

n = no. of individuals measured; X = mean; R = range

COMPARISON OF *O. VENUSTA* FORM VARIANTS WITH SPECIMENS FROM THE MEDITERRANEAN

Total body length of specimens from Naples recorded by Giesbrecht (1892) and Heron & Bradford-Grieve (1995) ranged between 1.09–1.27 mm for females, and 0.8–0.95 mm for males. This size range corresponds to that of *O. venusta* f. *typica* and most previous authors have regarded the mediterranean specimens as being conspecific with the typical form (e.g. Sewell, 1947; Tanaka, 1960). A comparison of morphological characters other than size between the two form variants from the Red Sea and specimens from the Gulf of Naples are summarized in Table 2. The Mediterranean specimens in fact seem to be more similar to the typical form than to the *venella* form. However, they also share some characters with f. *venella*, such as the form of the sclerotized structure between female genital apertures and the pore pattern of the male urosome. Two morphological characters of the Naples specimens were intermediate between the two Red Sea forms, the length to width ratio of the caudal ramus in both sexes and the length to width ratio of the genital somite in the male (Table 2). Based on these observations, it cannot be confirmed, which of the two form variants from the Red Sea is conspecific with *O. venusta* Giesbrecht sensu Heron & Bradford-Grieve. The length to width ratio of caudal ramus has been found to be very variable among specimens of *O. venusta* (Boxshall, 1977b) and this might also apply to the pore pattern. Malt (1983c) investigated the integumental pore patterns of females of the two *venusta* forms, based on material collected in the Atlantic, however, did not find any significant differences between them and/or the third 'robust' form variety. Males were not investigated during her study.

OTHER RECORDS OF *O. VENUSTA* FORM VARIANTS

The geographical distribution of the size morphs of *O. venusta* is poorly documented (Malt, 1983a). Farran (1936) reported a great size variation in specimens from the Great Barrier Reef, but could not distinguish the two form variants, which he previously had described from the temperate and tropical Atlantic and off New Zealand, because many specimens intermediate in size occurred.

Sewell (1947) recorded two variants of *O. venusta* from the northern Arabian Sea (discussed above), and concluded that they might have slightly different breeding seasons, since both exhibited different proportions of ovigerous females and of females bearing spermatophores in the samples. He summarized the geographical distribution of *O. venusta* known at that time and concluded that the smaller f. *venella* form was absent in the Mediterranean. However, both forms of *O. venusta* were recorded from Lebanese waters by Malt *et al.* (1989) without further descriptive details. In the quantitative study of Böttger-Schnack (1996) conducted in the Eastern Mediterranean, *O. venusta* was totally absent.

Tanaka (1960) recorded two size groups (1.13–1.39 mm and 0.90–1.0 mm, respectively) among female *O. venusta* from the Indian Ocean and off Cape of Good Hope, as well as from Antarctic waters; specimens from Japanese waters (South China Sea) belonged to the typical form only. He did not find any structural differences between the two forms, except for a somewhat more slender prosome in f. *venella* as compared to f. *typica*. The caudal rami were four times longer than wide in both forms, irrespective of sex; this is unusual for species of *Oncaea* s. str., which typically have

Table 3 Comparison of morphological characters of *Oncaea venusta* Giesbrecht from the Gulf of Naples with two forms, f. *typica* and f. *venella*, from the Red Sea.

	Gulf of Naples	Red Sea	
Species/form		f. *typica*	f. *venella*
Female			
Ornamentation on surface of prosome (ridges, etc)	very strong	strong	present, less strong
P2-bearing somite with dorso-posterior swelling	no	no	yes
Genital double-somite			
l : w ratio	1.4 : 1	1.5 : 1	1.8 : 1
anterior part produced dorsally	yes	yes	no
sclerotization between gen.ap.			
– form	double-scalloped	paired s-shaped	double-scalloped
– location	between gen.ap.	anterior to gen.ap.	between gen.ap.
Caudal ramus, l : w ratio	3.0 : 1	3.5 : 1	2.8 : 1
P4 enp-3, ratio of DS:ODS	1.5 : 1	1.3 : 1	1.5 : 1
Male			
Genital segment			
l : w ratio	1.7 : 1	1.5 : 1	1.7 : 1
no. of pores on dorsal surface	5	11	5
Caudal ramus, l : w ratio	2.2 : 1	2.5 : 1	1.9 : 1

DS = distal spine; ODS = outer distal spine; gen.ap. = genital apertures; P2, P4 = swimming legs 2, 4; enp-3 = third endopod segment; l = length; w = width; no. = number

a smaller length to width ratio of caudal ramus in the male (see above under 'Generic diagnosis'). The length to width ratio of the male genital segment was greater in f. *venella* (1.6 : 1) than in f. *typica* (1.3 : 1), which is in accordance with results from the Red Sea. The body lengths of males in Tanaka's study ranged between 0.74–1.07 mm, with no separation given for the two groups.

Corral Estrada (1970) recorded two forms of female *O. venusta* from the NE Atlantic, near Tenerife, which differed mainly in size (1.05–1.25 mm and 0.87–0.95 mm). Small differences were also found in overall body proportions, the *venella* form being more slender.

Ferrari (1975) recorded two size groups for both sexes of *O. venusta* from the Gulf of Mexico, measuring 1.1–1.2 mm or 0.92–0.99 mm (females) and 0.76–0.86 mm or 0.57–0.63 mm (males). Both groups occurred over the entire period (4 yrs) of his study, without exhibiting any overlap in size. No morphological differences other than size were noted by the author. His illustration of the male antenna of the typical form (his Fig. 6D) shows a long, plumose seta on the coxobasis, not the small naked one usually found in *O. venusta* (cf. Fig. 6H, 14G).

Boxshall (1977b) reported both size morphs of female *O. venusta* from the NE Atlantic, near the Cap Verde Islands, and in another report gave detailed information on their vertical distribution and diurnal vertical migration (Boxshall 1977a). The two forms differed only in size, with a mode length of 1.13 mm for f. *typica* and 0.98 mm for f. *venella*. No other detectable differences were recorded. The length frequency distribution of both forms (his Fig. 13) shows very little overlap in size between the two groups. Males were not distinguished into size groups during his study, their length ranged between 0.96–1.08 mm with a mean of 1.01 mm. Both sexual dimorphic characters of the male antenna (naked seta on coxobasis and modified seta on lateral armature) were illustrated by Boxshall (his Fig. 12b). The terminal accessory seta on the male caudal ramus, however, was figured as being less than twice the length of CR, whereas it is more than twice the length in *O. venusta* from Naples and the Red Sea. In addition to the two forms known at that time, Boxshall also recorded a few female specimens of a third 'robust form', which was more squat in general appearence and differed in the length to width ratio of the caudal ramus. The length of the specimens ranged between 0.88–1.4 mm, thus covering the length range of both other varieties of *O. venusta*. The 'robust form', however, seemed to have a limited distribution range, because it was not discovered again in subsequent collections from other North Atlantic localities (Malt 1983c).

Recently, Itoh [in: Chihara & Murano (1997)] recorded both size morphs of *O. venusta* from Japanese waters. His descriptions of female and male habitus exhibit the same differences in overall body morphology between the two morphs as recorded here for Red Sea specimens. Also, Itoh's illustration of the male antenna [Plate 223, Fig. 371(right) c] shows the two sexual dimorphic characters typical for the species. No overlap in size between the two groups was noted by Itoh, females measured 1.09–1.23 mm (*f. typica*) or 0.86–0.94 mm (f. *venella*) and males 0.89–0.98 mm (f. *typica*) or 0.62–0.65 mm (f. *venella*). Specimens of female *O. venusta* from the Sea of Japan examined during the present study, however, covered a wide size range from 0.80–1.3 mm, and many specimens intermediate in size (about 0.96 mm) occurred. Specimens at the upper and lower end of the size range exhibited nearly all morphological characters of f. *typica* and f. *venella*, respectively, while specimens intermediate in size could be assigned to neither morph. [The same phenomenon was observed in *O. venusta* specimens from Australian waters (McKinnon material).]

In summary, the two distinct size morphs of *O. venusta*, f. *typica* and f. *venella*, are widespread in tropical and temperate regions of the Atlantic (Corral Estrada, 1970; Ferrari, 1975; Boxshall, 1977b) and the western Indian Ocean and adjacent seas, including the Red Sea (Sewell, 1947; Tanaka, 1960; this report). Records of two corresponding size groups from the Eastern Indian Ocean and the Pacific are rare, because intermediate size forms occur, which make a clear separation of the groups more difficult. This had already been noted by Farran (1936), who found specimens of *O. venusta* from the Great Barrier Reef covering a wide size range, without being able to separate them into the two groups. Further studies on *O. venusta* from Pacific localities are required in order to define their morphological relationship to Atlantic and western Indian Ocean populations. The present results, based on both light and SEM microscopy, pointed to several morphological differences between the two *venusta* forms, which had not been noted before. However, these were not regarded as sufficient to warrant recognition of the two forms as separate species. Alternative taxonomic techniques, such as molecular analysis, may permit examination of any genetic differentiation between the forms of this ubiquitous species. A study on the molecular genetics of *O. venusta* size variants from the Atlantic is in progress and future morphological studies in other areas are recommended.

OTHER RECORDS OF *O. VENUSTA*

O. venusta is widely distributed at mid- and low latitudes, between approximately 50°S and 65°N (Malt, 1983a, b). Due to its relatively large size and the characteristic habitus of the female, it is one of the best documented oncaeid species in the world.

Halim (1969) listed *O. venusta* as one of the 'perennial-indigenous' species of the Red Sea, being distributed throughout the main basin and the Gulf of Suez all year round. His compilation of earlier records did not differentiate between the two forms of the species, which were found to exhibit considerable differences in regional and seasonal distribution in the Red Sea (see below under *Ecological notes*).

Wilson (1932) recorded *O. venusta* as the most abundant species of the genus in the Woods Hole region. The length range of his specimens (♀♀: 1.1–1.27 mm, ♂♂: 0.8–0.95 mm) indicates that he had collected the typical form, however, his illustration of dorsal aspect of the female (Fig. 213A; from W.M. Wheeler) shows the form of genital double-somite to be more similar to f. *venella*.

In the Western Pacific area, Mori (1937, reprinted 1964) figured *O. venusta* from Japanese waters and Dakin & Colefax (1940) recorded it as the commonest species in the coastal waters of Australia (New South Wales). Chen *et al.* (1974) described the species from the Yellow Sea and the East China Sea. Their illustration of P4 endopod (Plate 6, Fig. 3) shows 2 inner setae on distal segment which is not found in any species of *Oncaea* s. str. This requires confirmation. The length range reported by Mori (♀♀: 1.0–1.28 mm, ♂♂: 0.8–1.0 mm) was smaller than the sizes reported by Chen *et al.* (♀♀: 1.2–1.35 mm, ♂♂: 0.9–1.1 mm), but the dorsal habitus of females illustrated by these authors indicate that both were dealing with f. *typica*.

Olson (1949) recorded *O. venusta* from the East Pacific, off Oregon, which according to its size (♀♀: 1.25 mm, ♂♂: 0.9 mm) and female habitus might belong to the typical form. The author did not note any sexual dimorphism on the antenna or on the swimming legs.

Razouls (1974) figured *O. venusta* from the region of Banyuls-sur-mer (Golfe du Lion) and summarized previous records from the Mediterranean Sea. His illustrations lack many details, such as the genital apertures on the female genital double-somite, several elements on the antennule, antenna, P5 and the basal seta on P2–P4; moreover, the distal endopod spines in P2–P4 of his specimens are figured much longer than usually found in *O. venusta* (especially in P4). Further differences between his specimens and typical characters of *O. venusta* are found in the female caudal ramus, which is less than 3 times longer than wide and the length of caudal seta VI, which is unusually short in both sexes. The coxobasal seta on the male antenna was figured as long and plumose by Razouls, which is not the case in *O. venusta*. In summary, positive identification of his specimens can only be given after re-examination of his material.

Ho (1984) redescribed *O. venusta* based on several females collected from colonies of *Solandria secunda* (Inaba), a hydroid found at 10 m depth in Tassha Bay, Sado Island (Japan). His description differs from the present account in the setal formula of P1 endopod (4 instead of 5 setae on distal segment), in the armature of the antennule (some elements missing on segment 4 and 5), and in the armature of P6 (2 minute spinous processes not mentioned). Four females from his collection were kindly made available by J.-s. Ho. Re-examination showed that all specimens from Sado Island exhibit the typical setal formula on P1 enp-3 (5 setae). The insertion of the distalmost seta is hidden beneath the long terminal process (cf. Fig. 4A) and thus can easily be overlooked. Also, the armature of the antennule and on P6 is the same as described here. Due to their large size, Ho ascribed his specimens to f. *typica* and his opinion is followed here, although some characters, such as proportional spine lengths on P4 enp-3 were inconclusive in the two smaller specimens (0.92–0.96 mm) examined.

Humes (1988) described both sexes of a new species of *Oncaea* s.str., *O. praecalara*, collected with slurp guns or box corers during deep dives by manned deep-sea submersibles from the vicinity of deep-sea hydrothermal vents in the eastern Pacific. The main characters for the new species as summarized by Humes are: (1) its relatively large size [1.01–1.3 mm in the female], (2) extremely long caudal rami, about twice longer than anal somite and exhibiting a length to width ratio between 4.96–6.7 : 1 (measured halfway down the CR length), (3) sexual dimorphism on third segment of male antenna (not on fourth segment, as erroneously stated in his abstract), (4) labrum with nearly straight posteroventral margins. The female holotype as well as female and male paratypes of *O. praeclara* from the collection of the National Museum of Natural History, Smithsonian Institution, were re-examined, in addition to several samples of the species kindly made available by A.G. Humes. The following measurements taken of the female holotype gave strong evidence that *O. praeclara* is conspecific with *Oncaea venusta*: (1) length to width ratio of CR 4.2 : 1 (measured halfway down the CR length), 3.5 : 1 (measured proximally) [as reported in the present account], (2) maxillipedal basis with spinular row along palmar margin (not smooth as described by Humes, his Fig. 2h), (3) labrum bilobate [ornamentation on lobes not discernible without dissection of specimen], integumental pockets and slit-like pores on anterior face present. The male paratype of *O. praeclara* can be assigned to *O. venusta* on the basis of (1) the sexual dimorphism of antenna, with coxobasal seta short and naked (not noted by Humes), seta I on second endopod segment curved, and (2) the pore pattern on dorsal surface of genital segment (11 pores).

Humes' account of *O. praeclara* may have been based on two different species: the form of the genital double-somite and the position of the genital apertures differ considerably between his Fig. 1a (habitus, dorsal) and Fig. 1c (urosome, dorsal). The extremely elongate CR noted by Humes (his Fig. 1c, e) was found neither in the female holotype nor in any of the specimens re-examined, but may have been present in other specimens. Fig. 1c and 1e (caudal ramus) as well as Fig. 2h (maxilliped) of Humes (1988) are regarded here as belonging to a different species, which, however, could not be traced in his material, although some of the samples contained a mixture of oncaeid species (see 'Material examined' above). The remaining figures of Humes seem to be identical with *O. venusta*. Like Ho (1984), Humes erroneously figured the distal endopod segment of P1 with 4 outer setae, instead of 5. He also missed one seta on the distal armature in the male antenna.

Huys & Boxshall (1991) illustrated several appendages and a dorsal view of the female urosome of *O. venusta*, based on specimens from the North Atlantic. Their Fig. 2.10.10.A of the mandible shows 4 dentiform processes along the distal margin, whereas only 3 processes are found in specimens from the Red Sea (Fig. 3D, 7D) and in those from the Gulf of Naples (Heron & Bradford-Grieve 1995, their Fig. 14J). The authors erroneously figured the female P5 with 1 exopodal seta only (their Fig. 2.10.21.B), not with 2 setae as usually found in *O. venusta*.

Many more records of *O. venusta* from different localities of the world ocean are known [see Malt (1983a) for a review], but are not considered here, because they did not include figures or a description that positively identified the species.

ECOLOGICAL NOTES

O. venusta f. *venella* is much more abundant than f. *typica* in the Red Sea, exceeding the population densities of the latter by a factor of between 3 to 100, when both forms co-occur (Böttger-Schnack, 1990b, 1995).

GEOGRAPHICAL DISTRIBUTION

In the Red Sea, *O. venusta* f. *venella* is more widespread than *O. venusta* f. *typica*, it occurs throughout the main basin (Böttger-Schnack, 1990a, b, 1995) and was also found in samples from the northernmost part of the Gulf of Aqaba (unpubl. data). *O. venusta* f. *typica* is mainly restricted to the southernmost Red Sea and the Gulf of Aden, reaching the central Red Sea only during the winter months, when a strong seasonal inflow of southern Red Sea waters influences the plankton fauna in the central area (Böttger-Schnack, 1990b; see also Weikert, 1987; Beckmann, 1996).

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

O. venusta is mainly distributed in the epipelagic zone in the Red Sea, with maximum abundances in the 0–100 (150) m depth layer (Böttger-Schnack, 1990 a, b). Occasional finds of the species in the bathypelagic zone (unpubl. data, see also Beckmann, 1996) were usually regarded as moribund specimens or may be due to contamination of the nets.

When co-occurring, the two forms of *O. venusta* tend to be vertically separated: Both sexes of *O. venusta* f. *typica* were concentrated in the upper epipelagic zone at 0–20 m (Strait of Bab al Mandab) or at 0–40 m (Gulf of Aden) during summer, whereas female f. *venella* occurred deeper in the water column, with maximum concentrations at 20–60 m (Bab al Mandab) and (20)80–100 m (Gulf of Aden), respectively. Male f. *venella* occurred at the same depth horizon as females in the Gulf, but were concentrated somewhat shallower than females (0–40 m) in the Strait, thereby extending into the depth horizon where f. *typica* dominates. No corresponding vertical separation of the two forms became obvious in the central Red Sea during winter, when both forms stayed in the upper 50 m during day and night (Böttger-Schnack, 1990b). However, the sampled depth strata in the epipelagic zone were broader during winter (50 m-intervals) than during summer (20 m-intervals) and thus a vertical segregation may not have been detected due to the limitations in the sampling strategy.

In the central and northern Red Sea, *O. venusta* f. *venella* was mainly concentrated in the lower epipelagic zone, within and below the strong seasonal thermocline, during autumn (Böttger-Schnack, 1990a). Diurnal vertical migration of moderate intensity was observed during this season, with specimens showing a stronger tendency to concentrate within the depth range of maximum temperature gradients during the night than during the day. From autumn to winter, a conspicuous shift of the population centre from the lower epipelagic zone (40– 100 m) to shallower depths (0–50 m) was observed, which coincided with the weakening of the thermocline during the winter season (Böttger-Schnack, 1990b). Males of *O. venusta* f. *venella* generally exhibited the same depth distribution as females, but were evaluated semi-quantitatively during the autumn survey only.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

Seasonal variation in abundance in the central Red Sea was most conspicuous for *O. venusta* f. *typica*, which occurred in the central area only during winter, but was absent during summer and autumn (Böttger-Schnack, 1990b, 1995). By this, a strong inflow of southern Red Sea populations into the central area was indicated, and the species has been regarded as an indicator species of southern Red Sea waters, similar to other copepod species, such as species of *Eucalanus* (Beckmann, 1984, 1996). Abundances of *O. venusta* f. *venella* in the central Red Sea were highest during winter, but moderately high densities were also found during autumn, thereby indicating a lesser influence of the southern inflow than was observed for f. *typica*.

Oncaea mediterranea (Claus, 1863)

Antaria mediterranea Claus (1863): 159-160, Tafel XXX, Fig. 1–6 (♀), 7 (♂).

Oncæa mediterranea (Claus, 1863); *Oncäa mediterranea* (Claus, 1863).

OTHER DESCRIPTIONS. Giesbrecht (1892) [as *Oncäa mediterranea*]; Heron (1977); Heron & Bradford-Grieve (1995); for further details see Böttger-Schnack & Huys (1997b).

TYPE LOCALITY. Tyrrhenian Sea; Messina.

PRELIMINARY NOTE. A detailed redescription of *O. mediterranea*, based on material from the Red Sea and the Eastern Mediterranean, has recently been published by Böttger-Schnack & Huys (1997b), including a review of the taxonomic history of the species. The following corrective note describes additional morphological details, which were not mentioned in the previous account, but might be of importance for constructing phylogenetic relationships within the genus *Oncaea* s. str.

CORRECTIVE NOTE

(1) The labrum of *O. mediterranea* exhibits an additional patch of long spinules on posterior face at posterior part of each lobe, similar to *O. venusta* (cf. Fig. 3C), which was not figured by Böttger-Schnack & Huys.

(2) The endopodal spines of P1 exhibit a subapical tubular extension, similar to *O. venusta* (cf. Fig. 4A). These extensions seem to be widespread among oncaeids as they have been found in distantly related species, such as *Archioncaea arabica* (Böttger-Schnack & Huys, 1997a), species of *Triconia* (Böttger-Schnack, 1999), *O. subtilis* (Böttger-Schnack & Huys, in press) and species of the *atlantica*-group (unpubl. data).

(3) The coxa of P4 is ornamented with a patch of long setules on posterior face, similar to *O. venusta* (cf. Fig. 4D).

(4) The female P6 is ornamented with 1 spine and 2 spinous processes, as in all other species of *Oncaea* s.str., not only 1 spinous process as erroneously figured by Böttger-Schnack & Huys.

(5) In addition to the sexually dimorphic characters described by Böttger-Schnack & Huys, sexual dimorphism is expressed in the endopods of P1–P3, in the ornamentation of P5, and in the length of caudal setae: (1) in P1, the spinous outgrowth at the distal margin of the endopod is relatively longer in the male, reaching half the length of the distal spine, (2) in P2–P3, the conical projections on enp-3 are relatively longer in the male as compared to the female, similar to *O. venusta* (cf. Fig. 7B, C, E, F), (3) the outer long seta on P5 exopod is ornamented with triplicate row of minute spinules along entire length, not naked as in female, (4) caudal setae VI and IV are relatively shorter in the male as compared to the female, which was correctly figured by Böttger-Schnack & Huys (their Fig. 4A), but erroneously described as being equal in length to the female in the text.

Oncaea media Giesbrecht, 1891

Oncaea media Giesbrecht (1891): 477.

Oncäa media Giesbrecht (1892)

RELIABLE DESCRIPTIONS. Giesbrecht (1892): 591–600, 602, 603, 756, 757, 774, Plate 47, Fig. 1 (not Fig. 11), 29–33, 40 [as *Oncäa media*]; Tanaka (1960): 69,70, Plate XXXI, Figs. 4–9; Heron & Bradford-Grieve (1995): 36, 39, Figs. 15k, 16a–k, 17a–i, 26b; Itoh [in: Chihara & Murano 1997]: 980, Fig. 365a–f.

DOUBTFUL DESCRIPTIONS. Dakin & Colefax (1940): 117, Fig. 205C a [♀ only]; Chen *et al.* (1974): 41–42, Plate 6, Figs. 12–15; Mori (1937; reprinted 1964): 120–121, Plate 66, Figs. 14–18.

TYPE LOCALITY. not specified; original description based on material from various locations near the equator in the tropical Pacific.

PRELIMINARY NOTE. Giesbrecht's original material of *O. media* was not available for study, because it is not allowed to be sent out on loan (A. Ianora, Zoological Station Naples, pers. comm.). Heron & Bradford-Grieve (1995) gave an excellent redescription of *O. media* based on specimens from the Gulf of Naples and provided a summary of its distribution in the Pacific Ocean and other areas. They pointed to the great similarity between *O. media* and *O. scottodicarloi*, which they described as a new species, and cleared up the confusion in Giesbrecht's (1892) redescription with regard to these two species. Specimens from the Red Sea agreed in almost every detail with the redescription of Heron & Bradford-Grieve (1995). However, some morphological characters are described below, which were not noted by Heron & Bradford-Grieve and/or appeared to differ between the two areas. Also, the body dimensions of the species from the Red Sea calculated by the different methods used throughout this study are provided.

MATERIAL EXAMINED.

(1) Northern Red Sea, 22° 58.4'N, 37° 19.4'E: Stn. 663; *R/V Meteor* leg 5/5: collected 20 July 1987 with MSN 0.05 mm net (Haul 17/4); depth 50–100 m; total water depth ca 1200 m.
  (a) 2 ♀♀ in alcohol (BMNH 1998.2797–2798).
  (b) 1 ♂ in alcohol (ZMH K-39584).
  (c) 1 ♀ dissected on slides, 2 ♀♀ in alcohol; 1 ♂ dissected on slides, 2 ♂♂ in alcohol (RBS).
(2) Gulf of Aden, 11° 55.5'N, 43° 37.9'E: Stn. 631; *R/V Meteor* leg 5/5: collected 11 July 1987 with MSN 0.05 mm net (Haul 3/5); depth 0–50 m; total water depth ca 1400 m.
  (a) 2 ♀♀, 2 ♂♂ in alcohol (BMNH 1998.2799–2802).
  (b) 2 ♀♀, 2 ♂♂ in alcohol (ZMH K-39585).
  (c) 2 ♀♀ (1 ovigerous), 2 ♂♂ in alcohol, (RBS).

DESCRIPTION. Note illustrations are based on 1 (c).

ADULT FEMALE (Fig. 15).
Body length: 884 µm [traditional method: 710 µm, range: 650–770 µm, based on 22 specimens (Böttger-Schnack *et al.*, 1989)].

Exoskeleton moderately chitinized. Prosome 2.6 times length of urosome, excluding caudal rami, 2.2 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection visible in lateral aspect (Fig. 15B). Integumental pores on prosome as indicated in Fig. 15A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 13.0 : 62.7 : 8.5 : 6.1 : 9.7. Proportional lengths (%) of urosomites and caudal rami 11.4 : 55.2 : 7.5 : 5.3 : 8.5 : 12.1.

Genital double-somite 1.9 times as long as maximum width (measured in dorsal aspect) and 2.6 times as long as postgenital somites combined (Fig. 15C). Genital apertures with armature represented by 1 spine and 2 minute spinous processes (Fig. 15I) [the latter 2 not mentioned by Heron & Bradford-Grieve]. Double-curved sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 15C.

Anal somite 2.0 times wider than long; about 2/3 length of caudal rami (Fig. 15C). Ornamentation as in *O. venusta*.

Antennule with armature as for genus, small element on 6th segment (arrowed in Fig. 15 D) not mentioned by Heron & Bradford-Grieve.

Antenna as figured by Heron & Bradford-Grieve (their Fig. 16c), except for seta I of lateral armature on first endopod segment slightly longer than figured by these authors; additional surface ornamentation on coxobasis as in *O. waldemari* (cf. Fig. 25A).

Labrum (Fig. 15E, F) as for *O. venusta*, but lacking patch of setules on posterior face at posterior part of each lobe. [*O. media* is the only species of *Oncaea* s.str. that misses these setules.]

Mandible mainly as figured by Heron & Bradford-Grieve (their Fig. 16e), except for dorsal blade (C) ornamented with 4 dentiform processes at distal margin, 1 of them inserted subdistally, and 1 minute process halfway at dorsal margin (Fig. 16E). Maxillule, maxilla and maxilliped mainly as figured by Heron & Bradford-Grieve (their Figs. 16f–h), but with additional surface ornamentations and microstructures, such as 2 large secretory pores (not 1) on surface of maxilla and third single row of shorter spinules along outer margin of strong maxillary spine (similar to *O. waldemari*, cf. Fig. 25F). [Complete pattern of microstructures on surface of exoskeleton not additionally figured in present account, but generally similar to those observed for *O. venusta* and *O. waldemari*].

Swimming legs with armature as for genus and surface ornamentation similar to *O. waldemari* (cf. Figs. 26A–D). P1–P4 with spines on exp-1 longer than figured by Heron & Bradford-Grieve (their Figs. 16i–k, 17a), reaching beyond half length of spine on exp-2. P1 with inner basal element minutely pinnate (Fig. 15G), not naked as figured by Heron & Bradford-Grieve; distal margin of exp-1 and -2 ornamented with long spinules anteriorly as in *O. scottodicarloi* (cf. Fig. 23C).

P5 (Fig. 15H) with exopod longer than wide, length to width ratio 1.7 : 1.

P6 (Fig. 15I) armed with a spine and 2 small spinous processes [the latter 2 not mentioned by Heron & Bradford-Grieve].

Egg-sacs not observed.

ADULT MALE (Fig. 16).
Body length: 672 µm [traditional method: 560 µm, 1 specimen]. Sexual dimorphism in antennule, antennary setae, maxilliped, P1–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.2 times the length of urosome, excluding caudal rami, 1.9 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 12.3 : 66.4 : 4.3 : 3.7 : 4.3 : 8.6; proportional lengths (%) of urosomites (caudal rami included) 10.9 : 58.7 : 3.8 : 3.3 : 3.8 : 7.6 : 11.9. Caudal rami about as long as wide, much shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 2/3 the length of seta IV and 3 times the length of caudal ramus (Fig. 16A).

Antennule with armature as for genus.

Antenna (Fig. 16D) as in female, except for seta on coxobasis naked and shorter than in female [not mentioned by Heron & Bradford-Grieve]; lateral armature on distal endopod segment differing from female, with spiniform seta III much stouter and seta IV spiniform and curved, with row of dentiform processes along outer distal margin; both elements shorter than in female.

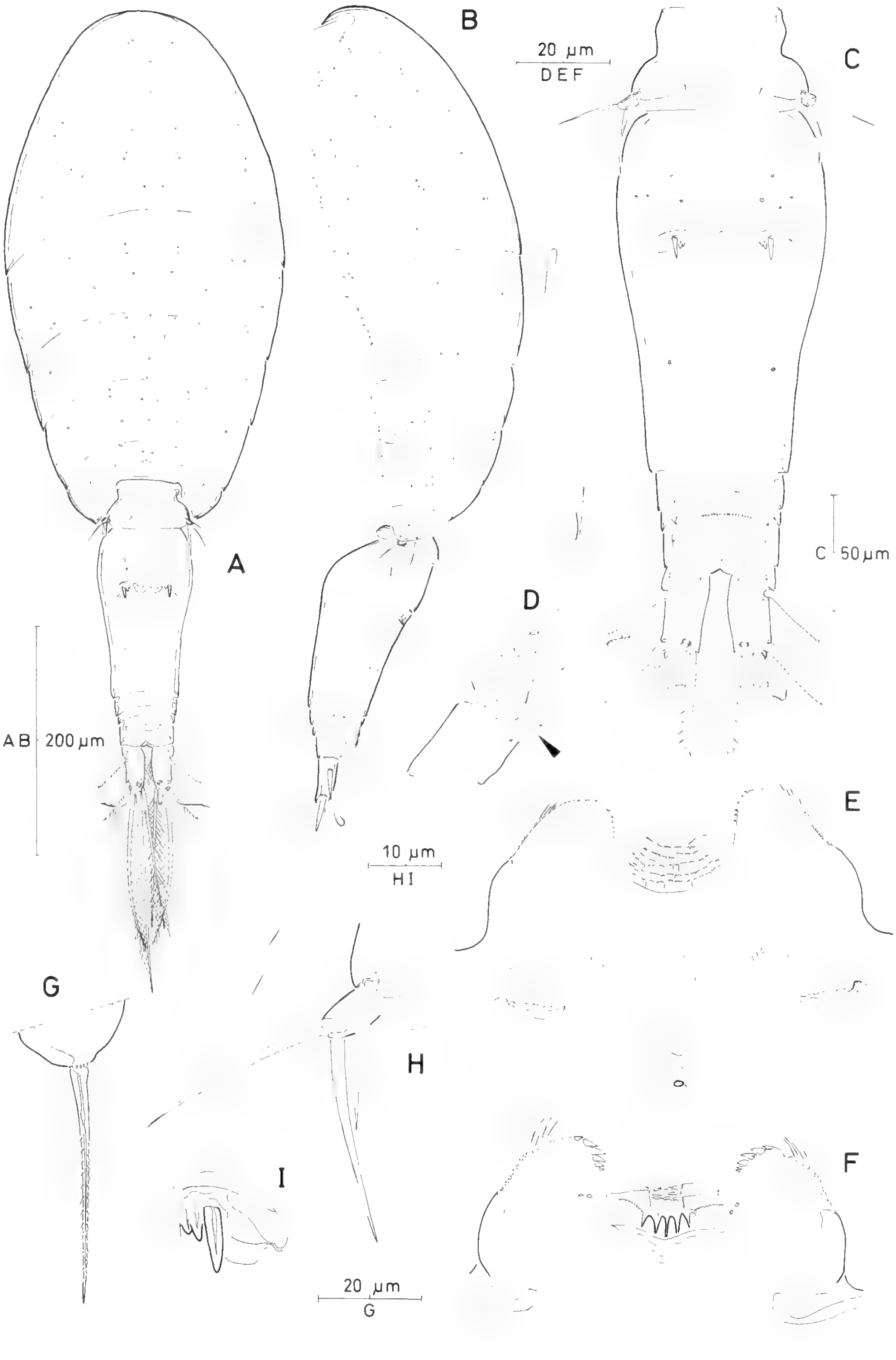

Fig. 15 *Oncaea media*, female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal; (**D**) antennule, 6th segment, small sensory element arrowed; (**E**) labrum, anterior: (**F**) same, posterior; (**G**) inner basal seta of P1; (**H**) P5, dorsal; (**I**) P6.

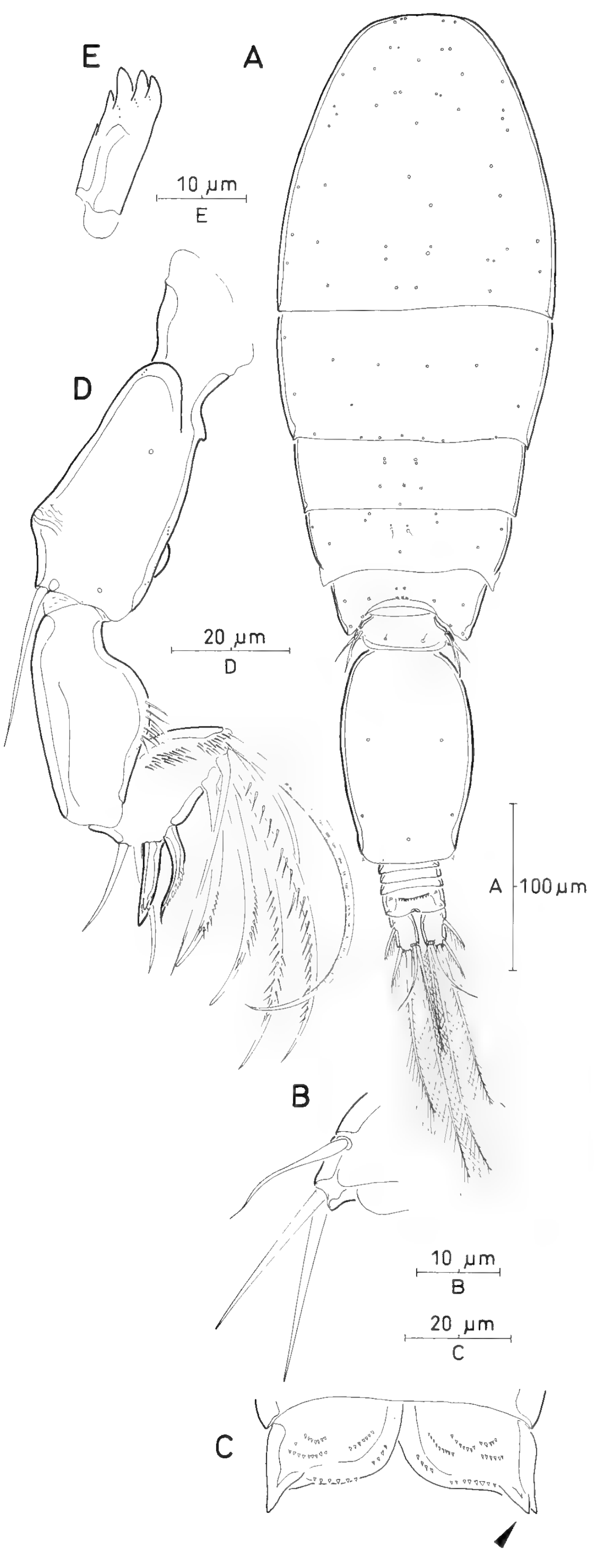

Fig. 16 *Oncaea media*, male (Red Sea) (**A**) Habitus, dorsal; (**B**) P5, dorsal; (**C**) P6, aberrant posterolateral corner arrowed. (**D**) antenna, anterior; (**E**) mandible, blade C.

