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The cranial muscles and ligaments of macrouroid fishes (Teleostei: Gadiformes); functional, ecological and phylogenetic inferences

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Contents

Introduction

> *If overall oceanic diversity could be expressed in numbers of individuals and species, rat-tails would surely emerge as the most diverse family of benthopelagic fishes.*

So wrote Marshall (1979) of the Macrouridae, a group assigned to that ill-defined assemblage of higher euteleostean fishes known as the Paracanthopterygii.

Marshall (1965) had earlier noted the sparsity of knowledge of the morphology and biology of macrourid fishes. Since then, the studies by Okamura (1970*a* & *b*) have contributed substantially to filling this gap. However, since Okamura studied only Japanese macrourid fishes, the work is taxonomically limited because morphologically more diverse taxa occur outside Japanese waters. The data Okamura has published, nevertheless are substantial enough to provide a foundation for further anatomical studies, particularly those aimed at producing cladistic analyses, which so far, have not been applied to macrourid taxa.

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Since Gilbert & Hubbs (1916) published their subfamilial arrangement of macrourid fishes, there have been few major taxonomic changes. Apart from the recognition of additional subfamilies (Parr, 1946) and the elevation of the Macrouroidinae to family level (Okamura, 1970*a* & *b*), the most noticeable rearrangement was that of Marshall (1966) who recognised the non-monophyletic nature of the family. Marshall (*op. cit.*) found that three taxa, previously recognised as macrourids, *viz*: *Steindachneria, Lyconus* and *Macruronus*, shared more characters in common with the gadoid family, the Merlucciidae. Although not all of Marshall's chosen characters are synapomorphic for merlucciids, there is every reason to agree that these three genera do not belong with the macrourids (see Cohen, 1984; Howes, 1988).

Most recent authors recognise four macrourid subfamilies (see Cohen, 1984), *viz*: the Bathygadinae, Trachyrincinae, Macrouroidinae and Macrourinae, the latter containing the majority (*ca* 30) of genera. Howes (1988), based largely on the data presented here, has challenged this concept of the Macrouridae (see below).

Most macrourid taxonomy has been based on ecological-evolutionary premises. For example, Okamura (1970*b*) viewed his hypothesised phylogenetic polarity of primitive to derived taxa as reflecting both ecological groups and an evolutionary sequence. McLellan (1977: 1034) devised an evolutionary scenario, based on her study of macrourid morphology and ecology, that reflected the invasion of continental slopes and deep ocean basins by taxa derived from pelagic ancestors; again, a sequence supposedly reflected in extant ecological groupings and ontogenetic development.

As pointed out by Marshall (1965; 1979) most macrourids are found in tropical seas but some areas contain more speciose taxa than others, e.g. the Sulu Sea, Gulf of Mexico and Caribbean. Most species are confined to continental slopes and few are common to more than one ocean. Marshall (1973; 1979) has hypothesised that the amphi-Atlantic distribution of 33% of the total Atlantic species and subspecies, might be attributable to continental drift. Merrett *et. al.* (1983) also note that species common to the Atlantic and Indian Oceans are inhabitants of continental slope, abyssal and pelagic regions, a distribution seeming to indicate a more general underlying factor than simply one of random dispersal.

In attempting to explain macrourid ecology and distribution, none of these authors has asked a fundamental taxonomic question; how closely related are the taxa under consideration? As yet, there exists no rigorously structured hypothesis of macrourid relationships.

Since previous studies of macrourid morphology have, to a large extent, been concerned with feeding mechanisms and because phylogenetic interpretations have been based on comparisons of those mechanisms, it is the objective of this study to re-assess the morphological basis of those ideas. The jaw musculature of some macrourid taxa has been described by McLellan (1977) and Casinos (1978), these descriptions were, however, made more from a functional rather than a taxonomic and phylogenetic viewpoint, and a taxonomically restricted range of taxa were used. A comparative analysis of macrouroids and other paracanthopterygians would, it was hoped, reveal morphological patterns that might indicate both related groups within the suborder and the relationships of macrouroids with other gadiforms. The limitations of using a single character complex for this purpose are well realised by the author, but past experience with basal euteleosts (Howes, 1984; 1985) has indicated that cranial muscles can provide rewarding information on which to base phylogenetic interpretations.

Where availability of material allowed, at least three specimens of each taxon were dissected to check the variability of the character described.

Okamura (1970*b*) has described other character complexes (osteology, scales, brain morphology, structure of light organs) and these have been used to a certain extent to test the congruency of relationships arrived at through the myological study. However, these other characters must themselves be evaluated by out-group comparisons, and it is evident in Okamura's analysis that many characters used to define sub-groups are plesiomorphic for Gadiformes. It remains, therefore, for future studies to make polarity assignments to osteological and other characters in order to produce a more refined hypothesis of macrourid interrelationships.

Howes (1988) in an account based principally on the findings presented here has reviewed the relationships of macrouroids and gadoids, and shown that the Macrouroidei (*sensu* Cohen, 1984) and the Macrouridae are non-monophyletic groups. Although, in that previous study, clades were identified they were not given formal taxonomic status. In this account two of those clades are recognised as families, namely, the Bathygadidae and the Trachyrincidae. More complete diagnoses and taxonomic reviews of both are in preparation. Since the Macrouroidei was restricted to containing a single family the Macrouridae (Howes, 1988), the terms macrouroid and macrourid are interchangeable. However, in this text the term macrouroid is used when making coordinate comparisons with Gadoidei (*i.e.* gadoids).

Classification used in this text
Suborder: MACROUROIDEI
  Family: Macrouridae
    Subfamilies: Macrourinae & Macrouroidinae

Suborder: GADOIDEI
  Family: Trachyrincidae, Bathygadidae, Moridae, Melanonidae, Steindachneriidae, Euclichthyidae, Merlucciidae, Gadidae, Ranicepitidae, Lotidae, Phycidae, Muraenolepididae & Bregmacerotidae

List of specimens used

All the specimens used in this study are in the collections of the British Museum (Natural History). Type of preparation is indicated as CS = cleared and stained; D = dissected; SK = dry skeleton.

MACROUROIDEI: *Abyssicola macrochir*, 1938.6.23: 12–13 (D); *Cetonurus globiceps*, 1986.4.22: 4–5 (D); *Chalinura mediterranea*, 1986.4.22: 3 (D); *Chalinura profundicula*, 1986.4.22: 9; *Chalinura* cf. *simula*, 1967.12.11: 2 (D); *Coelorinchus caribbaeus*, 1963.2.25: 244–250 (D; CS, 185 mm TL); *Coelorinchus coelorincus*, 1905.2.2: 18 (SK); *Coryphaenoides rupestris*, 1897.12.9: 82 (SK); *Coryphaenoides anguilliceps*, 1981.7.14: 1–4 (D); *Coryphaenoides mexicanus*, 1971.10.22: 24–25 (D); *Cynomacrurus piriei*, 1930.1.12: 952; *Echniomacrurus mollis*, 1967.12.11: 3–4 (D); *Hymenocephalus italicus*, 1973.3.5: 7–10 (D); *Kumba dentoni*, 1961.1.30: 6 (Holotype; superficial examination); *Lionurus carapinus*, 1934.12.19: 33–34 (D); *Macrosmia phalacra*, 1980.12.31: 2 (Paratype, D); *Macrouroides inflaticeps*, 1939.5.24: 684 (D); *Macrourus berglax*, 1965.6.22: 8–9 (D); *Malacocephalus laevis*, 1960.12.20: 2–3 (D); 1904.11.30: 33 (SK); *Mataeocephalus microstomus*, 1939.5.24: 723–24 (D); *Nematonurus armatus*, 1986.4.22: 1–2 (D); *Nezumia aequalis*, 1973.3.5: 60–64 (CS, 130 mm, tail broken); *Nezumia hildebrandi*, 1963.2.25: 138–153 (D); *Odontomacrurus murrayi*, 1967.12.11: 5 (D); *Sphagemacrurus hirundo*, 1934.12.19: 30 (D); 1986.4.22: 6–7 (D); *Squalogadus modificatus*, 1963.2.1: 10 (D); *Trachonurus villosus*, 1963.2.25: 226–228 (D); *Ventrifossa occidentalis*, 1965.2.25: 61–71 (D; CS, 190 mm TL).

GADOIDEI: *Antimora rostrata*, 1903.9.29: 7 (D); 1986.4.22: 10–11 (CS); *Austrophycis marginata*, 1936.8.26: 424–431 (D; CS); *Bathygadus favosus*, 1963.2.25: 28–30 (D); *Bathygadus macrops*, 1973.3.5: 3–6 (D); *Bathygadus melanobranchus*, 1969.6.26: 3227–3231 (D, CS); *Bathygadus vaillanti*, 1963.2.2: 31–35 (D); *Bregmaceros atlanticus*, 1984.11.14: 4 (D); *Bregmaceros maclellandi*, 1939.5.24: 792, 799 (D); *Brosme brosme*, 1892.6.8: 9 (SK); *Ciliata mustela*, 1983.8.3: 13–26 (D); *Enchelyopus cimbrius*, 1980.12.18: 3–12 (D); *Euclichthys polynemus*, 1986.5.14: 1–3; 4–9 (D); *Gadomus longifilis*, 1963.2.25: 7–17 (D; CS, 190 mm TL; 1890.6.16: 43 (SK); *Gadus morhua morhua*, 1971.2.16: 634–635 (D); 1971.2.16: 628–633 (CS, 81 mm SL); *Gadus morhua callaris*, 1985.9.6: 7–14 (D); *Gaidrospsarus mediterraneus*, 1971.10.7: 65–77 (D); uncat. (CS, 122, 54 mm SL); *Halargyreus affinis*, 1973.10.29: 384–440 (D; CS, 117 mm TL); *Lepidion eques*, 1981.3.16: 422–427 (D); 11981.3.16: 437–440 (CS, 110 mm TL); 1902.10.30: 6 (SK); *Lota lota*, 1953.6.26: 15–18 (D); 168.6 (SK, skulls only); *Lotilla marginata*, 1974.9.28: 6–7 (CS, 118 mm TL); *Lyconus brachycolus*, 1907.6.20: 15 (Holotype, partly dissected); *Macruronus magellanicus*, 1936.8.26: 352–357 (D); *Macruronus novozealandi*, 25, 120 (SK); *Merlangius merlangus*, 1971.2.16: 329–331 (D); *Melanonus gracilis*, 1930.1.12: 933 (D); *Melanonus zugmayeri*, 1981.3.16: 377 (D); 1986.4.22: 8 (CS, 140 mm TL); *Merluccius merluccius*, 1963.5.14: 94–109 (D); 1971.7.21: 44–57 (CS, 130 mm TL); *Merluccius productus*, 1896.9.25: 6 (SK); *Molva molva*, 1976.6.29: 2–5 (D); *Mora moro*, 25.370 (SK); *Muraenolepis microps*, 1937.7.12: 24–29 (D); 1937.7.12: 11–17 (CS, 95 mm TL); 1937.7.12: 24–29 (skull); *Physiculus argyropastus*, 1901.1.30: 22 (SK); *Phycis blennoides*, 1973.10.29: 4411-448 (D); 1976.7.30: 119 (CS); 1898.4.30: 14 (SK); *Pseudophycis brevisculus*, 1873.12.13: 30 (SK); *Phycis phycis*, 25.400 (SK); *Raniceps raninus* 1967.1.1: 4 (D); 1893.7.6: 2 (D) 1971.2.16: 640 (CS, 40 mm SL); 1864.8.26: 3 (SK); *Salilota australis*, 1936.8.26: 394–404 (CS, 58 mm TL); *Steindachneria argentea*, 1963.2.25: 335–339 (D); 1963.2.25: 344–354 (CS, 130 mm TL); *Trachyrincus trachyrincus*, 1904.11.30: 34–35 (D); 1976.7.30: 42–53 (D, CS, 110 mm TL); 1888.6.15: 7 (SK); *Urophycis regia*, 1985.6.6: 109–119 (D).

OUT-GROUP SPECIES: *Atherina presbyter*, 1983.4.21: 28–37; *Aulopus filamentosus*, 1953.11.1: 10–13; *Brotula jayakari*, 1891.2.9: 30 (SK); *Cataetyx messieri*, 1936.8.26: 1060–61 (D); *Centropomus ensiferus*, 1984.8.8: 85–95 (D); *Cynoscion jamaicensis*, 1961.9.1: 107–113 (D); *Dicrolene introniger*, 1939.5.24: 1441–1444 (D); *Diplacanthopoma brachysoma*, 1972.10.24: 4 (D); *Electrona antarctica*, 1948.5.14: 128–138; *Eleotris obscurus*, 1903.5.14: 93–99 (D); *Esox lucius*, 1971.11.19: 45–46 (D); *Genypterus blacodes*, 1936.8.26: 1052–57 (D); 1898.6.17: 73 (SK); *Glyptophidium macropus*, 1939.5.24: 1456–1465; *Gobiesox nudus*, 1985.3.18: 110–114 (D); *Gobius guineensis*, 1984.7.29: 1021–22 (D); *Harpadon nehereus*, uncat. (D); *Hoplostethes melanopus*, 1939.5.24: 817–8 (D); *Lampanyctus crocodilus*, 1976.7.30: 26–33 (D); *Lamprogrammus niger*, 1939.5.24: 1483–87 (D); *Lophiodes mutilus*, 1939.5.24: 1869–75 (D); *Lycodes frigidus*, 1969.6.26: 3145–49 (D); *Monomitopus metriostoma*, 1964.8.6: 43–46 (D); *Ophidion rochei*, 1971.12.17: 6–8 (D); *Percichthys trucha*, 1981.10.14: 28 (D); *Percopsis omiscomayus*, 1973.3.20: 468 (D); *Photichthys argenteus*, 1930.1.12: 299–306; *Plagioscion squamosissimum*, 1970.4.2: 5–8 (D); *Pogonias chromis*, 1886.1.21: 11–13 (D); *Polymixia nobilis*, 1862.4.22: 17–18 (D); *Porichthys porosissimum*, 1948.8.6: 1460–72 (D); *Serranus cabrilla*, 1960.6.10: 6–8 (D); *Siniperca knerii*, 1981.2.3: 1–4 (D); *Stephanoberyx monae*, 1972.10.24: 2–3; *Tilapia mariae*, uncat. (D).