Maxilliped as figured by Heron & Bradford-Grieve (their Fig. 17f).

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in (1) terminal process on P1 endopod (obscuring insertion of distalmost seta), being relatively longer than in female (similar to *O. scottodicarloi*, Fig. 23I), (2) terminal conical projections on distal endopod segment of P3 (not on P2) longer than in female, reaching 2/3–3/4 the length of outer distal spine and (3) reduced spine lengths in endopod spines of P2–P4 (Table 4).

Table 4 Sexual dimorphism in spine length (µm) on distal endopod segment of P2–P4 in *O. media* from the Red Sea. (Data represent single measurements).

	Spine length		
	Female	Male	Male : female (%)
P2			
Outer subdistal spine	20.0	10.0	50
Outer distal spine	18.1	7.5	41
Distal spine	26.3	11.3	43
P3		left/right	
Outer subdistal spine	18.8	10.6/11.3	57/60
Outer distal spine	19.4	10.6/13.8	55/71
Distal spine	32.5	25.6/25.6	79
P4			
Outer subdistal spine	24.3	16.3	67
Outer distal spine	26.3	20.6	78
Distal spine	43.8	31.3	72

P5 (Fig. 16B) exopod fused to somite, length of segment shorter than in female; proportional lengths of exopodal setae as in female.

P6 represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as in Fig. 16C; posterolateral corners with single pointed tip, occasionally with bifid tip (arrowed in Fig. 16C).

TAXONOMY

Giesbrecht (1891: 477) presented a short latin diagnosis of *O. media* and subsequently described the species in more detail from the Mediterranean, Naples area (Giesbrecht, 1892). Recently, Heron & Bradford-Grieve (1995) redescribed *O. media* from the Gulf of Naples and in the same account described a closely related species, *O. scottodicarloi*, which co-occurred with *O. media* in the Gulf. The authors pointed out an important discrepancy in Giesbrecht's (1892) description of *O. media*: all of his figures of the species matched *O. media* as re-examined by Heron & Bradford-Grieve, except for his Plate 47, Fig. 11, dorsal view of female urosome, which resembled that of the newly described *O. scottodicarloi*. [In this context it should be noted that Heron & Bradford-Grieve (1995) recorded several undescribed species similar to *O. media* and *O. scottodicarloi* in their Gulf of Naples samples, indicating that a complex of species close to *O. media* exists, which is as yet undescribed. One of the species belonging to this complex is undoubtedly *O. waldemari*, whose taxonomic position will be re-evaluated below.]

Specimens of *O. media* from the Red Sea met all important characters described by Heron & Bradford-Grieve, including patterns of integumental pores on the prosome of both sexes. Slight differences in Red Sea specimens included (1) the armature on 6th segment of antennule, the minute sensory element not noted by Heron & Bradford-Grieve, (2) additional surface ornamentation on coxobasis of female antenna and (3) spine lengths on P2–P4 enp-3 in the male. The first two characters are difficult to discern and may have been overlooked in the previous description. The reduction of spine lengths on P2–P4 enp-3 in male *O. media* was less pronounced in specimens from the Red Sea than had been reported by Giesbrecht (1892, Pl. 47, Figs. 32, 33) and Heron & Bradford-Grieve (their Fig. 17g–i). In particular the outer distal spine on P2 enp-3 was longer in Red Sea specimens, measuring about 3/4 the length of the outer subdistal spine (cf. Table 4), whereas it was figured being only 1/3–1/2 that length by the authors mentioned above. Proportional spine lengths on P2 enp-3 of *O. media* males from Japanese waters as recorded by Itoh (in: Chihara & Murano, 1997: his Fig. 365f) were similar to those found in Red Sea specimens.

O. media is closely related to *O. scottodicarloi*, with which it has often been confused. According to Heron & Bradford-Grieve (1995), important distinctions between females of the two species are found in (1) proportional lengths of urosome segments, (2) form and location of sclerotization between genital apertures, and (3) relative lengths of endopod spines of P4. Comments on the first two characters will be given below. A further character separating females of the two species as observed during the present study is the proportional length of exopodal setae on P5, the outer one being relatively shorter in *O. media* than in *O. scottodicarloi*.

(1) The typical elongate form of the genital double-somite of *O. media* as figured by Heron & Bradford-Grieve appears to be of great significance, because it enables unequivocal separation of *O. media* from other species of the *media* complex. In the original account of Giesbrecht (1892), however, the urosome is concealed underneath the paired egg-sacs of the ovigerous specimen in the illustration of female habitus (Plate 47, Fig. 1) and his illustration of the female urosome in dorsal aspect (Fig. 11) was assigned to *O. scottodicarloi* by Heron & Bradford-Grieve. Therefore it cannot be decided definitely, whether this character had also been present in Giesbrecht's specimen and the conspecificity of Giesbrecht's *O. media* with *O. media* sensu Heron & Bradford-Grieve can only be confirmed after re-examination of his type material. The lateral view of *O. media* as figured by Giesbrecht (Plate 2, Fig. 12) shows the genital segment being twice as long as the remaining part of the urosome, which is similar to *O. media* sensu Heron & Bradford-Grieve; also, the proportional lengths of spines on P4 enp-3 P4 figured by Giesbrecht are more similar to *O. media* than to *O. scottodicarloi*. Since both characters support Heron & Bradford-Grieve's conclusion, their opinion is followed in the present account.

(2) The integumental sclerotization located between the genital apertures is a reinforced attachment site for the insertion of the dorsal longitudinal trunk muscles (R.Huys, pers. commn.). These usually insert on the anterior rim of each somite, or in the case of the female genital double-somite near the genital apertures, marking the original plane of fusion. The sclerotization is always located at about 1/3 to 40% the distance from the anterior margin and does not differ between species, but as the position of genital apertures on the genital double-somite is different, the sclerotization changes its position relative to the genital apertures. In *O. media*, the genital apertures are located more laterally than in *O. scottodicarloi*, and thus the sclerotization changes its position accordingly.

Males of *O. media* can be separated from those of *O. scottodicarloi* most easily by the sexual dimorphism in the coxobasal seta of the antenna, which is short and naked (Fig. 16D) in *O. media*, but long and plumose as in the female in *O. scottodicarloi*. Giesbrecht and Heron & Bradford-Grieve did not notice the sexual dimorphism of this seta in *O. media*. In the present study, however, this character was found in all species of *Oncaea* s.str., except for *O. scottocarloi* and *O. waldemari*. The sexual dimorphism in spine lengths of P2–P4 enp-3, on the other hand, which had already been reported for males of *O. media* in both previous account mentioned above, cannot be used to distinguish between males of both species, since it was also found in *O. scottodicarloi* during the present study (Fig. 23J, M) and seems to be a typical character for males of *Oncaea* s.str. (cf. *O. venusta*, *O. waldemari*).

OTHER RECORDS OF *O. MEDIA*

A summary of the world-wide records of *O. media* has been compiled by Heron & Bradford-Grieve (1995). They point to the great confusion caused by Sewell (1947), who described two size variants, f. *major* and f. *minor*, from the Arabian Sea. The *major* form (♀♀: 0.73–0.82 mm, ♂♂: 0.53–0–62 mm) exhibited a smaller length to width ratio of caudal ramus (2:1) than the *minor* form (3:1), which would correspond to the observed differences between *O. media* and *O. scottodicarloi*. However, Sewell described the distal spine on P4 enp-3 of f. *major* measuring about 2/3 the length of distal endopod segment (p.261), which is longer than reported by Giesbrecht (1892) and Heron & Bradford-Grieve for *O. media*, the spine being only

Table 5 List of important characters separating *O. media* and related species. Data of *O. curta* after Sars (1918), remaining data from present study.

Species	*media*	*scottodicarloi*	*curta*	*waldemari*
Female				
GDS				
– l:w ratio	1.9:1	1.5:1	1.5:1	1.7:1
– Form	very el.	oval-el.	squarish	elongate
– ratio GDS : rest of urosomites[1] (excl.CR)	3.9:1	2.5:1	1.5:1	1.9:1
– position gen.ap., distance from lateral margin	1/4	1/3	ca 1/5	1/4
L. ratio caudal setae				
– seta VI:IV	2/3	1/2	ca 1/2	3/4
– seta VI:CR	3.8:1	2.2:1	ca 1:1	1.6:1
– seta VII:III	slightly longer	slightly longer	?	longer
Labrum, anterior face, paired patch of setules	no	yes	?	yes
P5 exopod				
– l:w ratio	1.9:1	1.7:1	ca1.5:1	1.3:1
– outer:inner seta	equal	slightly longer	1/2length	equal
Male				
Antenna				
– coxobasal seta	short naked	long, plumose	?	long, plumose
– endopod 2, element IV	strong-curved	curved	?	slightly curved
l. ratio caudal seta VI:VII	longer	longer	?	equal

GDS = genital double-somite; CR = caudal ramus; gen.ap.= genital apertures; el. = elongate; l = length; w = width

[1] Calculated by traditional method (i.e. telescoping of segments not considered)

1/2 length of the segment. Confusingly, Sewell refers to his figures of swimming legs, but these are not given in his account. A relatively long distal spine on P4 enp-3 is found in *O. scottodicarloi*, and it might be that Sewell had mixed up the characters of both species in his report. Since all three species of the *O. media*-complex (*O. media, O. scottodicarloi* and *O. waldemari* are found in the Arabian Sea (Böttger-Schnack, 1996, as *O. media* f. *major, O. media* f. *minor* and *Oncaea* sp. B, respectively), it is conceivable that he included the latter species in the lower size range of females as well.

Mori (1937, reprinted 1964) described the species from Japanese waters and Chen *et al.* (1974) recorded two size groups of *O. media* from the East China Sea and the Yellow Sea. In both accounts, the female genital double-somite is much shorter than in *O. media* sensu Heron & Bradford-Grieve and also seta VI on caudal ramus is too short. The same argument applies for the record of Dakin & Colefax (1940) from Australian waters. Although the illustration of the male antenna by Mori (his Plate 66, Fig. 17) shows a naked coxobasal seta, positive identification cannot be made without a closer examination of the specimens, especially in view of the extremely wide size range that was recorded for females (0.5–0.92 mm) in his account. However, the occurrence of *O. media* in the marine plankton of Japan has been confirmed in a recent excellent account by Itoh [in Chihara & Murano, 1997].

Tanaka (1960) recorded *O. media* from various locations in the East China Sea, Indian Ocean and south of Cape of Good Hope. He mentions the occurrence of two size groups, f. *major* and f. *minor*, which covered an overall size range of 0.55–0.79 mm. Sizes of the two groups were not recorded separately. His Plate XXXI, Fig. 4 clearly shows the dorsal view of female *O. media* sensu Heron & Bradford-Grieve, although he identified them as f. 'minor'. The different length ratio between subdistal and distal spines on P4 enp-3, which according to Heron & Bradford-Grieve (1995) separate *O. media* from *O. scottodicarloi*, is not apparent between Tanaka's f. *major* and f. *minor* (his Figs. 5 and 6). So it cannot be judged whether his small sized specimens are identical to *O. scottodicarloi* or probably belong to another closely related species, such as *O. waldemari*.

O. media f. *minor* sensu Malt (1982b) was assigned to *O. waldemari* during the present study and will be discussed below. In the identification key of oncaeids (Malt, 1983b) the separation between males of *O. media* and *O. venusta* needs to be revised, since the sexual dimorphism on antenna is found in both species, not only in *O. venusta*, as was erroneously stated by Malt.

GEOGRAPHICAL DISTRIBUTION

Oncaea media had been reported as *O. media* f. *major* in the previous quantitative accounts of Böttger-Schnack (1990b, 1994, 1995, 1996, 1997). The species is distributed throughout the Red Sea, but exhibits very variable abundances both seasonally and regionally. During summer, the species occurred in minimal numbers in the southern Red Sea, but exhibited higher values to the north, in the central-northern Red Sea, as well as to the south, in the Gulf of Aden and Bab al Mandab area (Böttger-Schnack, 1995).

In the northern Arabian Sea, *O. media* was found in appreciable numbers, with abundances being one to two orders of magnitude higher than in the Gulf of Aden and/or in the central Red Sea (Böttger-Schnack, 1996). The species also occurred in the Eastern Mediterranean Sea (Böttger-Schnack, 1997) in comparably low numbers.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

O. media was recorded from the central-northern Red Sea during winter (Böttger-Schnack, 1990b) and summer (Böttger-Schnack, 1995), but not during autumn, when it was completely absent or occurred as solitary finds only (Böttger-Schnack, 1990a, b). Due to its seasonality, the species had previously been assumed to be of southern origin (Böttger-Schnack, 1990b), but subsequent data from the summer season did not point to a consistent seasonal variation in the central Red Sea (Böttger-Schnack, 1995).

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

O. media was generally confined to the epipelagic zone (0–150 m) in the Red Sea, with few, isolated finds down to 900 m. The species had a unimodal distribution pattern with maximum densities in the upper epipelagic (0–50 m) and was classified as non-migratory during winter in the central Red Sea (Böttger-Schnack, 1990b). In the Gulf of Aden and Strait of Bab al Mandab, maximum densities were found at a depth of 0–20 m and 0–60 m, respectively, during summer (unpubl. data). By this, the species tended to be vertically separated from the two related species, *O. scottodicarloi* and *O. waldemari*, which generally occurred deeper and over a much wider depth range in that area.

Oncaea clevei Früchtl, 1923

Oncea clevei Früchtl (1923): 455, Tafel 26, Figs. 19–22 (♀only).

Oncaea conifera Cleve, 1901

RELIABLE DESCRIPTIONS. Früchtl (1924): 22–23, 89–91, Figs. 14,15, 60–70 (♀only); Itoh [in: Chihara & Murano (1997)]: 979, Fig. 361a, d, f (♀only).

DOUBTFUL DESCRIPTIONS. Sewell (1947): 258 [as *Oncæa clevei*]; Tanaka (1960): 66, Plate XXVIII, Figs. 7–13; Chen *et al.* (1974): 42, Plate 7, Figs. 4–7.

TYPE LOCALITY. Aru Archipelago, Indo-Pacific area.

PRELIMINARY NOTE. The original description of Früchtl (1923, 1924) lacks many details, particularly in the mouthparts, of which he described only the maxilliped. A detailed redescription of *O. clevei* from the Red Sea is given below, including a description of the hitherto unknown males. During the course of the study a closely related species was found, which is described as a new species, *O. paraclevei* sp. nov. A comparison of morphological characters separating the two species is included under *O. paraclevei* see *Remarks*.

MATERIAL EXAMINED.

(1) Central Red Sea, 21° 25.53'N, 38° 01.91'E: Stn. 130; *R/V Valdivia* leg 29: collected 28 October 1980 with MSN 0.1 mm net (Haul 117/5); depth 0–20 m; total water depth 1960 m.
  (a) 2 ♀♀ in alcohol (BMNH 1998.2803–2804).
  (b) 2 ♀♀ in alcohol (ZMH K-39574).
  (c) 1 ♀ partly dissected (maxilliped and maxilla on slides), 1 ♀ in alcohol (RBS).
(2) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m.
  (a) 1 ♂ partly dissected (urosome on slide), remaining specimen in alcohol (BMNH 1998.2805), 3 ♂♂ in alcohol (BMNH 1998.2806–2808).
  (b) 1 ♂ dissected on 10 slides (ZMH K-39575a–i), 1 ♀, 3 ♂♂ in alcohol (ZMH K-39576).
  (c) 2 ♀♀, 3 ♂♂ in alcohol (RBS).
(3) Gulf of Aden, 11° 55.5'N, 43° 37.9'E: Stn. 631a; R/V Meteor leg 5/5: collected 11 July 1987 with MSN 0.05 mm net (Haul 3/5); depth 0–50m; total water depth 1400 m.
  (a) 1 ♀, 1 ♂ (mating position, ♂ lacking urosome) in alcohol (BMNH 1998.2809–2810).
  (b) 1 ♀, 1 ♂ (mating position) in alcohol (ZMH K-39577).

(c) 1 ♂ (from mating pair) dissected on 9 slides, 1 ♀(ovigerous, from mating pair) in alcohol, 1 ♀, 1 ♂ (mating position) in alcohol (RBS).

(4) Northern Arabian Sea, 19° N, 65° E: Stn. 247; R/V Meteor leg 32/3: collected 14 May 1995 with MSN 0.05 mm net (coll. L. Postel); depth 0–50m; total water depth ca 3000 m: 1 ♀dissected on 11 slides, 1 ♀in alcohol (RBS).

(5) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; *R/V Meteor* leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 6 ♀♀in alcohol (RBS).

(6) Pacific Ocean, Great Barrier Reef; further sampling data not specified; leg G.P. Farran, 1928–1929, cf. Farran (1936); 10 specimens in alcohol, labelled *Oncaea clevei* (BMNH 1949.12.31.516): this vial contains 5 ♀♀of *O. clevei*, 1 prosome with dorsal hump and 4 damaged prosomes; 2 urosomes (1 of *O. clevei*, 1 possibly of *O. paraclevei* sp. nov.), and 2 bits of calanoid copepods).

(7) Pacific Ocean, Great Barrier Reef; further sampling data not specified; leg G.P. Farran, 1928–1929, cf. Farran (1936); more than 10 specimens in alcohol, labelled *Oncaea clevei* (BMNH 1948.4.28.140): this vial contains 22 ♀♀ of *O. clevei*, 1 ♂ Corycaeidae indet., 1 calanoid copepod.

DESCRIPTION. Note illustrations are based on (2a–2c) and (4).

ADULT FEMALE (Figs. 17–19, 21A).

Body length: 810 µm [traditional method: 640 µm, range: 620–680 µm, based on 4 specimens].

Exoskeleton well chitinized. Prosome 2.4 times length of urosome, excluding caudal rami, 2.1 times urosome length including caudal rami. P2-bearing somite with conspicuous dorso-posterior projection in lateral aspect (Fig. 17B), not varying in size between specimens examined. Integumental pores on prosome as indicated in Fig. 17A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 11.4 : 55.3 : 10.1 : 10.1 : 13.1. Proportional lengths (%) of urosomites and caudal rami 9.6 : 46.5 : 8.5 : 8.5 : 11.0 : 16.0.

Genital double-somite almost rectangular in dorsal aspect, 1.4 times as long as maximum width (measured in dorsal aspect) and 1.6 times as long as postgenital somites combined (Fig. 17C); largest width measured near anterior margin, lateral margins of genital double-somite rounded at anterior quarter, posterior part tapering slightly. Paired genital apertures located very close to dorsolateral margin at about 2/5 the distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 17H). Sickle-shaped sclerotization between, but slightly posterior to genital apertures, pore pattern on dorsal surface as indicated in Fig. 17C.

Anal somite 1.4 times wider than long; slightly shorter than caudal rami (Fig. 17C). Surface ornamentation mainly as in *O. venusta*.

Caudal ramus (Fig. 17F) about 2.3 times as long as wide. Seta VI more than 4/5 length of seta IV and 2.5 times longer than caudal ramus; seta VII about half length of seta VI and longer than seta III (Fig. 17C, F). Inner margin of somite with few long setules.

Antennule (Fig. 17E) with relative lengths (%) of segments measured along posterior non-setiferous margin 6.7 : 26.1 : 38.3 : 11.1 : 4.4 : 13.3. Armature as for genus.

Antenna (Fig. 18A) similar to *O. venusta*, except for coxobasis with fewer surface ornamentation and seta III on second endopod segment bipinnate.

Labrum (Fig. 18B,C) as in *O. venusta*, except for long fine setules missing latero-distally on outer margins of lobes. Anterior surface (Fig. 18B) with row of stout denticles on proximal part of each lobe, which are not found in *O. venusta*.

Mandible (Fig. 18D) as in *O. venusta*, except for blade C ornamented with 1 additional dentiform process halfway on dorsal margin. Maxillule (Fig. 18E), maxilla (Fig. 18F), and maxilliped (Fig. 18G) mainly as in *O. venusta*.

Swimming legs (Fig. 19A–D) with armature as for genus and surface ornamentation similar to *O. venusta*, except for less surface ornamention on coxae and bases, most obvious in P4 coxa, lacking patch of long setules on posterior surface. Endopodal and exopodal spine lengths mainly as in *O. venusta*, except for terminal spines on endopods of P1, P2 and P4 relatively longer, particularly in P4, reaching more than half the length of distal endopod segment. P2 with outer subdistal spine reaching insertion of outer distal spine; P4 with outer distal spine shorter than in *O. venusta*, about 1/2 length of distal spine. Inner basal seta on P1 naked; outer basal seta on P3 plumose.

P5 (Fig. 17G) comprising small naked seta arising from lateral surface of somite, and free unornamented segment representing exopod. Exopod twice as long as wide, bearing 2 spiniform, naked setae equal in length, which are straight.

P6 (Fig. 17H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes.

Egg-sacs paired, oval-shaped; each sac containing appr. 15–20 eggs (diameter 40–48 µm) (Böttger-Schnack *et al.*, 1989).

ADULT MALE (Fig. 20, 21A–C).

Body length: 630 µm [traditional method: 540 µm, range: 490–570 µm, based on 4 specimens]. Sexual dimorphism in antennule, antenna, maxilliped, P2–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.5 times the length of urosome, excluding caudal rami, 2.2 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 12.5 : 66.9 : 4.3 : 4.3 : 4.3 : 7.6; proportional lengths (%) of urosomites (caudal rami included) 11.0 : 58.9 : 3.8 : 3.8 : 3.8 : 6.7 : 12.0. Caudal rami about 1.8 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 3/5 the length of seta IV and 2.2 times length of caudal ramus; seta VII longer than in female, reaching about 2/3 length of seta VI (Fig. 20A).

Antennule (Fig. 20B) relative lengths (%) of segments measured along posterior non-setiferous margin 10.0 : 24.1 : 38.2 : 27.6. Armature formula as for genus.

Antenna (Fig. 20H) as in female, except for seta on coxobasis naked and shorter than in female; lateral armature on distal endopod segment differing from female, with element III being much stouter and element IV spiniform and distinctly curved; both elements shorter than in female.

Maxilliped (Fig. 20C) similar to *O. venusta*.

Swimming legs 1–4 with armature and ornamentation as in female; terminal process on P1 endopod as in female; P4 with outer distal spine half length of distal spine as in female; sexual dimorphism expressed in size of terminal conical projections on distal endopod segment of P2–P3, being relatively longer than in female, reaching 2/3 length (P2) or almost same length (P3) of outer distal spine (Fig. 21B1, B2, C). Variation in spine length as shown in Fig. 21B1, B2.

P5 (Fig. 20G) exopod not delimited from somite, general shape and armature as in female, except for exopodal setae shorter than in female.

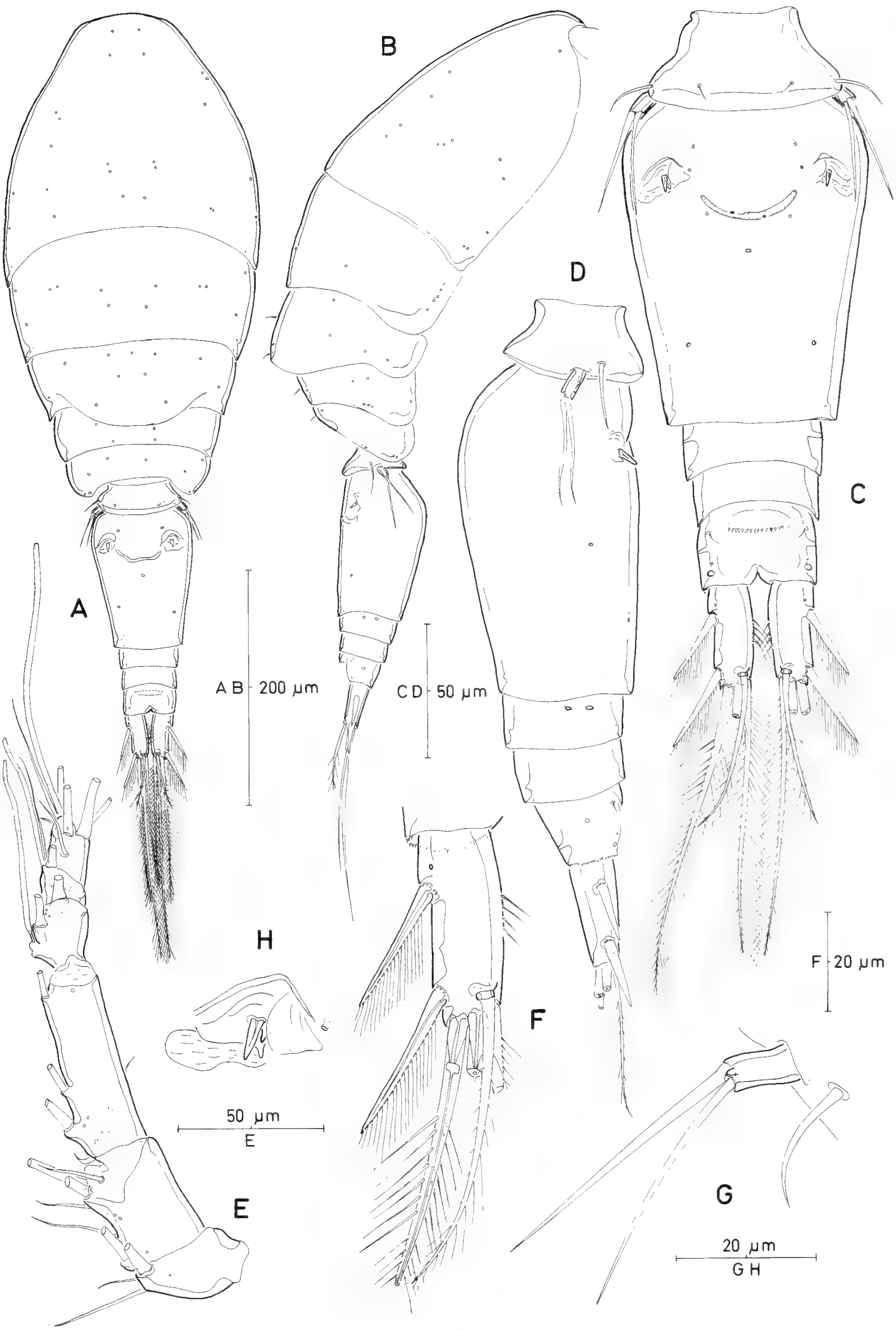

Fig. 17 *Oncaea clevei*, female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal; (**D**) urosome, lateral; (**E**) antennule; (**F**) caudal ramus, dorsal; (**G**) P5, dorso-lateral; (**H**) P6.

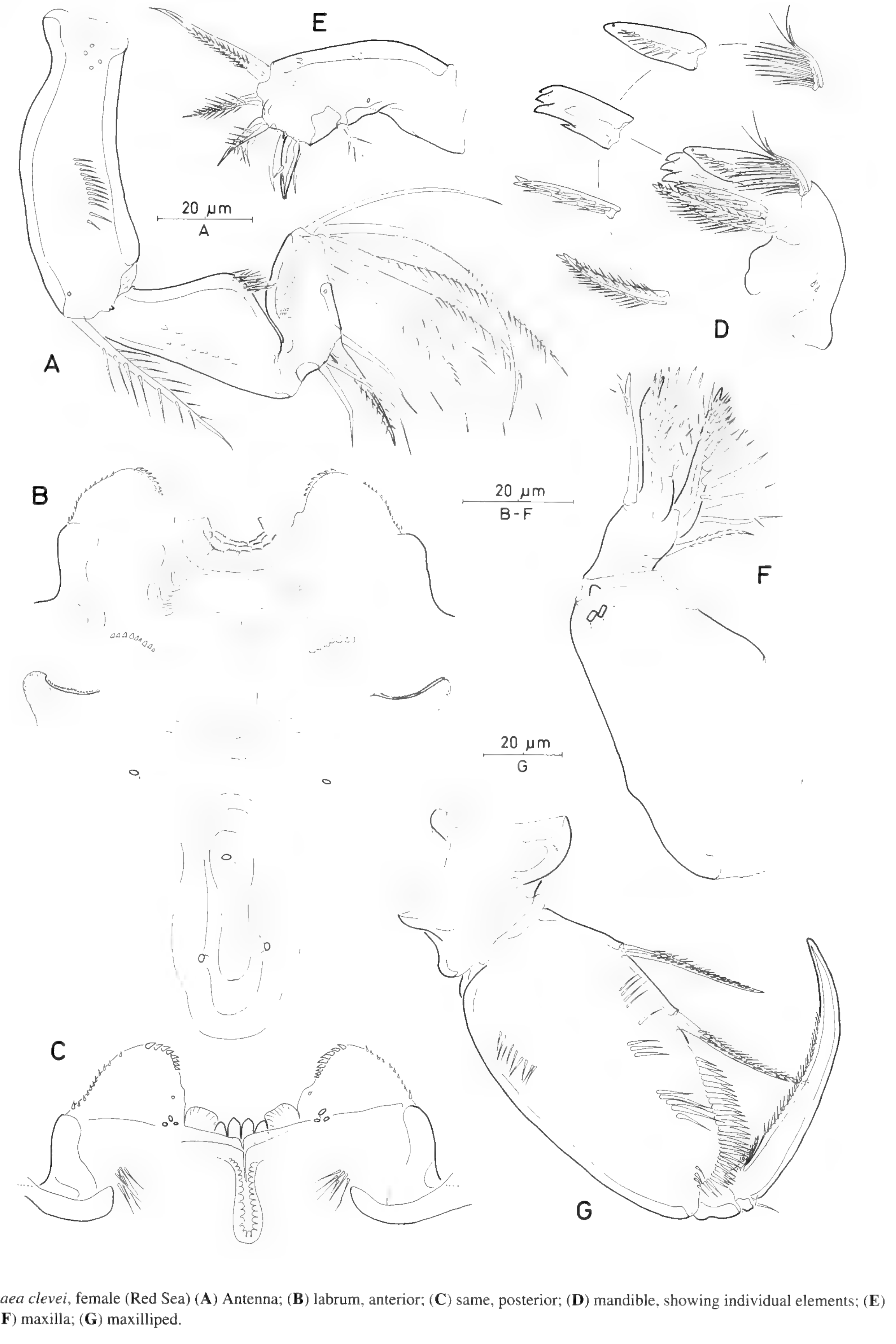

Fig. 18 *Oncaea clevei*, female (Red Sea) (**A**) Antenna; (**B**) labrum, anterior; (**C**) same, posterior; (**D**) mandible, showing individual elements; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

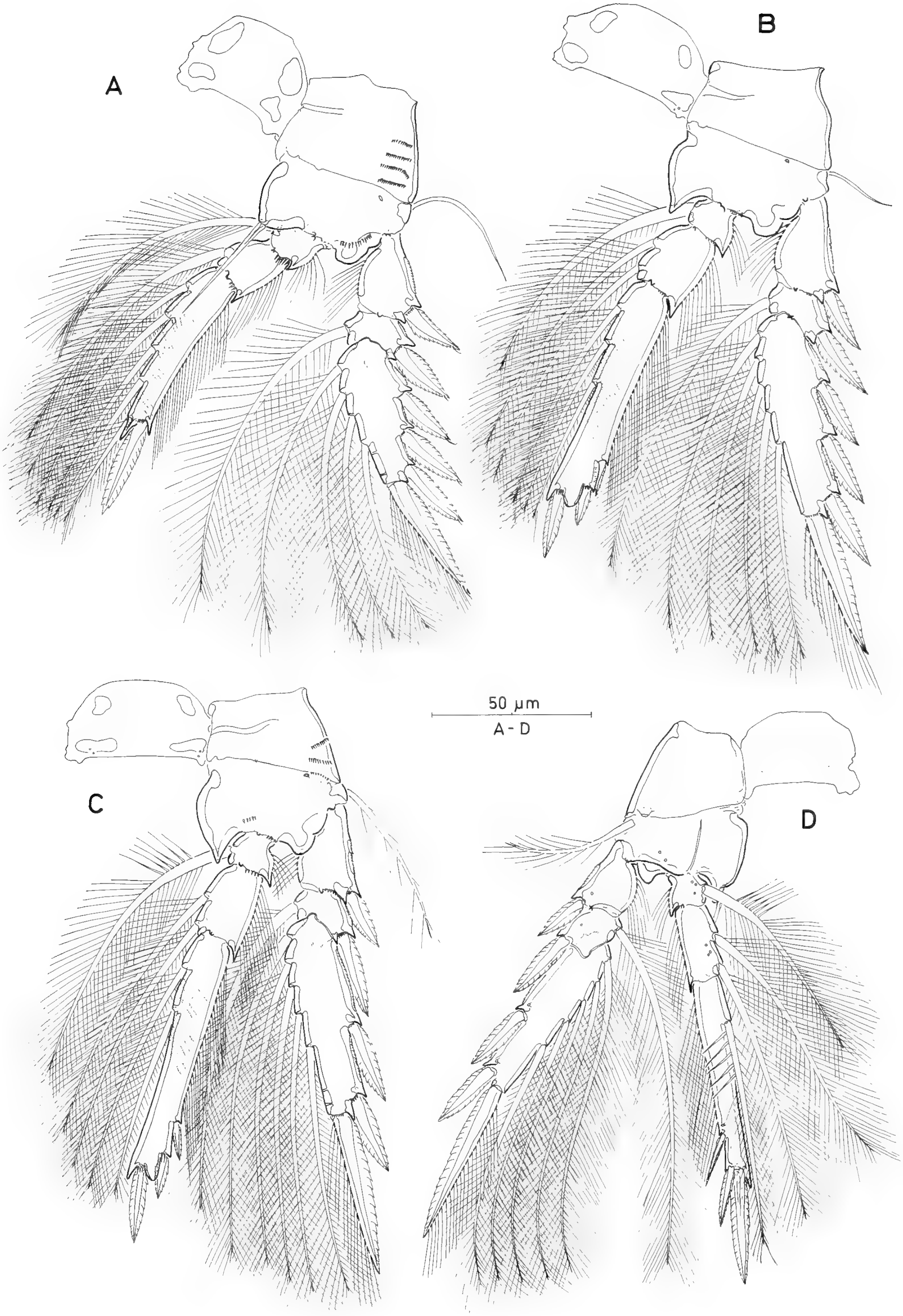

Fig. 19 *Oncaea clevei*, female (Red Sea) (**A**) P1, anterior; (**B**) P2, anterior; (**C**) P3, anterior; (**D**) P4, posterior.