Abbreviations used in the text figures

NB. Scale bars in all figures are in divisions of 1 mm.
A1, A1α, A1β, A1γ, A2, A2d, A2v, A3, Aω Divisions of the *adductor mandibulae* musculature

Aa	Anguloarticular
aap	*adductor arcus palatini* muscle
ad	*adductores* muscle
AH	Anterohyal
bf	buccalis facialis of trigeminal nerve
bpm	bucco-pharyngeal membrane of 1st gill-arch
Bsr	Branchiostegal membrane
Cb	Ceratobranchial
ce	chondroid element
Cmb	Coronomeckelian bone
Cmc	Coronomeckelian cartilage
ct	connective tissue
De	Dentary
Dh	Dorsohyal
do	*dilatator operculi* muscle
Eb	Epibranchial
Ent	Entopterygoid
epx	*epaxialis* muscle
ey	eyeball
fA2	fascia of muscle A2
Hb	Hypobranchial
ht	heart
hyab	*hyohyoideus abductores* muscle
hyad	*hyohyoideus adductores* muscle
Hyo	Hyomandibula
Hyop	Opercular process of hyomandibula
ica	*infracarinalis anterior* muscle
iA1β	internal aponeurosis of muscle A1β
IO	Interoperculum
im	*intermandibularis* muscle
lap	*levator arcus palatini* muscle
le	*levator externus* muscle
Let	Lateral ethmoid
lcdh	ceratobranchial-dorsohyal ligament
lee	lateral ethmoid-entopterygoid ligament
lei	entopterygoid-infraorbital ligament
lep	lateral ethmoid-palatine ligament
les	lateral ethmoid-suspensorial ligament
li	*levator internus* muscle
lip	interopercular-preopercular ligament

lla	labial ligament
lmh	mandibulo-hyoid ligament
lmi	mandibulo-interopercular ligament
lmm	maxillo-mandibular ligament
lmn	maxillary-nasal ligament
lmp	maxillary-premaxillary ligament
lmq	mandibulo-quadrate ligament
lo	*levator operculi* muscle
lpl	palatine-lachrymal ligament
lsm	supramaxillary ligament
lsc	semicircular ligament connecting 3rd hypobranchials
ludh	urohyal-dorsohyal ligament
lVII	maxillary-rostral cartilage ligament
lIX	maxillary-premaxillary ligament
lX	palatine-maxillary ligament
lXI	ethmoid-maxillary ligament
lXII	palatine-premaxillary ligament
Men	Meniscus
Met	Metapterygoid
Mmc	Mentomeckelian cavity
Mvp	Maxillary ventromedial process
Mx	Maxilla
Mxh	Maxillary head
nm	neuromast
NII	Optic nerve
NV	Trigeminal nerve trunk
NVII	Facial (hyomandibularis) nerve
NVIIh	Hyoid branch of facial nerve
NVIIm	Mandibular branch of facial nerve
obd	*obliqui dorsales* muscle
obp	*obliquus posterior* muscle
obs	*obliquus superior* muscle
obv	*obliqui ventrales* muscle
oi	*obliquus inferior* muscle
Op	Operculum
Pal	Palatine
Pb	Pharyngobranchial
pce	*pharyngoclavicularis externus* muscle
pci	*pharyngoclavicularis internus* muscle
Ph	Posterohyal
phy	*protractor hyoideus* muscle
Pmx	Premaxilla
Po	Preoperculum
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Ptt	Posttemporal
Q	Quadrate
Rc	Rostral cartilage
rd	*retractor dorsalis* muscle
Ra	Retroarticular
Rbv	Buccal branch of trigeminal nerve
rc	*rectus communis* muscle
rd	*retractor dorsalis* muscle
re	*rectus externus* muscle
rei	*rectus inferior* muscle
ri	*rectus internus* muscle
RmV	Mandibular branch of trigeminal nerve
RmxV	Maxillary branch of trigeminal nerve

rs	*rectus superior* muscle
rv	*recti ventrales* muscle
Scl	Supracleithrum
sh	*sternohyoideus* muscle
shl	lateral segment of *sternohyoideus*
So	Suboperculum
Tp	Toothplate
tv	*transversus* muscle
tvd	*transversi dorsalis* muscle
tA1α, t1, t2	insertion tendons of *adductor mandibulae* A1 muscles
tA2	insertion tendon of *adductor mandibulae* A2 muscle
Vo	Vomer

Cranial ligaments

Ligaments of the upper jaw and pterygoid bones

In the following account the terminology and numbering system for ligaments follows that of Stiassny (1986).

Stiassny (1986) recognised two synapomorphic arthrological characters uniting the acanthomorph lineages 'Paracanthopterygii' and Acanthopterygii, namely:

the absence of a median palato-maxillary ligament (ligament IV) *and*

the subdivision of the palato-vomerine ligament (ligament VI).

I would confirm Stiassny's findings that a median palato-maxillary ligament (IV) is absent in all paracanthopterygian taxa examined.

In macrouroids there is a single, undivided *palato-vomerine ligament*, which, from its points of attachment to the centre of the palatine and the head of the vomer, corresponds with Stiassny's ligament V (the posterior palato-vomerine ligament). The ligament runs parallel to the medial face of the palatine and varies in size from a long slender strap to a broad band. In the latter case the palatine is deep and is closely applied to the ethmo-vomerine bloc (e.g. *Coryphaenoides, Hymenocephalus*).

In Gadoidei the palato-vomerine ligament is also single. The presence of a single rather than a double ligamentous connection in gadoids and macrouroids may indicate that there has either been a derived loss of the anterior palato-vomerine ligament (ligament VI) or that it represents the plesiomorphic condition found in non-acanthomorph fishes. A broad investigation of the condition among paracanthopterygians is necessary to support one or other of these hypotheses.

The *maxillo-rostroid ligament* (ligament VII) is well-developed in all macrouroids. As in other acanthomorphs it runs from the medial portion of the folded maxillary head to the dorsolateral face of the rostral-cartilage. In all macrouroids ligament VII appears to be continuous across the dorsal surface of the cartilage. In gadoids, a similar situation obtains in *Bathygadus* and the Moridae where the ligament lies in a groove in the cartilage. In many other gadoids, however, ligament VII is broader and inserts on the lateral face of the rostral cartilage (Figs 13 & 17).

In some macrouroids, ligament VII runs parallel to the palato-maxillary ligament (XII), e.g. *Coryphaenoides* (Fig. 1) whereas in others it runs at *ca.* 45° to that ligament (Fig. 3). Ligament VII passes medial to the tips of the premaxillary ascending processes and is not attached to them. According to Stiassny (1986) in acanthomorphs ligament VII inserts on the premaxillary ascending processes. I have not found this attachment in any gadiform and the condition she reports is probably a derived one for acanthopterygians. Gosline (1981) has commented on the functional significance of ligament VII (Gosline's ligament rc) believing it to be the primary cause of upper jaw protrusion in at least some acanthomorphs (see p. 50).

Casinos (1978) although identifying ligament VII in macrouroids incorrectly states that it is absent in the Gadidae. In fact the ligament is present in all gadoid taxa (see comments on p. 51 concerning function).

An *anterior maxillo-premaxillary ligament* (ligament IX of Stassny, 1986; ligament 'am' of Gosline, 1981) is present in all macrouroids and other gadiforms examined. In macrouroids however, the ligaments of either side meet ventroposteriorly to the rostral-cartilage forming an X-shaped ligament connecting the maxillary heads (their menisci) and the premaxillary ascending processes (Figs 28B & C).

In gadoids ligament IX is variously developed and attached. In *Bathygadus* and *Trachyrincus*, there is a complex attachment of the ligament to the maxillary head *via* a cylindrical chondroid or fibrous element whose posterior tip joins a thin ligament stretching caudally, which becomes incorporated with the connective tissue stretching between the maxilla and premaxilla (Figs 29A & B). In melanonids and merlucciids, ligament IX attaches directly to the medial process of the maxillary head, although it may be associated with a thick wedge of fibrous connective tissue (Fig. 29C). In advanced gadoids, there is sometimes no discrete ligament but only tough connective tissue (e.g. *Euclichthys*) although in the majority there is a short ligament and a thin meniscus between the medial maxillary process and the premaxillary ascending process (Fig. 29D); see further comments on p. 39.

An *anterior palato-maxillary ligament* (ligament X) is present in all macrouroids and gadoids examined. It generally connects the base of the palatine prong with the inner central portion of the maxillary head. However, in the macrouroids *Coryphaenoides* and *Hymenocephalus*, the ligament attaches to the medial aspect of the maxillary head then passes forward to attach to the anterior process of the premaxilla.

An *ethmo-maxillary ligament* (ligament XI) is well-developed in all macrouroids and passes beneath the palato-premaxillary ligament (XII). Its attachments are to the lateral prong of the mesethmoid and the anterolateral face of the maxilla.

In two macrourid genera, *Cetonurus* (Fig. 4) and *Echinomacrurus*, a ligament extends transversly from the ethmoid to the palatine. In this respect, the situation corresponds with that in the percomorph *Morone* illustrated by Stiassny (1986, fig. 10). According to Stiassny the additional ligament is a branch of a bifurcated ligament XI. Such may also be the case in the two macrourid taxa. It is noted that in both these genera the dorsal palatine process is higher than in others and that a lateral ethmo-palatine ligament is absent. Thus the 'additional' ligament may serve to brace the palatine against too great a lateral movement.

In all Macrourinae there is a short ligament running from the head of the maxilla to the inner face of the extended nasal bone (Fig. 2). The ligament branches from the base of ligament XI; it is absent in *Bathygadus, Gadomus, Trachyrincus* and all other gadiform fishes. A maxillary-nasal ligament is apparently present in some acanthopterygians (Cichlidae, P. H. Greenwood, pers. comm.). I have not found the ligament in other paracanthopterygians examined, nor in berycoids or polymixiids.

A *palato-premaxillary ligament* (ligament XII of Stiassny, 1986) is present in all macrouroids and runs from the base of the palatine prong to the contralateral premaxillary ascending process. Often, the ligament attaches to the antero-dorsal surface of the rostral cartilage prior to its insertion on the premaxillary process. Gosline (1963, fig. 5A) shows a similar situation in the percopsiform *Aphredoderus* where ligament XII as well as attaching to the rostral cartilage is united with its antimere in the midline. In *Percopsis*, however, the ligament of each side attaches to its respective premaxillary ascending process, there being no contralateral attachment. The percopsiform situation may represent the plesiomorphic condition of ligament XII.

A *lateral ethmoid-palatine ligament* is present in all macrouroids examined. This ligament, commonly present in nearly all teleosts, connects the posterior face of the lateral ethmoid wing with the dorsomedial surface of the palatine. In macrouroids, there are often two ligaments, the medial occupying the usual position, while the lateral ligament connects the outer margin of the lateral ethmoid to the lateral surface of the palatine. In the macrourines *Nezumia* and *Ventrifossa* the medial ligament extends posteriorly to the entopterygoid. *Cynomacrurus* and *Odontomacrurus* are exceptional among macrouroids in lacking a lateral ethmoid-palatine ligament.

In the gadoid families Melanonidae, Merlucciidae and Steindachneriidae there is a single, stout lateral ligament connecting the lateral ethmoid with the palatine, which in *Gadomus* (Bathygadidae) extends medially to attach to the entopterygoid.

In the Euclichthyidae there is a unique form of ligamentous connection between the lateral ethmoid and suspensorial elements. The lateral ethmoid ligament fans out to attach along the dorsolateral surface of the palatine; it continues forward as a broad band along the dorsolateral border of the entopterygoid, enters to *adductor arcus palatini* muscle, curves ventrolaterally, leaves the muscle and attaches to the antero-medial face of the hyomandibula (Fig. 15).

In the Moridae there are both separate lateral and medial lateral ethmoid-palatine ligaments, and a lateral ethmoid-entopterygoid ligament. In the Gadidae, however, there are no definite ligamentous connections between the posterior face of the lateral ethmoid and the palatine. In most gadids, the palatine's only ligamentous connection with the neurocranium is with the vomer (ligament V; see above). The lateral ethmoid wing of gadids is often reduced and the palatine articulates not with the wing but with the anterior part of the lateral ethmoid where it contacts the ethmovomerine bloc. In the Muraenolepididae, for example, the palatine bears a high dorsal process which contacts the dorsomedial face of the (considerably reduced) lateral ethmoid. The palatine process is tightly bound by connective tissue to the lateral ethmoid but is not connected to it by a discrete ligament.

Among more 'advanced' gadoids there is a noticeable shift in the articulation of the palatine toward a more anteromedial position. Among macrouroids and plesiomorphic gadoids (Bathygadidae; Melanonidae), the palatine articulates with the ventral surface of the lateral ethmoid wing to which it is also ligamentously attached. In other gadoid taxa, however, the palatine articulates with the anterior, ethmoidal part of the lateral ethmoid and there is a correlated loss of ligamentous connection between the bones. In acanthopterygians, the lateral ethmoid-palatine connection may be *via* one or more ligaments (see for example, Stiassny, 1981: 74; Greenwood, 1985: 158). The widespread occurrence of discrete ligamentous connections between the lateral ethmoid and palatine in teleosts indicates that their absence, often coupled with that of an intimate articulation between the two bones (Howes, 1987) represents a derived condition.

Ligaments of the lower jaw and opercular bones

There is a single, strong mandibular-interopercular ligament present in all macrouroids. The ligament is variable in length and width, from long and strap-like to short and triangular. The mandibular attachment of the ligament is the retroarticular, which is usually dorso-ventrally elongate. Okamura (1970*b*) has drawn attention to the varying types of retroarticular among macrouroids.

Casinos (1978) refers to a 'circumbuccal' ligament in macrouroids and gadids which he describes as a '... tendon that contours all the mouth'. Casinos postulates that this ligament plays an important role in protrusion of the upper jaw (see p. 52). The 'circumbuccal' ligament of Casinos is present in some form or other in all gadiform fishes examined. It does not surround the perimeter of the jaw as is implied by Casinos, but is attached anteriorly to each dentary. I thus refer to it as the 'labial ligament'. The ligament varies in degree of thickness and complexity of anterior attachment, among gadoids being least in the Gadidae and most in the Bathygadidae, Moridae, Melanonidae and Merlucciidae. In macrouroids the ligament is also well-developed, but less so than in the four gadoid families.

In *Bathygadus* (Fig. 9) where it is most highly developed, the labial ligament is a thick rope-like element having a bifurcate attachment on the anterior aspect of the dentary. At the rictus of the jaws, the ligament curves around to attach to the premaxilla, at the point of curvature sending off a posterior branch which anchors to the maxillary rim.

A separate element, with the same gross consistency as the main ligament, forms a stump on the posteromedial surface of the maxilla, rising above the border of the bone. Rosen & Patterson (1969: 425) refer to this non-osseous structure in *Melanonus* (Melanonidae) as resembling a supramaxilla. I therefore refer to it as the 'supramaxillary ligament'.

Histological sections of the labial and supramaxillary ligament, stained specifically for elastin, reveal the 'ligaments' to consist of a collagenous core surrounded by an elastin coat. This tissue is ligament-like in the nature of its attachments (it is free from the dentary, although closely adhering to it by a sheet of connective tissue, which is highly innervated by subranches of the ramus mandibularis facialis (VII) nerve.

The distribution of the labial ligament among euteleosts is yet to be ascertained but is possibly a

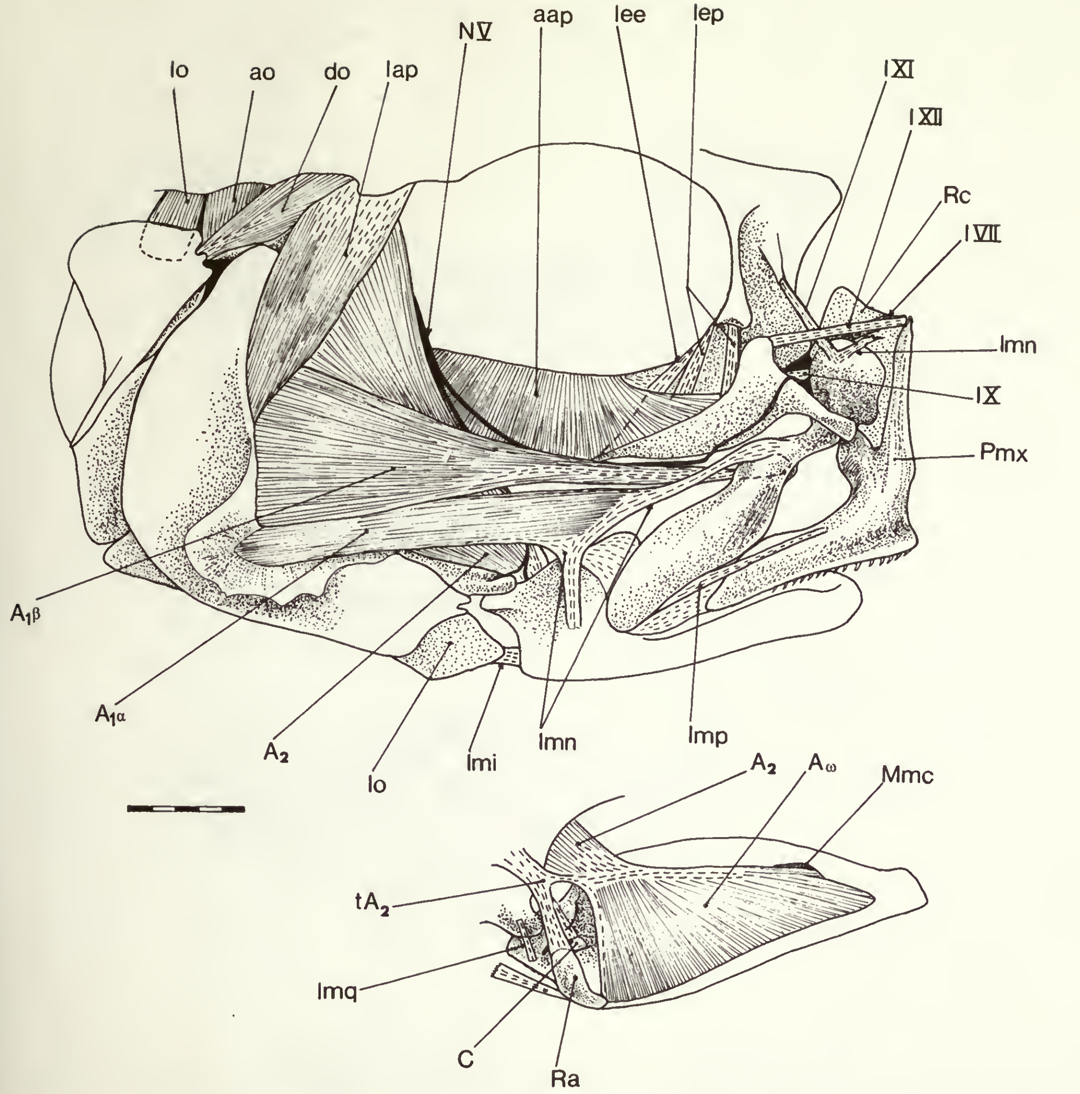

Fig. 1 *Coryphaenoides mexicanus*; cranial muscles and ligaments. Above, in lateral view. Below, medial view of the lower jaw adductor musculature and ligamentous connections.

eurypterygian character (Stiassny, pers. comm.). However, its complex posterior ramification in the gadoids listed above appears to be a derived specialization, whose functional significance is commented upon elsewhere (p. 52).

The ligament which in euteleosts connects the posterior tip of the interoperculum to the anterior border of the suboperculum is, in *Bathygadus* and *Gadomus* reduced and supplemented by another ligament stretching from the dorsal midpoint of the interoperculum to the preoperculum and hyomandibula. In most gadoids the interoperculum and suboperculum are connected by thin connective tissue, the dorsally directed ligament spanning the two bones and attaching to the preoperculum and hyomandibula. In the Merlucciidae, the dorsal ligament is a broad band attaching the interoperculum to the preoperculum. The Trachyrincidae have a unique condition whereby the interoperculum is connected by dorsally directed ligaments to the preoperculum and opercu-

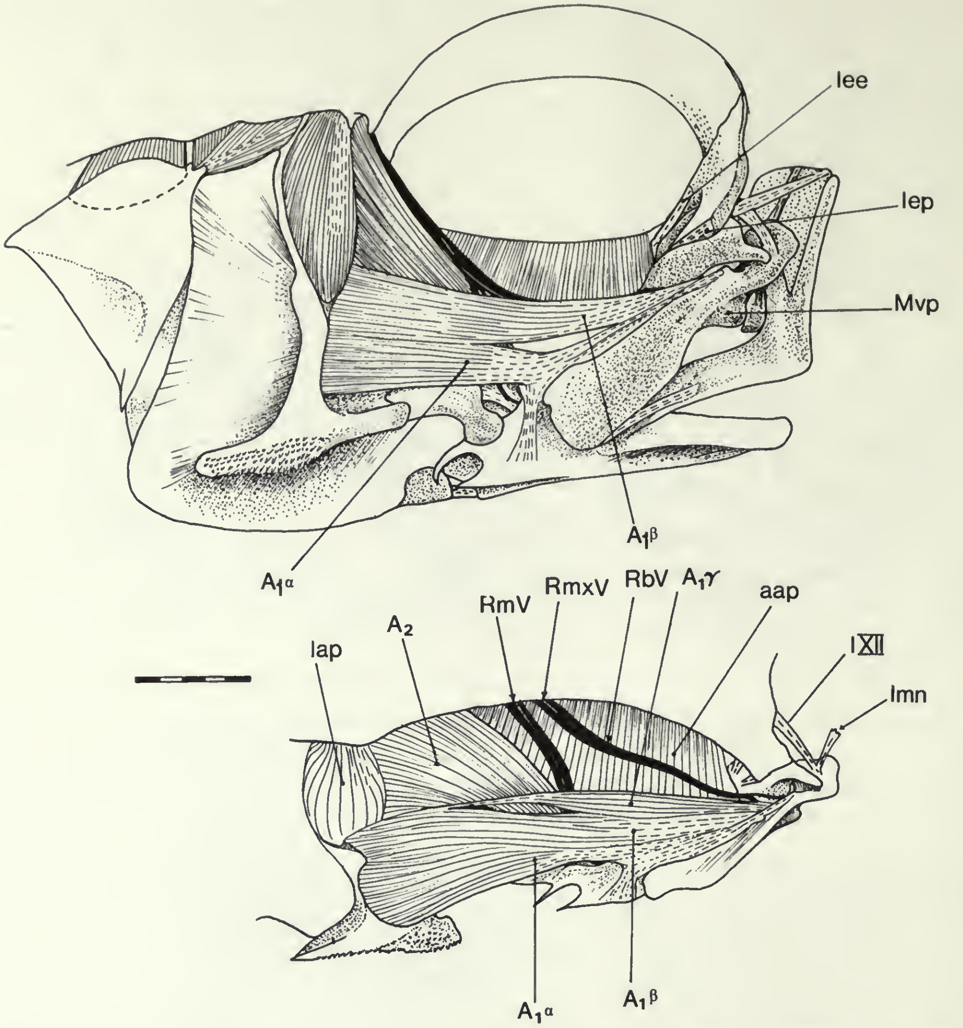

Fig. 2 *Coelorinchus caribbaeus*; cranial muscles and ligaments. In lateral (above) and dorsal (below) views.

lum (see Howes, 1988, figs 2 & 3). The ligamentous connection between the interoperculum and hyomandibula/preoperculum is considered to be a derived condition for gadoid fishes; its taxonomic and phylogenetic implications are discussed more fully in Howes (1988). The functional aspects of this linkage are discussed below, p. 54.

Cranial muscles

The *adductor mandibulae* and muscles of the suspensorium in macrouroids

The muscles of the jaws and suspensorium in macrourids have been described for some taxa by Dietz, 1921, McLellan , 1977 and Casinos, 1978; 1981. Dietz gave a brief description of the muscles in *Coleorinchus coelorinchus*; McLellan referred to, and illustrated the adductor muscles of *Bathygadus* and *Coelorinchus,* and Casinos those of *Coryphaenoides* and *Trachyrincus*. The two

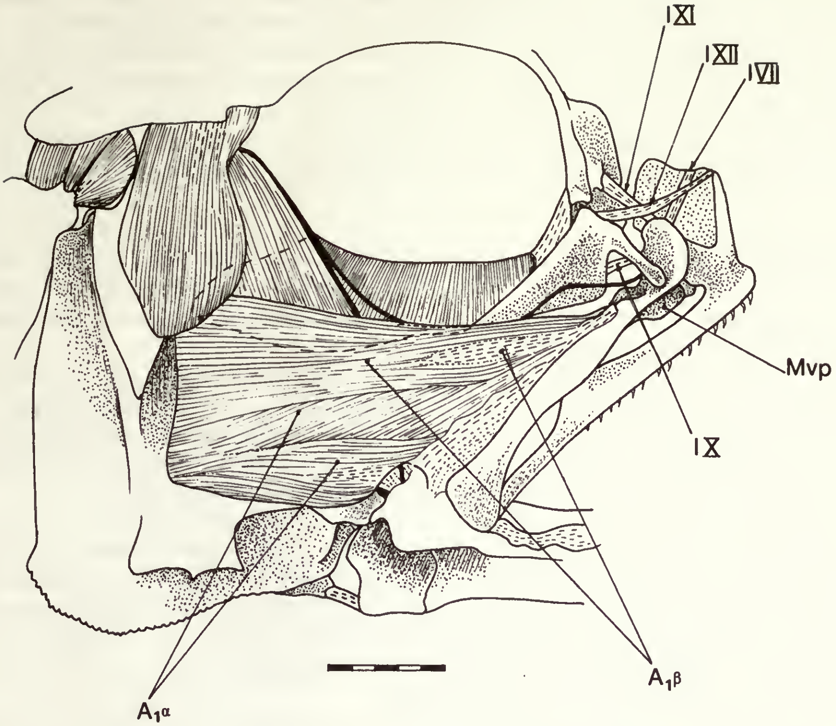

Fig. 3 *Ventrifossa occidentalis*; cranial muscles and ligaments in lateral view.

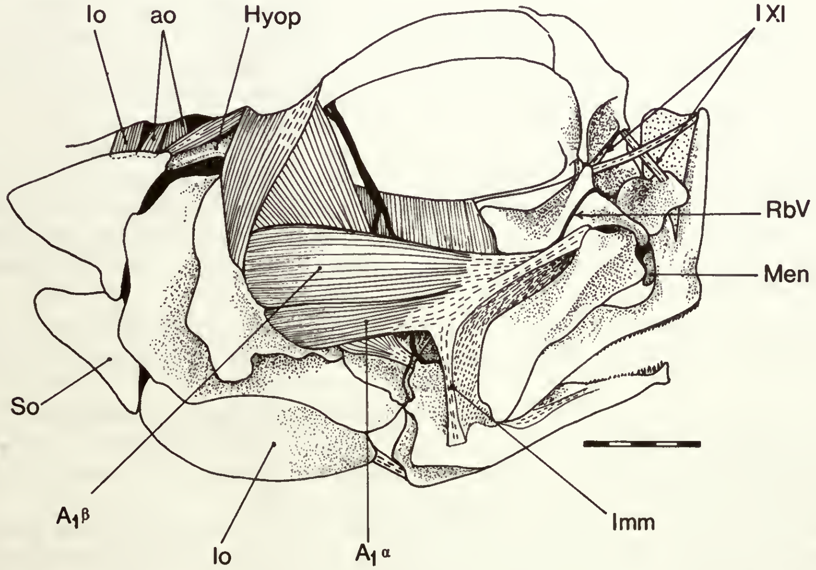

Fig. 4 *Cetonurus globiceps*; cranial muscles and ligaments in lateral view.

latter authors were concerned with describing the musculature in a functional context, although Casinos (1978) made some observations regarding the homology and evolution of certain adductor muscles. The taxonomic range of these authors' works is limited and the applicability of their functional conclusions to macrouroids in general requires a reappraisal in the light of morphological variations of which they were unaware.

NB. In the following descriptions the dorsal muscle of the adductor element (*levator maxillaris superioris* of authors) is referred to as A1β; its homology is discussed later, p. 34.

MACROURINAE

Type 1 morphology: two subgroups are recognised, (*a*) *Coryphaenoides, Abyssicola, Nezumia, Coelorinchus, Lionurus* (synonymised with *Coryphaenoides* by Iwamoto & Stein, 1973); *Nematonurus, Chalinura*; (*b*) *Macrourus, Trachonurus.*

The overall morphology of the adductor musculature is similar in the two subgroups, the only difference being the presence of an additional adductor element, A1γ, in subgroup (*a*).

In all the taxa included in the Type I group the mouth is inferior or subinferior and the jaws relatively short; the premaxillary ascending process is at least 80% the length of the dentigerous ramus; the maxilla is a deep, stout bone with a markedly convex dorsal border.

The outer adductor muscle is thin but relatively deep and divisible into upper and lower parts which are either entirely separated (e.g. *Coryphaenoides*, Fig. 1), or partially so (e.g. *Coelorinchus*, Fig. 2). The lower part (A1α) originates from the preopercular limb, and in *Coryphaenoides* from a prominent lateral flange of that bone (Fig. 1). The muscle inserts tendinously along the lower part of the maxillo-mandibular ligament. The upper part of the adductor (A1β) originates from the preopercular limb and inserts *via* a stout tendon on to a ventromedial process of the maxilla; it is not joined to the maxillo-mandibular ligament.

Running dorsomedially to A1β is a long spindle-shaped muscle here designated A1γ (Fig. 3); see below. The fibrous part of the muscle originates from a long tendon which in turn stems from the fascia of A1β. Insertion is *via* a cord-like tendon on the same medial process of the maxilla as A1β. In *Lionurus*, there is a marked difference in the relative proportion of the fibrous part to the posterior tendinous part of the muscle between small and large-sized specimens. In a specimen of 150 mm TL, the muscle is 50% tendinous and 50% musculose, whereas in a specimen of 225 mm TL, 75% of the muscle is fibrous. In *Abyssicola macrochir*, muscle A1γ is a larger and deeper element than in any other taxon examined. Also, unlike other taxa of this group the muscle originates from a broad tendinous sheet stemming from the rim of the hyomandibula.