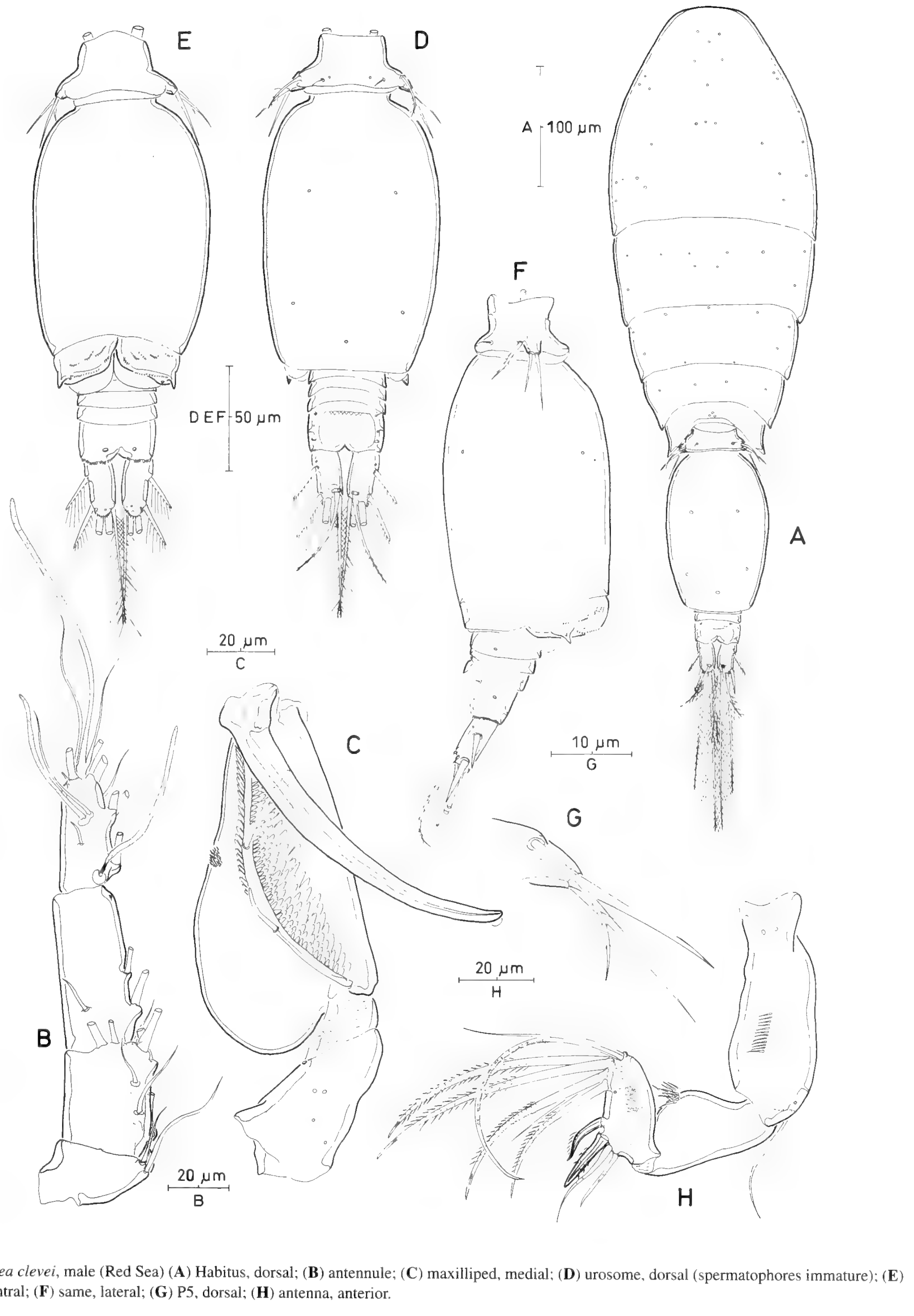

Fig. 20 *Oncaea clevei*, male (Red Sea) (**A**) Habitus, dorsal; (**B**) antennule; (**C**) maxilliped, medial; (**D**) urosome, dorsal (spermatophores immature); (**E**) urosome, ventral; (**F**) same, lateral; (**G**) P5, dorsal; (**H**) antenna, anterior.

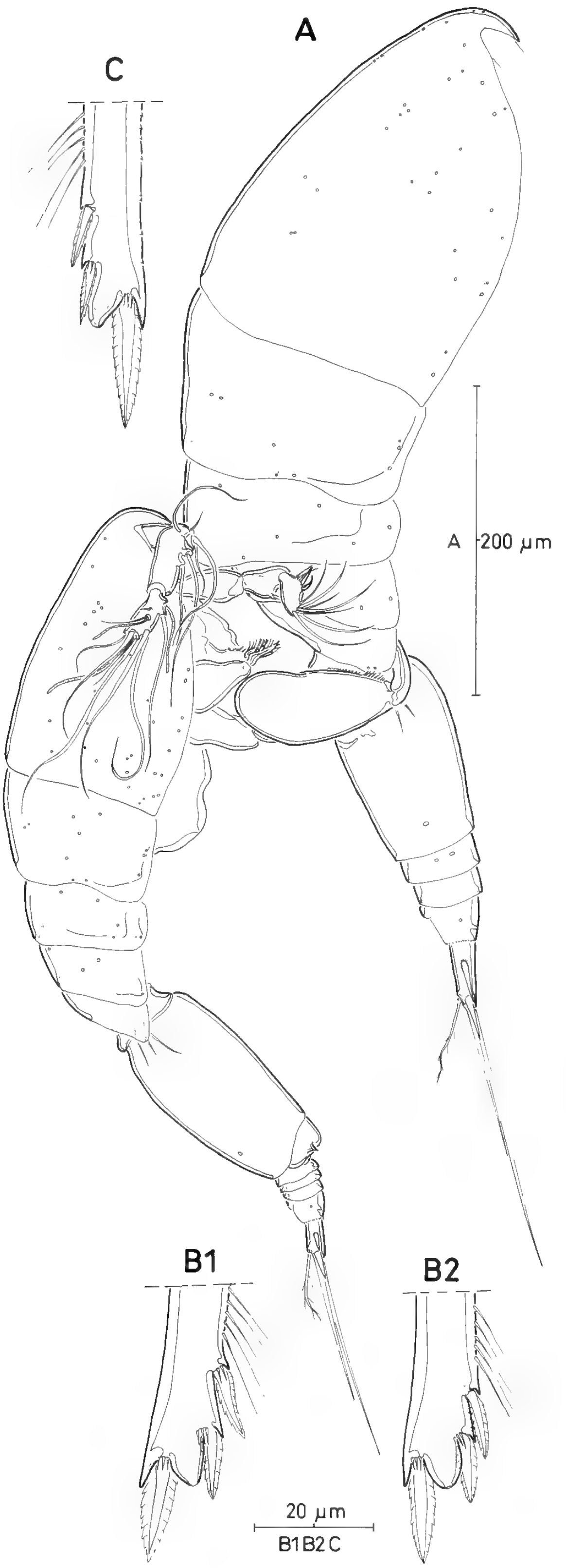

Fig. 21 *Oncaea clevei* (Red Sea) (**A**) Female and male, mating position, lateral, appendages of female and swimming legs of male omitted. *Oncaea clevei*, male (Red Sea) (**B1, B2**) P2, distal part of endopod, showing variation in spine length. (**C**) P3, distal part of endopod.

P6 (Fig. 20E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 20E.

Spermatophore oval (Fig. 20E, F), of variable size according to state of maturity.

TAXONOMY

Früchtl(1923) gave a first short diagnosis of *O. clevei* based on a single female collected near the Aru Archipelago, off Wokam, and subsequently described it in more detail (Früchtl,1924). The second account included additional specimens of *O. conifera* sensu Cleve (1901) from the Indo-Malayian Archipelago, which had been sent to Früchtl by G.O. Sars (Früchtl, 1924, footnote to p.89 (111)), and which he had synonymized with *O. clevei* after re-examination. Früchtlš figures of the female urosome (1923: Tafel 26, Fig. 19; 1924: Fig. 24) show an extremely lateral position of the genital apertures and a sickle-shaped sclerotization between, but slightly posterior to, the genital apertures. This combination of characters enables unequivocal identification of the Red Sea specimens with Früchtlš *O. clevei*. The closely related *O. paraclevei* sp. nov., which co-occurs with *O. clevei* in the Red Sea, differs in the location of genital apertures and in the form of sclerotization (see below under 'Remarks' of *O. paraclevei*). Red Sea specimens of *O. clevei* differ slightly from the original account in the length of the outer distal spine on P4 enp-3, which is about half the length of the distal spine, whereas it is shorter in *O. clevei* sensu Früchtl.The length of the outer subdistal spine on enp-3 in P2 (shorter in Red Sea specimens) and P3 (longer in Red Sea specimens) is also slightly different between the two descriptions.

Früchtl (1924) erroneously recorded the armature of P1 enp-3 with 4 inner setae (his Fig. 66 and p. 91), but in the same account described the 'aberrant' condition of the type specimen from Wokam, which exhibited 5 inner setae (his Fig. 15). The 5th inner seta on P1 enp-3 has repeatedly been overlooked in previous descriptions of this and other species of *Oncaea* s.str. (see above e.g. *O. venusta*), because the base of the seta is concealed beneath the long anterior spinous outgrowth of the segment (cf. Fig. 19A).

Males of *O. clevei* were not recorded by Früchtlor in any reliable subsequent account. Their description here is based on specimens taken from male-female pairs in mating position (Fig. 21A), which represents the highest probability of encountering a conspecific male of a given species (but see Heron & Bradford-Grieve, 1995 for exceptions). *O. clevei* males are very similar in size and habitus to those of *O. venusta* f. *venella*. However, differences in the ornamentation of the labrum (see below) as well as in proportional lengths of caudal setae separate the two species.

O. clevei is closely related to *O. paraclevei* sp. nov., from which it can be distinguished mainly by the location of genital apertures, the form of the genital double-somite and by further morphological characters summarized under *Remarks*, *O. paraclevei*. Together, the two species form a well-defined group within *Oncaea* s.str., which is characterized by the presence of a dorso-posterior projection ('hump') on the P2-bearing somite in the female and by the absence of long setules on the latero-distal margin of the lobes in the labrum. As the hump is a sexually dimorphic character, which is not found in males, males of the two subgroups can only be distinguished by differences in the ornamentation of the labrum, otherwise they are very similar.

OTHER RECORDS OF *O. CLEVEI*

Malt (1983a) summarized the published records of *O. clevei* and found it restricted to surface waters in low latitudes of the western Pacific and Indian Ocean. In view of the existence of a hitherto undescribed species, which is extremely close to *O. clevei*, it may be assumed that both *O. clevei* and *O. paraclevei* may have been recorded under the name *O. clevei* in previous records.

Sewell (1947, p. 258) recorded the species from the northern Arabian Sea, but it is not clear whether his material included *O. paraclevei* as well, because he stated that 'the dorsal projection on the 2nd thoracic segment varies considerably in its development', which is typical for the latter species.

Tanaka (1960) recorded both sexes of *O. clevei* from the South China Sea and off Cape Good Hope. His drawing of the female urosome (Plate XXVIII, Fig. 7) resembles that of *O. clevei* rather than *O. paraclevei*, but his description of the male is meagre and could also be assigned to any other oncaeid.

Chen *et al.* (1974) described the species from the Yellow Sea and the East China Sea. Their figure of female urosome lacks genital apertures and/or the sclerotization between them, which is necessary to separate *O. clevei* from the closely related *O. paraclevei*. Thus, a positive identification cannot be given without examination of their specimens.

More recently, Itoh [in: Chihara & Murano (1997)] recorded the species from Japanese waters; his dorsal view of the female shows the two characters typical for *O. clevei*.

Several other records of *O. clevei* from different localities in the Indo-Pacific are known [see Malt (1983a) for a review], but are not considered here because they did not include figures or a description that positively identified the species. In the Eastern Mediterranean Sea, neither *O. clevei* nor related species were found (Böttger-Schnack, 1997), thus corroborating the limitation of this subgroup to the Indo-Pacific area. The fact that *O. clevei* was not recorded in the detailed account of the oncaeid fauna from the New Zealand area by Heron & Bradford-Grieve (1995), confirms its restriction to low latitudes (Malt, 1983a).

GEOGRAPHICAL DISTRIBUTION
Oncaea clevei is distributed throughout the Red Sea, with lowest abundances in the northern area (Böttger-Schnack, 1990a, b, 1995). It was not found in small mesh net samples from the northernmost part of the Red Sea, in the Gulf of Aqaba (unpubl. data). In the southernmost Red Sea and at Bab al Mandab, abundances of the species were up to two orders of magnitude higher than in the central part (Böttger-Schnack, 1995). The data from both areas include an unknown number of *O. paraclevei* sp.nov., however, which was not separated from *O. clevei* during the quantitative counts. Thus, the actual regional difference in abundance remains uncertain.

In the northern Arabian Sea, *O. clevei* was recorded from the epipelagic zone by Böttger-Schnack (1996), however, the potential co-occurrence of *O. paraclevei* was not investigated.

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION
The depth distribution of *O. clevei* remains uncertain, as the species was counted together with *O. paraclevei* during the earlier quantitative investigations in the Red Sea (Böttger-Schnack, 1988, 1990a, b, 1995). Generally, the two species were confined to the epipelagic zone (0–100 m) with occasional occurrences below that depth. Individual specimens found down to 950 m depth during summer (unpubl. data) might be regarded as contaminants from shallower depths or as moribund specimens. Within the epipelagic zone, *O. clevei* and *O. paraclevei* exhibited a unimodal distribution in the upper epipelagic zone (0–20 or 0–40 m), staying above the strong seasonal thermocline, which usually develops during autumn (Böttger-Schnack, 1990a). No indication of a significant diurnal vertical movement became apparent and also no seasonal variation in the depth distribution of the two species was noted in the central Red Sea (Böttger-Schnack, 1990b).

In the deep southern Red Sea and in the Strait of Bab al Mandab/Gulf of Aden area, the depth distribution of the two species was similar to that observed in the central area, with maximum abundances in the upper 20 to 40 m layer (unpubl. data). In the shallow southern Red Sea, however, two population centres were found, situated at depths of 0–20 m and 100–125 m. Re-investigations of the southern plankton samples are required to find out whether *O. clevei* might be vertically separated from *O. paraclevei* in that area. For other oncaeid species or forms, which are closely related to each other, such as *O. media* and *O. scottodicarloi* and the two forms of *O. venusta*, a corresponding vertical separation had been observed in the shallow parts of the southern Red Sea.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)
O. clevei / *O. paraclevei* exhibited a strong seasonal variation in abundance in the central Red Sea, with highest abundances during winter, but low numbers during summer and autumn (Böttger-Schnack, 1995). This indicates a substantial recruitment for populations of the *clevei*-subgroup in the central area due to the inflow of southern Red Sea waters during the NE monsoon, which is similar to that observed for *O. venusta* f. *typica*. It remains uncertain, however, whether this effect applies likewise for both species of the *clevei*-subgroup, as the two species were not separated earlier.

Oncaea scottodicarloi Heron & Bradford-Grieve, 1995

Oncaea scottodicarloi Heron & Bradford-Grieve (1995): 39–41, Figs. 17j–r, 18a–k, 27a.

Oncäa media Giesbrecht, 1892 (partim); Giesbrecht 1892, Pl. 47, Fig. 11 only; H.Itoh [in: Chihara & Murano (1997)]: 981, Fig. 369a–f.

TYPE LOCALITY. Gulf of Naples, western Mediterranean Sea.

MATERIAL EXAMINED
(1) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/3); depth 20–40 m; total water depth ca 190 m.
   (a) 2 ♀♀, 1 ♂ in alcohol (BMNH 1998.2811–2813).
   (b) 2 ♀♀, 2 ♂♂ in alcohol (ZMH K-39581).
   (c) 2 ♀♀ dissected on slides, 1 ♀ in alcohol; 1 ♂ dissected on slides, 1 ♂ in alcohol (RBS).
(2) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/2); depth 40–60 m; total water depth ca 190 m.
   (a) 2 ♂♂ in alcohol (BMNH 1998.2814–2815).
   (b) 1 ♀, 1 ♂ (mating position) in alcohol (ZMH K-39582).
   (c) 2 ♂♂ in alcohol (RBS).
(3) Central-northern Red Sea, 22° 58.4'N, 37° 19.4'E: Stn. 663; *R/V Meteor* leg 5/5: collected 20 July 1987 with MSN 0.05 mm net (Haul 17/2); depth 150–200 m; total water depth 1200 m: 1 ♀on slide in lactophenol, numerous ♀♀and ♂♂ for length measurements (RBS).
(4) North-East Atlantic, upwelling area off Northwest-Africa, 17° 36'N, 16° 26'W: Stn. 262 (DIV); R/V Meteor leg 64: collected March 1983 with Messhai [= multiple opening-closing modified Gulf III type sampler, Pommeranz *et al.* (1979), Pommeranz & Moser (1987)] mesh size 0.05 mm; depth 80 m; total water depth 100 m: 1 ♀dissected on 1 slide in polyvinyl-lactophenol (RBS).
(5) North-East Atlantic, upwelling area off Northwest-Africa, 16° 09,N, 16° 48'W: Stn. 284 (DV); R/V Meteor leg 64: collected 27 March 1983 with Messhai [cf. (4)], mesh size 0.05 mm; depth

10–20–40 m; total water depth 100 m: 1 ♀dissected on 1 slide in polyvinyl-lactophenol (RBS).

(6) Eastern Indian Ocean, NW Cape Australia, 21° 49.86'S, 114° 30.3,E: Stn. B; NWC 005/2; RV 'Lady Basten' leg 1630; collected 26 October 1997 with 0.5 m WP-2 net with 0.073 mm mesh, vertical haul; depth 0–20 m (leg. D. McKinnon): 4 ♀♀ (RBS).

DESCRIPTION. Note illustrations are based on 1(c).

ADULT FEMALE (Figs. 22, 23A–E).
Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 803 μm [traditional method: (a) 600 μm, range: 540–610 μm, based on numerous specimens from southern Red Sea and Gulf of Aden; (b) 510 μm, range: 480–520 μm, based on 12 specimens from central Red Sea (Böttger-Schnack *et al.* (1989)].

Exoskeleton moderately chitinized. Prosome 2.8 times length of urosome, excluding caudal rami, 2.4 times urosome length including caudal rami. Integumental pores on prosome as indicated in Fig. 22A, B.

Proportional lengths (%) of urosomites 10.6 : 63.8 : 7.7 : 7.2 : 10.6. Proportional lengths (%) of urosomites and caudal rami 9.2 : 55.3 : 6.7 : 6.3 : 9.2 : 13.4.

Genital double-somite 1.5 times as long as maximum width (measured in dorsal aspect) and 2.5 times as long as postgenital somites combined (Fig. 22C); straight sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 22C. Armature of genital apertures represented by 1 spine and 2 minute spinous processes (Fig. 22G).

Anal somite 1.8 times wider than long; about 3/4 length of caudal rami (Fig. 22C). Ornamentation as for *O. venusta*.

Caudal ramus (Fig. 22F) about 2.3 times as long as wide, shorter than reported by Heron & Bradford-Grieve. Dorsal seta (VII) half the length of terminal accessory seta (VI), not 2/3 the length as reported by Heron & Bradford-Grieve, plumose and bi-articulate at base.

Antennule with minute element on 6th segment (arrowed in Fig. 22E), which was not mentioned in the original account.

Antenna as figured by Heron & Bradford-Grieve (their Fig. 17m), except for additional surface ornamentation on coxobasis similar to *O. waldemari* (cf. Fig. 25A) and 2 patches of spinules (not only 1) on anterior surface of distal endopod segment.

Labrum (Fig. 23A, B) similar to *O. waldemari*, but fewer dentiform processes medially on each lobe and free margin of integumental pockets distinctly serrate (Fig. 23A).

Mandible generally as figured by Heron & Bradford-Grieve, dorsal blade ornamented with 1 additional minute dentiform process at dorsal margin (Fig. 22H). Maxillule, maxilla and maxilliped similar to *O. waldemari*, some ornamentation elements on syncoxa of maxilla and on basis of maxilliped missing in the account of Heron & Bradford-Grieve.

Swimming legs 1–4 with armature as for genus and surface ornamentation similar to *O. waldemari* (Fig. 26A–D), except for anterior face of P1 enp-1 and -2 with stronger spinules on distal margin (Fig. 23C). P1 exp-3 with outer distal spine slightly longer than figured by Heron & Bradford-Grieve. P4 exp-3 and enp-3 (Fig. 23E) with outer distal spines somewhat longer than in original account, outer endopodal spine reaching almost 1/2 length of distal spine.

P5 (Fig. 22F) with exopodal segment longer than figured by Heron & Bradford-Grieve, ornamented with 3 spinules ventrally; inner one of exopodal setae stouter and slightly shorter than outer one.

P6 (Fig. 22G) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes.

Egg-sacs paired, oblong-oval; each sac containing 6 eggs (diameter 40–45 μm) (Böttger-Schnack, 1989, as *O. media* f. *minor*).

ADULT MALE (Fig. 23F–M).
Body length: 607 μm [(a) 440–480 μm, based on several specimens from southern Red Sea and Gulf of Aden; (b) 410 μm, range: 410–440 μm, based on 7 specimens from central Red Sea (Böttger-Schnack *et al.* (1989)]. Sexual dimorphism in antennule, antenna, maxilliped, endopods of P2–P4, P5–P6, caudal ramus and in genital segmentation.

Prosome 2.5 times length of urosome, excluding caudal rami, 2.2 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 11.2 : 69.2 : 3.8 : 3.8 : 3.8 : 8.3; proportional lengths (%) of urosomites (caudal rami included) 10.0 : 61.1 : 3.3 : 3.3 : 3.3 : 7.3 : 11.6. Caudal rami about 1.6 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI 2.6 times the length of caudal ramus, and dorsal seta VII 2/3 the length of seta VI.

Antennule with armature as for genus.

Antenna with seta on coxobasis long and plumose as in female; lateral armature on distal endopod segment differing from female, element III much stouter and element IV spiniform and curved, ornamented with dentiform processes along distal margin (arrowed in Fig. 23H); both elements shorter than in female.

Maxilliped as figured by Heron & Bradford-Grieve, except for endopodal segment (claw) with concave margin naked, not ornamented with short spinules pinnate as figured in their Fig. 18j.

Swimming legs 1–4 with armature and ornamentation as in female; terminal conical projections on P2–P3 enp-3 as in female. Sexual dimorphism expressed in reduced spine lengths on enp-3, most obvious in P3 (Fig. 23D, J) and in outer subdistal spine of P4 (Fig. 23E, M). Spine lengths on P2 enp-3 less reduced.

P5 (Fig. 23K) exopod not delimited from somite, shape and armature as in female, except for exopodal setae more spiniform and shorter than in female; small plumose seta arising from lateral surface of somite shorter than in female.

P6 represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 23L.

Spermatophore not observed.

TAXONOMY
O. scottodicarloi is the species previously referred to as *O. media* f. *minor* in the quantitative studies of Böttger-Schnack (1990a, b, 1994, 1995). Specimens from the Red Sea agreed in almost every detail with the original account of Heron & Bradford-Grieve (1995) from the Mediterranean, except for their smaller size, which is discussed below under 'Size variation'. The only other remarkable difference in female morphology between the two regions was the length to width ratio of caudal ramus, which was smaller in Red Sea specimens (2.3:1) than in the original account (about 3:1). [In the closely related *O. waldemari*, the length to width ratio of the caudal ramus turned out to be a variable character at closer examination (see below), which might also apply to *O. scottodicarloi*]. Other slight differences between the two descriptions, such as the surface ornamentation on mouthparts and antenna, as well as the minute element on 6th segment of antennule, which was not mentioned by Heron & Bradford-Grieve, are not regarded as substantial and/or might have been overlooked in the original account.

Males of *O. scottodicarloi* from the Red Sea differed from the original account in the ornamentation of maxillipedal claw, which was naked, while it had been described as having short spinules along the concave margin by Heron & Bradford-Grieve (1995, p. 40,

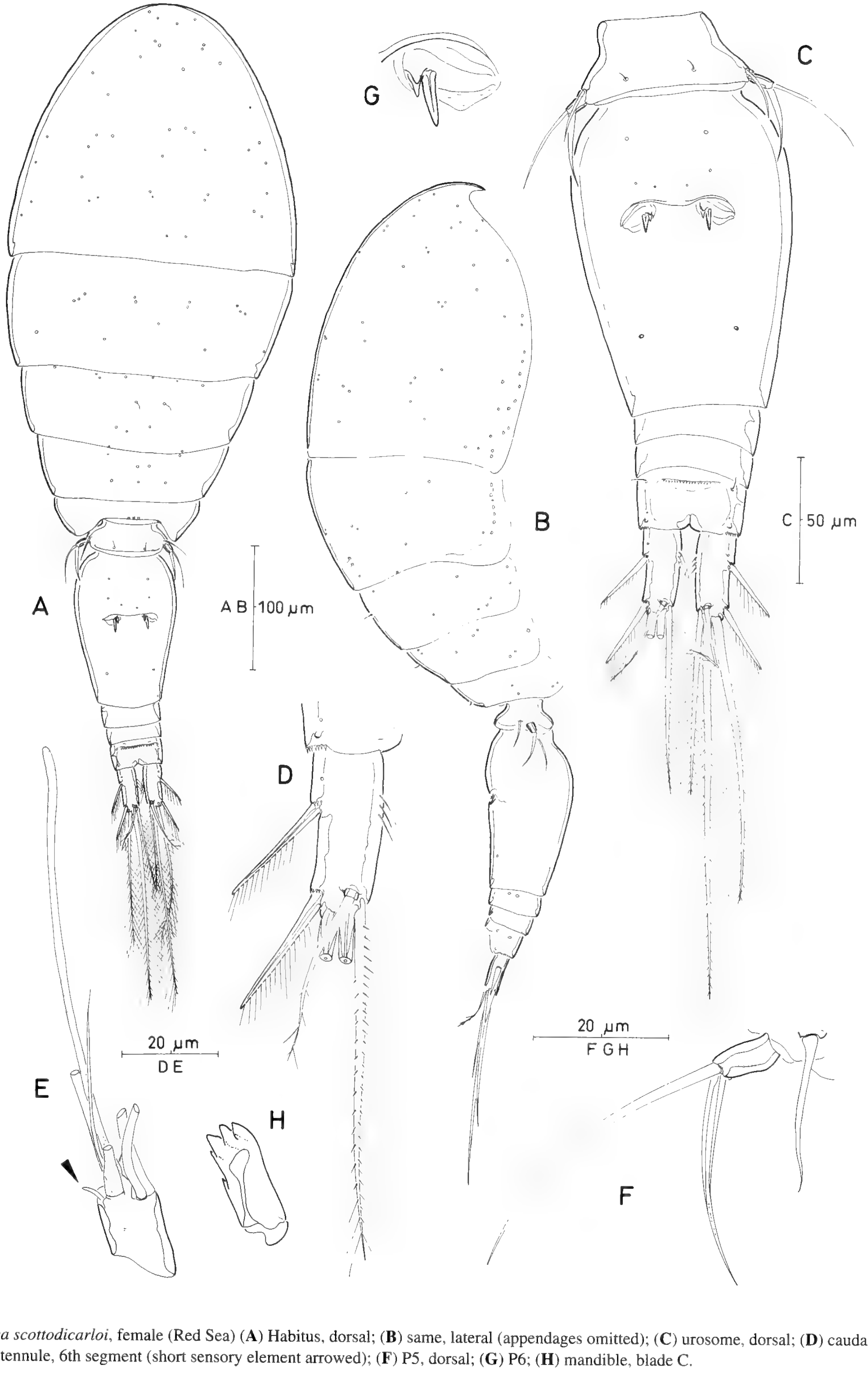

Fig. 22 *Oncaea scottodicarloi*, female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal; (**D**) caudal ramus, dorsal; (**E**) antennule, 6th segment (short sensory element arrowed); (**F**) P5, dorsal; (**G**) P6; (**H**) mandible, blade C.

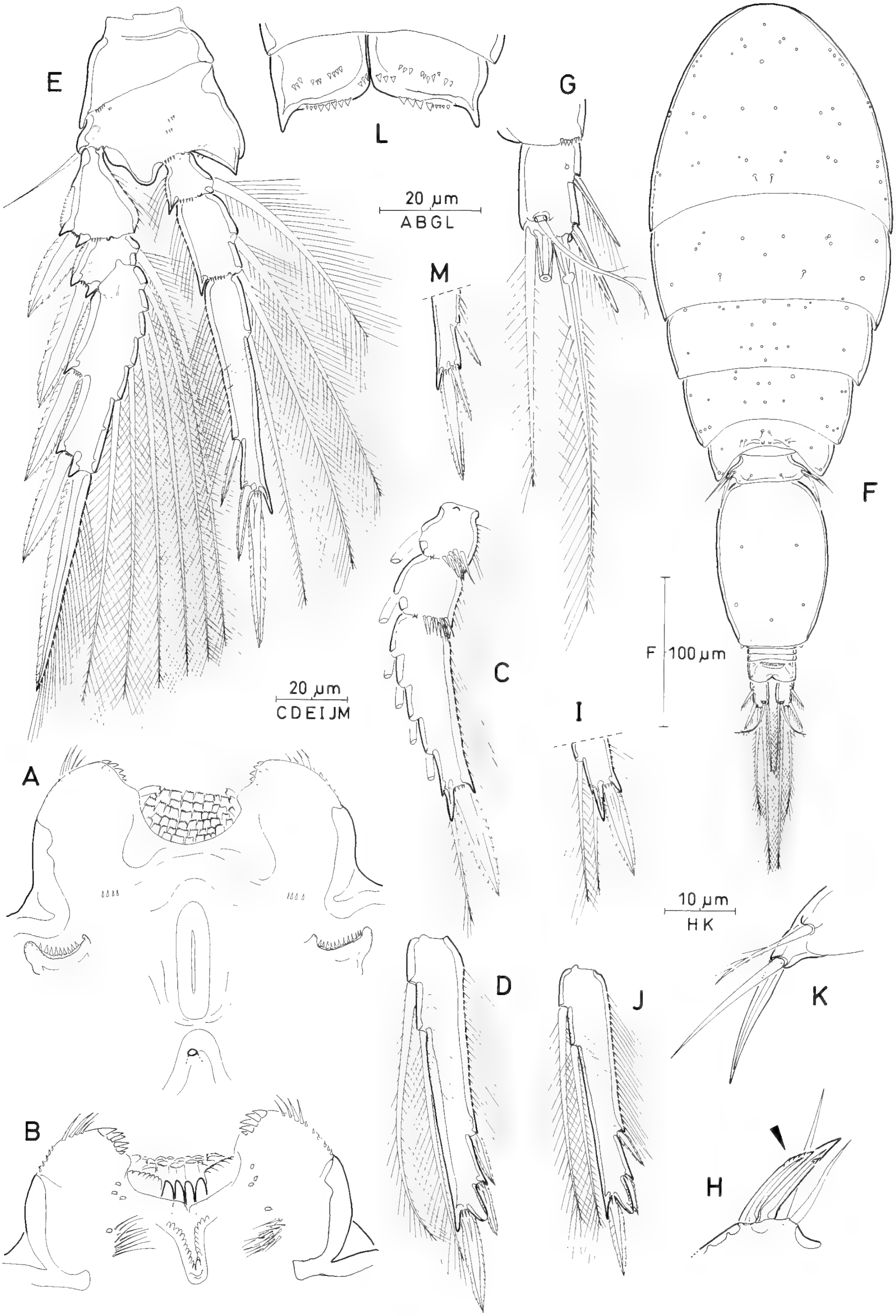

Fig. 23 *Oncaea scottodicarloi*, female (Red Sea) (**A**) Labrum, anterior; (**B**) same, posterior; (**C**) P1, endopod, anterior; (**D**) P3, distal endopod segment, anterior; (**E**) P4, anterior. – *Oncaea scottodicarloi*, male (Red Sea) (**F**) Habitus, dorsal; (**G**) caudal, ramus, dorsal (seta V not drawn); (**H**) antenna, lateral armature of second endopod segment (ornamentation of seta IV arrowed); (**I**) P1, distal part of endopod; (**J**) P3, distal endopod segment; (**K**) P5, dorsal; (**L**) P6; (**M**) P4, distal part of endopod.

Fig. 18j). Males of oncaeid species usually exhibit a naked maxillipedal claw, with few exceptions only [*Epicalymma schmitti* and *Oncaea englishi* (Heron, 1977); *O. mollicula* (unpubl. data)]. In the case of *O. englishi* the ornamentation seems to be variable, as it was lacking in some individuals (Heron, 1977). A further difference between the original description and the present account is the sexual dimorphism in spine lengths on enp-3 in P2–P4, which was not reported for *O. scottodicarloi* before. The sexual dimorphism of this character seems to be typical for species of the genus *Oncaea* s.str., however, as it was found in almost all species described in the present account. Nonwithstanding these differences between the two descriptions, both sexes of the species found in the Red Sea are regarded as conspecific with *O. scottodicarloi*.

O. scottodicarloi is closely related to *O. media*, *O. waldemari*, and *O. curta*. Major distinctions between the four species have been summarized in Table 5. Female *O. media* can most easily be separated from the three other species by the length ratio of urosome somites, particularly of the genital double-somite, which is much longer. This character enables rapid identification of the species during quantitative counts. The three remaining species are morphologically very similar, except for differences in the length ratio of urosome somites, the length of exopodal seta on P5 and the relative lengths of caudal setae. The morphological relationships of *O. curta* within this species complex remain uncertain, however. Sars' original account of *O. curta* is the only reliable description of the species. He described several important characters, such as the unequal exopodal setae on P5, which need to be affirmed, as they are difficult to discern. The species could not be re-examined during the present study due to the lack of material. Heron & Bradford-Grieve (1995) recorded *O. curta* from the Gulf of Naples, but their summary of morphological distinctions between the species and *O. scottodicarloi* was based on Sars' original account, rather than on own observations (G. Heron, pers. commn to R. Huys). The authors noted several as yet undescribed species close to *O. scottodicarloi* in their samples from Naples, one of which probably had been *O. waldemari*, which is also present in the Mediterranean. However, Heron & Bradford-Grieve were not aware of this species, because the original description of *O. waldemari* (dated 1994) did not appear until 1996.

Males of *O. scottodicarloi* can easily be separated from those of *O. media* by the lack of sexual dimorphism in the coxobasal seta on the antenna, which is long and plumose as in the female. Males of *O. waldemari*, however, share this character and can be distinguished from *O. scottodicarloi* only by minor details in the form and ornamentation of seta IV on the antenna as well as in proportional lengths of caudal setae (Table 5). For males of *O. curta* corresponding sexual differences still need to be investigated.

SIZE VARIATION

Female *O. scottodicarloi* from the central and northern Red Sea were considerably smaller (0.48–0.52 mm, Böttger-Schnack *et al.*, 1989) than those from the southern Red Sea and Gulf of Aden, which measured between 0.54–0.61 mm (numerous specimens measured by the traditional method used by Böttger-Schnack *et al.*, 1989). No morphological differences other than size became apparent for specimens from the two regions. Re-examination of specimens from the central populations confirmed that the small morph had not been confused with *O. waldemari*, which is similar in size. The observed regional size difference of *O. scottodicarloi* (which occurred also in the males) does not seem to be a temporary phenomenon, as the lengths of specimens in the central Red Sea did not vary during different seasons. Generally, *O. scottodicarloi* seems to exhibit a wide range in body length: Heron & Bradford-Grieve reported females between 0.59–0.72 mm, with distinct differences between different oceanic areas. Female *O. scottodicarloi* from the northern Arabian Sea and Eastern Mediterranean Sea as well as those collected of Australia's NW Cape (eastern Indian Ocean) measured between 0.58–0.62 mm (unpubl. data) and were thus in the upper size range of specimens from the Gulf of Aden. Itoh [in: Chihara & Murano (1997)] recorded females between 0.50–0.64 mm and males between 0.38–0.54 mm in size, however, the author was not aware of *O. waldemari*, which might have been included in the lower size range of his specimens. [A recent examination of two forms of female *O. scottodicarloi* from the Western Subtropical Pacific kindly made available by H. Itoh and S. Nishida showed that females of the smaller form (0.49–0.62 mm) were conspecific with *O. waldemari*, while the larger form (0.58–0.71 mm) belonged to *O. scottodicarloi*.] Compared to these data, specimens of *O. scottodicarloi* from the central Red Sea appear to be even smaller than the lowest values reported for this species so far. The occurrence of the small morph seems to be a local phenomenon for this area. A possible explanation for the reduced size of central populations may be the more extreme environmental conditions in the central Red Sea as discussed by Böttger-Schnack et al. (1989). Similar to *O. venusta* f. *venella*, the small morph of *O. scottodicarloi* in the central Red Sea seems to be a self-sustaining population, with no substantial recruitment from the South.

OTHER RECORDS OF *O. SCOTTODICARLOI*

Heron & Bradford-Grieve (1995) recorded *O. scottodicarloi* from various regions in the Atlantic and Pacific and recently Itoh [in: Chihara & Murano (1997)] described it from Japanese waters. The species was also found in great abundance in the Eastern Mediterranean as well as in the northern Arabian Sea (Böttger-Schnack, 1994, 1996, as *O. media* f. *minor*). Sewell (1947) had reported *O. media* f. *minor* from the Indian Ocean, however, the identity of his size morph with *O. scottodicarloi* cannot be confirmed as the specimens of Sewell are not available. The specimens might have been confused with *O. waldemari*, which was found to co-occur with *O. scottodicarloi* in both areas (see below). The identity of *O. media* f. *minor* (*sensu* Malt, 1982b) will be discussed below under *O. waldemari*.