Muscle A2 is a deep, broad element whose medial fibres originate from the frontal, and those more lateral in position from the prootic and hyomandibula. A2 has a complex insertion in the lower jaw. Its posteromedial fibres insert into an aponeurosis which bifurcates into a vertical and a horizontal tendon. The vertical tendon inserts onto the coronomeckelian bone and continues to the dorsomedial surface of the narrow retroarticular, while the horizontal tendon runs forward into the mandibular cavity. The majority of fibres of A2 insert on the horizontal tendon, from which also originate those of the *mandibularis* section of the adductor Aω (Fig. 1). Muscle Aω lies mostly outside the mentomeckelian cavity, but with a small bundle of lateral fibres running forward into it.

The *levator arcus palatini* (Figs 1 & 2) is a long, pyramidical muscle running between the sphenotic and the lateral face of the hyomandibula; its outermost fibres insert on the edge of the preopercular limb.

The *dilatator operculi* (Figs 1 & 2) originates from the lateral hyomandibular fossa and inserts on the rim of the opercular facet. The *adductor* and *levator opercularis* muscles extend from the lateral border of the pterotic, the *adductor* inserting on the opercular process of the hyomandibula and the *levator* on the anteromedial face of the operculum (Figs 1 & 2).

The *adductor arcus palatini* occupies the floor of the orbit, its anterior fibres inserting on the broad concave surface of the palatine (Figs 1 & 2). Posteriorly, the muscle runs between the parasphenoid and the lateral faces of the entopterygoid and metapterygoid and the medial face of the hyomandibula.

Type II morphology. Macrourinae (part): *Ventrifossa, Cetonurus, Echinomacrurus, Malacocephalus, Hymenocephalus, Odontomacrurus, Sphagemacrurus, Cynomacrurus, Mataeocephalus.*

Taxa of this group have a terminal or subterminal mouth, with the exception of *Echinomacrurus* in which it is inferior. The ratio of premaxillary ascending process to dentigerous ramus length varies from 30–33% in *Odontomacrurus* and *Chalinura* to 50% in *Ventrifossa*. An opposite extreme is *Mataeocephalus* where the premaxillary ramus is 50% of the length of the ascending process (cf. Macrouroidinae, p. 15); in *Echinomacrurus* and *Cetonurus*, the ramus and ascending process are of almost equal length.

The characteristic myological feature of this morphotype is that A1 is a single, or incompletely divided, deep element. *Ventrifossa occidentalis* is taken to illustrate the morphotype, representative of the majority of taxa (Fig. 3). *Echinomacrurus* and *Cetonurus* which differ somewhat in detail from *Ventrifossa* are considered below.

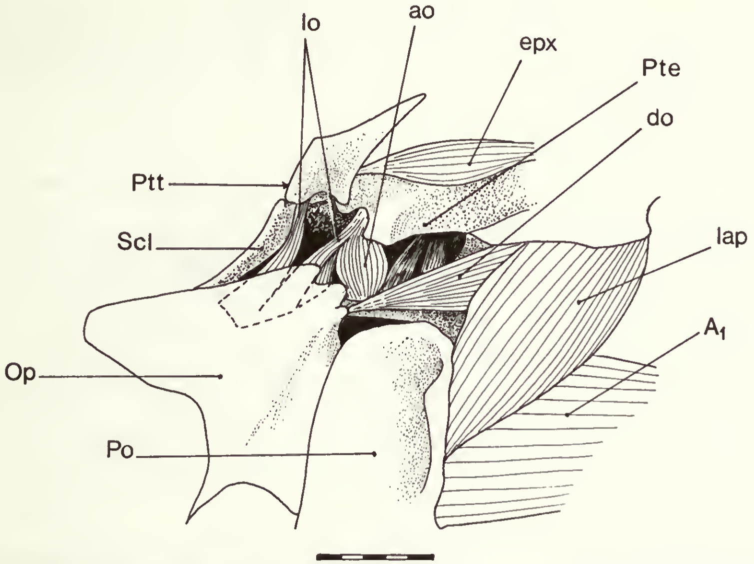

Fig. 5 *Cynomacrurus piriei*; *levator arcus palatini* and opercular muscles in lateral view.

Muscle A1 originates posterodorsally from the upper part of the preopercular limb and ventrally from the preoperculum and quadrate (Fig. 3). The dorsal border of the muscle is almost horizontal, there being a slight concavity and tendinous area below the orbit. Dorsal fibres of the muscle insert on the inner aspect of the maxilla, while the remainder of the muscle, separated from the upper part by an internal aponeurosis, inserts into the anterior third of the maxillo-mandibular ligament. Along the centre of the muscle is an aponeurosis which is marked laterally by a change in muscle fibre direction—from almost horizontal (dorsally) to oblique (ventrally). The position of the aponeurosis is marked in taxa belonging to morphotype I by a complete or partial division of the muscle. In this respect *Cetonurus* resembles the latter taxa (Fig. 4).

Muscle A2 is a deep element originating from a cavity formed between the prootic and frontal, with fibres stemming from both bones. In *Cynomacrurus* and *Odontomacrurus* the anterior muscle fibres are vertically aligned or posteroventrally angled, in contrast to the more usual anteroventral angle present in *Ventrifossa* (Fig. 3). The insertion of muscle A2 in the lower jaw is *via* a cord-like tendon carrying outer fibres to the coronomeckelian bone and into a broad aponeurosis from which originates muscle Aω. The muscle is short, barely extending halfway along the mandible; only its dorsal fibres enter the mentomeckelian cavity.

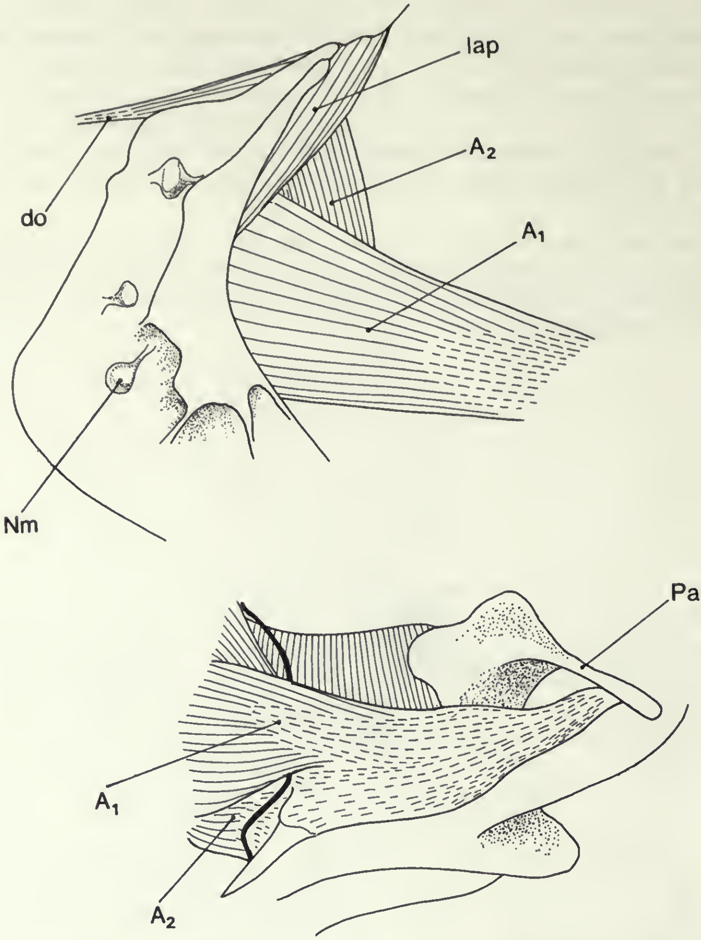

Fig. 6 Macrouroidinae; above, *Squalogadus modificatus*, preoperculum and associated muscles; below, *Macrouroides inflaticeps*, anterior of adductor musculature.

The *levator arcus palatini* is a large muscle in all Type II genera, extending from the sphenotic and pterotic to the lateral face of the hyomandibula, its anteroventral portion covering the posterodorsal margin of A1. In *Cynomacrurus* the *levator* is angled forward to a greater degree than in the other included taxa (Fig. 5).

The *dilatator, adductor* and *levator operculares* muscles are all well-developed. The *dilatator operculi* originates from a lateral hyomandibular fossa and the *adductor* from the ventral surface of the pterotic. Some fibres of the *adductor operculi* insert with those of the *dilatator* on the rim of the opercular condyle, but the majority insert on the opercular process of the hyomandibula. In *Cetonurus* the separate insertions of the muscle are further marked by the complete division of its body. The *levator operculi* is a long, deep muscle originating from the ventral surface of the pterotic and inserting along the anteromedial border of the operculum. In *Cynomacrurus* the *adductor operculi* inserts entirely on the opercular process of the hyomandibula and the *levator operculi* is divided. The anterior segment of the *levator* shares a common origin with the *adductor operculi*, but the posterior segment originates from the posttemporal (Fig. 5); both segments insert together on the anteromedial face of the operculum. With respect to its posttemporal origin, the *levator* of *Cynomacrurus* is similar to that of the gadoid *Lota* (see p. 32 and Howes, 1988).

The *adductor arcus palatini* extends the length of the parasphenoid and anteriorly inserts on the palatine; posteriorly it inserts on the ento- and metapterygoids and the medial face of the hyomandibula. In *Cetonurus* the muscle extends only halfway along the length of the parasphenoid (Fig. 4).

MACROUROIDINAE

Two monotypic genera are included in this subfamily, *Macrouroides* and *Squalogadus*. Of the former, only a single, poorly preserved specimen of *Macrouroides inflaticeps* was available for examination. The specimen has a damaged and partially disarticulated skull and it has been impossible to ascertain precisely the configuration and insertions of the adductor muscles. Likewise, only a single specimen of *Squalogadus modificatus* is available for examination and only a partial dissection of the posterior region of the cheek musculature has been possible (Fig. 6).

Muscle A1 is a single element originating from the preopercular limb and inserting on to the upper part of the maxilla *via* the maxillo-mandibular ligament.

Muscle A2 is a thick, crescentic muscle stemming from the frontal and prootic; its insertions in the lower jaw and the extent of muscle Aω have not been ascertained in either taxon.

Table 1 Grouping of Macrourinae based on jaw and ventral gill-arch muscle morphotypes (see text, p. 58), compared with Okamura's (1970*b*) groupings

	Jaw muscles		Gill-arch muscles	Okamura's groups
Type 1*a*	*Abyssicola*	(*a*)	*Abyssicola*	*Abyssicola*
	Coryphaenoides		*Coryphaenoides*	*Coelorinchus*
	Nezumia		*Coelorinchus*	*Macrourus*
	Lionurus		*Lionurus*	
	Nematonurus		*Nematonurus*	
	Chalinura		*Chalinura*	
			Macrourus	
Type 1*b*	*Macrourus*		*Trachonurus*	
	Trachonurus		*Malacocephalus*	
			Mataeocephalus	
			Cetonurus	
			Echinomacrurus	
Type II	*Ventrifossa*	(*b*)	*Ventrifossa*	*Ventrifossa*
	Malacocephalus		*Hymenocephalus*	*Malacocephalus*
	Hymenocephalus		*Nezumia*	
	Odontomacrurus		*Odontomacrurus**	*Odontomacrurus*
	Cynomacrurus		*Cynomacrurus**	*Cynomacrurus*
	Mataeocephalus			
	Macrosmia			
	Cetonurus			*Cetonurus*
	Echinomacrurus			*Echinomacrurus*
	Sphagemacrurus			*Sphagemacrurus*

NB. * these two genera lack a palatine-lateral ethmoid ligament. According to Iwamato & Stein (1973), *Lionurus*, *Nematonurus* and *Chalinura* should be treated as subgenera of *Coryphaenoides*.

The following macrourine genera have not been examined, *Astenomacrurus*, *Cetonurichthys*, *Haplomacrourus*, *Lepidorynchus*, *Paracetonurus*, *Parakumba*, *Pseudocetonurus*, *Pseudonezumia*.

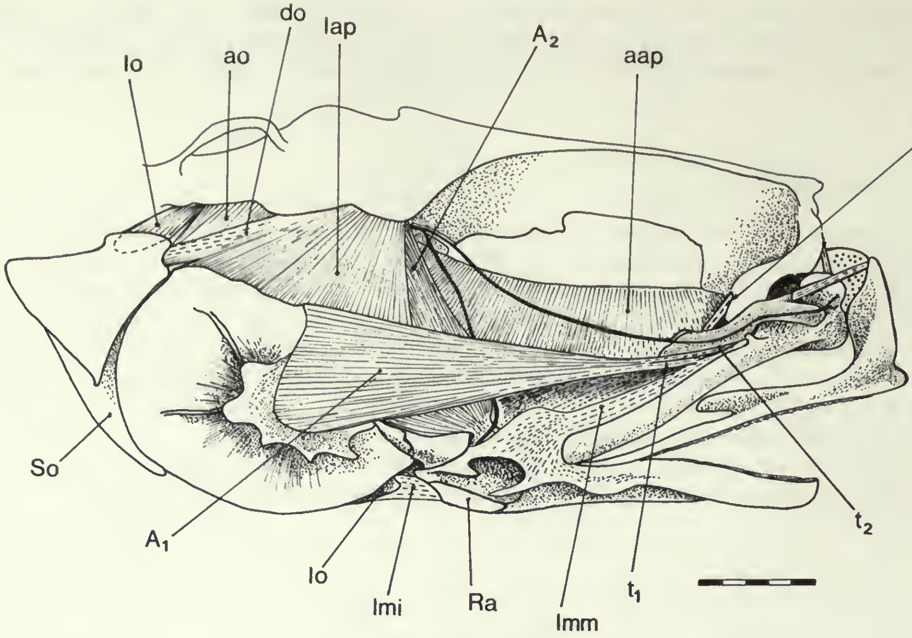

Fig. 7 Trachyrincidae: *Trachyrincus trachyrincus*; cranial muscles in lateral view.

The *levator arcus palatini* and *operculi* muscles are missing from the specimen of *Macrouroides*, but in the *Squalogadus* specimen there is a small *levator arcus palatini*, lying posterolaterally to the *adductor mandibulae* complex (Fig. 6).

The *adductor arcus palatini* is a thick element flooring the orbital cavity, inserting anteriorly on the palatine and posteriorly on the lateral surface of the ento- and metapterygoids.

Comparisons with gadoids

The presence of a dorsal section of the *adductor mandibulae* originating from the palatoquadrate was considered by Rosen & Patterson (1969: 361 *et seq.*) to be a specialisation of paracanthopterygian fishes. Fraser (1972) commented that a muscle of this type had developed in several acanthopterygian groups and could not be used as a character indicating phyletic relationships. He also pointed out that the number of taxa examined for this character by Rosen and Patterson was too few to make generalisations as to its occurrence and homology. Marshall & Cohen (1973) in referring to the so-called *levator maxillaris superioris* muscle note that '. . . character has received little comment; its distribution and taxonomic significance are at present in need of fuller survey'.