GEOGRAPHICAL DISTRIBUTION

Oncaea scottodicarloi is distributed throughout the Red Sea proper (Böttger-Schnack, 1988, 1990a, b, 1995, as *O. media* f. *minor*) and can also be found in the northernmost part of the Gulf of Aqaba (own unpubl. data). The species is one of the most abundant oncaeids in the central Red Sea, usually accounting for 2–10% of the total number of Oncaeidae in the water column down to 450 or 1050 m depth, depending on region and season. In narrower depth layers, even higher percentages, up to 15%, of all oncaeids are found (epipelagic zone, winter, central Red Sea). Similar to *O. media*, *O. scottodicarloi* exhibited a 2-tailed horizontal distribution during summer, with high abundances in the central-northern Red Sea as well as in the Strait of Bab al Mandab and Gulf of Aden, but low abundances in the intermediate southern parts of the Red Sea (Böttger-Schnack, 1995: Table 6). Consequently, its relative abundance in the southern Red Sea was rather low (0.4/1.6%), but strongly increased again further south. The proportion of *O. scottodicarloi* in the Gulf was possibly underestimated, since samples in that area covered only the upper 250 m of the water column, thereby excluding a potential mesopelagic population. In Table 8 of Böttger-Schnack (1995), the abundance values of *O. scottodicarloi* in the uppermost depth zone (0–100 m) were inadvertently changed between stations. The correct data for *O. scottodicarloi* are given in Table 6 of the present account.

Table 6 Abundance (individuals beneath 0.25m²) of *O. scottodicarloi* adults in the Gulf of Aden and different regions of the Red Sea during summer 1987.

	Gulf of Aden		Bab al Mandab	South, shallow	Red Sea Main Basin		
					South, deep	Central	North
Stn.	631	633	717	708	703	682	663
Sampling Time	N	D	D	D	D	D	D
Total water depth (m)	1400	1300	250	190	970	1890	1200
Depth layer (m)							
0–100	2800	2000	5000	380	300	770	850
100–250	160	–	330	620*	81	220	380
250–450	–	–			91	350	620
450–1050	–	–			7**	28	130

Corrected data of Table 8 in Böttger-Schnack (1995)
D = Day; N = Night; – = no data; Stn. = Station number
* = Depth range 100–175m
** = Depth range 450–950m

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

In the Red Sea, *O. scottodicarloi* had an epi- and mesopelagic distribution mainly between the surface and 600 m depth in the Red Sea; individual finds occurred down to 1250 m. Females exhibited a bimodal vertical distribution pattern, with maximum abundances in the epipelagic zone (0–100m) and in the mesopelagic zone, at 200–400(450) m depth (Böttger-Schnack, 1990a, b and unpubl. data from summer 1987). The depth horizon of the two population centres varied seasonally, with the epipelagic mode shifting to shallower depth during winter, due to absence of a strong thermocline, as well as regionally, with the mesopelagic mode shifting to shallower depth in the South as compared to the central-northern area. In general, however, the bimodal pattern was consistent. Diurnal vertical migration of moderate intensity was observed only for the epipelagic part of the female population during autumn, which migrated upwards at night. During winter, the vertical migration behaviour of the species was not investigated.

In contrast to females, males of *O. scottodicarloi* exhibited a unimodal distribution pattern in the epipelagic zone, with highest densities in the upper 50 m (winter, summer) or in the 50–100 m zone (autumn). Within this depth zone, their diurnal vertical migration was stronger than in the females.

The mesopelagic population centre of *O. scottodicarloi* did not show a regional downward shift between the central and northern Red Sea in relation to the regional differences in oxygen profiles, as had been observed for other oncaeids exhibiting bimodal distribution patterns in the area, such as *O. mediterranea* and *Lubbockia squillimana* (Böttger-Schnack, 1990b). During summer, however, the lower part of the population occurred somewhat shallower in the southern Red Sea (200–300 m) than in the central-northern area (250–400/450 m) (own unpubl. data). This might be related to a corresponding regional shift in the depth of the oxygen minimum (Böttger-Schnack, 1995). However, as the sampling variability within each area was not investigated during the summer, the data are inconclusive.

In the shallow part of the southern Red Sea (SRS) and in the Strait of Bab al Mandab (BaM), both sexes of *O. scottodicarloi* were found more or less evenly distributed between 40 m and the near-bottom layer at 175 m (SRS) or occurred in maximum concentrations between 20–60 m depth (BaM) during summer (unpubl. data). In this area, the population occurred at the same depth as *O. waldemari*, but the two species were vertically separated from *O. media*, which was concentrated much shallower, at 0–20 m (BaM).

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

O. scottodicarloi exhibited no consistent seasonal variation in abundance in the central Red Sea, indicating that the species is not markedly influenced by seasonal inflow of southern Red Sea waters (Böttger-Schnack, 1995, see also above under 'Size variation').

Oncaea waldemari Bersano & Boxshall, 1994

Oncaea waldemari Bersano & Boxshall (1994): 29–41, Figs.1–6.

Oncaea media f. *minor* Malt (1982b): 130–133, Figs. 1a–i, 2a–j, 3a–z', 4a–o, 5a–h.

TYPE LOCALITY. Southern Brazilian shelf (31°40'–33°45'S, 51°00'–52°20'W) .

PRELIMINARY NOTE. The type description by Bersano & Boxshall (1994) includes some inconsistencies between text and figures, in particular with regard to P5 exopod, that severely hampers a positive identification of the species. Re-examination of the type material of *O. waldemari* during the present study gave unequivocal evidence that specimens from the Red Sea are conspecific. The species is redescribed based on Red Sea specimens (figures) and the type material. It includes several morphological details which were not mentioned in the original account (e.g. labrum). Also, body dimensions of specimens from the Red Sea, calculated by the different methods used throughout this study, are provided. The urosome segmentation of a typical female Copepodid Stage V, which has been incorrectly described for oncaeid copepods in the literature before, is described and briefly discussed.

MATERIAL EXAMINED.

(1) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/3); depth 20–40 m; total water depth 190 m.
  (a) 2 ♀♀ in alcohol (BMNH 1998.2816–2817).
  (b) 2 ♀♀, 1 ♂ in alcohol (ZMH K-39583).
  (c) 2 ♀♀, 3 ♂♂ dissected on slides; 2 ♀♀, 1 ♂ in alcohol (RBS).
(2) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/2); depth 40–60 m; total water depth 190 m.
  (a) 2 ♂♂ in alcohol (BMNH 1998.2818–2819).
  (b) 3 ♀♀, 3 ♂♂ (RBS).
(3) Southern Brazilian shelf, 31° 40'–33° 45'S, 51° 00'–52° 20'W, collected between 1988–1991 with cylindrical-conical closing net (mesh size 0.15 mm); depth 0–25m: holotype ♀ (Stn. 319, BMNH 1994.6213), 2 ♀♀ paratypes (Stn. 309), 2 ♂♂ paratypes (Stn. 319) (BMNH 1994.6214–6223).
(4) Eastern Mediterranean Sea, 34° 25.3'N, 26° 14.8'E, Stn. 35; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm

net (Haul 24/5); depth 0–50 m; total water depth 3400 m: 1 ♀in alcohol (RBS).

(5) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; *R/V Meteor* leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 5 ♀♀, 2 ♂♂ for length measurements (RBS).

(6) Plymouth Sound, BMNH 1981.229, labelled *Oncaea media* (*sensu* Malt, 1982): 3 ♀♀, 2 ♂♂ in alcohol.

(7) Adriatic Sea, 42° 38.5'N, 18° 02.0'E: Stn. 'Lokrum 100'; collected 26 September 1996 with 0.053mm Nansen type net; depth 0–25 m, vertical haul (leg. F. Kršinić): 2 ♀♀(1 ovigerous), 1CV ♀, 1 ♂ in alcohol (RBS).

(8) Eastern Indian Ocean, NW Cape Australia, 21° 49.86'S, 114° 30.3,E: Stn. B; NWC 005/2; *RV 'Lady Basten'* leg 1630; collected 26 October 1997 with 0.5 m WP-2 net with 0.073 mm mesh, vertical haul; depth 0–20 m (leg. D. McKinnon): 2 ♀♀in alcohol (RBS).

(9) Western Subtropical Pacific, off Sagami Bay (Japan), 34° 15.0'N, 139° 45.0'E: Stn. 1; *R/V Tansei-Maru* leg KT-00-5; collected 09 May 2000 with Norpac net with 0.1 mm mesh; depth 0–200 m, vertical haul (leg. S. Nishida; H. Itoh): > 30 ♀♀ in alcohol for molecular analysis (RBS)

REDESCRIPTION. Note illustrations are based on 1 (c) and (7) (CV ♀).

ADULT FEMALE (Figs. 24–26).
Body length: 637 µm [Traditional method: 420–500 µm, based on 21 specimens].

Exoskeleton well chitinized. Prosome 2.7 times length of urosome, excluding caudal rami, 2.3 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Fig. 24B). Integumental pores on prosome as in Fig. 24A, B.

Proportional lengths (%) of urosomites 10.3 : 56.6 : 10.7 : 8.7 : 12.6. Proportional lengths (%) of urosomites and caudal rami 8.8 : 48.1 : 9.1 : 7.4 : 11.6 : 15.1.

Genital double-somite (GDS) of Red Sea specimens 1.7 times as long as maximum width (measured in dorsal aspect) and 1.7 times as long as postgenital somites combined (Fig. 24C); GDS length to width ratio of three female paratypes from Brazilian waters ranging between 1.6–1.7 : 1, larger than reported by Bersano & Boxshall (1.4:1). Armature of genital apertures represented by 1 spine and 2 small spinous processes, as figured by SEM-micrograph by Bersano & Boxshall (their Fig. 5D), the second minute one hardly discernible with light microscope in Red Sea specimens (Fig. 24H).

Anal somite shorter than caudal rami (Fig. 24C), 3/4 the length of caudal rami in Red Sea specimens; variable in paratype specimens due to differences in length of caudal rami (see below).

Caudal ramus (Fig. 24F) about 2.3 times as long as wide in Red Sea specimens, longer in paratypes, varying between 2.4–2.8 : 1. Seta VI longer than dorsal seta VII and less than twice the length of caudal ramus; seta VII distinctly longer than seta III.

Antennule (Fig. 24E) with armature formula as for genus, some elements missing in original account of Bersano & Boxshall (their Fig. 2A); pore pattern as figured (Fig. 24E).

Antenna 3-segmented (Fig. 25A). Coxobasis with row of long, fine spinules or setules near outer margin and with few additional denticles on proximal part of outer (exopodal) margin, not figured in the original account of Bersano & Boxshall.

Labrum (Fig. 25B, C) as for *O. venusta*, except for additional surface ornamentation (paired row of denticles) on anterior face, and integumental pockets either side of median swelling more pronounced (Fig. 25B).

Paragnaths (not figured) as in *O. venusta*.

Mandible (Fig. 25D) with surface of coxa unornamented; armature elements as for *O. venusta*, but dorsal blade with 2 additional dentiform processes along dorsal margin (not only one as figured by Bersano & Boxshall).

Maxillule (Fig. 25E) as for *O. venusta*, with the 3 innermost elements on outer lobe similar in length, not innermost one shortest, as erroneously figured by Bersano & Boxshall (their Fig. 3C).

Maxilla (Fig. 25F) and maxilliped (Fig. 25G) similar to *O. venusta*. Proximal basal seta of maxilliped slightly longer than distal one (Fig. 25G), not shorter, as erroneously figured by Bersano & Boxshall (their Fig. 3E).

Swimming legs 1–4 with armature as for genus, surface ornamentation as shown in Fig. 26A–D. Exopods and endopods with ornamentation and spine lengths similar to *O. venusta*, except for terminal spine on P4 endopod relatively longer and hyaline lamella more narrow (Fig. 26D).

P5 with small exopodal segment clearly delimited from somite (Fig. 24G), not fused as stated by Bersano & Boxshall (p. 35). Exopod slightly longer than wide, ornamented with minute subapical pore and bearing 2 naked setae nearly equal in length, inner one spiniform. Small naked seta arising from lateral surface of somite.

P6 (Fig. 24H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes, smaller one hardly discernible in Red Sea specimens.

Egg-sacs paired, oval-shaped; each sac containing appr. 10–12 eggs (diameter ca 50 µm).

ADULT MALE (Fig. 27).
Body length: 454 µm [Traditional method: 340–360 µm, based on 6 specimens]. Sexual dimorphism in antennule, antenna, maxilliped, P1 and P3 (endopod), P5–P6, caudal ramus and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.3 : 66.8 : 3.3 : 4.7 : 4.2 : 11.5; proportional lengths (%) of urosomites (caudal rami included) 8.3 : 59.6 : 3.3 : 4.2 : 3.8 : 10.0 : 10.8. Caudal rami about 1.4 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI shorter than in female, about same length as seta VII and 2.0 times length of caudal ramus. The extreme shortness of seta VI recorded by Bersano and Boxshall (about half the length of seta VII, according to their Fig. 1D) could not be confirmed upon re-examination of male paratypes. Surface of genital flaps ornamented with several rows of small spinules and area of minute pits as in Fig. 27E.

Antennule (Fig. 27B) with armature as for genus, pore pattern as figured [distalmost element on segment 2 erroneously figured as belonging to segment 3 in original account, Fig. 2B of Bersano & Boxshall].

Antenna as in female, except for third spiniform element on lateral armature being somewhat stouter than in female and fourth element curved and ornamented with vestigial dentiform processes along distal margin (arrowed in Fig. 27H). Seta on coxobasis long and plumose as in female.

Maxilliped (Fig. 27C) similar to *O. venusta*.

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in terminal process on P1 enp-3, being relatively longer than in female (Fig. 27J), and in longer terminal conical projection on P3 enp–3, reaching 2/3 the length of outer distal spine (Fig. 27K).

P5 (Fig. 27G) exopod not delimited from somite, general shape and armature as in female, except for setae slightly shorter than in female; small naked seta arising from lateral surface of somite as in female.

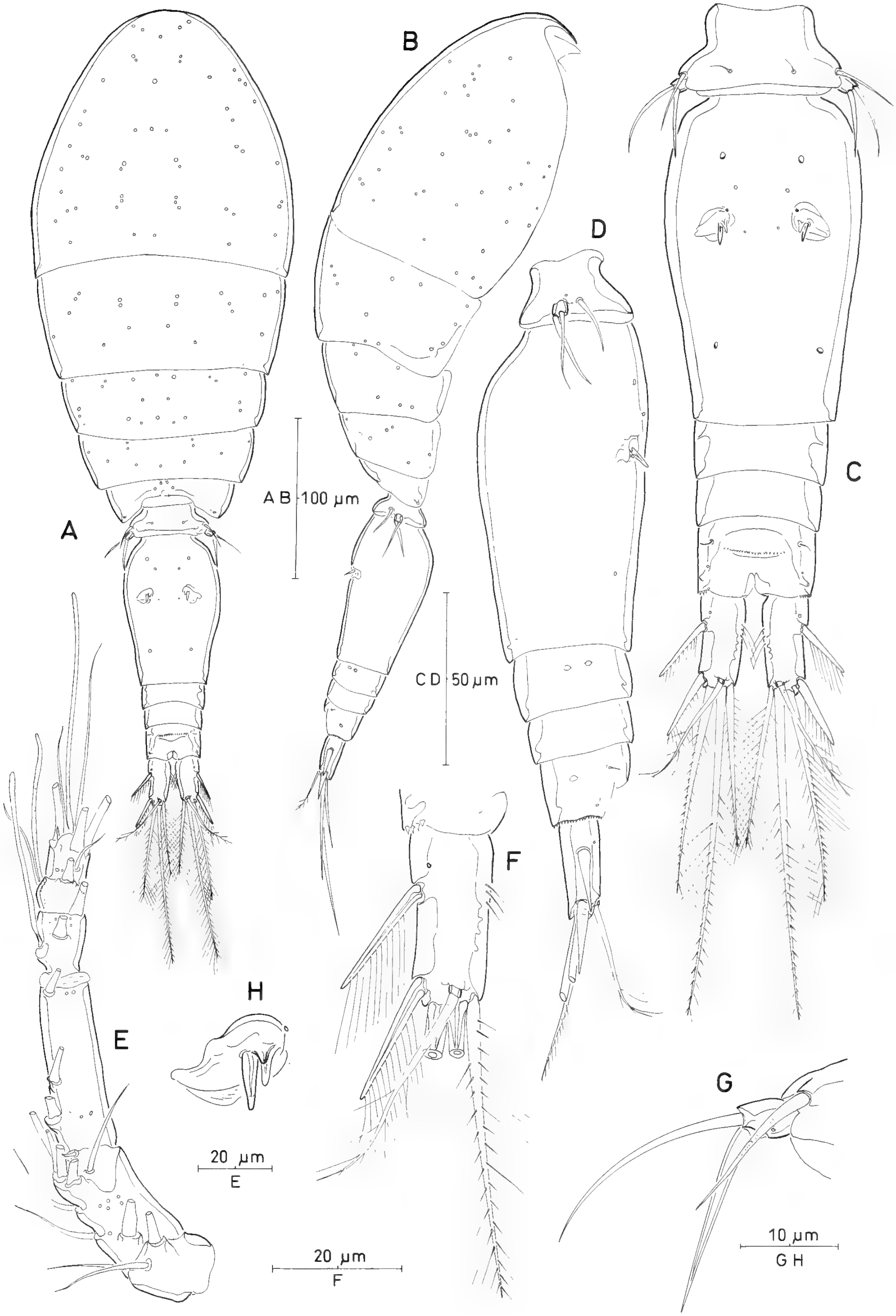

Fig. 24 *Oncaea waldemari*, female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal; (**D**) urosome, lateral; (**E**) antennule; (**F**) caudal ramus, dorsal; (**G**) P5, dorsal; (**H**) P6.

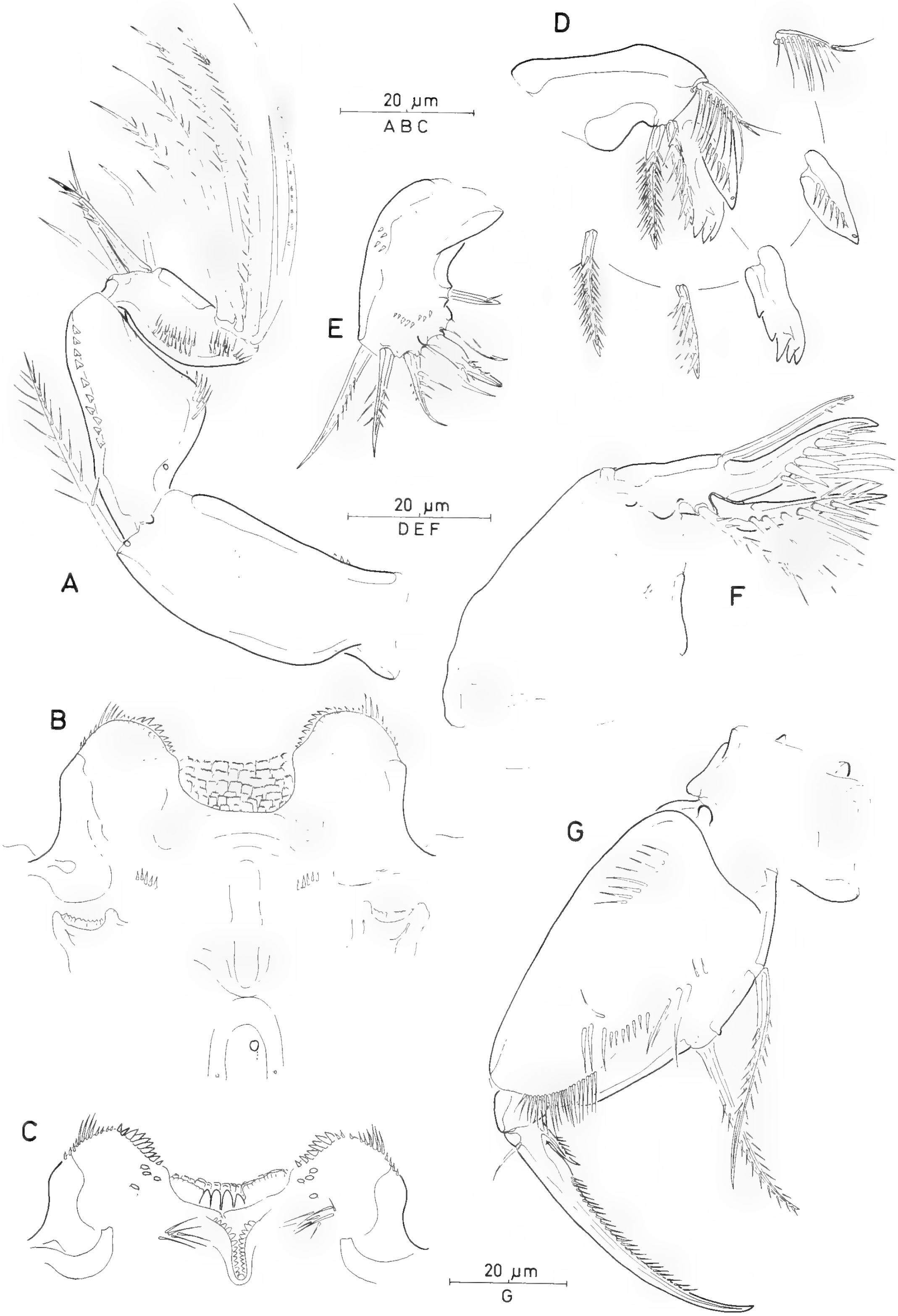

Fig. 25 *Oncaea waldemari*, female (Red Sea) (**A**) Antenna, posterior; (**B**) labrum, anterior; (**C**) same, posterior; (**D**) mandible, showing individual elements; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

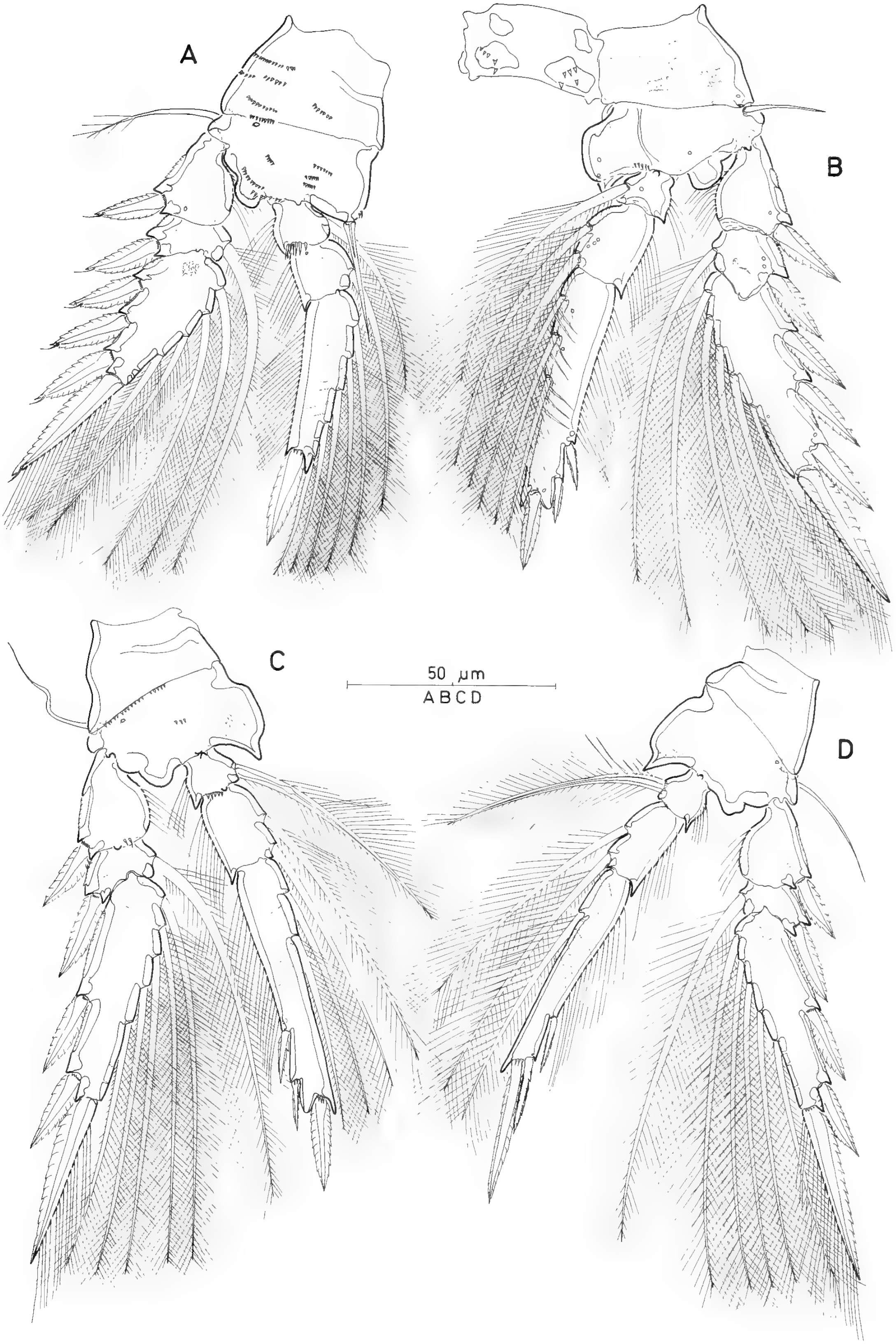

Fig. 26 *Oncaea waldemari*, female (Red Sea) (**A**) P1, anterior; (**B**) P2, posterior; (**C**) P3, anterior; (**D**) P4, anterior.

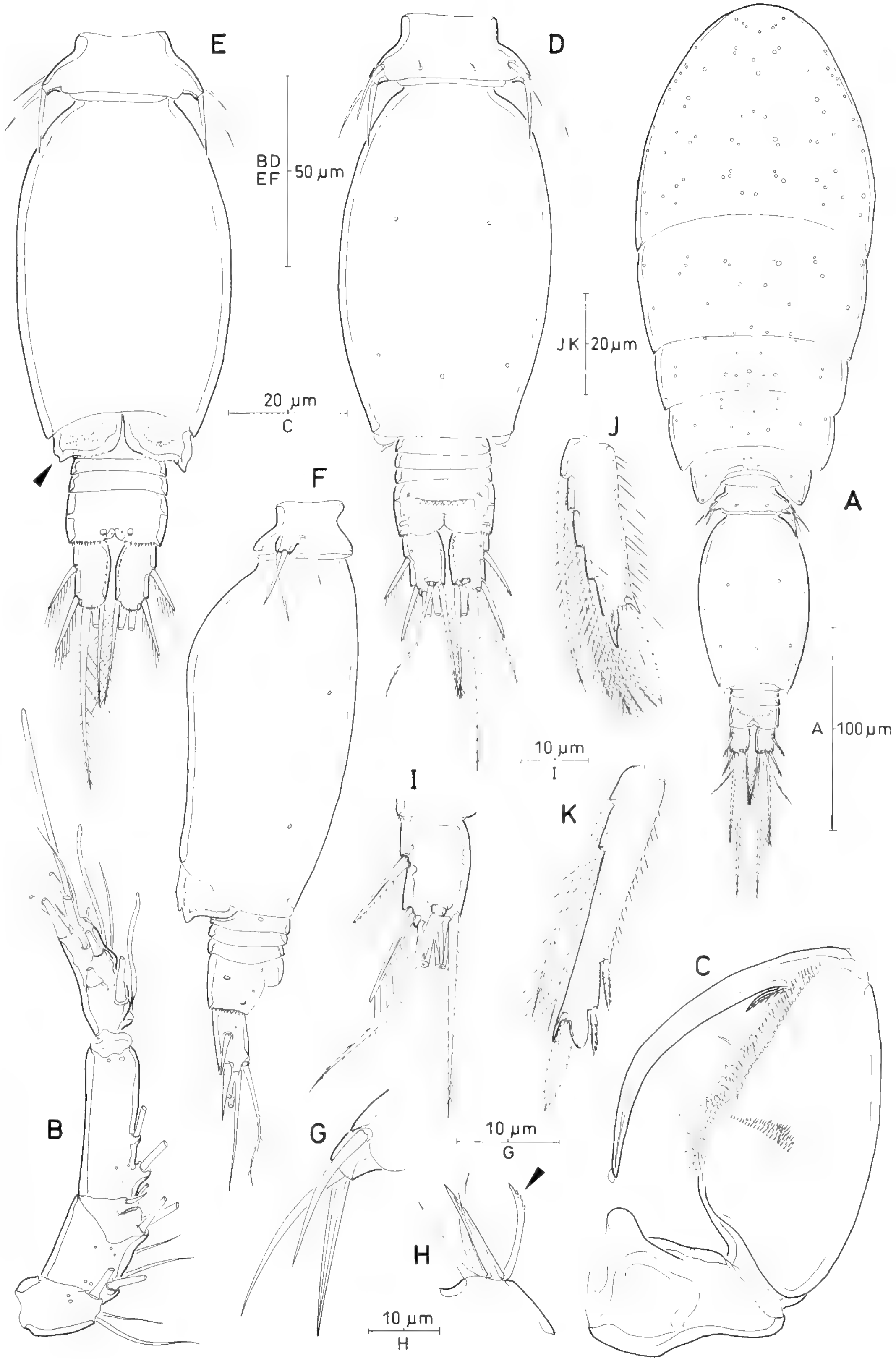

Fig. 27 *Oncaea waldemari*, male (Red Sea) (**A**) Habitus, dorsal; (**B**) antennule; (**C**) maxilliped, anterior; (**D**) urosome, dorsal; (**E**) urosome, ventral (spermatophores immature), modified tip of posterolateral corner on P6 arrowed; (**F**) same, lateral; (**G**) P5, dorsal; (**H**) antenna, lateral armature of distal endopod segment (ornamentation of seta IV arrowed); (**I**) caudal ramus, dorsal; (**J**) P1, distal endopod segment, anterior; (**K**) P3, distal endopod segment, anterior.

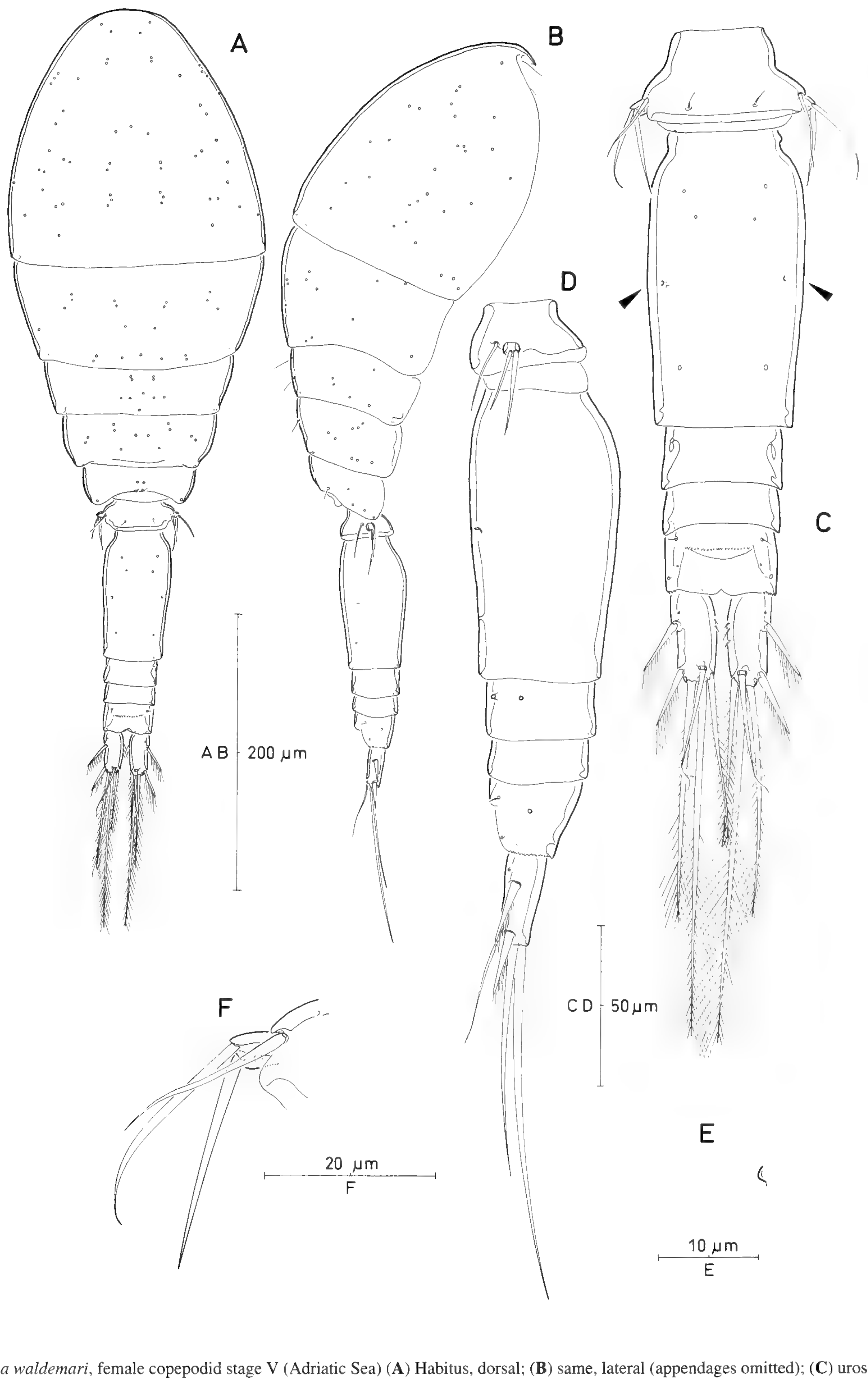

Fig. 28 *Oncaea waldemari*, female copepodid stage V (Adriatic Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal, slit-like structures arrowed; (**D**) urosome, lateral; (**E**) slit-like structure; (**F**) P5, dorsal.

P6 (Fig. 27E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles and area of minute pits as in Fig. 27E; posterolateral corners rounded, generally with bifid tips, as in Fig. 27F (aberrant stunted corner on right side arrowed in Fig. 27E).

Spermatophore oval (Fig. 27E, F), of variable size according to state of maturity; swelling of spermatophore during development not affecting shape and relative size of genital somite.

FEMALE COPEPODID STAGE V (Fig. 28).

Body length: 640 µm [Traditional method: 550 µm].

Prosome 2.4 times length of urosome, excluding caudal rami, about 2.1 times urosome length including caudal rami. Integumental pores on prosome as in Fig. 28A, B.

Urosome 5-segmented; proportional lengths (%) of urosomites 11.7 : 51.7 : 11.5 : 8.9 : 16.2. Proportional lengths (%) of urosomites and caudal rami 10.0 : 44.0 : 9.8 : 7.6 : 13.8 : 14.8.

Second urosomite 1.8 times as long as maximum width (measured in dorsal aspect) and 1.4 times as long as postgenital somites combined (Fig. 28C). Paired slit-like structure located close to dorso-lateral margin at about midlength along second urosomite (Fig. 28C), representing precursors of adult genital apertures (Fig. 28E). Pore pattern on dorsal surface similar to adult female; entire surface covered with numerous small pits.

Anal somite shorter than caudal rami.

Caudal ramus with length to width ratio 2.0 : 1. Caudal setae with proportional lengths as in adult female.

P5 (Fig. 28F) similar to adult female.

Antennule, antenna, mouthparts and swimming legs not examined.

TAXONOMY

Oncaea waldemari has been referred to as *Oncaea* sp. AD (Böttger-Schnack, 1994, 1995) or *Oncaea* sp. B (Böttger-Schnack, 1996) in previous ecological studies. The original description of *O. waldemari* by Bersano & Boxshall (1994) shows an inconsistency between text and figures with regard to the exopod segment of female P5, which is described as being fused to the somite (p. 35), but is figured as being delimited (their Fig. 1B). Re-examination of the holotype and female paratypes of the species during the present study gave clear evidence, that the exopod of female P5 is free (as in Fig. 24G), and that specimens from the Red Sea are conspecific. Slight differences in body dimensions between the two descriptions are mainly brought about by the different methods used throughout this study (telescoping of somites) or appear to be variable between specimens (e.g. length to width ratio of caudal ramus as discussed below).

Based on the erroneous assumption of a fused P5 exopod in the female, Bersano & Boxshall (1994) placed *O. waldemari* in a small group of oncaeids together with *O. petila*, *O. ovalis*, *O. brocha* and *O. compacta*. The present redescription undoubtedly shows that the species belongs to *Oncaea* s.str. and within this genus is most closely related to *O. curta*, *O. scottodicarloi* and *O. media*. Major distinctions between the three species are summarized in Table 5. Further differences between *O. waldemari* and *O. scottodicarloi* include the relative lengths of endopodal spines on P4, which are shorter in *O. waldemari*. Males of *O. waldemari* can be separated from those of *O. media* by the sexually dimorphic coxobasal seta of the antenna (Table 5). Males of *O. scottodicarloi* lack this character; they can be distinguished from *O. waldemari* by slight differences in element IV on the antenna, the length of seta VII on the caudal ramus and the ornamentation of the P6.