There has been much confusion concerning the identity of the dorsal adductor muscle in paracanthopterygians. Rosen (1962) and Rosen & Patterson (1969: 341 *et seq.*) referred to the element as a *levator maxillaris superioris* (*i.e.* the homologue of that muscle in the halecomorph *Amia*; see Allis, 1897). Previous authors, *viz*. Holmquist (1911) and Dietz (1921) had referred respectively to the muscle as A4 and A1β. Later, Rosen (1973: 417) reformulated his ideas and, following Dietz, referred to the muscle as A1β, a view supported by Winterbottom (1974*a*) and most subsequent authors. Casinos (1978: 443) continued to use the term *levator maxillaris superioris* '. . . because of functional reasons'.

Because the muscle in question lies lateral to the mandibular branch of the trigeminal (V) nerve, I concur with Winterbottom (1974*a*) in recognising it as part of muscle A1. Allis (1897: 581–2) comments that the '. . . course and position of the inferior maxillary nerve . . . seems to lie always between A1 and A2 . . .'; see similar remarks of Freihofer (1978: 17) and Howes (1985: 275).

In all gadiform fishes I have examined, apart from some macrouroids noted above and the Trachyrincidae (see below), a dorsal division of muscle A1 is present. The various conditions of this, and other cranial muscles are as follows:

TRACHYRINCIDAE

(Figs 7 & 8)

The family (formerly recognised as a macrouroid subfamily) contains two genera *Trachyrincus* and *Idiolophorynchus*. Species are characterised by their unique adductor muscle arrangement (described below), interopercular-preopercular-opercular ligamentous arrangement, nasal morphology, caudal skeleton (see Howes, 1988) and other features such as dorsal scutes (given in diagnosis for subfamily by Marshall, 1973). In trachyrincids the jaws are long, the length of the premaxillary ascending process being 50% of the ramus.

Muscle A1 is a single, narrowly triangular element which extends from the anterolateral face of the preoperculum to insert *via* a double tendon on the maxilla. The upper tendon (t2, Fig. 7) passes medially to insert close to the maxillary head while the lower (t1, Fig. 7) joins the maxillo-mandibular ligament to insert on the lateral face of a maxillary dorsal process. Casinos (1978: 443) is incorrect in stating that a maxillo-mandibular ligament is absent in *Trachyrincus*. A ventral tendon runs from the aponeurosis to the coronomeckelian bone; muscle Aω extends from the anterior part of the aponeurosis, the majority of fibres lying medial (outside) the mentomeckelian cavity.

The *levator arcus palatini* in contrast to that of macrouroid taxa, is extended posteriorly and its anteroventral part is covered by the *adductor mandibulae*. The muscle originates dorsally from the sphenotic and pterotic, and medially from the hyomandibula; insertion is across the extensive dorsal face of the preoperculum.

The *dilatator operculi* originates from a common aponeurosis with the *levator arcus palatini* and has a strong tendinous insertion on the rim of the opercular condyle. The *adductor operculi* is a long muscle originating from the ventral surface of the pterotic and inserting for much of its length on the opercular process of the hyomandibula. Only the posterior fibres insert on the operculum, just medial to the insertion of the dilatator muscle. The *levator operculi* is a thin, narrow element running postero-laterally and inserting on the medial face of the small operculum.

The *adductor arcus palatini*, although extending the length of the parasphenoid is weakly developed anteriorly (of single fibre thickness) and does not insert on the palatine.

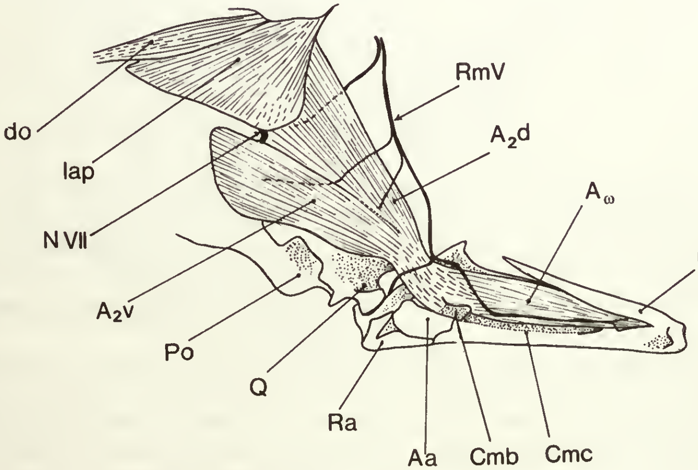

Fig. 8 *Trachyrincus trachyrincus*; medial view of inner adductor muscle and lower jaw.

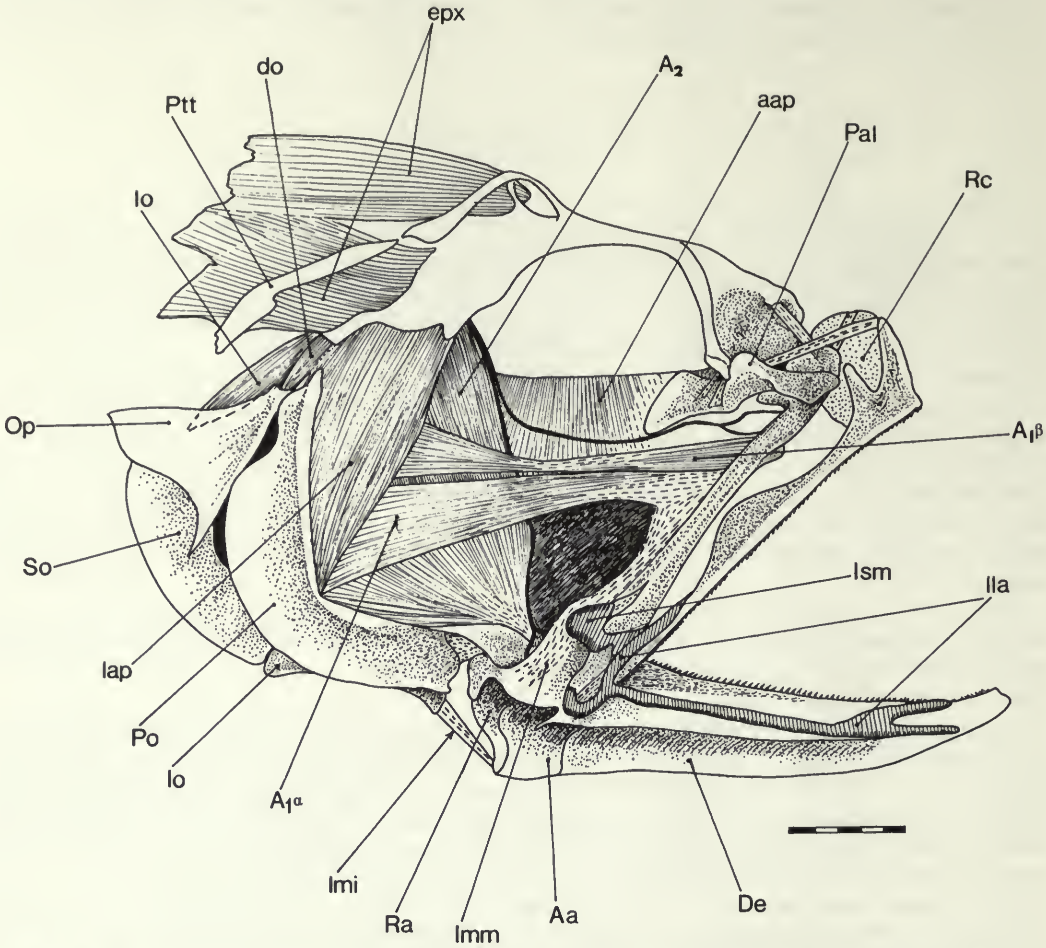

Fig. 9 Bathygadidae: *Bathygadus melanobranchus*; cranial muscles and ligaments in lateral view.

BATHYGADIDAE

(Figs 9 & 10)

Formerly recognised as a subfamily of macrouroids, Howes (1988) referred the 'bathygadine' genera *Bathygadus* and *Gadomus* to the Gadoidei as a clade, here recognised as a family. A complete taxonomic diagnosis is in preparation but it can be stated here that the family is distinguished from other gadoid families by its lack of a caudal skeleton, derived RLA pectoral nerve pattern, reduced gill-filaments, reticulate scale pattern and myological synapomorphies detailed here.

Bathygadus and *Gadomus* have a terminal mouth with a wide gape, the jaws are long and slender. The outer adductor muscle is a thin, shallow sheet of fibres originating from the preoperculum and posterior margin of the hyomandibula. In most *Bathygadus* species it is clearly divided into ventral (A1α) and dorsal (A1β) parts. However, in *B. favosus*, the two muscles can only be distinguished by their separate tendinous insertions on the maxilla. In the species where the A1α and A1β parts remain separated, A1α joins a broad aponeurosis with the maxillo-mandibular ligament halfway along the length of the maxilla. Muscle A1β originates from the medial fascia of the *levator arcus palatini* muscle and is divided into anterior and posterior segments, the division being brought about by the muscle's tendinous constriction below the orbit. The anterior segment of A1β inserts on the medial face of the maxillary process.

In *Gadomus* muscle A1α has a definite insertion on the outer aspect of the anterior part of the maxilla, and the maxillo-mandibular ligament is longer and narrower than in *Bathygadus*.

Muscle A2 is a large element originating from the hyomandibula, prootic and frontal and inserting on the lower jaw. Insertion is partly *via* a vertical tendon stretching down the medial face of the anguloarticular, and partly on a tendon inserting on the coronomeckelian bone and medial face of the anguloarticular. From these tendinous insertions stem the fibres of the mandibularis part of the adductor muscle (Aω). The anterior half of Aω enters a long mentomeckelian cavity.

The *levator arcus palatini* is a large, deep element which inserts halfway down the preopercular limb and entirely covers the origin of muscle A1. The lateral posterodorsal fibres of the *levator* are inseparable from those of the *dilatator operculi*.

The *adductor arcus palatini* extends nearly the entire length of the parasphenoid, but anteriorly it is feebly developed, with widely spaced, tendinous bands of fibres; posteriorly the muscle inserts on the lateral face of the metapterygoid and the medial face of the hyomandibula.

As noted above, the anterior fibres of the *dilatator operculi* intermesh with the dorsoposterior fibres of the *levator arcus palatini*; those respective groups of fibres of both muscles originate from the hyomandibula, inserting together with the *adductor operculi* on the opercular condyle. The *levator operculi* is a well-developed element stemming from the pterotic and inserting along the posteromedial border of the operculum.

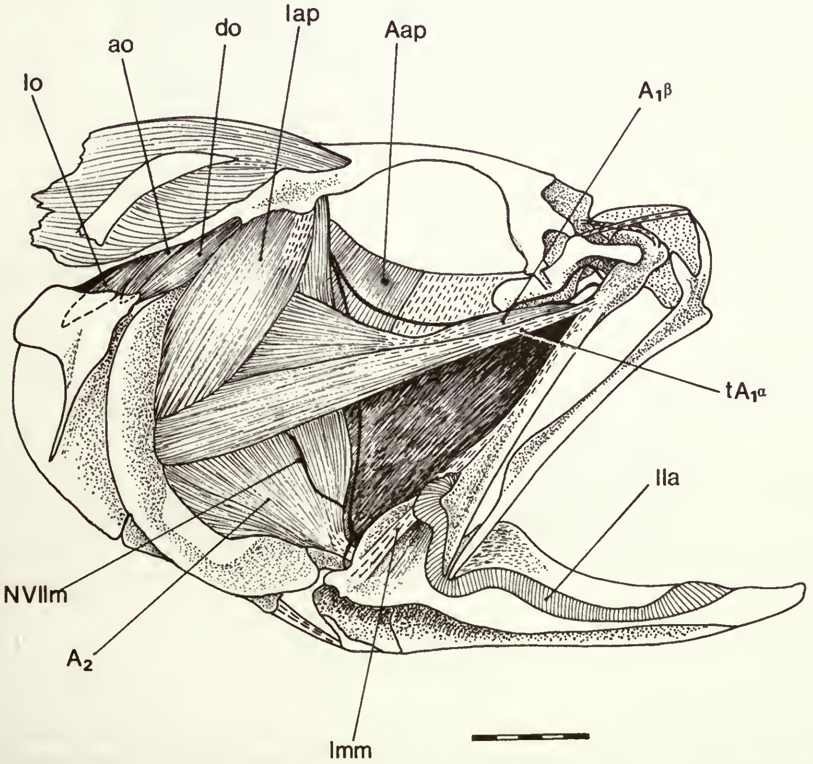

Fig. 10 Bathygadidae: *Gadomus longifilis*; cranial muscles and ligaments in lateral view.

MORIDAE

(Fig. 11)

In their overall morphology, the cranial muscles of morids are most similar to those of the Bathygadidae and *Gadomus* (Melanonidae). In *Halargyreus* (Fig. 11), *Pseudophycis* and *Antimora*, muscles A1α and A1β originate laterally to A2; A1β is tendinously constricted below the orbit, its anterior expansion joining the insertion tendon of A1α.

The *levator arcus palatini* is large, its ventral tip extending to a point halfway down the preopercular limb (cf. *Bathygadus*). The *adductor arcus palatini* is divided into posterior and anterior parts, the latter inserting on the entopterygoid and not the palatine as in most other gadoids.

In *Lepidion* (Fig. 10), muscles A1α and A1β are incompletely separated; both segments originate from a single body. The dorsal (A1β) and ventral (A1α) bundles insert on separate tendons beneath the orbit, which then join into a single muscle body lateral to the palatine before separating into their respective medial and lateral maxillary insertions.

The *levator arcus palatini* covers the upper part of A2, dorsally it joins the *dilatator operculi* along an aponeurosis. The *adductor arcus palatini* is feebly developed in its central portion; the anterior fibres insert on the palatine.

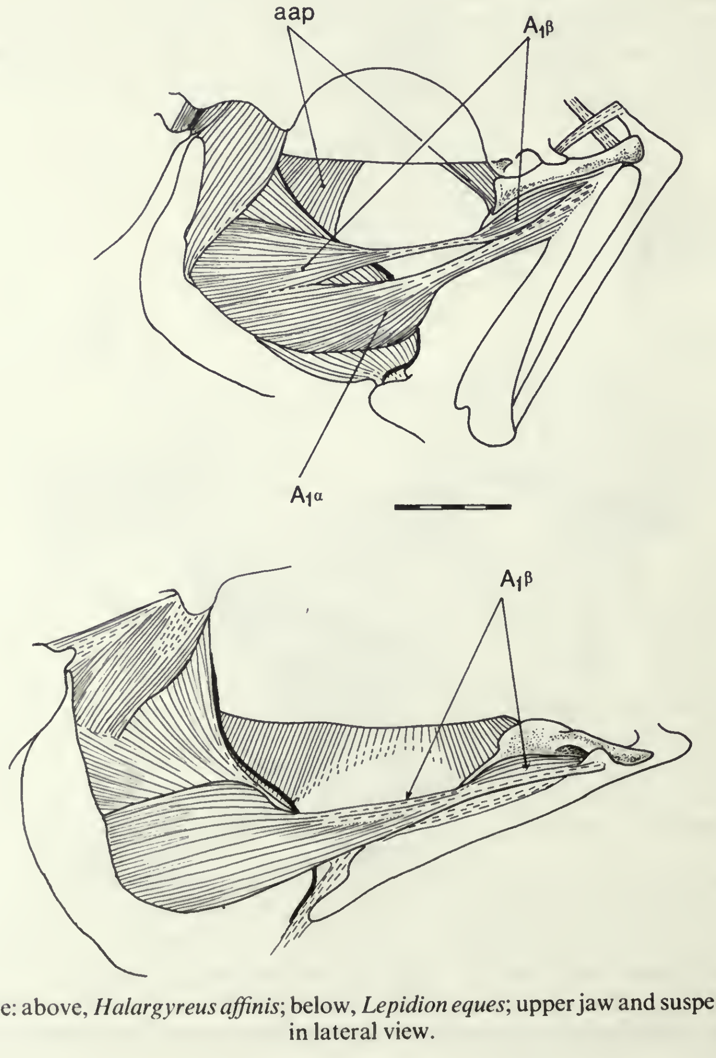

Fig. 11 Moridae: above, *Halargyreus affinis*; below, *Lepidion eques*; upper jaw and suspensorial muscles in lateral view.

MELANONIDAE

(Fig. 12)

In *Melanonus* muscles A1α and A1β are inseparable at their origins which is from the fascia of muscle A2. The individual elements only become apparent above the jaw articulation. A1β is constricted into a tendon halfway along its length at the point where it is crossed transversely by a ligament running from the posterolateral edge of the palatine and the entopterygoid to the medial face of the second infraorbital. The anterior expansion of A1β inserts on the inner part of the maxillary head. The outer element, A1α, inserts *via* a separate tendon on to the outer face of the maxilla.

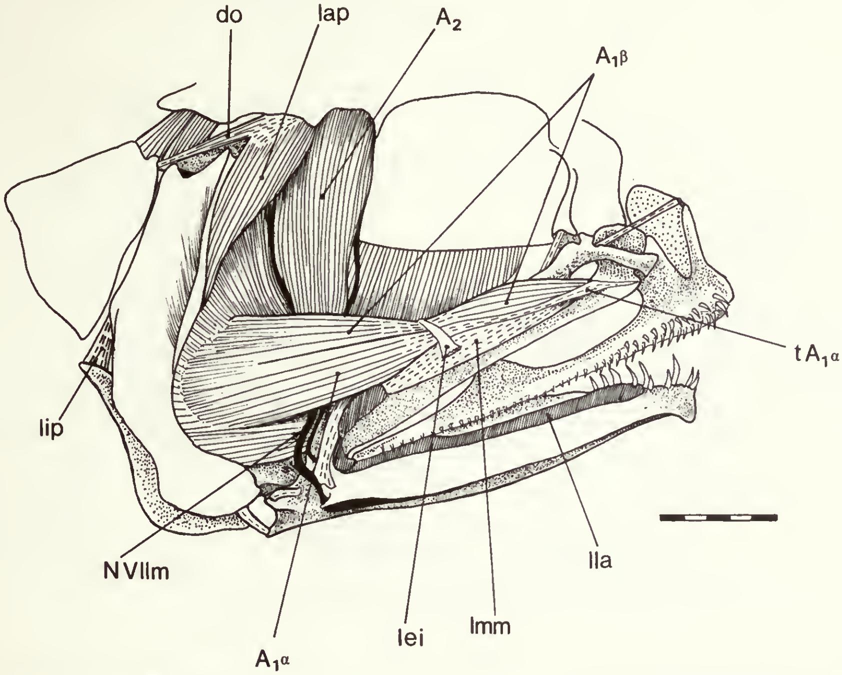

Fig. 12 Melanonidae: *Melanonus zugmayeri*; cranial muscles in lateral view (suboperculum removed).

Muscle A2 is strongly developed, its anterior fibres being almost vertical. The muscle is partially divided by a hypertrophied *ramus mandibularis internus facialis* of the hyomandibularis VII nerve trunk (Fig. 12).

The *levator arcus palatini* shares an aponeurotic origin with the *dilatator operculi*. The *adductor arcus palatini* is well-developed, flooring the orbital cavity, and inserting anteriorly on the palatine.

The *adductor* and *levator operculares* muscles share a common origin from the ventral surface of the pterotic shelf. The *adductor* inserts both on the dorsomedial rim of the opercular condyle and the opercular process of the hyomandibula; the *levator* inserts along the dorsomedial border of the operculum:

STEINDACHNERIIDAE

(Fig. 13)

In *Steindachneria* muscle A1 is large, originating from the lower half of the preopercular limb. Its fibres are angled anterodorsally, and dorsally the muscle is divided. The posterodorsal group of fibres insert on an aponeurosis from which stems a sausage-shaped segment of fibres running forward to meet, laterally, the maxillo-mandibular ligament. From this point, the muscle becomes separated from the ligament and almost immediately inserts on the medial aspect of the maxillary head. This part of the muscle is identified as A1β. The ventrolateral group of fibres inserts directly on the maxillo-mandibular ligament and is identified as A1α.

Muscle A2 originates from the prootic, the sphenotic process and the upper part of the hyomandibula, its anterior fibres running almost vertically.

Insertion in the lower jaw is *via* a strong vertical tendon to the coronomeckelian bone and a broad aponeurosis from which originates Aω. No fibres of A2 insert on the anguloarticular. Muscle Aω is lanceolate, the majority of its fibres filling the mentomeckelian cavity.

The *levator arcus palatini* is moderately developed, originating from the sphenotic process and pterotic, and inserting in a lateral cavity of the hyomandibula. The muscle lies lateral to A2, but its

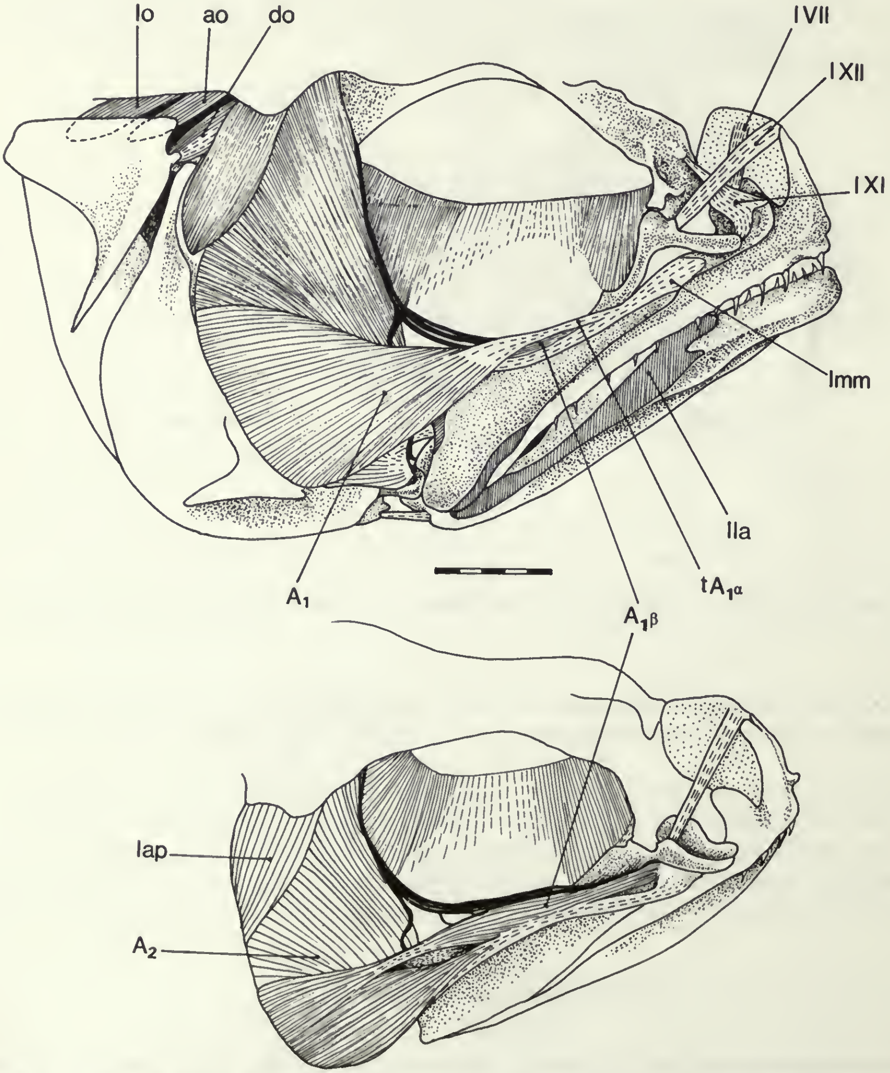

Fig. 13 Steindachneriidae: *Steindachneria argentea*: cranial muscles in lateral (above) and dorsolateral (below) views. NB. Not all the upper jaw ligaments are shown in the lower drawing.

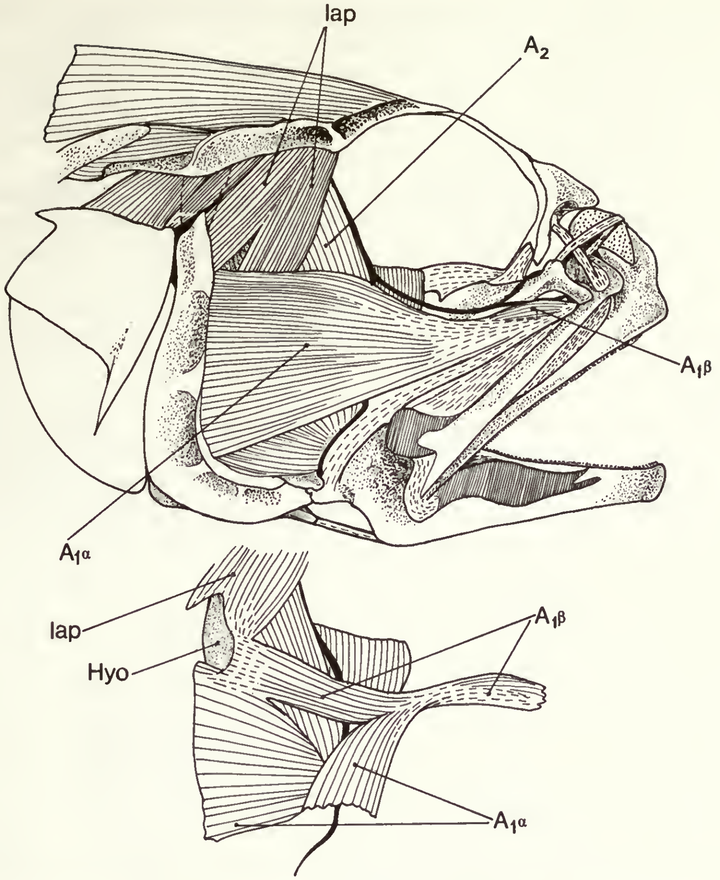

Fig. 14 Euclichthyidae: *Euclichthys polynemus*; above, cranial muscles in lateral view; below, posterior associations of muscle $A_1\beta$; $A_1\alpha$ reflected.

ventral tip does not reach as far as the origin of muscle A1. The *adductor arcus palatini* is well-developed posteriorly and anteriorly, where it inserts on the palatine but its central portion is reduced to a few widely spaced fibres which are well-separated from the dorsal margin of the pterygoid series.

Rosen & Patterson (1969, fig. 44a) depict the adductor musculature of *Steindachneria*. However, my observations are not completely in accord with theirs, since they show muscles A1α and A1β separated for their entire lengths, and a fully developed *adductor arcus palatini*.

The *dilatator, adductor* and *levator operculares* muscles are as described for *Melanonus*.

EUCLICHTHYIDIDAE

(Figs 14 & 15)

The *adductor mandibulae* muscle is a thick, deep element originating from the upright limb of the preoperculum; it comprises superficial, A1α, and medial, A1β, elements which have complex associations posteriorly.

Muscle A1β is, posteriorly, a shallow, band-like muscle, having its origins aponeurotically from, dorsally, the *levator arcus palatini*, and ventrally, the dorsomedial surface of A1α, thus partially dividing the latter. Anteriorly, muscle A1β becomes bulbous and transversely expanded, joining with A1α before separating from it to insert on the ventromedial surface of the maxillary head.

Muscle A1α is tendinous anteriorly and joins the maxillo-mandibular ligament together with A1β; its insertion is on the dorsolateral surface of the maxilla.

Muscle A2 is well-developed, originating from the sphenotic and the dorsolateral surface of the hyomandibula. In the lower jaw, A2 joins a band-like aponeurosis, from which originates Aω; a strong vertical tendon runs from the aponeurosis to the coronomeckelian bone. Muscle Aω is long and shallow, lying within the mentomeckelian cavity for most of its length.

The *levator arcus palatini* originates from the sphenotic and pterotic; it bifurcates ventrally, the anterior branch inserting on the hyomandibula and having an aponeurotic connection with muscle A1β (see above and Fig. 14); the posterior branch inserts on the preoperculum and overlaps the posterodorsal edge of A1α.

The *adductor arcus palatini* is confined to the posterior part of the parasphenoid; it inserts on the lateral faces of the ento- and metapterygoids. A unique feature of this muscle is that it is divided by a strong ligament running from the lateral ethmoid and palatine to the medial face of the hyomandibula (see p. 7 and Fig. 15).

The *dilatator operculi* is a spindle-shaped muscle extending from the pterotic to the opercular process. The *adductor operculi* runs almost laterally from the underside of a pterotic shelf to insert entirely on the opercular process of the hyomandibula; the *levator operculi* is an extensive muscle whose insertion extends along the entire dorsal border of the operculum.

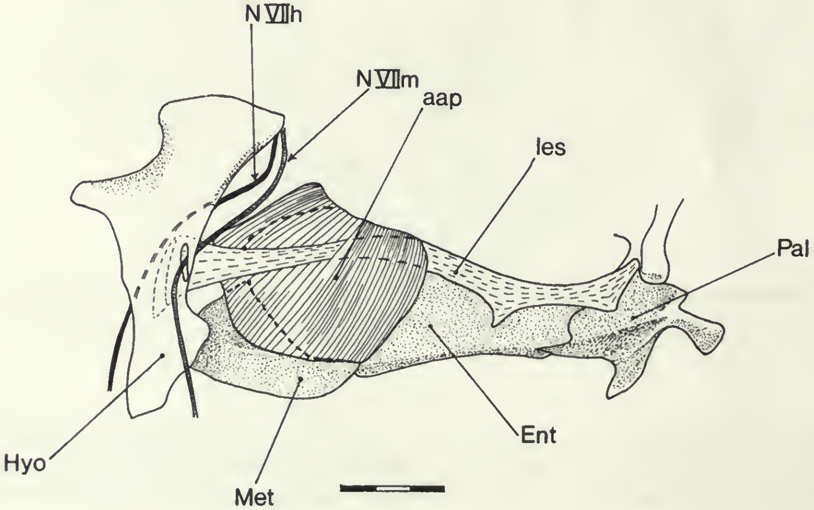

Fig. 15 Euclichthyidae: *Euclichthys polynemus*; *adductor arcus palatini* muscle and associated elements.