SIZE VARIATION

The body length of *O. waldemari* varies considerably in different geographic regions (Table 7). Lengths of specimens from the Red Sea were in the lower end of the size range observed for other regions or were smaller.

Table 7 Body length (mm) and length to width ratio of female caudal ramus (CR) of *O. waldemari* from various locations.

Region	♀	♂	CR
South Atlantic, Brazilian waters*	0.49–0.58	0.36–0.41	2.4–2.8 : 1
Mediterranean			
(a) Adriatic Sea	0.51–0.60	0.40–0.46	2.4 : 1
(b) Eastern Medit.	0.50		
Plymouth Sound	0.62–0.69	0.50–0.52	2.5 : 1
Red Sea	0.42–0.50	0.34–0.36	2.3 : 1
Arabian Sea	0.47–0.52	0.34;0.38	no data
Eastern Indian Ocean, NW Cape Australia	0.48–0.54	–	2.2–2.4 : 1
Western Subtropical Pacific, off Sagami Bay (Japan)	0.49–0.62	–	no data

*after Bersano & Boxshall (1994)

Beside the difference in size, the length to width ratio of caudal ramus (Table 7) and the form of the genital double-somite seemed to be variable within an area as well as outside. Female paratypes of *O. waldemari* from Brazilian waters exhibited a variable length to width ratio of caudal ramus, which was not noticed the Red Sea material. Specimens from Plymouth (see below) had a somewhat shorter genital double-somite than the type collection, and within the populations from the Adriatic and from Australian waters, differences in length to width ratio of the genital double-somite, as well as of the caudal ramus, were noted. This indicates considerable intraspecific variation (morphs) in *O. waldemari*, which makes it difficult to identify the species. More detailed taxonomic studies on this small and widespread species, including alternative methods such as molecular analyses, are necessary to ascertain the taxonomic status of these morphs.

The form of the bifid corners of genital lappets on male P6 was slightly variable in Red Sea specimens. A corresponding variation in male morphology was observed in *O. media* (cf. Fig. 16C) and had previously been observed for another oncaeid, *Triconia hawii* (Böttger-Schnack, 1999). It may be more widespread among oncaeids than previously known.

OTHER RECORDS OF *O. WALDEMARI*

Malt (1982b) described the developmental stages of *O. media* from Plymouth Sound and assigned the species to f. *minor* on the basis of size. Re-examination of adult specimens from her collection indicated that they are conspecific with *O. waldemari*, based on the following characters (cf. Table 5): (1) ratio of genital double-somite to rest of urosomites (2.0 : 1), (2) position of genital apertures (1/4 the distance from lateral margin), (3) length ratio of seta VI on CR (3/4 length of seta IV), and (4) length to width ratio of P5 exopod (1.3 : 1). The length to width ratio of genital double-somite of Malt's specimens was somewhat smaller (1.5 : 1) than in typical *O. waldemari* and its form was not as elongate as in specimens from the Red Sea, but resembled more that of *O. scottodicarloi*. However, such variation was also observed in specimens from the Adriatic during various seasons, and thus may indicate some intraspecific variation. Males of *O. media* sensu Malt were assigned to *O. waldemari* on the basis of antennary seta IV, which was slightly curved and setiform (cf. Fig. 27H), rather than being spiniform as in *O. scottodicarloi*.

The records of *O. waldemari* from very distant localities in tropical and temperate regions of the three great oceans indicate a world-wide distribution of the species. However, some morphological differences were observed between these morphs, which need to be clarified.

DEVELOPMENTAL STAGE CV ♀ OF *O. WALDEMARI*

The developmental stages (NI–NVI, CI–CVI ♀ and ♂) of *O. waldemari* were described by Malt (1982b, as *O. media* f. *minor*), based on individuals reared in the laboratory and collected at sea. According to her report, the female CV exhibits a 4-segmented urosome (1 segment between genital double-somite and anal somite), which is very unusual among copepods exhibiting the full complement of urosomites in the adult. Typically, the number of somites between female CV and CVI does not change in female copepods possessing a genital double-somite because the addition of one abdominal somite from CV to CVI is compensated for by the fusion of the genital somite and the first abdominal somite in the female (e.g. Itoh & Nishida, 1995). Remarkably, the only other taxonomic report of copepodid stages of oncaeids by Björnberg (1972) also describes the female CV of an unidentified *Oncaea* sp. with a 4-segmented urosome. So both Malt and Björnberg must in fact have been dealing with a CIV. In the present study, late female copepodid stages of *O. waldemari* and related species, such as *O. venusta*, *O. mediterranea*, and *O. scottodicarloi*, were found with a 5-segmented urosome, which exhibited no genital apertures (cf. Fig. 28C, E). According to the general rule mentioned above, these stages should be regarded as the typical female CV. A more detailed re-examination of developmental stages of *O. waldemari* and other oncaeid species is in progress.

GEOGRAPHICAL DISTRIBUTION

O. waldemari was confined to the Gulf of Aden / Strait of Bab al Mandab area and the southernmost, shallow parts of the Red Sea. It was not found in the deep oceanic area of the southern Red Sea or further north in the central/northern regions (Böttger-Schnack, 1995, as *Oncaea* sp. AD). Thus, it cannot be regarded as a typical Red Sea species. In the Arabian Sea, it was present in somewhat greater numbers near Oman than in the central Arabian Sea (Böttger-Schnack, 1996, as *Oncaea* sp. B). The species is also present in the Eastern Mediterranean, but was not separated from the closely related *O. scottodicarloi* during earlier quantitative counts in that area (Böttger-Schnack, 1997, as *O. media* f. *minor*).

VERTICAL DISTRIBUTION

Both sexes of *O. waldemari* occurred in the lower epipelagic zone, with maximum concentrations between 20–60 m in the Gulf of Aden and the Strait of Bab al Mandab. In the southern, shallow region of the Red Sea (total water depth 190 m), the populations showed a strong tendency to submerge: they were generally found between 20–175 m, with maximum concentrations between 125–175 m (females) or 100–150 m (males).

Oncaea paraclevei sp. nov.

TYPE LOCALITY. Southern Red Sea, oceanic area, 15° 34.8'N, 41° 54.9'E, at 0–50 m; total water depth 970 m.

MATERIAL EXAMINED.

(1) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m.
   (a) holotype ♀ dissected on 11 slides (urosome partly damaged after documentation (ZMH K-39578a–j); paratypes: 6 ♀♀ in alcohol, some ovigerous (ZMH K-39579).
   (b) additional paratypes: 1 ♀ dissected on 10 slides (BMNH 1998.2820), 5 ♀♀ in alcohol (BMNH 1998.2821–2825).
   (c) additional paratypes: 1 ♂ dissected on 10 slides, 1 ♀ dissected on 11 slides, 6 ♀♀ (1 ovigerous, 2 with spermatophores, 1 with small dorsal projection, 1 without dorsal projection) in alcohol (RBS).

(2) Central Red Sea, 21° 25.53'N, 38° 01.91'E: Stn. 130; *R/V Valdivia* leg 29: collected 28 October 1980 with MSN 0.1 mm net (Haul 117/5); depth 0–20 m; total water depth ca 1960 m.
   (a) 1 paratype ♀ in alcohol (BMNH 1998.2826).
   (b) 2 paratype ♀♀ in alcohol (ZMH K-39580).
   (c) 1 paratype ♀ dissected on 10 slides (RBS).

(3) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; *R/V Meteor* leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 2 ♀♀ in alcohol (RBS).

DESCRIPTION. Note illustrations are based on the holotype, except for habitus, maxilliped and labrum.

ADULT FEMALE (Figs. 29–31).

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 770 μm [traditional method: 650–660 μm, based on 2 specimens].

Exoskeleton well chitinized. Prosome 2.1 times length of urosome, excluding caudal rami, 1.8 times urosome length including caudal rami. P2-bearing somite with dorso-posterior projection in lateral aspect (Fig. 29B), variable in conspicuousness according to degree of telescoping of somites (Fig. 29a–c). Integumental pores on prosome as indicated in Fig. 29A, B. Pleural areas of P4-bearing somite elongate and with rounded posterolateral corners.

Proportional lengths (%) of urosomites 9.4 : 58.5 : 9.9 : 10.4 : 11.8. Proportional lengths (%) of urosomites and caudal rami 7.9 : 49.2 : 8.3 : 8.7 : 9.9 : 15.9.

Genital double-somite oval-elongate, 1.6 times as long as maximum width (measured in dorsal aspect) and 1.9 times as long as postgenital somites combined (Fig. 29C); largest width measured at anterior third, lateral margins of genital double-somite rounded anteriorly, tapering posteriorly. Paired genital apertures located near dorsolateral margin at about 1/3 distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 29H). Double-curved sclerotization between genital apertures, varying in form as in Fig. 28d, e; pore pattern on dorsal surface as in Fig. 29C.

Anal somite 1.3 times wider than long; about 3/4 length of caudal rami (Fig. 29C). Anterior margin of anal opening (vestigial anal opening) with transverse row of minute denticles, which are variable in number, ranging between 4 (holotype) and 10. Other surface ornamentation as in *O. venusta*.

Caudal ramus (Fig. 29F) about 2.3 times as long as wide, variation within (Fig. 29F) and between specimens ranging between 2.1–2.4 : 1 (4 specimens). Surface ornamentation and length ratios of caudal setae as in *O. clevei*, except for longer outer terminal seta (IV), reaching 4/5 the length of inner terminal seta (V).

Antennule (Fig. 29E) with relative lengths (%) of segments measured along posterior non-setiferous margin 6.0 : 24.5 : 42.9 : 10.9 : 4.3 : 11.4. Armature formula as for genus.

Antenna (Fig. 30A) as in *O. clevei*, except for seta III on second endopod segment unipinnate.

Labrum (Fig. 30B,C) as in *O. clevei*, except for anterior surface lacking row of denticles on proximal part of each lobe.

Mandible (Fig. 30D) similar to *O. clevei*, except for number of dentiform processes along distal margin of blade C varying between 3 or 4 (Fig. 30D, d).

Maxillule (Fig. 30E), maxilla (Fig. 30F), and maxilliped (Fig. 30G) as in *O. clevei*.

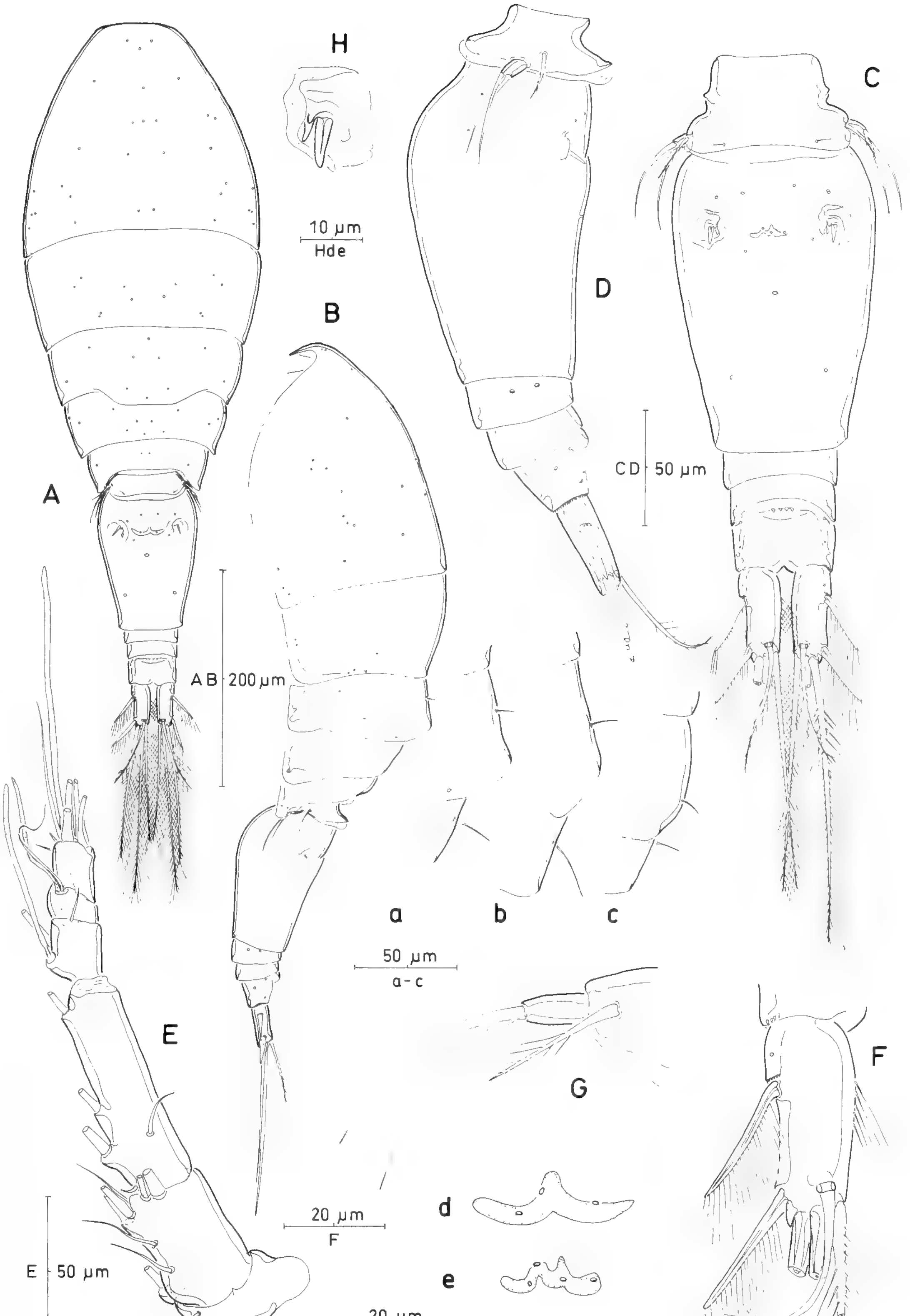

Fig. 29 *Oncaea paraclevei* sp. nov., female (Red Sea) (**A**) Habitus, dorsal; (**B**) same, lateral (appendages omitted) [**a–c:** different degrees of telescoping of somites, causing variation in conspicuousness of dorso-posterior projection on P2-bearing somite]; (**C**) urosome, dorsal, setae V and VI (right) not figured [**d, e:** variation in form of sclerotization between genital apertures]; (**D**) urosome, lateral; (**E**) antennule; (**F**) caudal ramus, dorsal; (**G**) P5; (**H**) P6.

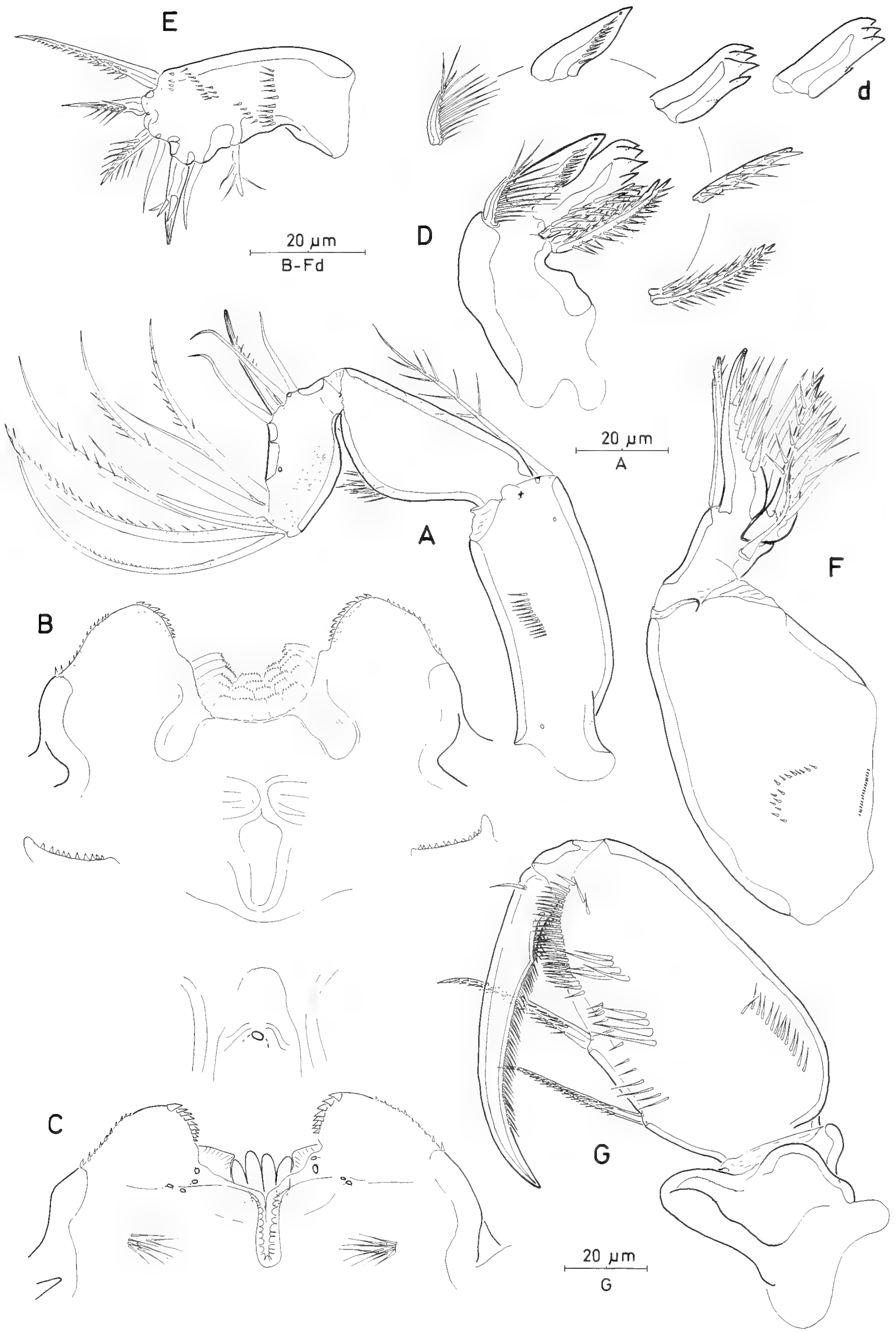

Fig. 30 *Oncaea paraclevei* sp. nov., female (Red Sea) (**A**) Antenna, anterior; (**B**) labrum, anterior; (**C**) same, posterior; (**D**) mandible, showing individual elements [**d:** blade C, showing variation in number of dentiform processes]; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

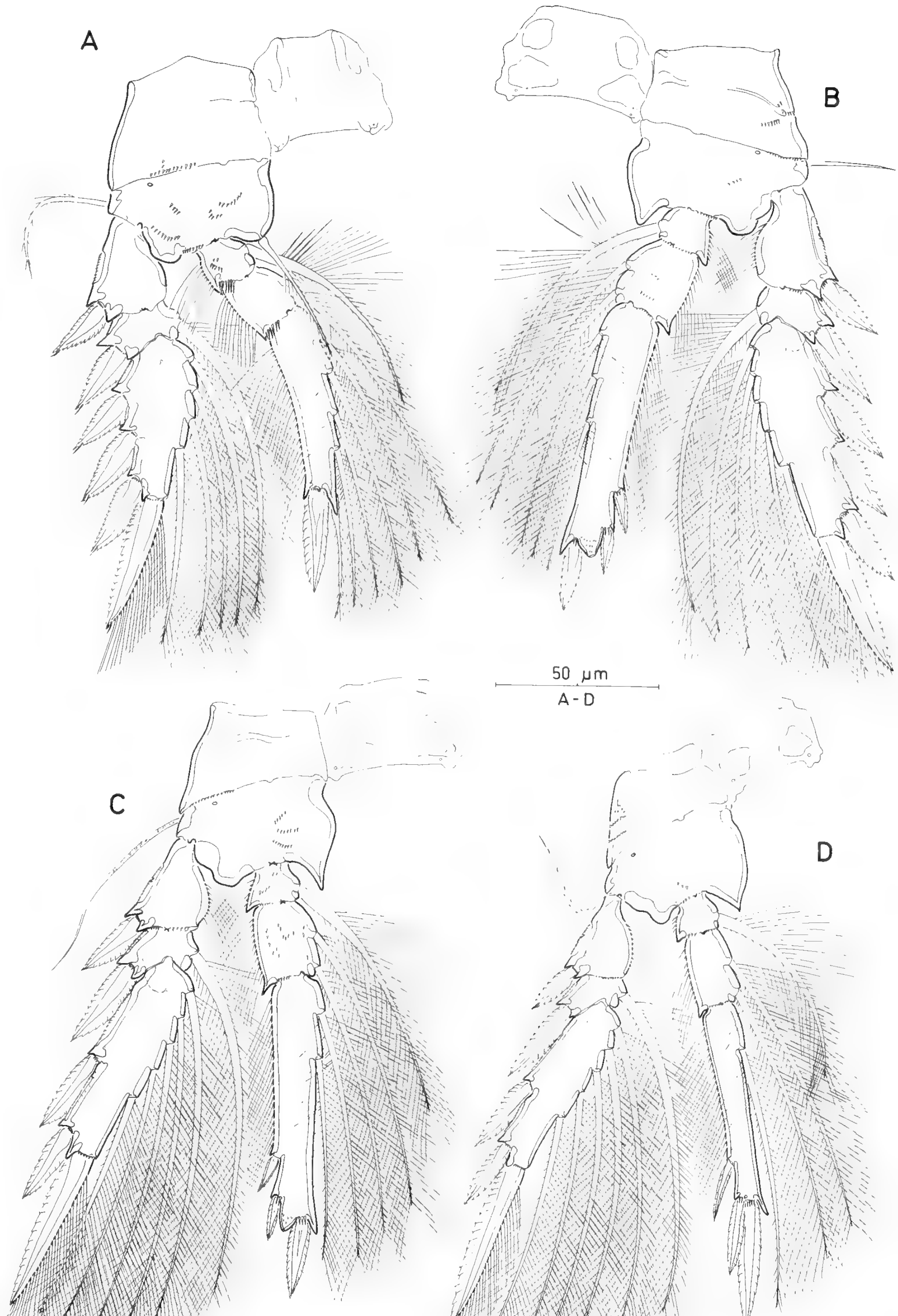

Fig. 31 *Oncaea paraclevei* sp. nov., female (Red Sea) (**A**) P1, anterior; (**B**) P2, anterior; (**C**) P3, anterior; (**D**) P4, anterior.

Swimming legs 1–4 (Fig. 30A–D) with armature as for genus and surface ornamentation as in *O. clevei*. Spine length of exopodal and endopodal segments not substantially different between the two species, except for outer distal spine on P4 endopod, which is slightly longer, measuring > 1/2 to 3/5 length of distal spine (Fig. 30D).

P5 (Fig. 29G) as for *O. clevei*, except exopodal setae slightly curved, and small seta arising from lateral surface of somite plumose.

P6 (Fig. 29H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes.

Egg-sacs as in *O. clevei*.

ADULT MALE. Unknown.

ETYMOLOGY. The Greek prefix *para-*, meaning beside, refers to the great similarity of the species with *O. clevei*.

TAXONOMY

O. paraclevei is closely related to *O. clevei*, from which it can be distinguished by differences in the form of the genital double-somite, which is more elongate, location of genital apertures, which are more medial and somewhat more posterior than in *O. clevei*, and by the resulting differences in form and location of sclerotization between genital apertures. The combination of these characters enables rapid separation of the two species during routine counts. Further minor differences are found in ornamentation of the labrum, in proportional spine lengths on P4 enp-3, and in P5 setae.

Males of *O. paraclevei* were not encountered during the present study, although ovigerous females and specimens carrying spermatophores were observed in the samples. Those males co-occurring with females of *O. clevei* and *O. paraclevei* were all assigned to the first species at closer examination, based on the proportional length of endopodal spines on P4. However, as this is a variable character in *O. paraclevei*, it might not be adequate to separate males of these two species. Further investigation using alternative methods, such as molecular analysis, may help to identify males of *O. paraclevei*, which cannot be distinguished morphologically.

SIZE VARIATION

O. paraclevei exhibited variable body morphology, most obviously in the form and size of the dorso-posterior projection on P2-bearing somite, which varied greatly in size and conspicuousness according to the degree of telescoping of somites (cf. Figs. 29a–c). Variation was also expressed in the form of sclerotization on the dorsal surface of genital double-somite, in the ornamentation of the anal opening, in length to width ratio of caudal ramus and in proportional lengths of terminal spines on P4 endopod.

GEOGRAPHICAL DISTRIBUTION

O. paraclevei was recorded from the central and southern Red Sea as well as from the Gulf of Aden and the northern Arabian Sea. Its potential distribution in the northern Red Sea still has to be confirmed, as the species was not separated from the closely related *O. clevei* during the earlier quantitative counts.

VERTICAL DISTRIBUTION

No quantitative data on the vertical distribution of *O. paraclevei* are available, because the species was not distinguished from *O. clevei* by Böttger-Schnack (1990a, b, 1995). It generally co-occurred with this species in the upper epipelagic zone, at 0–20 or 0–50 m depth, and was absent in the meso- and bathypelagic zones.

ACKNOWLEDGEMENTS. I am very grateful to Dr R. Huys (The Natural History Museum, London) for his encouragement, fundamental help and indefatigable advice in the study of oncaeid taxonomy and for arranging the loan of *O. waldemari* and *O. media* sensu Malt. His critical comments helped to improve the manuscript. Sincere thanks are due to Prof. J. Lenz, Prof. D. Schnack and Drs H. Weikert and K. Schulz for continuous support during the study. I wish to thank H. Itoh (Kawasaki, Japan) for translating the Japanese text of his recent taxonomic study on oncaeids into English. I appreciate assistance from the following persons or institutions, who provided specimens, samples or information pertinent to the study: Dr G.A. Heron (University of Washington, Seattle); Prof. J.-s. Ho (California State University, Long Beach); the late Prof. A.G. Humes (Boston University Marine Program, Woods Hole); Dr F. Kršinić (Laboratory of Plankton Ecology, Dubrovnik); Dr D. McKinnon (Australian Institute of Marine Science, Townsville); Dr S. Nishida (Ocean Research Institute, Tokyo); Dr S. Ohtsuka (Hiroshima University); Dr H. Postel (Institut fürOstseeforschung, Warnemünde);Dr D.K. Steinberg (Bermuda Biological Station); Dr C.T. Walter (National Museum of Natural History, Smithsonian Institution). The financial support for a visit to The Natural History Museum, London, under the EC-funded TMR Programme Bioresource LSF is gratefully acknowledged. This study was supported by Deutsche Forschungsgemeinschaft grant Le 232/18 to J. Lenz.

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Review of the False Smooth snake genus *Macroprotodon* (Serpentes, Colubridae) in Algeria with a description of a new species

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CONTENTS

SYNOPSIS. The characters used to define *Macroprotodon cucullatus mauritanicus* Guichenot are re-evaluated. The taxa, *M. c. cucullatus*, *M. c. brevis* and *M. c. mauritanicus* are considered to be full species. The populations occurring in northern Algeria-from Algiers eastwards to Northern Tunisia are retained as *M. mauritanicus*. Those populations from Algiers westwards into Morocco as far as Melilla are recognised as a new species, *M. abubakeri*. The populations inhabiting the regions further south are morphologically closer to *M. cucullatus* Geoffroy Saint-Hilaire and are assigned to that species. The status of *M. c. ibericus* Busack & McCoy is discussed.

INTRODUCTION

The subspecies of *Macroprotodon cucullatus* were first investigated across its range by Pasteur & Bons (1960) and Bons (1967) in which, on the basis of midbody scale differences, *M. c. brevis* was separated from *M. c. cucullatus*. The former race was restricted to the Iberian peninsula, Morocco exclusive of the east and northeast of that country and the Western Sahara; the populations elsewhere were retained in the nominate form (Fig. 1a).

Wade (1988), recognised the northern Algerian, northern Tunisian and Balearic populations as distinct from the nominate race mainly on the head and body pattern. He applied the available name, *M. c. mauritanicus* Guichenot 1850, to which the eastern and northeastern Moroccan populations were also assigned (without seeing any of these specimens). In all other respects there was agreement with Bons (Fig. 1b).

The latest review by Busack and McCoy (1990) rearranged the distribution of the subspecies and added a fourth (Fig. 1c). The distributions of the four subspecies are as follows:

M. c. cucullatus (Geoffroy Saint-Hilaire, 1827) is restricted to Libya, Egypt and southern Israel.

M. c. mauritanicus Guichenot, 1850, to which were assigned populations of *M. c. cucullatus sensu* Wade, 1988, occupies the whole of northern Algeria (south to 23°16'N), Tunisia (south to 33°42'N), and the Balearic Islands (Spain). The isolated populations of *Macroprotodon* (*M. c. cucullatus, sensu* Wade, 1988) from the Hoggar (Algeria) and Lampedusa Island (Italy) were assigned to *M. c. mauritanicus*.

M. c. brevis (Günther, 1862) was excluded from Iberia but stated to inhabit the whole of Morocco. The Western Saharan form of *M. c. cucullatus* (*sensu* Wade, 1988) together with the eastern Moroccan population of *M. c. mauritanicus* (*sensu* Wade, 1988) in the extreme northeast of that country were assigned to *M. c. brevis*.

M. c. ibericus Busack & M.Coy, 1990 (*M. c. brevis* auct.) inhabits the Iberian peninsula except the extreme north.

The sets of characters used by Busack & McCoy have been reappraised. *M. c. mauritanicus* has been redefined. The analysis revealed that more than one taxon is involved; the populations from Algiers eastwards comprising the nominate form, those to the west a new form extending into the extreme northeastern Morocco. (Fig. 7). The Balearic populations are considered to be sufficiently distinct as to merit separation at subspecific level and will be described by Dr J. M. Pleguezuelos.

The main aim of this work is the resolution of the conflict of opinions on the forms currently said to comprise *Macroprotodon cucullatus mauritanicus*, the bulk of which occur in Algeria. The value of the analysis would be diminished had the forms under investigation not been compared with extralimital forms in regions where the putative taxa meet. The Moroccan *M. c. brevis* whilst not being part of the present analysis is here nevertheless taken into account insofar as the populations which meet the western form of *M. c. mauritanicus sensu lato* (=the new species) and the adjacent populations of the nominate form are concerned.

With regard to *M. c. cucullatus*, the present analysis addresses only those populations (*sensu* Wade, 1988) which occur in Algeria, Tunisia and Lampedusa i.e. those which have been synonymised with *M. c. mauritanicus* by Busack & McCoy, 1990 and those extending to the Moulouya valley, northeast Morocco. Bons (1967: Carte no.16) depicts a good number of localities but unfortunately

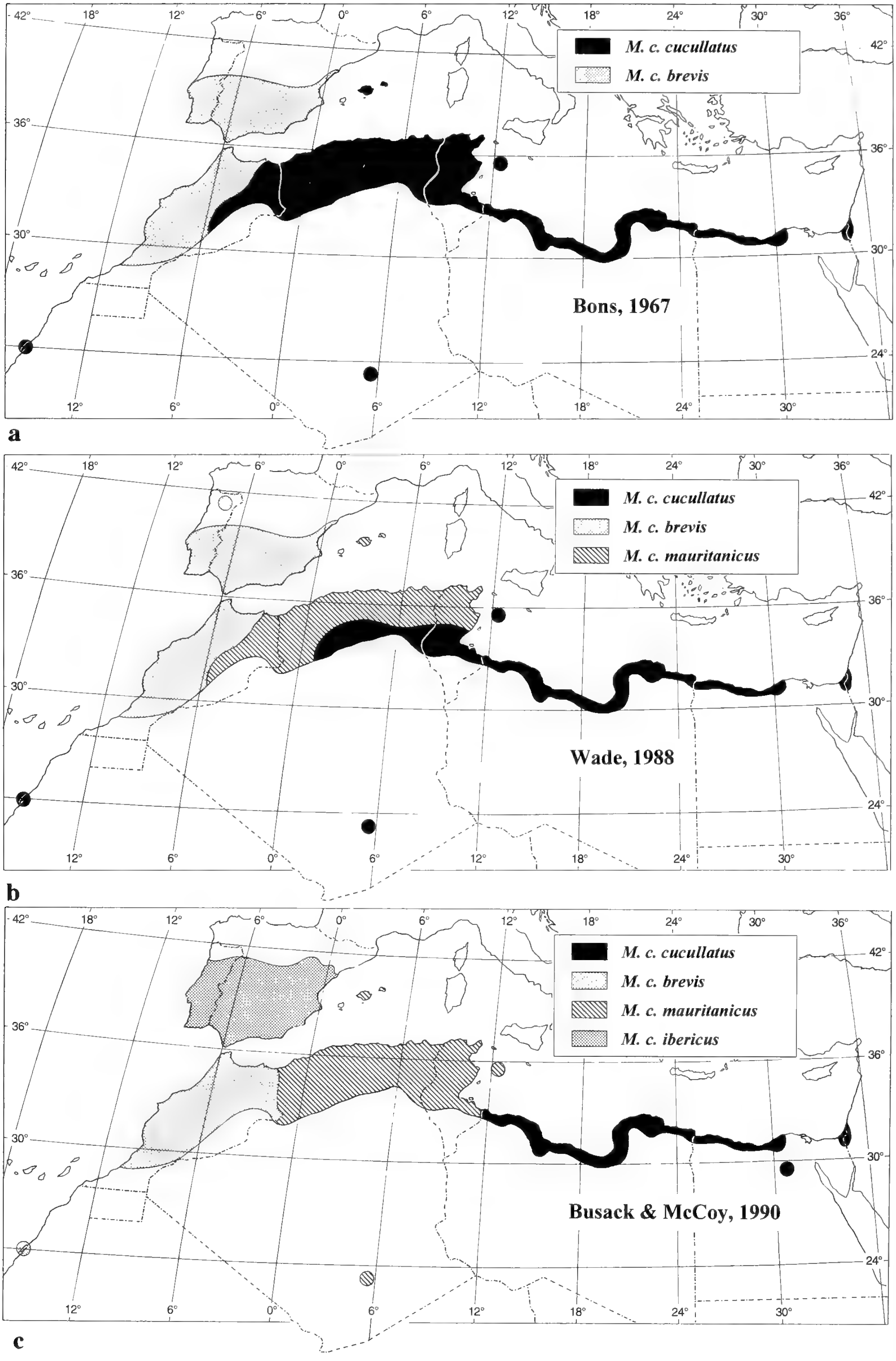


Fig. 1 Concepts of the distribution of *Macroprotodon* of various authors.

the deposition of these specimens is not indicated. *M. c. brevis*, with which the western population of *M. c. mauritanicus* (*sensu* Wade, 1988) is synonymised by Busack & McCoy (1990), is similarly poorly represented in collections from areas where it would meet neighbouring taxa. A full revision of *M. c. cucullatus* and *M. c. brevis* is postponed pending study of material from eastern and southern Morocco.

The subspecies are accorded full species rank. The balance of evidence suggests that the distinctness between them is maintained with little suggestion of any intergradation between the taxa.

MATERIALS AND METHODS

The material examined in the course of this work is listed at the end of each species treatment. Abbreviations used are as follows: Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard (MCZ); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Muséum d'Histoire naturelle, Genève (MHNG); Muséum National d'Histoire Naturelle, Paris (MNHN); Naturhistorisches Museum Basel (NMB); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Senckenberg Museum, Frankfurt am Main (SMF); University of Colorado Museum, Boulder (UCM); National Museum of Natural History, Washington, D.C. (USNM); Museum fürNaturkunde, Universität Humboldt, Berlin (ZMB); Zoologische Staatssammlung, München (ZSM); Zoologisches Museum der Universität Hamburg (ZMH); Naturhistorisches Museum, Wien (NMW); personal collection of the author (EW).

The primary source for Fig. 7 has been the bioclimatic map of Emberger *et al.* (1962) from which relevant data has been extrapolated and forms the substance of Fig. 12. Other maps have also been consulted. The bioclimatic map utilises meteorological data and quantifies dry season drought taking into account not only temperature and precipitation but also atmospheric humidity as the xerothermic index (x) or number of physiologically dry days in the dry season (Emberger *et al.*, 1962, pp. 12–19). The area under consideration broadly translates into north-south divisions of seven subregions with their respective xerothermic indices ranging from, in the more northern latitudes, the sub-mediterranean (x =<40) to those in the south, the desertic (x =300+). The xerothermo-mediterranean subregion (x =150–200) is seen as a transitional zone between the Mediterranean and the Arid-Saharan regions. Transliteration of indigenous place names mainly follows the Michelin (tourist) map 958 'Algérie-Tunisie'. The convenient symbols of Busack and McCoy (1990) have been used.