MERLUCCIIDAE

(Figs 16–18)

The following descriptions are based on three genera, *Merluccius, Macruronus* and *Lyconus*; *Lyconodes* has not been examined.

In *Merluccius* (Fig. 16) muscle A1α is a thin, shallow element, stretching from a tendinous origin on the preoperculum across the face of muscle A2 to insert *via* a cord-like tendon halfway along the maxilla where it joins the maxillo-mandibular ligament. Muscle A1β is a deep element having its origin from the meta- and entopterygoid and the palatine. It passes *medial* to the ramus mandibularis of the trigeminal nerve. The part of the muscle originating from the palatine is thick and bolster-like (Fig. 16). Insertion of A1β is across a wide area of the medial face of the maxilla.

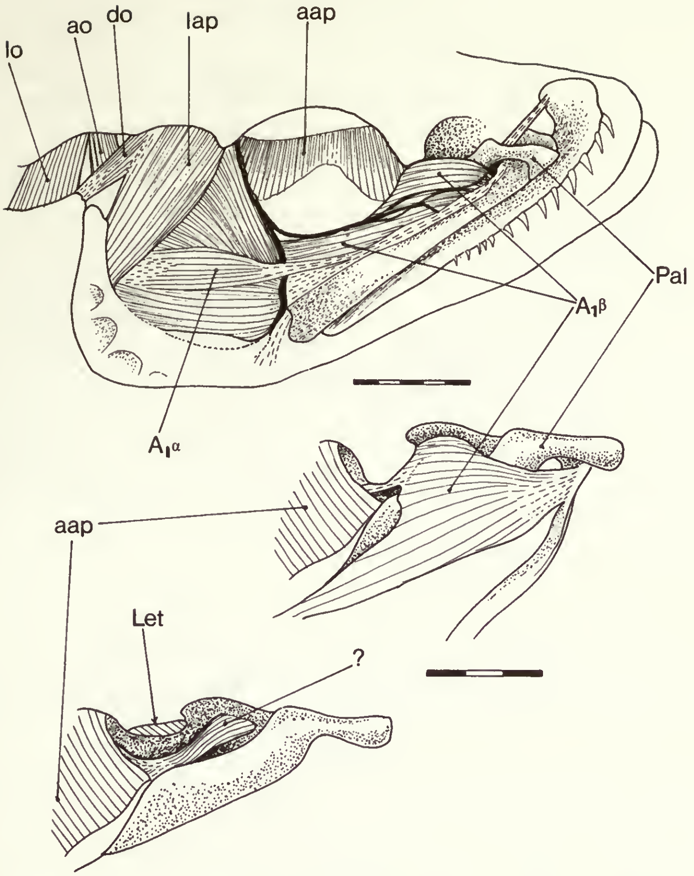

Fig. 16 Merlucciidae: *Merluccius merluccius*; cranial muscles in lateral view; above, entire; centre, palatine portion of muscle $A_1\beta$ (superficial); below, after removal of superficial muscle.

The *levator arcus palatini* is well-developed and lies lateral to the *adductor mandibulae* A2, but does not cover the origin of A1. The *adductor arcus palatini* floors the orbital cavity and inserts on the palatine. An unusual feature is the presence of a separate, small muscle running from the medial face of the palatine to the lateral face of the ethmoid bloc (Fig. 16). The muscle stems from the fascia of the *adductor arcus palatini*; in some specimens there are no muscle fibres, but only a narrow sheet of connective tissue.

The opercular muscles are well-differentiated, although the *dilatator operculi* shares an aponeurotic origin with the *levator arcus palatini*.

In *Macruronus* (Fig. 17), muscle A1α is a thick, bulky element almost covering the lateral face of A2. In the pinnate arrangement of its fibres, the muscle differs from that in the taxa so far considered. Insertion is on the dorsal maxillary process *via* a thick tendon. Muscle A1β originates from the outer rim of the quadrate, the entopterygoid and a lateral cavity of the palatine; insertion is one the medial face of the maxillary head. The position of the ramus mandibularis of the trigeminal nerve lies *posterior* to the origin of A1β.

Muscle A2 originates from the dorsomedial face and anterior rim of the hyomandibula and from the prootic. Insertion is *via* a lateral tendon to the coronomeckelian bone and a medial aponeurosis from which stems Aω; the latter lies entirely within the mentomeckelian cavity.

The *levator arcus palatini* is small, its ventral portion covered by A1α; insertion is into a small lateral hyomandibular cavity. The *adductor arcus palatini* is divided into anterior and posterior

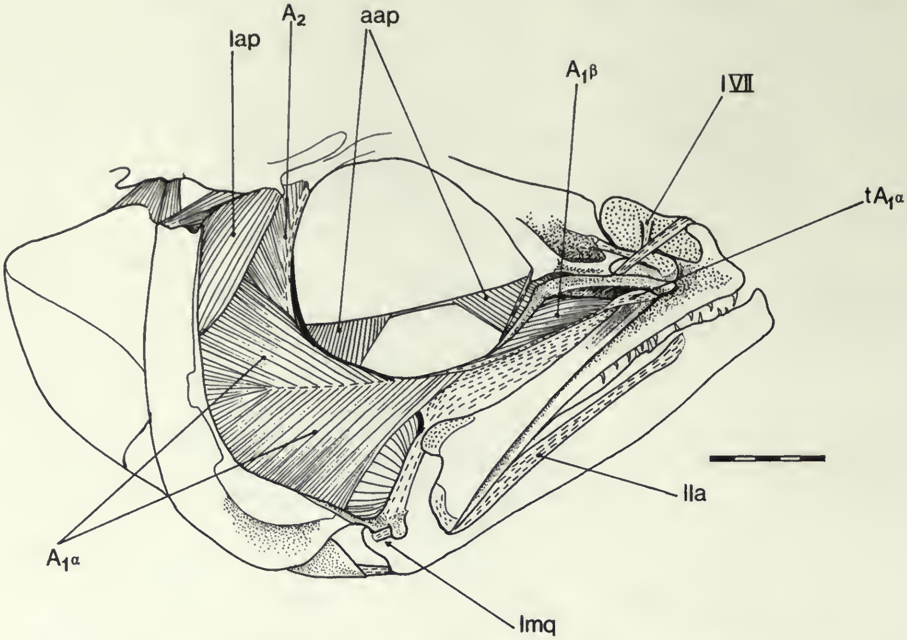

Fig. 17 Merlucciidae: *Macruronus magellanicus*; cranial muscles in lateral view.

portions, the former inserting into the medial cavity of the palatine. The *adductor operculi* inserts entirely on the opercular process of the hyomandibula.

In *Lyconus* (Fig. 18), muscle A1α is a narrowly triangular element whose area of origin extends from the central to the upper part of the preopercular limb. Fibre direction in the anteroventral section of the muscle is at almost 45° to that of the dorsal part. Insertion is *via* a long tendon on to the dorsal aspect of the maxilla. Muscle A1β resembles that of *Merluccius* in that it originates *medially* to the ramus mandibularis of the trigeminal nerve. The muscle's origins and insertions are complex; a posterior segment originates from the metapterygoid, a narrow, medial segment from the rim of the entopterygoid, and a long anterior segment from the concave lateral face of the palatine. The posterior segment runs into a long tendon, separate from that of the single tendon shared by the medial and anterior segments. The two tendons run forward to share a common insertion on the dorso-medial part of the maxillary head.

Muscle A2 is large, originating from the sphenotic and pterotic, its anterior fibres running almost vertically into the lower jaw.

The *levator arcus palatini* is a small unipinnate muscle originating from the sphenotic and pterotic; its insertion on the preopercular limb is above the origin of A1α. The *adductor arcus palatini* is well-developed, flooring the orbital cavity and, anteriorly, inserting on the palatine.

As only the type specimen of *Lyconus brachycolus* was available it has not been possible to make a sufficiently extensive dissection to ascertain the morphology of the other cranial muscles.

GADIDAE

(Fig. 18)

The following descriptions are based on three genera, *Gadus* and *Merlangius* (Fig. 18). These taxa differ from all those previously described in that muscle A1α is merely a thin, flat sheet of fibres stemming from the lateral body of A2 (as reported for *Microgadus* by Rosen, 1962). The separation of A1α from A2 is marked by the course of the ramus mandibularis of the trigeminal nerve, which passes medial to the segment; the separated fibres insert on the dorsal aspect of the maxilla *via* the maxillo-mandibular ligament.

Muscle A1β is a noticeably stout muscle and also differs from the previously described conditions in that it originates tendinously from the lateral face of the hyomandibula, passing forward between muscles A2 and A3 and lateral to the ramus mandibularis nerve (*cf.* medial in *Merluccius*). The muscle is deep and parallel fibred, running against, but not attaching to, the palatine; insertion is on the ventral medial edge of the maxillary head.

Holmquist (1911: 12–17) has adequately described and illustrated the origins and insertions of the deeper adductor and the suspensorial and opercular muscles in *Gadus*; I find little variation from this condition in other gadid genera examined. It should be noted here, however, that the *levator arcus palatini* inserts on a lateral shelf or slope of the hyomandibula. Although in *Gadus*, the *levator* is, for the most part, covered laterally by muscle A2, in *Merlangius*, A2 originates from below the hyomandibular shelf, thus leaving the *levator* exposed laterally and its outermost fibres lying in the same lateral plane as those of A2. The adductor muscles A2 and A3 are further discussed below (p. 41).

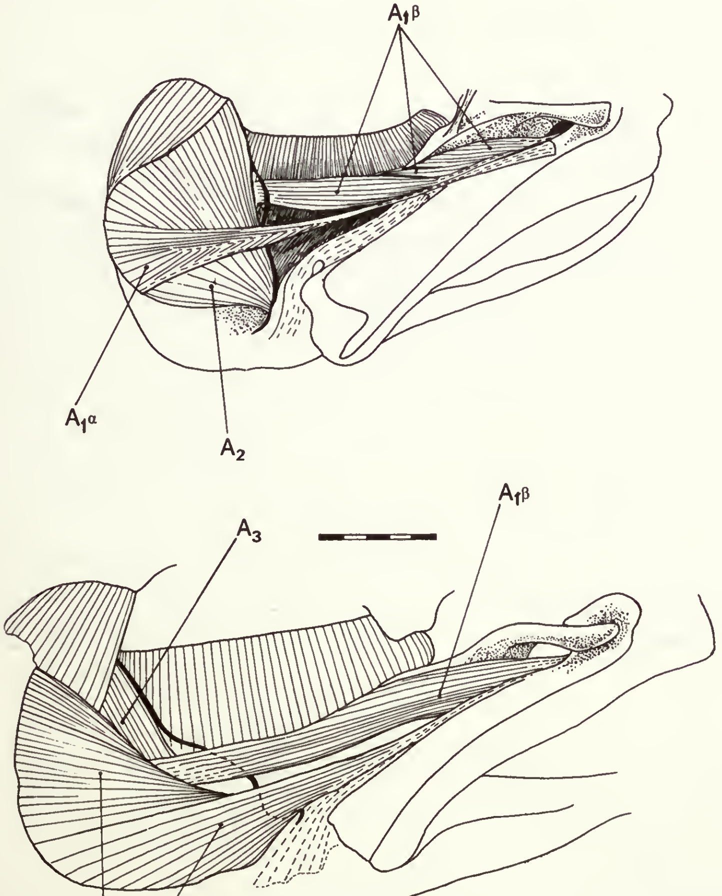

Fig. 18 Merlucciidae: above, *Lyconus brachycolus*, jaw and suspensorial muscles in dorsolateral view. Gadidae; below, *Merlangius merlangus*, jaw and suspensorial muscles in lateral view.

RANICEPITIDAE

(Fig. 20)

Howes (1987) recognised *Raniceps* as belonging to a distinct family on the basis of its sharing with certain phycids and the Muraenolepididae a tendinous attachment of the *rectus communis* muscle and the derived arrangement of the adductor musculature now described.

Muscle A1α is a small, spindle-shaped element, originating from the anterolateral face of A2. It runs alongside A1β, to which it is closely applied, and inserts *via* a long tendon on the dorsolateral face of the maxilla.

Muscle A1β is a broad, band-like element having its origin tendinously from the hyomandibula and passing between muscles A2 and A3; anteriorly, the muscle becomes bulbous and inserts on the ventral surface of the maxillary head.

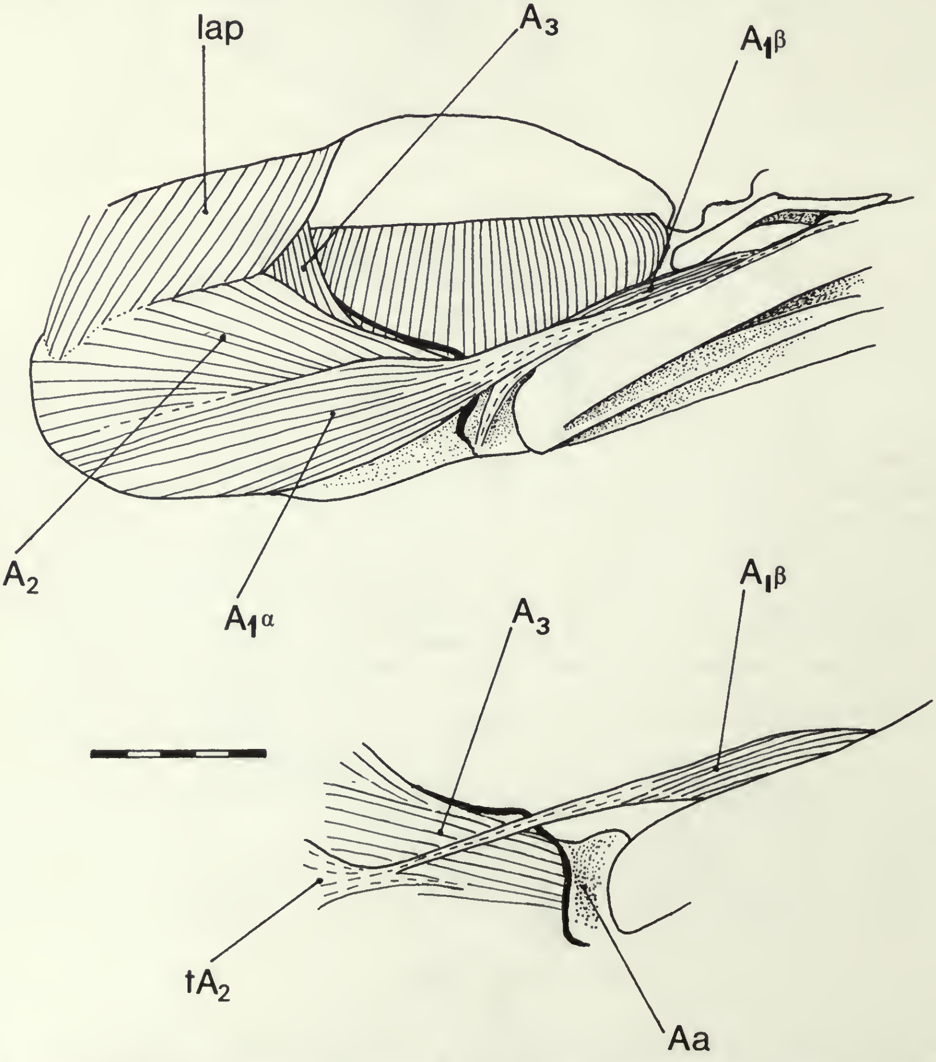

Fig. 19 Gadidae: *Molva molva*; jaw and suspensorial muscles in lateral view; above, entire; below, with outer adductor element removed to expose origin of $A_1\beta$. Mandibularis branch of trigeminal nerve in solid black.