Each synonymy includes most of the generic and specific combinations. Pages refer to citations of the taxa. Most of the references in which either sources are not given or the species is just mentioned, have been excluded.

CHARACTERS EXAMINED

All specimens were sexed. Morphological characters used by Wade (1988) and those used and considered by Busack & McCoy (1990) were re-evaluated. Of those of the latter the sum of the ventral + subcaudals, anterior temporals and postocular counts were not analysed; all their other characters were found to be useful in varying degrees. Additional characters such as maxillary tooth counts and scale row reductions were incorporated into the analysis.

Dorsal scales rows. These are normally understood to mean those counted arounud midbody. The reductions were recorded in the manner proposed by Dowling (1951b). They occur behind the head from 25 in four stages to 19 rows until anterior to the vent where the count falls to 17 or more rarely to 15. Occasionally after 19 there may be no further reduction. These are mostly due to fusion between the 4th and 5th rows but those of the 4th and even the 2nd and 3rd are not infrequently involved. Exceptionally, especially in individuals with aberrant dorsal scalation, fusion may occur in other rows, in particular the vertebral and paravertebral. For practical purposes only the reduction from 21 to 19 on the neck and 19 to 17 anterior to the vent, not taking into account any irregular fluctuations, have been considered. The length of the head is defined in this work as the distance from the snout to the retroarticular process of the mandible. The 1st ventral is situated at or slightly posterior to this point in vertical alignment.

In addition to dorsal counts at midbody Busack & McCoy (1990) considered counts at a point one head length (not specified) behind the head and one of same value anterior to the vent. These characters, especially the latter, were found to be significant. The histograms (Figs. 8 & 9) show (ordinate) each point of reduction at the relevant ventral scute expressed as a percentage of the total ventral number. A mean to the nearest integer was taken when the reductions were unequal on either side. Subsequent fusions and divisions after the main points of reduction were not quantified.

Ventral and subcaudal counts. These were counted in the manner of Dowling (1951a) and are summarised in Table 1. Addition of the ventrals to the subcaudals (Busack & McCoy, 1990) whilst not completely eliminating sexual dimorphism did, nevertheless, diminish it, whereas as discrete states they revealed clear sexual dimorphism in all the taxa (Fig. 11). With the exception of *M. c. cucullatus* (*sensu* Wade, 1988) interpopulational variation in these characters was usually slight or too discordant to permit determination of any geographic trends in either of the northern forms.

Supralabials. Nearly all the material examined here possessed 8 supralabials on each side of which the 4th & 5th meet the eye: one individual of *M. mauritanicus* had 9 on both sides.

Supralabial-parietal contact. (Table 2). In the North African material this character was useful in differentiating *M. mauritanicus* from *M. cucullatus* .

Infralabials. (Table 2). The anterior series, i.e. those in contact with the genials, normally numbered 6, there being few departures. Significant differences were found in the posterior or 'free' series of infralabials.

Maxillary teeth. (Table 2). The maxilla bears a series of six teeth increasing in size followed by a diastema and a second numbering from three to five of smaller size that precede the fangs. Duméril and Bibron (1854) gave the number of maxillary teeth as '6+3 ou 5+2' which is understood here to mean 6, followed by 3 or 5+II. Significant differences occurred in the second series of teeth, i.e. that which precedes the fangs.

Head pattern. The variability in the elements of head pattern first noted by Boulenger has been analysed by Wade (1988) and Busack and McCoy (1990). From the confusing array of configurations in

Table 1 Variation (sample size, range, mean, and one standard deviation [SD]) in ventral and subcaudals in the species of *Macroprotodon*.

	M. cucullatus		*M. mauritanicus*		*M. abubakeri*	
	Males	Females	Males	Females	Males	Females
Character:						
Ventrals						
Sample size	23	28	44	39	16	15
Range	153–163	163–182	162–178	168–193	159–175	172–185
Mean	158.17	177.57	170.55	183.51	167.5	180.33
SD	3.25	4.04	3.99	4.56	5.54	3.72
Subcaudals						
Sample size	22	28	44	34	15	15
Range	42–54	39–53	46–59	43–54	45–50	41–51
Mean	48.41	44.57	57.91	48.38	49.7	45.27
SD	2.86	3.35	2.79	2.81	1.76	3.08
Ventrals + subcaudals						
Sample size	22	28	44	34	15	15
Range	196–217	207–226	212–235	222–241	209–224	213–237
Mean	207.05	216.36	222.45	231.65	216.74	225.7
SD	5.2	5.49	5.5	5.51	5.74	6.23

Table 2 Variation in character states the species of *Macroprotodon*.

	M. cucullatus	*M. mauritanicus*	*M. abubakeri*
Sample size:	51	83	31
Character:			
Labial-parietal contact (L/R)			
+/+	1 (1.96%)	74 (89.2%)	13 (41.9%)
+/– or –/+	0	7 (8.4%)	3 (9.7%)
–/–	50 (0.98%)	2 (2.4%)	14 (42.2%)
Posterior infralabials (L/R)			
3/3	5 (9.8%)	46 (54.4%)	2 (6.5%)
3/4 or 4/3	0	14 (16.9%)	1 (3.2%)
4/4 or more	46 (90.2%)	23 (27.7%)	28 (90.3%)
Posterior maxillary teeth			
3	0	83 (100%)	0
4	24 (47.1%)	0	30 (100%)
4/5 or 5/4	2 (3.9%)	0	0
5	25 (49%)	0	0
Nuchal collar			
Entire	1 (1.96%)	3 (3.6%)	22 (71%)
Divided	30 (58.8%)*	78 (93.4%)	6 (19.4%)
Partially melanocephalic	5 (9.8%)	0	1 (3.2%)
Melanocephalic	15 (29.4%)	2 (2.4%)	2 (6.5%)
'Pale' collar			
Present (uninterrupted)	5 (9.8%)	81 (97.6%)	20 (64.5%)
Present (interrupted)	1 (2%)	0	10 (32.3%)
Absent	24 (47.1%)	2 (2.4%)	0
Intermediate or indeterminate	4 (7.8%)	0	0
Obscured	17 (33.3%)	22 (2.4%)	1 (3.2%)
Postorbital streak			
Short	0	63 (75.9%)	0
Interrupted or fragmented	13 (25.5%)**	3 (3.6%)	5 (16.1%)
Entire	30 (58.8%)***	17 (20%)	26 (83.9%)
Embraces last supralabial	2 (3.9%)	82 (98.8%)	27 (87.1%)
Obscured or part. absorbed	8 (15.7%)	1 (1.2%)	0

* Laberal portions in most cases more forwardly situated and often united to the 'V'-mark; ** occasionally rather short but never less than two supralabials in length; *** highly variable in shape (see p. 89).

the pattern essentially three characters, the nuchal collar, the interspace between it and the head pattern elements (the 'pale collar') and the postorbital streak presented states which were useful in the differentiation of the taxa: these are summarised in Table 2. In some individuals, from north west Algeria in particular, there occurs a bar, more or less at the level of the mouth, connecting the posterior head pattern elements to the nuchal collar. The state of the forward position of the lateral portions of the nuchal collar (i.e. occupying the space of the 'pale collar') still serves to distinguish the taxa but there is some reduction in reliability where it has been used to differentiate some individuals of *M. cucullatus* from the eastern Hauts Plateaux + southern Tunisia from the populations further west and the *mauritanicus* complex to the north.

The V-mark is an inverted V or Y-shape which commences from around mid-frontal its posterior 'arms' extending, entire or fragmented to the last supralabials, or further. The state where it either embraces the last supralabial – where it may unite with the postorbital streak – or extends on to the 'pale collar' has significance in differentiating the taxa, in particular those of eastern Algeria and Tunisia.

The postorbital streak is highly variable in the forms from the southern and more arid regions (*M. c. cucullatus sensu* Wade, 1988) and less so in those from the north. In Table 2 the categories are as follows: 'short' denotes the condition in which the streak extends not much further than the 6th supralabial and is always associated with absence of labial smudging; there may occasionally be vestiges of the streak on the 7th or 8th supralabials but should this condition be unaccompanied by labial smudging it is counted as 'short': 'interrupted' or 'fragmented' covers the variety of conditions other than 'short' or 'entire' (Fig. 3): 'Embraces last supralabial' denotes the condition in which the the postorbital streak joins the posterior extensions of the V-mark; in the 'short' condition the partial embracing of the last supralabial is made up of the V-mark: 'Entire' denotes the uninterrupted condition. The short state (Fig. 4c & d) is of some taxonomic significance in evaluating the northern forms.

Body pattern. This essentially consists of a conspicuous series of vertebral spots or flecks, on one or both sides of each scale upon which they are situated (Fig. 6c & f), with less prominent ones alternating on the sides (Fig. 6a & e). These in varying degrees are connected diagonally: they are sometimes manifest only when the body is bent the imbrication being reduced thus exposing the parts of the scales which are normally hidden. This condition, the 'undifferentiated' pattern, may merge into one in which the spots expand to form a reticulated-tessellated pattern consistent with some darkening of the ground colour leaving the spaces so formed as discrete pale areas, the '*textilis*' pattern. A third condition sometimes occurs in which the ground colour differentiates into pale and dark longditudinal stripes, the '*taeniatus*' pattern. This character is of little value when applied to intraspecific differences between the northern forms but very useful in differentiating those from the southern populations.

Belly pattern. The chequered pattern and its variations and the immaculate condition are present in all the taxa. In the northern populations the progression from one to the other is by reduction in number and also the size and density of the spots whereas in those from the south the change is more often by progressive fading.

SYSTEMATIC ACCOUNT

Macroprotodon cucullatus (Geoffroy Saint-Hilaire)

Coluber cucullatus I. Geoffroy Saint-Hilaire, 1827:151, Pl. 6, Fig. 3. Type locality, 'Lower Egypt' Type lost.

?Coronella laevis (part), Schlegel, 1837:65 .

Coronella cucullata: Günther (part), 1858:35. Strauch, 1862:55. Lallemant, 1867:28. ?Olivier (part), 1894: 25; ?1896:124.

Lycognathus cucullatus: Duméril & Bibron (part), 1854:926. ?Gervais, 1857:511, Pl. 5, fig. 6; ?1869: 200, pl. XLIV, 2.

Lycognathus textilis: Duméril & Bibron, 1854:931.

Coronella textilis: Strauch, 1862b:67. Lallemant, 1867:29.

Psammophylax cucullatus: Jan, 1862:312.

Psammophylax cucullatus: Jan & Sordelli, 1866:312; Pl. i, Fig. 3A. Lataste, 1881: 399.

Psammophylax cucullatus var *textilis*: Jan & Sordelli, 1866:312; Pl. i, Fig. 4

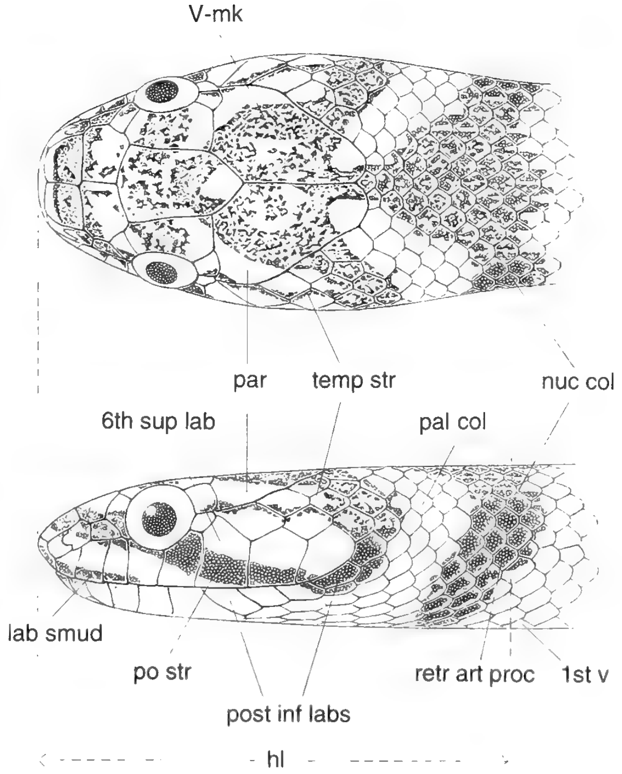


Fig. 2 Head of *Macroprotodon abubakeri* (MNHN 1899.273 Laghouat, Algeria) showing the characters used in the study): par = parietal, 6th sup lab = 6th supralabial, post inf labs = posterior infralabials, 1st v = 1st ventral, retr art proc = retroarticular process of the mandible, V-mk = V-mark, temp str = temporal streak, po str = postorbital streak, nuc col = nuchal collar, pal col = pale collar, lab smud = labial smudging, hl = head length.

Macroprotodon cucullatus: Rochebrune, 1884:160. Boulenger (part), 1891:149–150. (part), 1896:175–176. Mayet, 1903:24. Boulenger, 1920a (1919):290; 1920 (1919b):305. Pellegrin, 1926:161. Mosauer (part), 1934:58. Laurent, 1935:347. DeWitte, 1930:618. Angel & L'Hote, 1938: Tab. Angel, 1944b:419. Villiers, 1950:98. Chpakowski & Schnéour, 1953:135 (*forme méridionale*), Pl. XVI, 2. Domergue (part), 1959:166–167, photos. 16&17. Pasteur (part), 1959 (1960):136–7?. Lanza & Bruzzone, 1960:55; Fig. 2, Pl. xli. Davidson, 1964:15 (southern form). Slavtchev & Chadli, 1984:417.

Macroprotodon textilis: Rochebrune, 1884a:160.

Macroprotodon cucullatus melanocephala Mosauer & Wallis, 1927:305–310, Fig. 1. Type locality: Gafsa.

Macroprotodon cucullatus cucullatus: Pasteur & Bons (part), 1960:87. Bons & Girot (part), 1962:50. Kramer & Schnurrenberger (part), 1963:506. Villiers, 1963:133+134. Bons (part), 1967:29, 84, ?87, 90, 93, 162, 191,192, 231, fig. 16, map 16. Papenfuss, 1969:308. Bons (part), 1972:116; 1973:94. Villiers, 1975:134. Wade, 1988:242–243, Figs. 3b–c & 4b. Gruber (part), 1989: 149–151. (part) Sindaco, 1990:151.

Macroprotodon cucullatus mauritanicus: Busack & McCoy (part), 1990:268–269, Fig. 2 (Codes 2&4).

Macroprotodon cucullatus brevis: Busack & McCoy (part), 1990:269, 271.

DIAGNOSIS. A species of *Macroprotodon* characterised by four or five maxillary teeth in the series preceeding the fangs. Head pattern

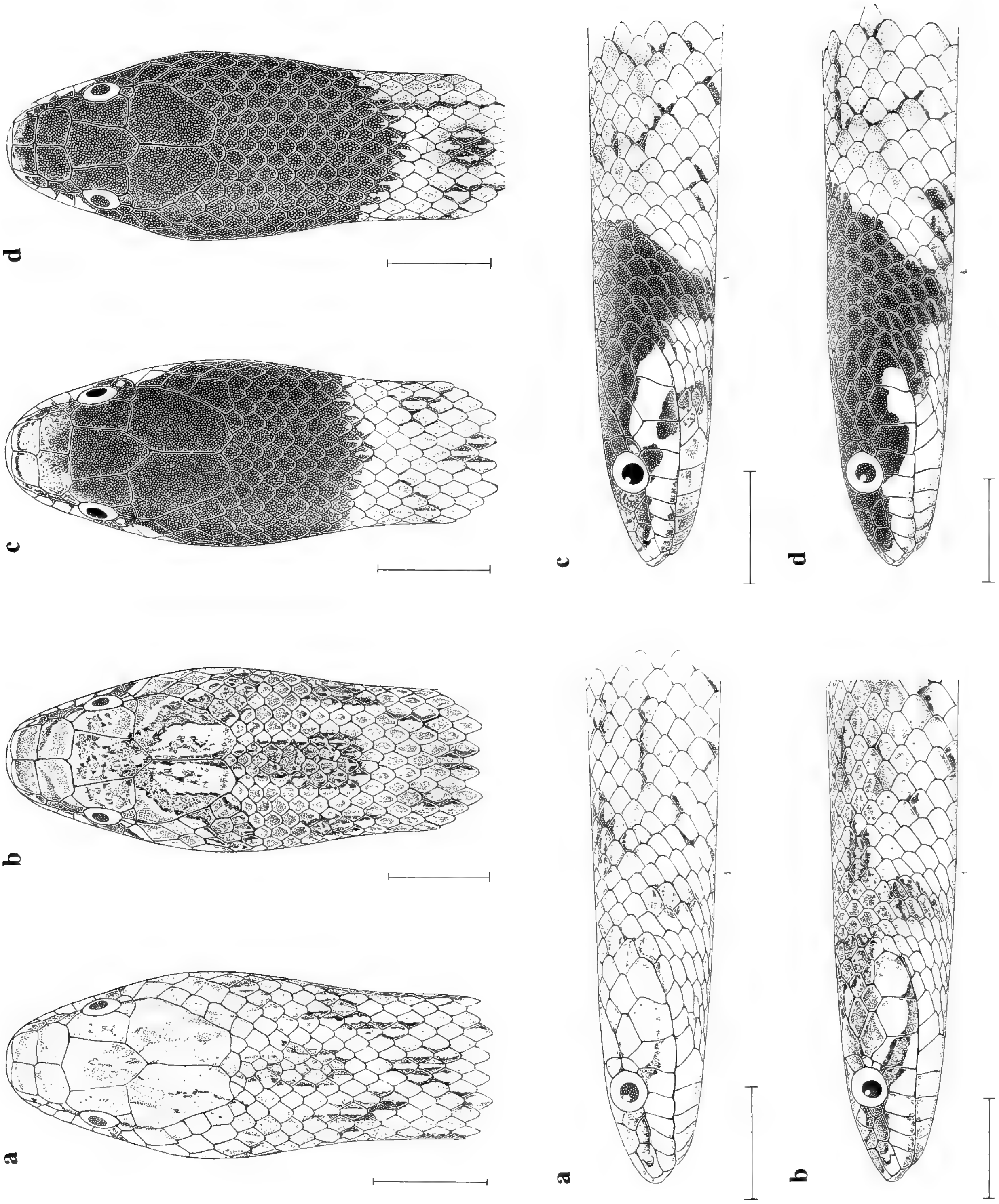


Fig. 3 Head and nape pattern in *Macroprotodon cucullatus*. **a.** MNHN 849; Deserts of Western Algeria (holotype of *Lycognathus textilis*). **b.** MNHN 1927.149; Bordj Douis, Algeria. **c.** MCZ 27501: Aïn Sefra, Algeria. **d.** MNCN 1802; Biskra, Algeria. (Scale=5mm).

variable, body pattern usually tessellated-reticulated (the *textilis*) pattern. Midbody scales in 19 rows. Sixth supralabial usually not in contact with parietal. Usually four posterior infralabials. Separable from *M. mauritanicus* mainly in the maxillary tooth count; 4 or 5 as opposed to 3 and from that race and the new species (see below) in its possession of the '*textilis*' pattern in contrast to the undifferentiated or the '*taeniatus*' pattern.

REDESCRIPTION OF THE HOLOTYPE OF *Lycognathus textilis* Duméril & Bibron 1854. Adult female MNHN 849, (Figs. 3a & 6a): snout-vent length 287 mm; tail 57 mm. Type locality, 'Deserts of Western Algeria', collected by F. Schousboé.

Scalation. Scales at midbody 19, ventrals 168, subcaudals 45+1. Dorsal scale row reduction formula:

$$\mathbf{21}\ \frac{3+4\ (8)}{3+4\ (7)}\ \mathbf{19}\ \frac{4+5\ (119)}{4+5\ (128)}\ \mathbf{17}\ \text{———}\ 168$$

Supralabials 8/8 the 6th well separated from the parietals on both sides; infralabials 6+4 /4+4.

Maxillary teeth. 6+4+II; a diastema occurs between the 1st and 2nd tooth in the second series (both sides) i.e. that which precedes the fangs.

Coloration. Spirit-faded, cream coloured the darker ground colour only just discernible; dark markings undiminished.

Head pattern. V-mark indistinct; postorbital streak fairly thin extending obliquely from the eye to the 6th supralabial whereupon it abruptly assumes a horizontal course, narrowing and petering out on the 7th; nuchal collar fragmented, consisting of a median and two lateral portions.

Body pattern. Conspicous black dorsal and dorsolateral markings in varying degrees on the margins of the scales they occupy are connected diagonally by black slivers usually confined to the inner margins of the scales: the ground colour faded and only just discernable thus poorly differentiating these from the pale patches.

Belly pattern. Immaculate, no trace of any markings visible.

Remarks. Doumergue (1901) believed the type locality to be in the region of El Aricha (34°13'N, 1°01'W). This is supported to a large extent by the character states of the holotype agreeing with almost all those of the nearest populations, allowing for variation in small sample sizes (Berguennt n=3; Tadmit-Djelfa n=3). Although the condition of 4 maxillary teeth in the second series is normal for material from eastern Morocco and western Algeria the diastema between the 1st and 2nd is but a small step from a socket into which an additional tooth would easily fit suggesting a recent departure from the 5-toothed condition and that its provenance may lie closer to the 5-toothed populations the nearest of which in Algeria is Oum Ali.

DESCRIPTION. Based on 51 specimens including the holotype of *Lycognathus textilis*. Restricted to material from north Africa between 3°W and 10°33'E. Lampedusa Island (Italy) is included.

Dorsal scale rows. 19 rows at midbody commencing from the 3rd to the 11th ventral. In one individual from the Hoggar for a distance of 20 ventrals and another from Gafsa for a distance of 1 the count dropped to 17 before the 40th ventral: in two from southern Tunisia the count was 18 in stretches of 4 and 5 ventrals. The count anterior to the vent varied from 17 to 15. Seventeen in 40% (n=19), decreasing to 15 in 30% (n=14) and reverting from 15 to 17 in 30% (n=14).

Ventrals. 153–182 (males 153–163, females 167–182).

Subcaudals. 43–54 (males 43–55, females 40–54).

Supralabials. Eight supralabials the 6th, with one exception (CAS 132803), always out of contact with the parietals.

Infralabials. Usually ten (6+4): one (USNM 195463b from Berguennt) exhibited 7+3. Four (MNHN1916.31 from Kebili, SMF 57648, CAS 132803 from near Gabès and MNHN 1930.181 from the Hoggar possessed nine (6+3).

Maxillary teeth. 6+4+II or 6+5+II.

Pattern. Nuchal collar, in specimens in which the pattern elements are sufficiently discrete, is usually divided and sometimes fragmented; the lateral portions are fragments may be either vertically aligned in relation to the median spot a few scales distant from the last supralabial displaying a 'pale collar', or are anteriorly situated so as to exclude it. Anterior head pattern very variable. V-mark conspicuous, indistinct or even absent; connecting the nuchal elements, discrete or fragmented. Postorbital streak highly variable: it may be curved, oblique-straight, or straight; thick, thin or tapering; entire or fragmented; a 'spur' may be present on its lower margin. Melanocephalism present in varying degrees: jet black or diluted, and/or partial to virtually complete.

Body pattern of the '*textilis*' type. Typically this consists of a vertebral and two lateral series of spots connected diagonally by black markings situated on the unexposed parts of the scales involved and expands to form a reticulated-tessellated pattern with some darkening of the ground colour leaving the spaces so formed as discrete pale areas. The black markings may be conspicuous or they may be occasionally reduced even to a condition in which the spots are barely discernible except when the scales have been parted.

Belly pattern presents conditions in which the spots may oppose, alternate or coalesce; they may progressively fade – often from the centre – be uniform or be completely absent.

REMARKS ON THE SYNONYMY. Two of the synonyms listed above, *Lycognathus textilis* Duméril & Bibron and *Macroprotodon cucullatus melanocephala* Mosauer & Wallis pertain to the form of *M. c. cucullatus* from the regions under consideration in this work. Only the holotype of *Lycognathus textilis* has been examined. With regard to *Macroprotodon cucullatus melanocephala* Mosauer and Wallis (1927) neither indicated the institution in which the single specimen was deposited nor did they give a full description. The general appearance of the specimen, its possession of the '*textilis*' pattern and its having originated in Gafsa confirm its belonging with *M. cucullatus* .

GEOGRAPHIC VARIATION. Some of the character states show distinct geographical variation. In specimens from the west, in the Hauts Plateaux as far as the Moulouya valley the nuchal collar fragments when sufficiently discrete, i.e. not obscured by encroaching melanocephalism, are often disposed to show a 'pale collar'. This state is also accompanied by that of 6+4+II maxillary teeth. There is an eastward trend towards exclusion of the 'pale collar' and an increase in the number of maxillary teeth, 6+5+II being the condition most frequently met with in populations from southern Tunisia. There is a noticable east-west reduction in the degree of chequering in the belly patterns. Supralabial-parietal contact was lacking in all except one individual CAS 132803 from near Gabès and 4 posterior infralabials, or more, were manifest in all except for three in USNM 196463b (near Berguennt, Morocco), MNHN 1916.31 (Kebili, Tunisia), SMF 47648 and CAS 132803 (near Gabès, Tunisia). From Libya eastwards the incidence of 6+5+II maxillary teeth increases, 6+4+II being of rare ocurrence in Egypt; labial-parietal contact in 33–50% of specimens (Busack & McCoy, 1990) and in none did the posterior infralabial count exceed three. It is likely that, given the magnitude of the range and the degree of variation in *M. cucullatus*, further work will result in the description of an additional subspecies. Should the character states which distinguish any of the western forms from that occuring further east be considered sufficiently trenchant as to warrant separation the name available for the Algerian and Tunisian population is *M. c. textilis* (Duméril & Bibron): it is to this form that those of the northeastern Moroccan steppe from Berguennt to the Moulouya valley belong. *M. c. melanocephala* Mosauer & Wallis would be a synonym of *M. c. textilis* (see also p. 91).

AFFINITIES. The infralabial count is an exceptionally stable character with respect to this species not only in the populations of the nominate form in the area of this study but in those from Libya eastward (Busack & McCoy, 1990). Any departures from the norm are regarded as significant. Thus specimens from Kebili and Gabès are seen as belonging to the eastern form of *M. c. cucullatus*.

The demarcation line drawn by Busack & McCoy (1990) between these populations and those further east is the Tunisian-Libyan border, approximates that which Cherlin (1990b) separates populations of *Echis arenicola* from those of *E. pyramidum.*

LOCALITIES

MOROCCO – Taourirt (34°25'N, 2°53'W) MNHN 1927.130–1: **El Agreb** (34°20'N, 3°,08'W); Bons & Geniez, 1996: **Aïn Fritissa** (34°09'N, 3°14'W); Bons & Geniez, 1996: **Rchida** (33°55'N, 3°13'W); Bons & Geniez, 1996: **El Ateuf** (33°51'N, 3°02'W) 1.5km S, aprox 11km S, aprox 20lm S; Bons & Geniez, 1996: **Berguennt** (34°01'N, 2°01'W); Pellegrin, 1926; Werner, 1929; Bons, 1960 MNHN 1925.219; 25km S; Bons, 1960; Bons & Geniez, 1996 and 43km W, Bons & Geniez, 1996: between **Missour** (33°03'N, 4°01'W) and **Talsinnt** (32°32'N, 3°26'W); Bons, 1967: **Aïn Benimathar** (34°05'N, 2°00'W) 10 km S; Busack & McCoy, 1990 USNM 196463a–b: **Meridja** (34°02'N, 2°24'W) approx 8kmW, approx 5km E; Bons & Geniez, 1996.

ALGERIA – 'Deserts of Western Algeria'=?**El Aricha** (34°13'N, 1°16'W) MNHN 849 (holotype of *Lycognathus textilis*), Duméril & Bibron, 1854; Gervais, 1857, 1869; Olivier, 1894: Wade, 1988; Busack & McCoy, 1990 **Aïn Sefra** (32°45'N, 0°35'W); Werner, 1929; Busack & McCoy, 1990 MCZ 27501: **Beni Ounif** (32°3'N, 0°15'W), Foley, 1922: **Méchéria** (33°33'N, 0°17'W), Doumergue, 1901: **Djelfa** (34°40'N, 3°15'E) NMB 13774: Douis=**Bordj Douis** (34°22'N, 2°43'E) MNHN 1927.149: Talmit=**Tadmit** (34°17'N, 2°59'E) MHNG 899.55: **Biskra** (34°51'N, 5°44'E), Jan & Sordelli, 1866; Busack & McCoy, 1990 MNCN 1802: Bir Oum Ali=**Oum Ali** (35°01'N, 8°19'E), Wade, 1988; Busack & McCoy, 1990; BMNH 1920.1.20.3859: **Djebel Ilâman, Hoggar** (23°16'N, 5°31'E), Angel & Lhote, 1938; Witte, 1930 MNHN 1930.181: '**Algeria**' Busack & McCoy, 1990 USNM 10940.

TUNISIA – no locality MNHN 1894; ZFMK 4844: **Fériana** (35°57'N, 8°34'E2), Slavtchev & Chadli, 1984; Wade, 1988; Busack & McCoy, 1990; BMNH 1920.1.20. 3109; MNHN 1885.447–8: **Redeyef** (34°24'N, 8°09'E) MNHN 1961.664–5: **Gafsa** (34°25'N, 8°48'E) (Oasis), Busack & McCoy, 1990 UCM 37371: **Djebel Hattig** nr **Gafsa**, Mayet, 1903: between **Gafsa** and **Redeyef** ('Bled Douara'), Busack & McCoy, 1990 UCM 37345–37358, 37360, 37363–37370, 48083; CM 54559: **Gabès** (33°53'N, 10°07'E) 15 km N, Busack & McCoy, 1990 SMF 57648 and16 km N, ibid CAS 132803: **Chott Fédjédj** (33°55'N, 9°20'E), Lataste, 1881: **Kebili** (33°42'N, 8°58'E), Chabanaud, 1916b MNHN 1916.31: **Tozeur** (33°55'N, 8°08'E); Lavauden, 1926: '**Mateur**' MHNG 1379.84.

SPAIN – Southern Spain, Busack & McCoy, 1990 SMF 20170.

ITALY – Lampedusa Island (35°31'N, 12°35'E), Camerano, 1891; Lanza & Bruzzone, 1959; Busack & McCoy, 1990; Sindaco, 1990 UCM 31078.

Macroprotodon mauritanicus **Guichenot**

Macroprotodon mauritanicus Gervais 1848 (nomen nudum). Guichenot 1850:22, Pl. ii. Fig. 2. Type locality: Algeria. Syntypes, MNHN 2172, 1994.2339–41. Müller, 1882b:169.

Macroprotodon mauretanicum: Müller, 1878:467; *Macroprotodon mauret.* [abbreviation for *mauretanicum*], ibid: 666.

?*Coronella austriaca*: Gervais (part), 1836:312 .

?*Coronella laevis*: Schlegel (part), 1837: 65 .

Lycognathus taeniatus: Duméril & Bibron, 1854:930. Wade, 1988:242. Busack & McCoy, 1990:268.

Coronella taeniata: Strauch, 1862b: 57.

Lycognathus textilis: Busack & McCoy, 1990:268.

Lycognathus cucullatus: Duméril & Bibron (part), 1854: 926. Bosca, 1877:55. Müller, 1890:692.

Coronella cucullata: Günther, 1958:35. Strauch, 1862b:055. Lallemant (part), 1867:29. Boettger (part), 1883; 1885:457–458; 1896:297. ?Olivier, 1894: 25; ?1896:124. Le Cerf (part), 1907:24.

Psammophylax cucullatus: Jan, 1862:312; Jan & Sordelli, 1866, Pl. i, fig. 3B.

Macroprotodon cucullatus: Tristram, 1859; Boulenger (part), 1891:149–150; (part), 1896:175–176. Escherich, 1896:279. Gough ?(part), 1903:468. ?Mayet, 1903:24. Chaignon, 1904:20–22. Gadeau de Kerville, 1908:95. Werner, 1892:352; 1894:85; (part), 1909:620–621. Lavauden (part), 1926:158, 159. Hediger (part), 1929:24–26. Mosauer (part), 1934:58 . Chpakowsky & Schnéour: 1953:134 (*forme septentrionale*), Pl. XVI, 3, XVII, 7. Mertens & Müller (part), 1940:53. Bellairs & Shute, 1954:226. Lanza & Bruzzone, 1954:55 Fig.2, Pl. xli. Mertens & Wermuth (part), 1960:184. Kramer & Schnurrenberger (part), 1963:508. Davidson, 1964:14,15. Schneider, 1969:250, Pl. ii. Johann, 1977:320–321. Sura,1983: 29. ?Blanc, 1988:22. Bischoff & In den Bosch, 1991:170.

Macroprotodon cucullatus cucullatus: Bons (part), 1967:192, Fig. 16. Sochurek (part), 1985:71. Sindaco (part), 1990:151.

Macroprotodon cucullatus melanocephala: Busack & McCoy, 1990:269.

Macroprotodon cucullatus mauritanicus: Wade (part), 1988:242, Figs. 3a, 5 & 4c. Busack & McCoy (part), 1990:268–269, Fig. 2, codes 2 & 4. Gruber (part), 1989. Joger & Bischoff, 1989:100, Pl. 3.

DIAGNOSIS. A species of *Macroprotodon* characterised by a series of three maxilliary teeth preceding the grooved fangs; divided nuchal collar; a short, or less frequently, an entire postorbital streak. Dorsal pattern of the 'undifferentiated' or the '*taeniatus*' state. Supralabial-parietal contact on both sides in the majority of specimens. Dorsal scales in 19 rows, sometimes 20 or 21 at points irregularly along the body but never in 21 rows continuously. Ventral scutes 162–193, subcaudals 43–61. Readily distinguishable from *M. abubakeri* and *M. cucullatus* by the number of maxillary teeth in the series preceeding the fangs (3 as opposed to 4 and 4 or 5 respectively). From *M. cucullatus* it is separable by the high incidence of supralabial – parietal contact (as opposed to virtually no contact) and possession of the 'undifferentiated'–'*taeniatus*' as opposed to the '*textilis*' body patterns.

DESCRIPTION OF THE SYNTYPES. Males: MNHN 2172 (Fig. 4a), 1994.2341; snout-vent length 386–462 mm, tail 83–95 mm. Females: MNHN 1994.2339 & 2340 (Figs. 4b–c & 6c) snout-vent length 384–392 mm, tail 68–95 mm.

Scalation. Dorsal rows 19 at midbody, reduction formula simple. MNHN 2172 (male)

$$\mathbf{21}\ \frac{1+2\ (5)}{2+3\ (5)}\ \mathbf{19}\ \frac{4+5\ (137)}{4+5\ (135)}\ \mathbf{17}\ \text{———}\ 174$$

MNHN 1994.2341 (male)

$$\mathbf{21}\ \frac{3+4\ (9)}{3+4\ (8)}\ \mathbf{19}\ \frac{4+5\ (144)}{4+5\ (146)}\ \mathbf{17}\ \text{———}\ 164$$

MNHN 1994.2339 (female)

$$\mathbf{21}\ \frac{4+5\ (12)}{4+5\ (12)}\ \mathbf{19}\ \frac{3+4\ (171)}{3+4\ (169)}\ \mathbf{17}\ \frac{3=3+4(173)\ 3+4(174)}{}\quad 184$$

MNHN 1994.2340 (female)

$$\mathbf{21}\ \frac{4+5\ (8)}{4+5\ (6)}\ \mathbf{19}\ \frac{4+5\ (168)}{4+5\ (165)}\ \mathbf{17}\ \text{———}\ 186$$

Ventrals. males 164–174, females 184–186 . Subcaudals: males 51–54, females 47–51. Three possessed eight supralabials, one MNHN 1994.2339 exhibited 9/8; the 6th in contact with parietal. Ten infralabials (6+4) in three specimens one of which, MNHN 1994.2339, possessed an incomplete suture between the 1st and 2nd shield in the second series on the left side (Fig. 4b). MNHN 1994. 2340 exhibited nine (6+3) infralabials.

Pattern. The nuchal collar is divided in all four specimens. A subsidiary study of the mouth, in Pl. 2 (Guichenot, 1850), clearly refers to MNHN 1994.2340 in which the infralabials number 9 (6+3) without any partial fusion. Pileal part of V-mark indistinct in MNHN 1994.2339 and 2341, discernible in MNHN 1994.2340 and most conspicuous in MNHN 2172 in which it unites with the temporal streak. Postorbital streak entire in MNHN 2172 and 1994.2339; short, terminating at the suture of the 5th and 6th supralabial in MNHN 1994. 2340 and 2341, (Fig. 4c).

The belly pattern varies from moderately strongly chequered as exemplified by MNHN 2172 in which the spots tend to be square and arranged alternately to immaculate in MNHN 1994.2341. In MNHN 1994.2440 the markings are somewhat reduced, squared rather than barred with more gaps; in MNHN 1994.2339 the spots are longer than deep, often with spaces 1–3v or more and positioned centre and off centre.

Guichenot's figure (1850, Pl. 2) appears to be a composite drawing. The head incorporating character states of MNHN 1994.2339, namely the slender median portion of the divided nuchal collar, the complete postorbital streak and the lack of the discernable V-mark. The belly pattern is portrayed somewhat fancifully as being entirely black except the distal portions of the ventrals uniting at intervals with transverse lateral bands enclosing ocelli. This is most closely approximated by belly pattern of MNHN 2172. which is the most densely chequered.

DESCRIPTION. Based on 83 specimens including the syntypes: the dubious specimen, (MHNG 1379.68 from 'Bordj Bou Arréridj') is excluded and is discussed below.

Scalation. Dorsal scales normally in 19 rows along the body but occasionally reaching 20 and 21 in short stretches (1–8 ventrals). Scale row reduction usually simple: 2nd + 3rd, 4th + 5th and sometimes 1st + 2nd, 5th + 6th and even vertebral and paravertebrals are involved.

In ten specimens fusions, divisions and reformations of scale rows at irregular intervals along the body occurred, where the counts should have been 19, reaching 20 and 21 from the position of the 1st ventral to virtually the entire distance . In two individuals, ZSM 1985 ('Annabes', Algeria) and ZMB 143381 (Tunis), the reduction on the neck from 21 to 19 was due to fusion of the 3rd + 4th and 4th + 5th rows; thereafter divisions and fusions occured erratically along the body involving the vertebral and paravertebral series alone until the count dropped to 17 where again fusion of the 3rd + 4th and 4th + 5th rows occurred.

Ventrals 162–193 (males 162–178, females 175–193); subcaudals 43–61 (males 46–61, females 43–59).

Supralabials. Normally eight but occasionally an additional scute may arise. Contact with parietal in seventy four (89%) of which fifty seven (74%) exhibited sutural contact, sixteen 'point' contact on one side and one 'point' contact on both sides. Contact was lacking on one side in seven and on both sides in two specimens, one of which possessed nine supralabials on both sides.

Infralabials. 6+3/6+3 in 44 individuals (53%); twenty four intermediates with mostly 6+3 or 6+4 on one side; 6+4/6+4, in thirteen (16%): two possessed 7+4/7+4.

Maxillary teeth. 6+3+II, 6+2+II (one specimen).

Pattern. nuchal collar divided in all specimens except three in which the collar was entire (BMNH 59.3.29.17, Algiers; NMB 2016, Médéa and BMNH 47.10.30.203A, Tunis) and two which were black headed (Médjana, Algeria). V-mark inverted 'Y', 'V', or lyre-shaped sometimes originating as a T-shaped mark on frontal and supraocular scutes, bifurcating, the 'arms' uniting posteriorly with the postorbital streak around the last supralabial. Anteriorly the V-mark may be in varying degrees obscured by the occasional dense concentrations of the pileal vermiculations and occasionally the 'arms' are separated from the pileal part.

Postorbital streak short in 76%, reaching the suture of the 5th & 6th supralabial but, save for a few instances, not extending much beyond it, recommencing at and embracing the last supralabial posteriorly, sometimes uniting with the temporal streak. It is always accompanied by unmarked anterior lips save for slight overspill beyond its suture with the loreal. Entire postorbital streak uniting with the V-mark together with the anterior part of the mouth along its line smudged with black in only 17 individuals (20.5%).

In one of the black headed individuals (Fig. 4, d.) most of the head above is ink-black save for a pale streak in the canthal region, involving the preocular, supraocular and prefrontal as far as the suture of that shield with the internasal. The lower part of the head, supralabials and adjacent lower parts of the temporals are creamy white: the postorbital streak terminates at the suture of the 5th + 6th supralabial and there is no smudging on the mouth. In the other black headed specimen the whole of the top of the head is black; the supralabials below the position of the postorbital streak and the infralabials are white, the underside of the head nearly so.

The body pattern usually consists of a vertebral series and three longditudinal rows of spots on each side of the body disposed at intervals of 1–3 scales. The vertebral spots vary in size from flecks barely covering a single scale to clusters of as many as 6 scales; where a whole scale is involved it is more or less bisected longditudinally. The dorsolateral and flank series of spots are less conspicuous and tend to occupy the margins of scales, in some specimens small spots less than a scale wide, paler than the ground colour distributed in conjunction with the dark spots dorsally and dorsolaterally sometimes giving the impression of imperfect ocelli. The ground colour may be uniform but is often differentiated into darker striae on the 2nd and 3rd scale rows from the ventral, and sometimes the adjacent portion of the fourth, and a darkening of the median 7–9 rows leaving a pale stripe some 2–2.5 scales wide. These spots are obliquely connected by diagonal series of black marks at the scale pockets, being often seen only when the scales are

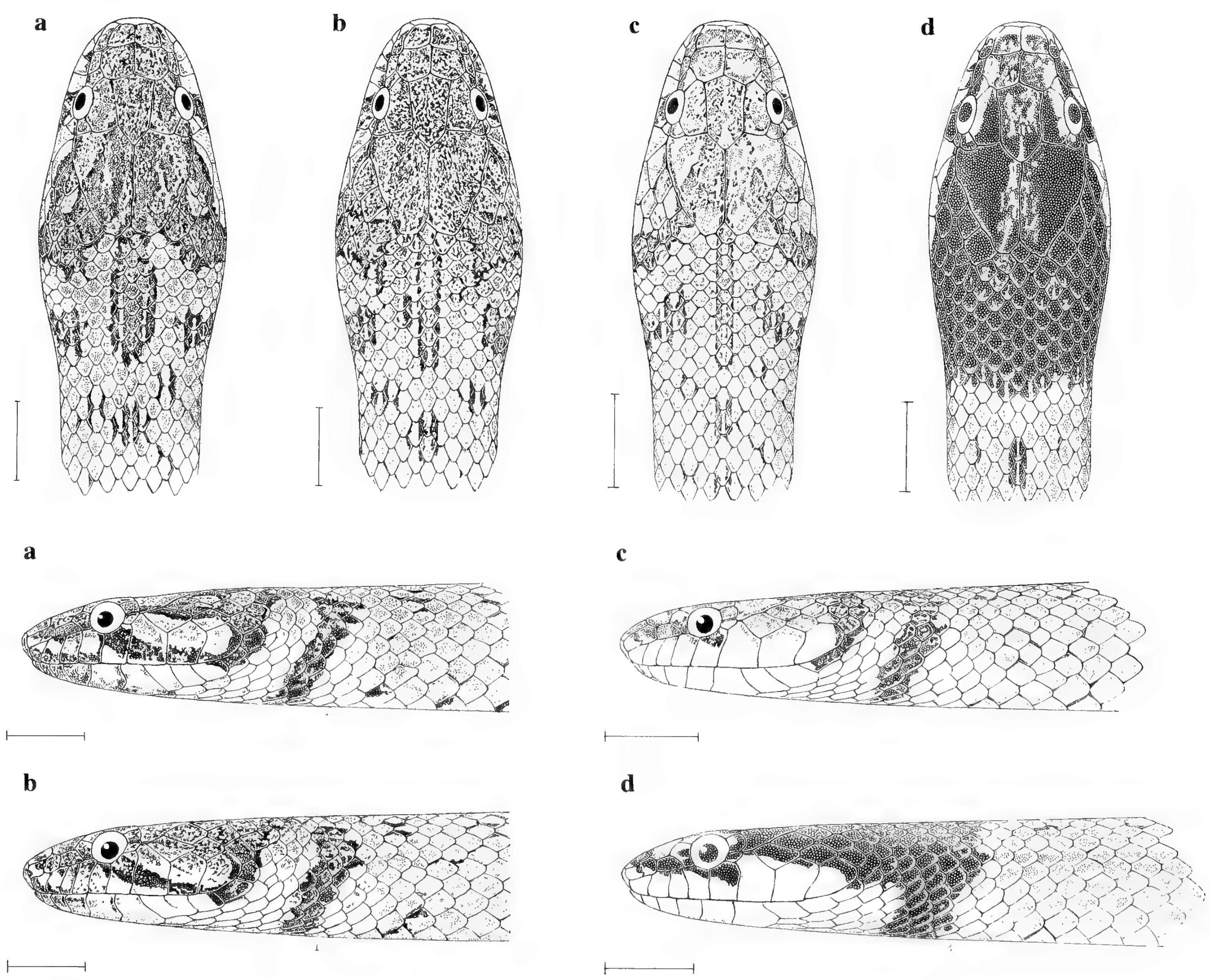


Fig. 4 Head and nape pattern in *Macroprotodon mauritanicus*. **a.** MNHN 2172. **b.** MNHN 1994.2339. **c.** MNHN 1994.2340 (**a–c** = syntypes, Algeria). **d.** EW.1992.5, Médjana, Algeria. (Scale=5mm).

separated. The outermost row of spots takethe form of oblique bars which border the ventrals.

Belly chequered in varying degrees (Fig. 6c, d & e). These markings vary from broad, angled bars and/or rectangles, centred or otherwise, with few separations to conditions in which the marks may be reduced and widely spaced and ultimately intergrading to the immaculate state. Belly immaculate or nearly so in about 40 individuals (48%): this condition is never associated with that in which labial smudging or entire postorbital streaks occur.

REMARKS ON THE SYNONYMY. The author was unable to locate the holotype of *Lycognathus taeniatus* Duméril & Bibron 1854. The specimen has been lost (Brygoo, in litt., Wade, 1988) for well over a century. At least neither Strauch, (1862) nor Doumergue, (1901) claim to have seen the specimen, although they both presented extracts from the original description. The type locality was given as 'Deserts of Western Algeria' (?= El Aricha) as for *L. textilis*. El Aricha is a region of subsaharan steppe in which neither of the two forms of the *M. mauritanicus* complex are likely to occur. The original description is principally concerned with the body pattern, the '*taeniatus*' pattern *sensu* Wade, (1988) shades of which may occasionally be found in any of the taxa. Clear evidence of any diagnostic features is lacking. F. Schousboé who collected the holotype was principal translator for the French Army in Algeria and was closely associated with the ornithologist Commandant V. Loche who travelled extensively in that country. In consequence Schousboé was unlikely to have restricted his activities solely to western Algeria: the specimen therefore could have originated from anywhere in Algeria. As defined here *Macroprotodon mauritanicus* is restricted to northeastern Algeria (Algiers eastwards) and northern Tunisia.

GEOGRAPHICAL VARIATION. Scarcely any geographic variation discernible: the only two melanocephalic individuals were found in the Médjana region, Algeria (38°04'N, 4°40'E).

AFFINITIES. Resembles most closely the new species described below (p. 105).

DISTRIBUTION. Northern Algeria from Algiers eastwards and south as far as Biskra (34°51'N, 5°44'E): northern Tunisia south to Sidi Bou Zit (32°02'N, 9°30'E).

LOCALITIES

ALGERIA – no locality Boulenger, 1896; Duméril & Bibron, 1854; Gervais, 1857; 1869; Olivier, 1894; Busack & McCoy, 1990 BMNH 93.11.30.2; MNHN 2172, 1994.2339–41 (syntypes of *Macroprotodon mauritanicus*) **Algiers** (36°47'N, 03°03'E); Günther 1858; Boulenger, 1896; Hediger, 1935; Busack & McCoy, 1990 BMNH 59.3.29.17; MNHN 3735; ANSP 3484; 3488; NMB 2422; USNM 56437 as *M. c. mauritanicus fide* Busack & McCoy, 1990=*Coronella girondica*; Maison-Carrée=**El Harrach**, 36°43'N, 30°08'E, Le Cerf, 1907: **Médéa** (36°16'N, 02°45'E); Hediger, 1935; Müller1882 NMB 2016: Ben Arous=**Bordj ben Arous** (36°01'N, 3°25'E) ZFMK 14316: **Lalla Khadidja** (36°27'N, 4°14'E) MHNG 847.69: **Médjana** (34°08'N, 4°40'E) 18 km NW EW 92.5, 92.9.1–6, 93.9.1–3: **Guellal** (36°02'N, 7'05°21'E); Sura,1983: **Sétif** (36°12'N, 05°24'E); Werner, 1909: Bougie= **Bejaïa** (36°45'N, 5°05'E); Jan & Sordelli, 1866; Bellairs & Shute,1954; Sura, 1983 BMNH uncatalogued: **Massif de l'Aurès**; Sindaco, 1990: **Col de Tibharine**, (35°21'N, 6°25'E) Gruber,1989; Bischoff & In den Bosch, 1991 ZFMK 49602: **Batna** (35°34'N, 6°11'E); Wade, 1988; Busack & McCoy, 1990 BMNH 1920.120.1525 (skeleton), 1920.1.20.3108; MCZ 6421; ZFMK 4841–2: **Biskra** (34°51'N, 5°44'E) Jan & Sordelli, 1866; Boettger, 1885; Busack & McCoy, 1990 MHNG 2031.98; SMF 20169 **Constantine** (36°22'N, 6°37'E); Werner, 1929; Busack & McCoy, 1990 MCZ 144.371: **Guelma** (36°28'N, 7°26'E); Gough, 1903: **Hammam Meskoutine** (36°27'N, 7°16'E); Anderson, 1882; Busack & McCoy, 1990 BMNH 91.5.4.14: Bugeaud=**Seraïdi** (36°55'N, 7°40'E); Busack & McCoy, 1990 BMNH 1920.1.20.1186; CM 58420–1: Bône, Bona, ?Annabes=**Annaba** (36°54'N, 7°46'E); Hediger, 1935; Wade, 1988; Busack & McCoy, 1990 BMNH 1920.1.20.1620; NMB 2018–2024; MNHN 1981.31; 30km E ZSMH 77/1985.1–4: **Mt Edough** (36°53'N, 7°37'E), Werner, 1892: **Teniet** (locality unknown) MNHN 8507. The specimens NMW 25840 **Algiers** and MHNG 1379.68 **Bordj Bou Arréridj** (36°4'N, 04°46'E) have been identified as *Macroprotodon brevis*:

TUNISIA – no locality Busack & McCoy, 1990 MNHN 1891.316,1908.88; ZFMK 4843, 4845; FMNH 83650–1: **Îles Galita** (37°32'N, 8°56'E); D'Albertis, 1878; Davidson, 1964; Lanza & Bruzzone, 1960; Schneider, 1969): **Aïn Drahm** (36°47'N, 8°42'E); Gadeau de Kerville, 1908; Busack & McCoy, 1990 BMNH 1906.8.29.20–21, MNHN 1891.316–322: road to **Sedjenane** (37°03'N, 9°14'E) just past junction to **Cap Serrat** (37°14', 9°13'E); Busack & McCoy, 1990 USNM 165874: **Bizerte** (37°17'N, 9°52'E); Busack & McCoy, 1990: **Bulla Regia** (36°33'N, 8°44'E); Davidson, 1964: **Mateur** (37°03'N, 9°40'E) MHNG 1379.81–83: **Mégrine** (36°46'N, 10°14'E); Chpakowski & Chnéour, 1958: **Zaghouan** (36°24'N, 10°09'E); Chaignon, 1904: **Tunis** (36°48'N, 10°11'E); Günther 1858; Boulenger, 1896; Escherich, 1896; Werner, 1909; Busack & McCoy, 1990 BMNH 47.10.203.1–3; ZMB 14338, 14381, 14854, 51650–1; between **Sidi bou Said** (36°47'N, 9°49'E) and **Hammam Lif** (36°44'N, 10°20'E); Busack & McCoy, 1990 SMF 34340: **Cap Bon** (36°45'N, 10°45'E); Blanc, 1988: **Soukra** (36°53'N, 10°15'E; Mosauer, 1934: Bir el Bey=**Bordj el Bey** (36°02'N, 10°18'E); Davidson, 1964: **?Sfax** (34°44'N, 10°45'E) MNHN 1982.115: **Sidi bou Zit** (35°02'N, 9°30'E); Chaignon, 1904; Busack & McCoy, 1990 FMNH 75967. NMW 19193.3 **Tunis** has been identified as *Macroprotodon brevis*.

NORTH AFRICA – no locality ZMH R04321.

'LEVANT' – MNHN 3736b.

Macroprotodon abubakeri sp. nov.

Lycognathus cucullatus: ?Gervais, 1857: 511, Pl. 5, Fig. 2.

Coronella cucullata: Strauch (part), 1862: 55. Lallemant (part), 1867:28.

Macroprotodon cucullatus: Doumergue (part), 1901: 282–288; Pl. XXI, fig.12a. Gough (?part), 1903: 468 . Werner (part), 1909 161; 1929: 11–12, ?20; (part), 1931: 300–301. Zulueta (part), 1909: 354. ?Maluquer, 1917b: 564. Hediger (part), 1935: 24–26. Sochurek, 1956: 87+ pl. (part), 1979:221.

Macroprotodon cucullatus cucullatus: Pasteur (part), 1959 (1960):136–7 ?. Bons (part), 1960: 64, 74; (part), 1967: 29, ?87, 192, Fig. 16, Map no.16; (part), 1972: 116. Pasteur & Bons (part), 1960: 116. Bons & Girot, 1962: 50.

Macroprotodon cucullatus brevis: Busack & McCoy (part), 1990: 269–271.

Macroprotodon cucullatus mauritanicus: Wade (part), 1988: 242, Fig.1. Busack & McCoy (part), 1990: 268–269. Bons & Geniez (part), 1996: 226–228, (314, appendix in English).

HOLOTYPE. BMNH 1913.7.3.14 (Figs. 5a & 6f) from Oran, Algeria; collected by the Hon. Walter Rothschild and Dr. Ernest Hartert. Named in honour of M. Aboubakeur Sid-Ahmed, a naturalist from Tlemcen, Algeria.

PARATYPES. MNHN 3734 (Fig. 5b); MCZ 27502, 29919; FMNH 42840: all from the region of Oran (see end of species description for locality data).

DIAGNOSIS. A species of *Macroprotodon* characterised by a series of four maxillary teeth preceding the fangs, nuchal collar entire or sometimes divided; postorbital streak usually entire uniting with the 'arms' of the V-mark. Dorsal body pattern of the 'undifferentiated' or '*taeniatus*' state. Belly usually chequered. Supralabials separated from the parietals or in contact with them. Four posterior infralabials in the majority of specimens.

Close to *M. mauritanicus* from which it is readily separated by possession of an additional maxillary tooth. Postorbital streak usually unbroken. Separable from *M. c. brevis* by 19 dorsals or in patches of 21 along the body (cf 21 uninterrupted rows); sutural contact

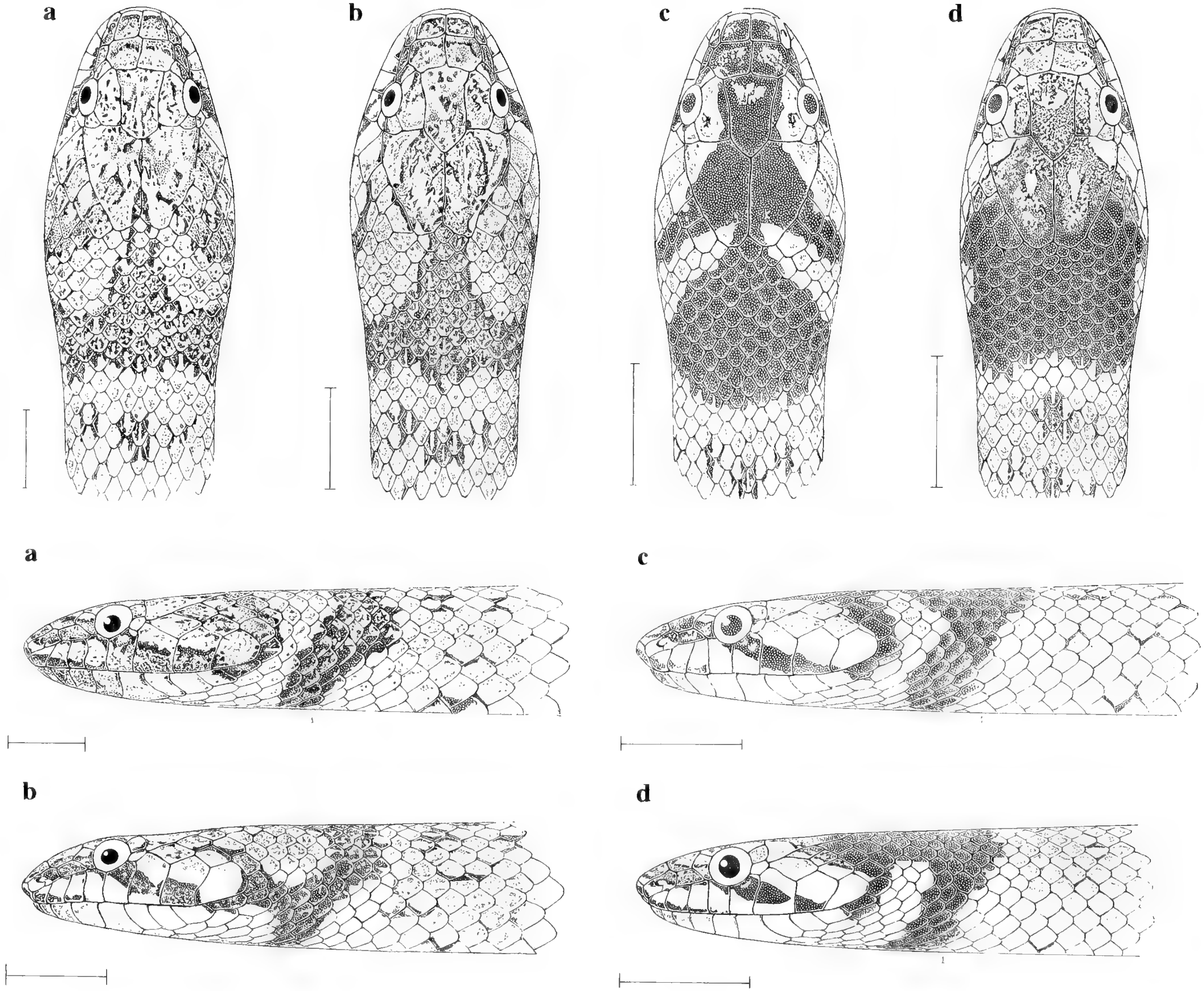


Fig. 5 Head and nape pattern in *Macroprotodon abubakeri*. **a.** BMNH 1913.7.3.14 (holotype). **b.** MNHN 3734 (paratype) (**a–b**, Oran, Algeria). **c.** NMB 9401, Algiers. **d.** MNHN 3731, Algeria without precise locality. (Scale=5mm).

between supralabials and parietal in less than half; 4 as opposed to 3 in the posterior series of infralabials; postorbital streak usually separate from the 'arms' of the V-mark. The entire nuchal collar and lack of the '*textilis*' pattern distinguishes it from the parapatric *M. cucullatus* .

DESCRIPTION OF THE HOLOTYPE. Adult male snout-vent length 386 mm; tail 78 mm from Oran, Algeria.

Scalation. Scales at midbody 19, ventrals 170, subcaudals 51+1. Dorsal scale row reduction formula:

$$\mathbf{21}\ \frac{3+4\ (6)}{3+4\ (6)}\ \mathbf{19}\ \frac{4+5\ (115)}{4+5\ (121)}\ \mathbf{17} - \text{vertebral}\ (170)\ \mathbf{16} \text{———} 170$$

Supralabials 8/8, the 6th falling short of contact with the parietal on both sides; infralabials 6+4/6+4.

Maxillary teeth. Arranged in a series of six teeth increasing in size followed by a diastema and a series of four smaller in size preceding the fangs on both sides of the maxilla.

Coloration. Colour (in alcohol) grey with black and light brownish markings.

Pattern. V-mark poorly defined at its apex becoming more distinct posteriorly where it unites with the postorbital streak around the 8th supralabial and the 10th infralabial extending also beyond the suture on the 9th. Postorbital streak dark, black on its upper margin commencing on the 5th, occupying most of the 6th and 7th supralabials and extending on to the 9th and the whole of the 10th infralabial where it unites with the V-mark. From the anterior margin of the eye it continues as a widening, forwardly directed emarginate band its lower margin crossing the apices of the 3rd–5th supralabials and enclosing the loreal and most of the nasal including the nostril, extending on to the anterior parts of the prefrontals and most of the internasals but failing to contact the rostral. Anteriorly, the rostral, supralabials and less conspicuously the infralabials are smudged with black along the mouth. Temporal streak ill defined. Nuchal collar not divided dorsolaterally being about three scales wide at the narrowest point, extending forwards sagittally and terminating to a point some two fifths along the suture dividing the parietals.

Body pattern consists of a uniform ground colour; a vertebral series of somewhat darker, emarginate, more or less 'x' shaped spots, at points of articulation of 4–6 scales, is disposed at intervals of about two scales distance along the body. Two other series of alternating dorsolateral and lateral spots reduced in size, not visible much beyond the imbrications of the scales, are imperfectly connected by markings situated at the scale pockets: these being best seen on exposure of the scales by bending the specimen. The belly is marked by rectangular bars sometimes alternating, occasionally disposed sequentially in single or fused units; these are occasionally separated by unmarked ventrals (Fig. 6f).

DESCRIPTION. Based on 31 specimens including the holotype: the dubious specimen, (MHNG 1214.40 'Chellala') is excluded and is discussed below (p. 105).

Scalation. Dorsal scales in 19 rows along the body but reaching 20 and 21 in stretches of 1 to 51 and in one male (BMNH 1931.2.9.2 from Algeria, without precise locality) the count, save for two short intervals (1v) where the count dropped to 19, the dorsals numbered 21 from the 3rd to the 118th ventral. As in *M. mauritanicus* the counts can fluctuate as much as fifteen times. Ventrals in males (n=16), 154–175; females (n=15), 172–185. Subcaudals in males (n=15), 46–53; females (n=15), 42–52.

Supralabials. Eight supralabials on each side. in which thirteen individuals exhibited contact between the 6th supralabial and the parietal, in eleven of these contact was sutural, two exhibited 'point' – contact; three showed contact on one side and in fourteen contact was lacking.

Infralabials. Contact on both sides (n=25), single specimens with 6+5/6+4, 6+5/6+4s, 5+4 on both sides, 6+4/6+3 and two individuals with 6+3 on both sides.

Maxillary teeth. 6+4+II in all the material examined.

Pattern. Nuchal collar entire n=22 (71%), divided n=6 (19%). V-mark variable; indistinct, solid or obscured by vermiculations, fragmented and/or discrete in varying degrees but often (approximately 40%) entire. In all except four individuals the V-mark unites with the postorbital streak. Postorbital streak embracing the 8th supralabial (n=28), either entire (n=21) or interrupted (n=3).The V-mark-postorbital streak connection is separated from the nuchal collar by 2–4 scales (n=18) but may be connected to the nuchal collar by a bar at the level of the mouth of 0.25–2 scales thickness.

Extensive melanocephalism occurs in two individuals: the top of head and snout is black, save for a white streak on the first 5 or so supralabials and another, oblique, occupying the upper part of the supralabials+the lower parts of the temporals extending from the eye to the corner of the mouth, or beyond. In one (BMNH 1931.2.4.23 from Algeria without locality) the white streak commencing at the eye continuing uninterrupted beyond the 8th supralabial for 3 scale rows abruptly changing course downwards and forwards terminating near the last infralabial from which it is separated by a single scale. The throat is heavily smudged with black: the penultimate infralabial save for its posterior margin is white. The other specimen, (MCZ 27502 from Djebel Mourdjadjo) is similar but differing in that the white streak is shorter, more oblique and terminates at the posterior margin of the 8th supralabial; the black pigment on the last two infralabials and the postorbital streak formes its lower margin. the black pigmentation is concentrated on the anterior part of the lower jaw. The configuration of the pattern of the melanocephalic specimen purportedly from 'Bona' (NMB 2017) approximates the last specimen very closely.

Body pattern very similar to that in *M. mauritanicus* but slightly more variable, consisting of a vertebral series of dark spots 2–2.5 scales apart, each 1–3 or more scales wide; each of the contributing scales is longditudinally bisected and emarginate. These are accompanied by a dorsolateral series of spots or flecks of reduced size. As in *M. mauritanicus* these spots are diagonally connected by smaller series which are often obscured by imbrication: pale flecks may accompany the vertebral or paravertebral spots. Ground colour uniform or darkening at the median 7 or so rows and the 2nd and/or 3rd from the ventrals leaving a paler stripe the equivalent of two scales wide. A melanocephalic and partially melanocephalic specimen, both from Algeria but lacking further locality data exhibited diffuse pale interspaces between the vertebral spots.

Belly pattern likewise similar to that of *M. mauritanicus*, consisting of squares, bars, occasionally chevrons of varying size but with a somewhat greater tendency towards central disposition, n=3 (9.7%) cf n=1 (1.2%).

GEOGRAPHIC VARIATION. None discernible.

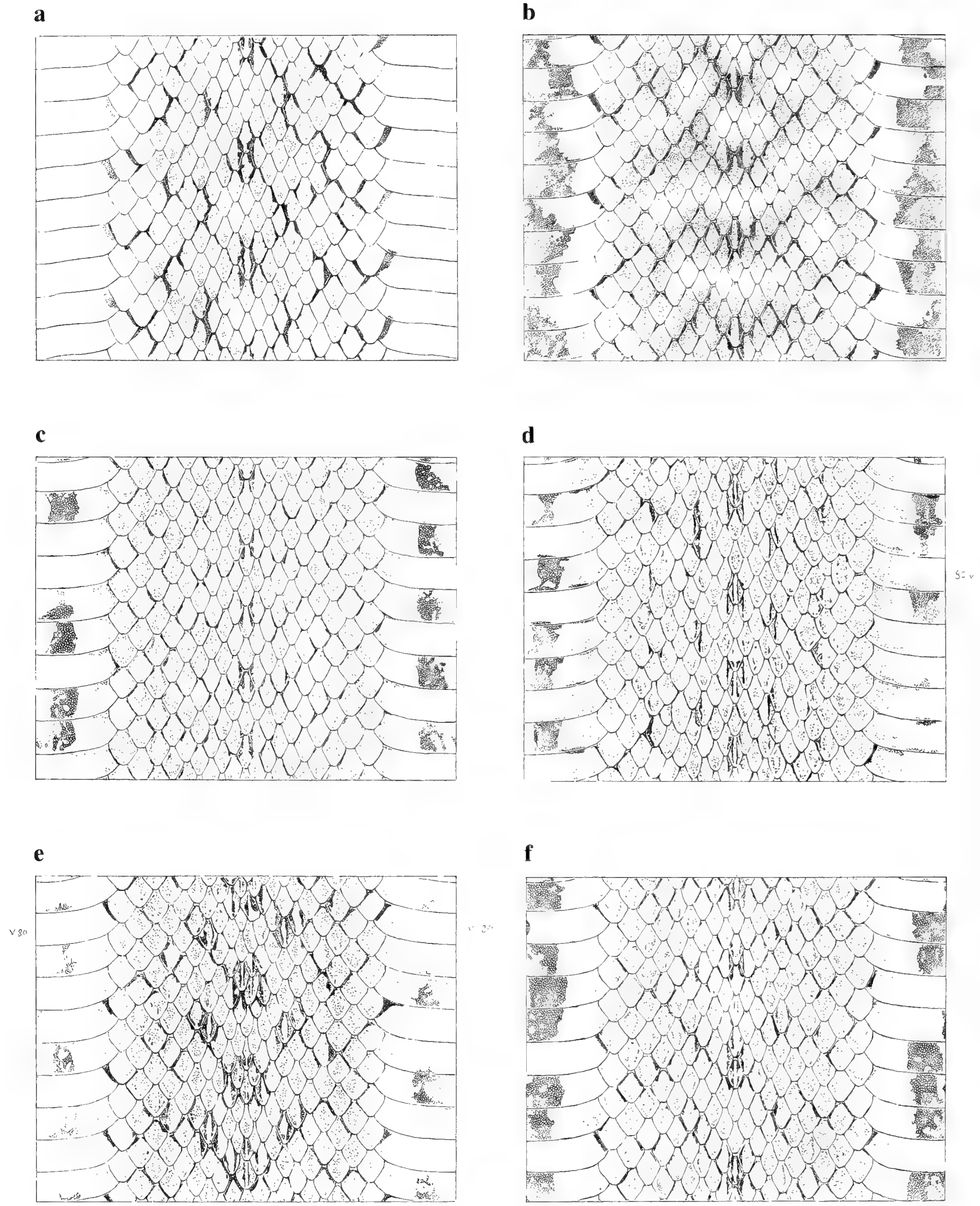


Fig. 6 Dorsal patterns in *Macroprotodon*. *Macroprotodon cucullatus*. **a.** MNHN 849, Deserts of Western Algeria (holotype of *Lycognathus textilis*). **b.** MNHN 1930.181, Djebel Ilâman, Hoggar, Algeria. *Macroprotodon mauritanicus*. **c.** MNHN 1994.3439 (syntype). **d.** BMNH 1920.1.20.3108, Batna, Algeria. **e.** ZMB 51650, Tunis. *Macroprotodon abubakeri*. **f.** BMNH 1913.7.3.17, Oran, Algeria (holotype).

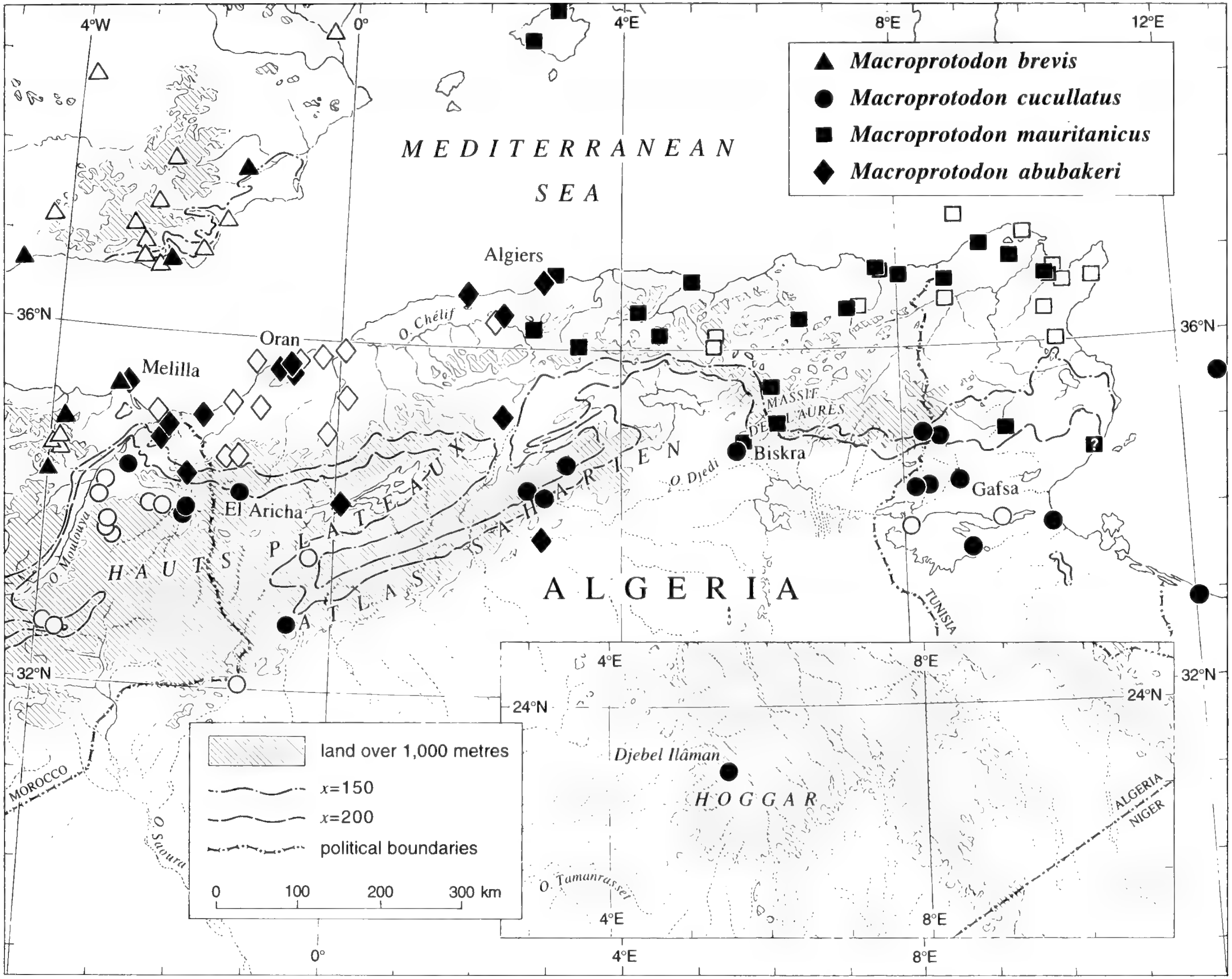


Fig. 7 Distribution of *Macroprotodon*; solid symbols represent specimens examined, open symbols, literature reports: place names refer to type localities and places of abuttment in the ranges of the species. Inset: the Hoggar region (to the same scale). *x*=xerothermic index (number of physiologically dry days in the dry season).

AFFINITIES. Close to the preceding species with which it shares the frequent irregularities in dorsal scalation and identical body pattern. In scale characters (supralabial-parietal contact, ventral, subcaudal and infralabial counts, points of reduction) it appears intermediate between *M. mauritanicus* and *M. cucullatus* . However, the condition of the head and body patterns suggest intermediacy between *M. mauritanicus* and *M. brevis*.

DISTRIBUTION. Northwestern Algeria from the coast towards the Hauts Plateaux at altitudes below 1,000 metres, Extends eastwards as far as Algiers, westwards to northeastern Morocco as far as Melilla (35°19'N, 2°57'W). Specimens having been taken from localities as far south as El Kreider (34°09'N, 0°04'E) and Laghouat (33°48'N, 2°53'E).With respect to the natural and bioclimatic range of the species the last named locality is unexpected and may be erroneous: it is possible that the specimen (MNHN 1899.273 presented by Secques) could have originated from further north.

LOCALITIES

SPAIN (North African possessions) – Melilla (35°19'N, 2°57'W); Zulueta, 1909 MNCN 1795.

MOROCCO – **Ras el Ma** (35°08'N, 4°26'W); Bons & Geniez, 1996: **Berkane** (34°56'N, 2°40'W); Bons, 1960; 1967; Bons & Geniez, 1996 MNHN 1912.221: **Guenfouda** (34°29'N, 2°03'W) 19 km S (photographs + exuviate); D. Donaire in litt.. **Taforalt (Beni Snassene)** (34°49'N, 2°14'W); Werner, 1931; Bons & Geniez, 1996 MCZ 29920.

ALGERIA – **no locality** BMNH 1931.2.4.23; MNHN 3731; MHNG 524.59: **Sebdou** (34°38'N, 1°20'W); Doumergue, 1901: Beni Snous=**Khemis** (34°38'N, 1°35'W); Doumergue, 1901: Arlal=**Aghlal** (35°12'N, 1°04'W); Doumergue, 1901: Nemours=**Ghazaouet** (35°06'N, 1°51'W); Busack & McCoy, 1990 MCZ 144369–70: Oued Sefioun (34°59'N, 0°07'W); Doumergue, 1901: Saint Leu=**Bettioua** (35°48'N, 0°16'W); Doumergue, 1901: **Beni Saf** (35°18'N, 1°23'W); Doumergue, 1901: **Mostaganem** (35°56'N, 0°05'E); Strauch, 1862: **Mascara** (35°24'N, 0°08'E); Doumergue,1901: **Djebel Mourdjadjo** (35°40'N, 0°45'W); Werner, 1929; 193; Busack & McCoy, 1990 MCZ 27502 (paratype): **Îles Habibas** (35°44'N, 1°08'W); Doumergue, 1901: **Oran** (35°43'N, 0°38'W); Doumergue, 1901; Werner, 1909; Busack & McCoy, 1990 BMNH 1913. 7.3.14 (holotype); MNHN 3734 (paratype); **Oran, Battérie Espagnole**; Werner, 1931; Busack & McCoy, 1990 MCZ 29919 (paratype): Arcole=**Bir el Djir** (35°43'N, 0°34'W); Sochurek, 1956: **Es-Sénia** (35°39'N, 0°38'W) Busack & McCoy, 1990 FMNH 42840 (paratype): **El Kreider** (34°9'N, 0°04'E); Werner, 1929; Busack & McCoy, 1990 MCZ 27500: Chellala=**Ksar Chellala** (35°13'N, 2°41'E) MHNG 1379.85–86, 1379. 88–89: **Miliana** (36°19'N, 2°14'E); Strauch, 1862: **Hammam Righa** (36°23N, 2°24'E) ZMH RO4327: **Algiers** (36°47'N, 3°03'E); Wade, 1988; Busack & McCoy, 1990 BMNH 53.2.4.23, MNHN 3732, ANSP 3486, RMNH 212a–b, ZMH RO4322, ZSMH 2095/0, NMB 9401: 100 km W EW 91.1: **Laghouat** (33°48'N, 2°53'E) MNHN 1899.273: 'Bona'= '**Annaba**'(36°54'N, 7°46'E); Hediger, 1935 NMB 2017. MHNG 1214.40 Chellala=**Ksar Chellala** (35°13'N, 2°41'E) has been identified as *Macroprotodon brevis*. For NMB 2015 (**Oran**) see under *Macroprotodon mauritanicus*.

'LEVANT' – MNHN 3736a.

KEY TO THE SPECIES

1 Usually 19 scale rows at midbody 2

(21 or 23 scale rows at midbody .... *M. brevis*)

2 Body with '*textilis*' pattern; maxillary teeth 4–5 in series preceeding the fangs; 'pale' collar usually indistinct or absent .... *M. cucullatus*

Body with undifferentiated or '*taeniatus*' pattern; 3 or 4 maxillary teeth in series preceeding the fangs; 'pale'collar nearly always present 3

3 Three maxillary teeth in series preceeding the fangs; nuchal collar divided; postorbital streak often short .... *M. mauritanicus*

Four maxillary teeth in series preceeding the fangs; nuchal collar entire in majority; postorbital streak never short .... *M. abubakeri*

DISCUSSION

The distribution pattern of the forms of *Macroprotodon cucullatus* as understood by Wade (1988) (Fig. 1b) followed naturally that of Bons (1967) (Fig. 1a). However, that conceived by Busack & McCoy (1990) (Fig. 1c), purportedly in accord with bioclimatic parameters was probably the result of dismsissal of certain characters and application of heavier weighting in others, notably that of infralabial counts. With the exception of midbody counts characters states used were shared at least in part by most of the taxa. The diagnoses of Busack & McCoy (op. cit. pp 268–271) do not adequately differentiate the subspecies. Their conclusions, insofar as Morocco is concerned, have been accepted by Fahd & Plegezuelos (1992) but rejected by Bons & Geniez (1998): Schleich *et al.* (1996) present both conceptions. The results of this analysis supplement that of Wade (1988) and resolve the uncertain status of many of the populations from areas from which hitherto no material had been seen by the author. The subspecies *cucullatus*, *brevis*, *mauritanicus*, are raised to full species, the population from northwestern Algeria and extreme northeastern Morocco (*mauritanicus* auct.), is recognized as a new distinct species, *abubakeri* and the forms *textilis* and *ibericus* are for the present retained as populations (or varieties) of *cucullatus* and *brevis* respectively (Fig. 10).

Of the species of *Macroprotodon*, *M. mauritanicus* presented the greatest areas of conflict of opinions in respect of its distribution and composition. This is due in part to different interpretations of some of the character states.

The position on the neck at which the count reduces from 21 to 19 is variable in all of the taxa (Fig. 8). The variability is most

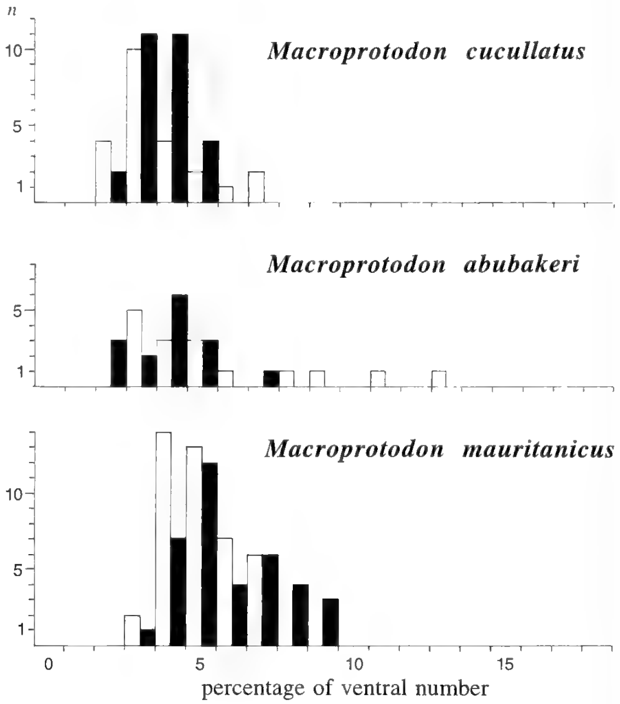


Fig. 8 Histogram showing anterior reductions (nuchal) from 21 to 19 scale rows. Percentage of ventral number (ordinate); number of specimens (abscissa). Open bars = males, solid bars = females.

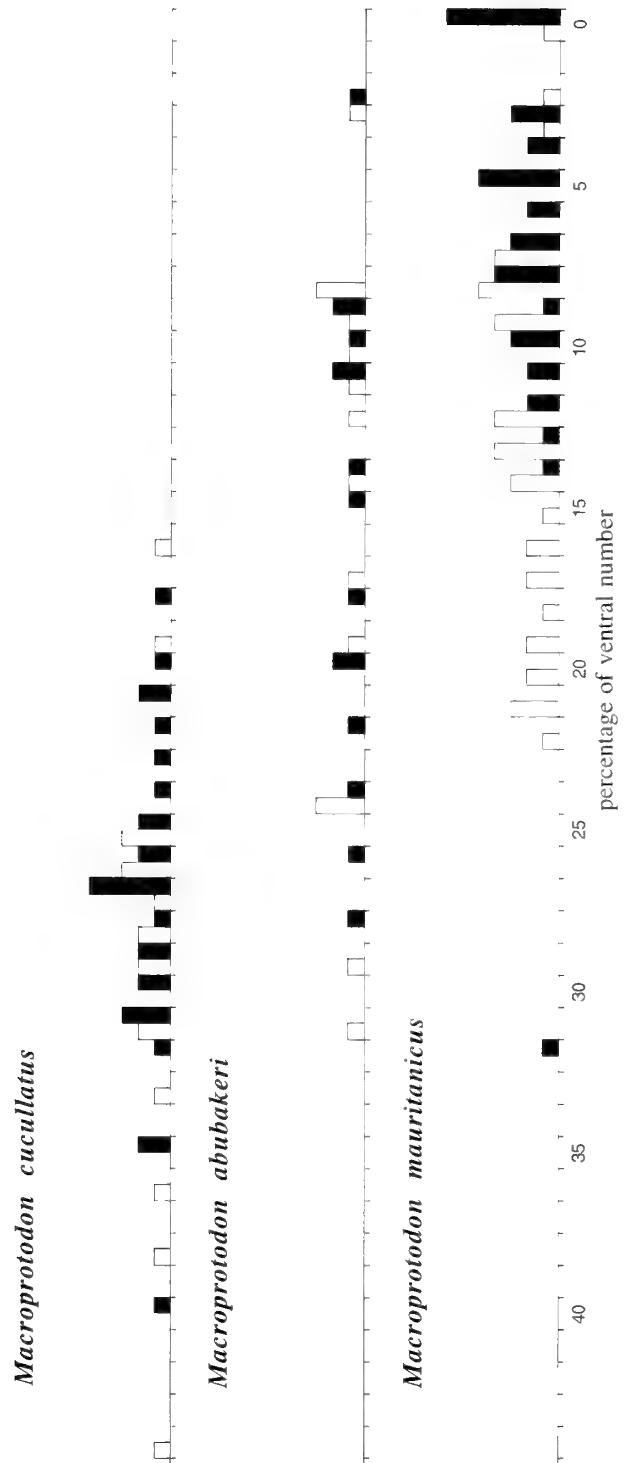


Fig. 9 Histogram showing posterior reductions from 19 to 17 scale rows. Symbols and values as for Fig. 8.

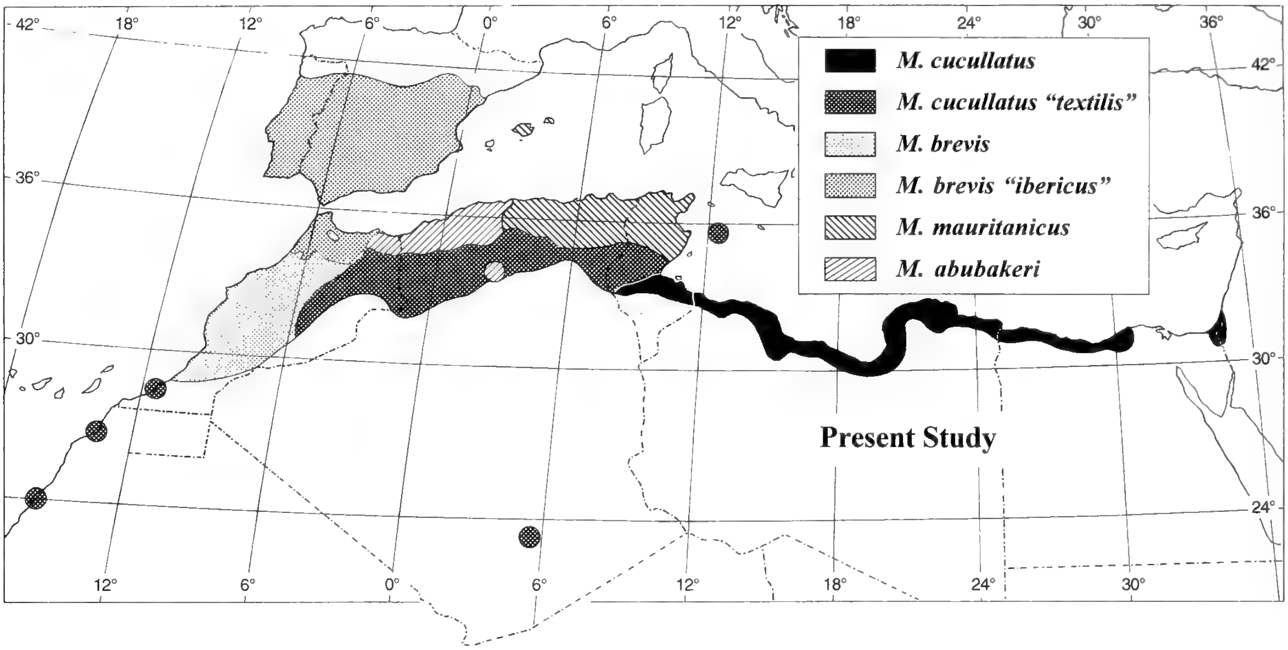


Fig. 10 The author's concept of the distribution of the species of *Macroprotodon*.

pronounced in *M. mauritanicus* the reduction occuring at the 3rd to the 16th ventral averaging at about the 10th (5.4%). *M. abubakeri* exhibits a similar condition. The range in the position of the reduction for *M. cucullatus* in the region under investigation is narrower, being from the 3rd to the 11th ventral and averaging at around the 7th ventral (3.7%). For the Libyan populations and those further east the average positions of reduction occur progressively closer to the head (Wade, pers. obs.) suggesting that at least between these populations the differences are clinal.

The differences in the position of reduction from 19 to 17 anterior to the vent between the taxa, however are much sharper (Fig. 9). In *M. mauritanicus* the position ranges from zero (i.e. no reduction) to 38 ventrals distance from the vent ($\bar{x}$=10.5%), the majority exhibiting positions of reduction much less distant. The range is widest in *M. abubakeri* from the 3 to the 54 ventrals and the positions more evenly distributed ($\bar{x}$=15.7%). The positions of reduction are the most distant from the vent in *M. cucullatus* ranging from 25 to 71 ventrals, the most frequent being from 40 to 47 ($\bar{x}$=28.6%).

Characters such as labial-parietal contact dismissed by Wade (1988), Busack & McCoy (1990) and infralabial counts overlooked by Wade were found to be exceptionally valuable in the resolution of the *mauritanicus* problem. The sample of Busack & McCoy, 1990 (Fig. 1c) of '*M. c. mauritanicus*' (n=73) is a heterogeneous assemblage which includes material from the Balearics (n=8), northwestern Algeria =*M. abubakeri* (n=9) and that which is assigned in this work to *M. cucullatus* (n=33): only twenty two of the specimens from northern Algeria and northern Tunisia are referrable to *M. mauritanicus*. Populations here recognised as *M. cucullatus* (n=3) and *M. abubakeri* (n=2) where they extended into Morocco were assigned to *M. c. brevis*. These authors found supralabial-parietal contact in 40/47% (L/R) of '*M. c. mauritanicus*'. This character in the present study was found to sharply differentiate *M. mauritanicus* from *M. cucullatus* . The species showed no intermediacy in any of the diagnostic character states where they occur at Biskra, the only known point of contact. The scatter diagram (Fig. 11) also shows the species to be well differentiated. Two specimens of *M. mauritanicus*, SMF 20169 (closely resembling syntype MNHN 1994.2340, Fig. 4c.) and MHNG 2031.98 showed, in addition to undifferentiated body patterns and the state of 6+3+II maxillary teeth, 6+3 infralabials in conjunction with good supralabial-parietal contact. Two black headed individuals of *M. cucullatus* MNCN 1802 (Fig. 3d) and one originally from the Museo Civico di Storia Naturale di Milano (Jan & Sordelli, 1966 Livr. 19e, Pl. I, Fig. 3A) shared the following states: a pronounced '*textilis*' pattern, 6+4 infralabials and supralabials separated widely from the parietals: the former possessed 6+4+II maxillary teeth as did presumably also the latter (lost due to destruction of Jan's collection during the 2nd World War, Dr M. Podestà, in litt., 1998). Busack & McCoy (1990) found 23% (n=16) of '*M. c. mauritanicus*' to possess 'entirely' black heads. Melanocephalism is rare in *M. mauritanicus* but common in *M. cucullatus* (Table 2).

Three specimens of *M. mauritanicus* from a sample of 83 were found to possess an entire nuchal collar, the common state in *M. abubakeri*, of which two (BMNH 59.3.29.17 Algiers and NMB 2016 Médéa) originated in boundary zones between the two species. However both possessed the states of short postorbital streak and less than 4 maxillary teeth in the series preceding the fang; indeed the Médéa specimen exhibited 6+2+II on both sides. In four other specimens from Algiers, NMB 2422, MNHN 3735, ANSP 34847 and 34848 the nuchal collar was divided, supralabial-parietal contact was pronounced but the infralabial state was equivocal (6+3 n=3, 6+4 n=2). By contrast in the nine specimens of *M. abubakeri* from the same locality the nuchal collar was entire in all except MNHN 3732 in wich it was divided: all possessed 6+4 infralabials (6+5 on one side in one individual)whereas the supralabial-parietal condition was equivocal (contact n=3, non-contact n=4 contact one side n=2).

The evidence presented above shows that *M. mauritanicus* and *M. abubakeri* are distinct taxonomic entities and behave as good species without any evidence of intergradation: both being distinguishable

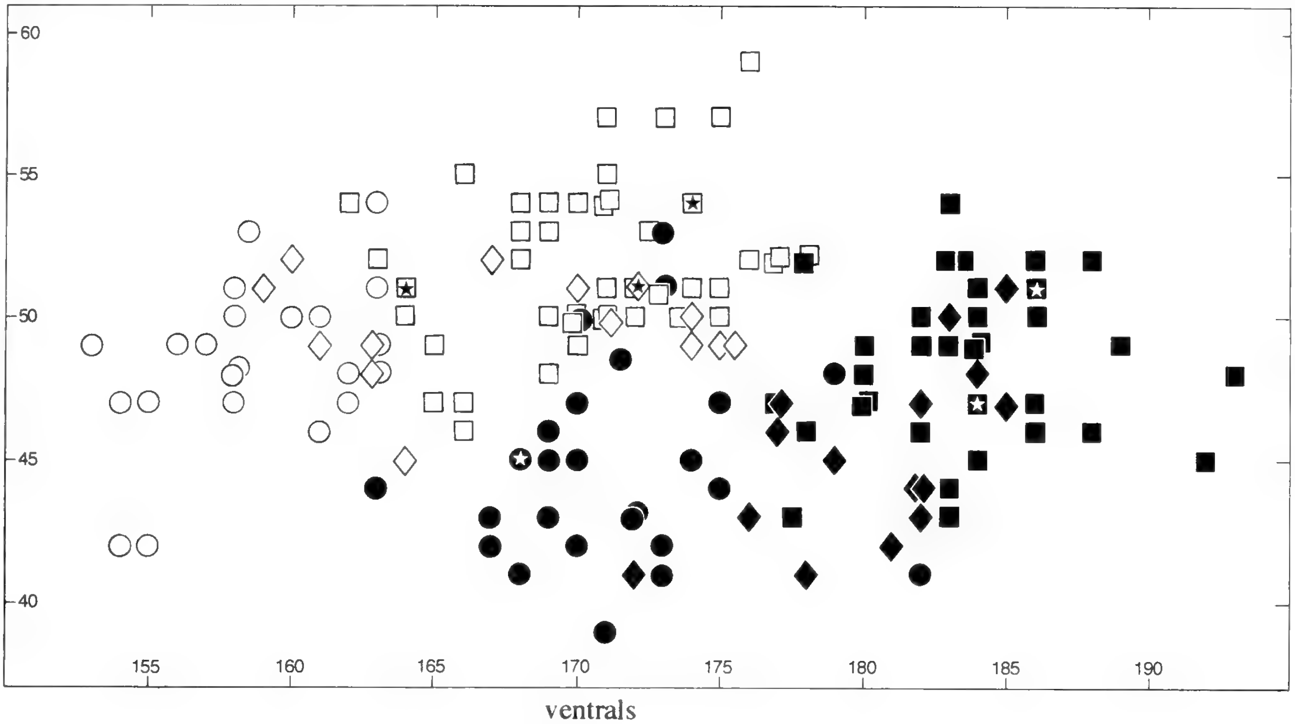


Fig. 11 Scatter diagram showing intraspecific variation for ventrals (ordinate) and subcaudals (abscissa) in *Macroprotodon*. Open symbols=males, closed symbols=females, symbols enclosing stars refer to type specimens. Symbols as in Fig. 7.

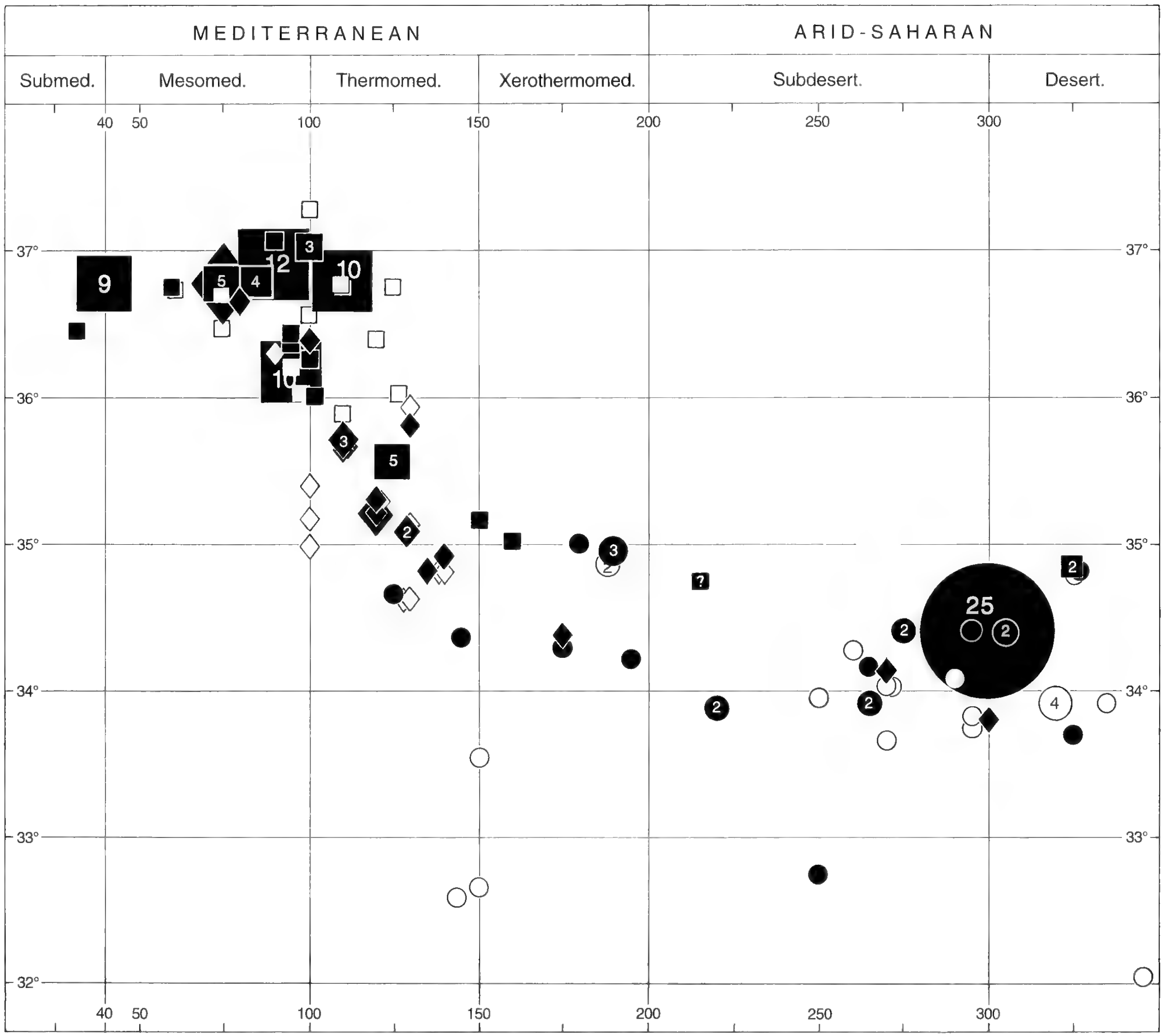
from the *M. cucullatus* populations in the south, and *M. abubakeri* from *M. brevis* in the west. Almost inevitably there are a few exceptional cases where the odd individual may be divergent in one of the character states.

Aside from the nuances of the nebulous concept of 'general appearance' the characters by which *M. abubakeri* can be distinguished from *M. brevis* (excluding the Iberian populations) are the lower number of dorsals and the usual state of the postorbital streak meeting the 'arms' of the V-mark around the last supralabial. *M. mauritanicus* exhibits the greatest degree of homogeneity in its character states and the distinction from *M. abubakeri* is similarly clear cut. Compared with *M. mauritanicus*, *M. abubakeri* is somewhat less homogeneous in its character states. In five specimens the dorsal count rose to 21 in stretches from 2 to 24 ventral scales. Two of these from the extreme northeast of Morocco, MNHN 1912.221 Berkane and MCZ 29920 Taforalt (Beni Snassène Mountains) whilst exhibiting counts of 21 in maximum stretches of 24 and 21 ventrals respectively conformed in all other respects to the diagnostic states of *M. abubakeri*. The single specimen of this species out of a total of four from Melilla the boundary zone, MNCN 1795, makes no approach to *M. brevis* in any of its characters: it has an uninterrupted run of 19 rows, 3+4 infralabials and no contact between the supralabials and parietals. The other three, MNCN 1783, 1796, 1797 all have 21 rows, good supralabial-parietal contact and, except for the last in which the infralabials number 7+4, the count is 6+3. Bons & Geniez (1996) '...examined numerous specimens from eastern Morocco all of which possessed 19 rows'. The count anterior to the vent is normally 17 but may decrease further: in one specimen which originated from Dj. Bou Keltoum (south of Guenfouda) the count actually fell to 15 for a distance of 2 ventrals before settling at 16. In three individuals (including the holotype and one of the paratypes) it decreased to 16. Other characters the states of which may resemble those of neighbouring taxa such as infralabial counts and nuchal collar are scattered within the body of the populations.

M. cucullatus and *M. brevis* (including populations of *ibericus*) have wide geographic ranges and possess intraspecific variations which often lack consistencey from one locality to another. Although *M. cucullatus* shows little of the variability in dorsal counts found in *M. brevis* (19 as opposed to 19–25) it exhibits a polymorphism in head pattern at least as great, being unique in that a significant number of its populations lack the 'pale collar'. By contrast *M. abubakeri* and more particularly M. *mauritanicus* are restricted in their ranges showing considerably less intraspecific and virtually no geographic variation when their ranges are compared to those of similar dimensions of populations of *M. cucullatus* .

Most of the character states which could be said to define *M. c. ibericus*, e.g. supralabial-parietal contact, 3 posterior infralabials, complete nuchal collar, occasional melanocephalism apply also to some populations of *M. brevis* occuring east of Tangiers including those parapatric with *M. abubakeri* (Wade, unpublished). Pleguezuelos (1998) noted melanocephalism in examples bordering the strait of Gibraltar. The variations are greatest in *M. brevis* of which the Tangiers-Melilla populations form only a part. The distinction between these *ibericus*-like forms from *M. abubakeri* is readily made but from *M. brevis* elsewhere in Morocco it is not easy to make as there is considerable overlapping of character states over wide areas. Nineteen midbody scale rows has been found to occur in some of the Iberian populations and very exceptionally in the Moroccan but this state has not been found in any of the populations from Tangiers to Melilla. Busack & McCoy (1990) presented a case for *M. c. brevis* giving rise to *M. c. ibericus* in Iberia largely on evidence of electrophoresis. It is regrettable that they restricted their samples for that analysis to populations from either side of the Strait

Fig. 12 Scatter diagram showing the position of the species of



Macroprotodon in relation to the bioclimatic regions and subregions: xerothermic indices (ordinate), degrees latitude (abscissa). Symbols as in Fig. 7; figures within symbols represent number of specimens.

of Gibraltar and not from the other regions in which they altered the ranges. Definition of the states that constitute *M. c. ibericus* and determination of its range requires further investigation.

There is to a large extent correlation between the distribution of the species and bioclimatic parameters. The xerothermomediterranean demarcation line (x=150–200) separating the Mediterranean from the arid-Saharan regions is a convoluted band of variable width which commences at the Atlantic and extends eastwards to the Tunisian coast (Fig. 7). The line becomes particularly narrow as it reaches the Moulouya valley to the west of which lie the Anti Atlas, an area of moderate humidity (mesomediterranean) where *M. brevis* is found: to the east of it stretches the arid region along the Moulouya valley to less tan 50 kilometres from the Mediterranean coast. From thence the line extends along the the Hauts Plateau for some 400 kilometres whereupon it reverses to almost as far as Aïn Sefra only to again reverse and continue along the Atlas Saharien from whence it extends in an arc across the Monts du Hodna to the southern part of the Massif de l'Aurès before proceeding eastwards to the coast. *M. cucullatus* inhabits largely the arid or Saharan regions to the south of the line and the *abubakeri-mauritanicus* assemblages the Mediterranean to the north of it (Fig. 7).

M. abubakeri could be viewed as an eastern mesomediterranean-thermomediterranean extension of the northern Moroccan populations of *M. brevis* which it resembles at least as closely as it does to *M. mauritanicus*. Further east *M. abubakeri* is replaced by *M. mauritanicus* which is most densly concentrated in the mesomediterranean but extends into the more humid submediterranean subregions. The two northern forms extend southward, although with considerably less frequency, into the xerothermomediterranean and enter the desertic subregions (Fig. 12). *M. abubakeri*, unlike *M. cucullatus* or *M. mauritanicus* which do not eschew the high ground, is restricted to land below 1,000 metres, at least in Algeria. The localities Taforalt, Djebel Bou Keltoum (Morocco), Khemis and Sebdou (Algeria) although appearing on the map (Fig. 7) in the shaded area showing land above 1,000 metres do in fact lie below that altitude. The scale of the map is not large enough for the smaller valleys and similar low lying areas to be shown.

Individual specimens that do not conform to the taxon or population from which they are supposed to have originated occasionally appear: this may be due to error of attribution or more likely as a result of human introduction. Four specimens of *M. brevis* three of which possess 23 midbody scale rows from 'Algeria' (NMW 25840.5), Bordj Bou Arréridj (MHNG 1379.68) and Tunis (NMW 19193.3) – i.e. well within the range of *M. mauritanicus* – agree with material from the Essaouira-Marrakesh region; the other with 21 uninterrupted rows from Ksar Challala (MHNG 1214.40) most closely resembles the northern Moroccan population. There is no evidence of intergradation but instead there is some suggestion of character displacement thus arguing against expanding the description of *M. mauritanicus* to accomodate the additional states: rather, it provides further support for the recognition of the taxa at specific level.

The melanocephalic specimen mentioned by Hediger (1935) p. 24 from 'Bona' NMB 2017 with four posterior infralabials and four teeth preceding the fangs, presents a head configuration resembling so closely that from Djebel Mourdjadjo that its discovery in the eastern sector of Algeria is most likely to be due to accidental introduction. This individual is listed in the current NMB catalogue as one of eight specimens collected by Hagenmüller Müller(1890 p. 692) lists only seven specimens presented by that collector from around Annaba. Although noteworthy particulars are recorded no individual is singled out as being black headed. A further specimen, NMB 2015 also listed by Müller 1878: 567 & 666 under 'Algerien und Aegypten', the provenance of which is stated in the actual catalogue to be Oran. However, possession of sutural labial-parietal contact, 6+3 infralabials and 3 posterior maxillary teeth suggests that it originated from further east: it is identical to *M. mauritanicus*. It is of some significance that both individuals were collected from long established seaports rather than from inland.

A specimen (SMF 20170) collected in 'southern Spain' which is identical to material from Egypt is surely the result of an accidental introduction. *Macroprotodon* not infrequently occurs near human habitations. Some of the specimens from Médjana were rescued, both as adults and particularly as hatchlings, from domestic chickens. Secretive, adventitious little snakes abroad at dusk or early morning hiding in human artefacts, could easily be transported by accident.

ACKNOWLEDGEMENTS. I am indebted to Drs E. N. Arnold and C. McCarthy for permitting me to re-examine the *Macroprotodon* collection in the NHM and for numerous other courtesies. For the loan and making available material for examination I thank Drs V. Mahnert and B. Schätti (MHNG), E. Stöckli (NMB), J. Rosado (MCZ), G. Zug (USNM), J. Cadle (ANSP), E. J. Censky (CM), R. L. Humphreys (UCM), R. Günther(ZMB), G.E. Gonzales (MNCN), M. Hoogmoed (RMNH), I. Ineich (MNHN), W. Böhme (ZFMK), M. Laudahn (SMF), U. Gruber (ZSMH), H. Koepecke (ZMH), A. Resetar (FMNH), J. Vindum (CAS), Prof. F. Tiedemann (NMW). I thank Dr G. Vogel for the donation of a specimen and Mr D. Donaire for photographs and an exuviate. Dr G. Underwood and Mr B. Hughes provided constructive criticism and Mr J. Pether provided advice and assistance during the course of this work.

I thank my senior colleagues at Middlesex University, the late Professor J. Lansdown who authorised the study and particularly Professor Ian McLaren who approved leave for travel and provided invaluable help. The visits to Algeria were financed by grants RO31/1109 and RO31/6180. Colin Rattray and Phil Wilson took over my responsibilities during my absence.

I owe a debt of gratitude to Dr Nebbache Mounir and M. Médani Kerim for providing facilities and assistance whilst I was in Algeria and Dr Mohamed Bey and M. Nebbache Djemaï for hospitality. Messrs Aboubakeur Sid-Ahmed, Nebbache Riyadh, Ouali Nour ed-Dine and O. Abbas provided hospitality and companionship in the field. To all I extend warmest thanks.

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Bulletin of The Natural History Museum

ZOOLOGY SERIES

Vol. 67, No. 1, June 2001