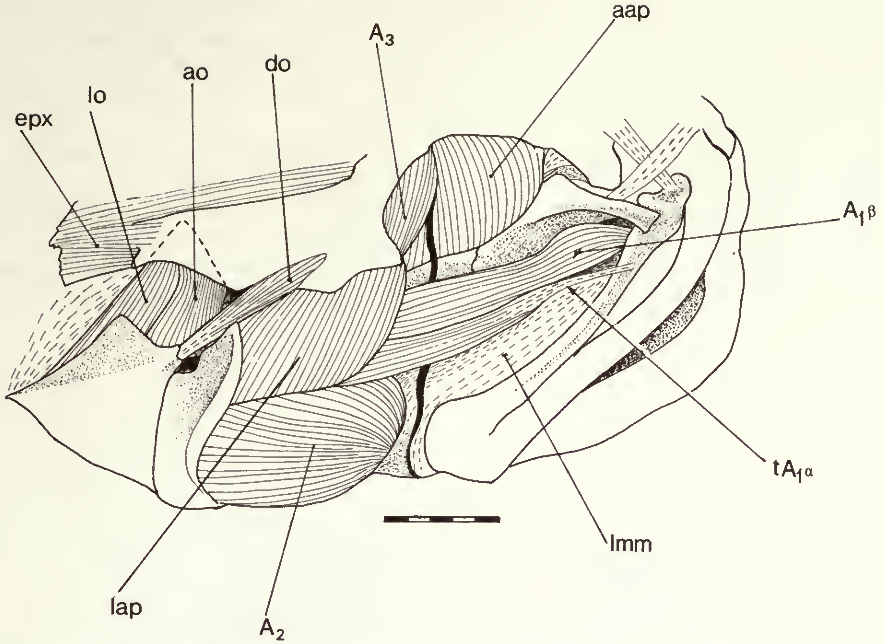

Fig. 20 Ranicepitidae: *Raniceps raninus*; cranial muscles in dorsolateral view.

Muscles A2 and A3 are thick, bulbous elements, the former originating from the preoperculum and hyomandibula, and the latter from the pterosphenoid and prootic. Both muscles join a common aponeurosis in the lower jaw from which Aω originates.

The *levator arcus palatini* is also a thick, bulbous element, stemming from the sphenotic and pterotic to insert on the hyomandibula and preoperculum. The lateral fibres of the *levator* meet those of adductor A2 along a near vertical raphe. The *adductor arcus palatini* is well-developed and floors the orbital cavity. The anterior fibres do not, however, insert on the palatine but remain within the confines of the entopterygoid.

The *dilatator operculi* is a narrow, ribbon-like muscle sharing a common origin with the posterior fibres of the *levator arcus palatini*; it inserts tendiously on the rim of the opercular facet. The *adductor* and *levator operculares* muscles share a common origin from beneath the pterotic and are separable only because of their insertions. The *adductor* inserts entirely on the opercular process of the hyomandibula; the *levator* along the dorso-medial surface of the operculum.

PHYCIDAE

(Fig. 21)

Urophycis is taken as the taxon representing this family but in at least one myological character both it and *Phycis* differ from other genera regarded as belonging to the family (see below).

In *Urophycis* (Fig. 21), fibres of muscle A1 share a common origin from the preopercular margin with those of A2. A1 separates from the body of A2 above the jaw articulation, its fibre direction varying from horizontal to 45°, and inserts *via* a long tendon on the anterodorsal process of the maxilla. Ventromedially, the insertion of A1α joins the maxillo-mandibular ligament.

Muscle A1β is a thick, cylindrical element originating, medially to A2, from the anterior rim of the hyomandibula. The muscle passes laterally to the ramus mandibularis of the trigeminal nerve, becoming slightly indented on its medial face below the orbit, and inserting musculously on to the ventral surface of the maxillary head.

Muscles A2 and A3 join a common aponeurosis medial to the anguloarticular (only a few fibres insert on the dorsal rim of the bone); the aponeurosis divides into medial and lateral tendons, the lateral one inserting on the coronomeckelian bone, while the medial branch forms the site of origin for muscle Aω. This muscle fills the mentomeckelian cavity with only a thin layer of fibres passing outside the cavity along the medial face of the dentary.

The *levator arcus palatini* is extensive and lies between A2 and A3; its dorsoposterior part can only be distinguished as a *dilatator operculi* by the insertion of those fibres on the rim of the opercular facet. The *adductor operculi* runs from the pterotic to the opercular process of the hyomandibula; the *levator operculi* inserts on the medial rim of the operculum. *Urophycis* is unusual in that a segment of epaxial muscle runs anteroventrally from the supracleithrum to insert on the medial face of the operculum. The posteroventral border of the muscle meets a part of the

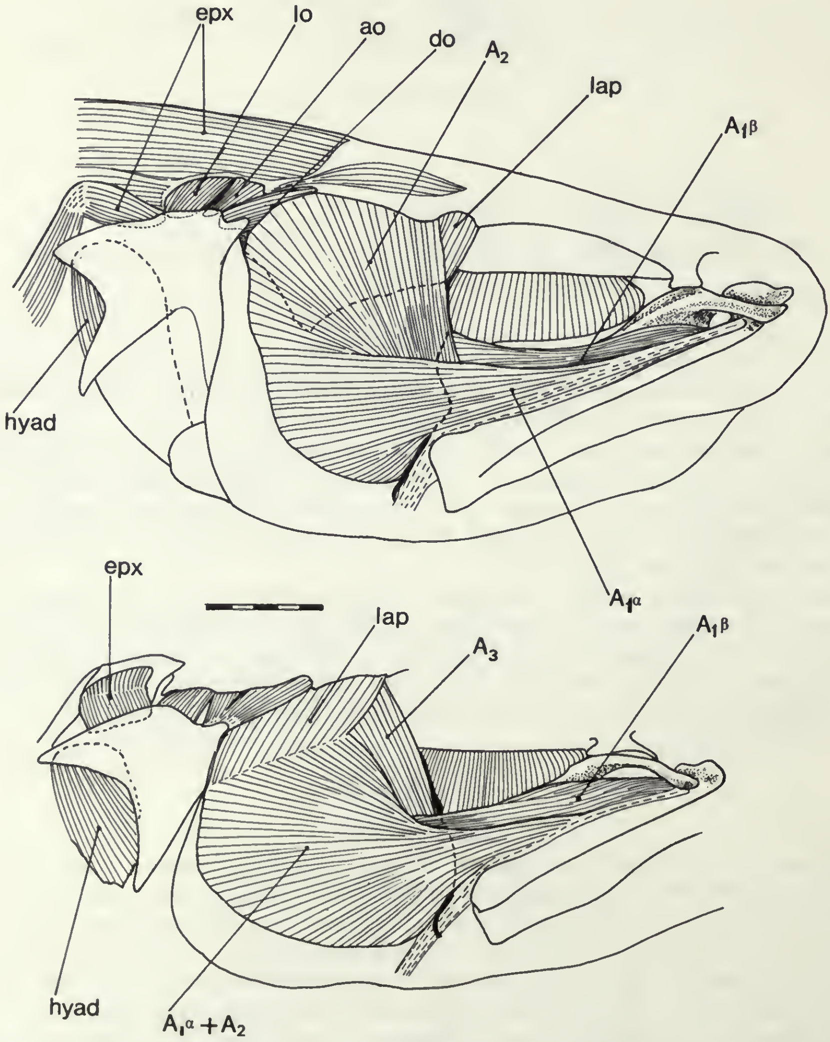

Fig. 21 Phycidae: above *Urophycis regia*; cranial muscles in lateral view. Lotidae: below, *Lota lota*; cranial muscles in lateral view; extent of *levator arcus palatini* and pathway of ramus mandibularis are indicated by dashed lines.

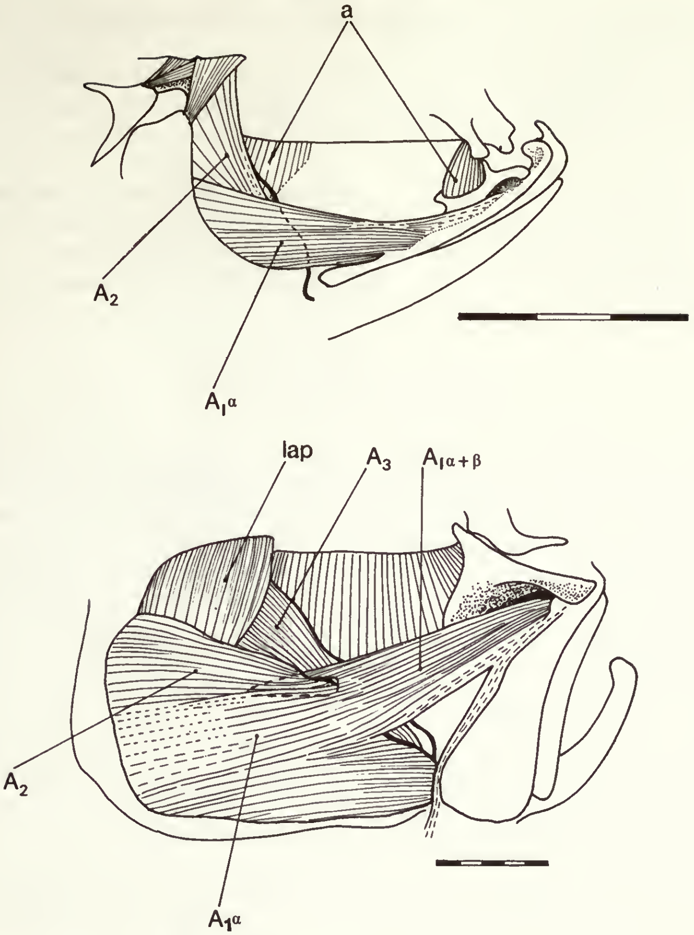

Fig. 22 Bregmacerotidae (above): *Bregmaceros atlanticus*. Muraenolepididae (below): *Muraenolepis microps*. Cranial muscle in lateral view (posterior extent of $A_1\beta$ indicated by dashed lines).

hyohyoidei adductores which extends from the last branchiostegal ray almost to the dorsal margin of the operculum. The *epaxialis* segment is less well-developed in *Phycis* and such an arrangement is absent in other phycids (see Howes, 1988).

LOTIDAE

(Figs 19; 21)

In *Lota* (Fig. 21) muscle A1α is only differentiable from A2 anteriorly by the separation of a bundle of lateral fibres which insert, *via* a long tendon, on the dorsal process of the maxillary bone. Muscle A1β originates from the anterior rim of the hyomandibula, medial to A2. A ventral tendon of A1β meets A1α at the anterior border of A2; the fibres of muscles A1α and A1β are indistinguishable for a short distance prior to separation. A1β inserts on the ventromedial face of the maxillary head. The ramus mandibularis of the trigeminal nerve passes medial to A1β, crosses above the lower jaw insertion of A2+3, and then passes medial to A1α.

Muscle A3 is separated dorsally from A2 by A1β, the two former elements joining in a common aponeurosis from which Aω originates.

The *levator arcus palatini* is not covered by A2 as in the Phycidae, its lateral fibres lying in the same plane and meeting aponeurotically those of A2. The ventral surface of the levator is bevelled to accommodate the medial surface of A2.

The opercular muscles are similar to those described for *Urophycis* and, as in that taxon, a segment of epaxial muscle inserts on the medial border of the operculum. Its site of origin, however, is the posttemporal rather than the supracleithrum as in *Urophycis* (but cf. *Muraenolepis*, below).

In *Molva* (Fig. 19), muscle A1β occupies a position similar to that in *Gadus* and *Merlangius* but comprises a long tendon stemming from the point of origin on the hyomandibula and expanding anteriorly into a thick bundle of fibres which inserts on the maxillary head.

Muscle A2 runs from the lateral face of the hyomandibula and preoperculum to insert with A3 on an aponeurosis from which muscle Aω also originates.

MURAENOLEPIDIDAE

(Fig. 22)

In *Muraenolepis* (Fig. 22) muscle A1 has its origins lateral and medial to A2. Its lateral origin is from a thin tendinous sheet covering the face of A2; its medial origin is from a tendinous fascia on the inner aspect of that muscle. The two bodies of the muscle join into a single element anterior to the border of A2. The lateral part of A1 (A1α) inserts tendinously on the dorsal aspect of the maxilla; the ventral border of the insertion tendon joining the maxillo-mandibular ligament. The main portion of A1 (A1β) inserts on the ventromedial aspects of the maxillary head.

Muscle A2 is large, covering most of the *levator arcus palatini* laterally. It converges with muscle A3 into a thick tendon medial to the anguloarticular. A stout subbranch of the tendon inserts on the coronomeckelian bone. Muscle Aω extends from the principal part of the tendon; only its anterior tip enters the small mentomeckelian cavity. Muscle A3 is divided from A2 by the *levator arcus palatini* which is a large, laterally bulbous muscle, originating from the sphenotic and inserting into a shallow cavity on the lateral face of the hyomandibula. The *adductor arcus palatini* is well-developed, flooring the orbital cavity and inserting anteriorly on the palatine.

The opercular muscles are well-differentiated from one-another; the *dilatator* is a narrow, spindle-shaped element inserting on the long anterior process of the operculum; the *adductor* and *levator operculares* originate from the underside of the pterotic and insert close together on the anteromedial face of the operculum (see Howes, 1988, fig. 5). As in *Urophycis* and *Lota*, a segment of epaxial musculature inserts on the medial face of the operculum, being narrowly separated from the *hyohyoidei adductores*. As in *Lota*, the site of origin of the epaxial segment is the posttemporal (see Howes, 1988, fig. 5).

BREGMACEROTIDAE

(Fig. 22)

In *Bregmaceros* (Fig. 22) muscle A1 is thin and shallow and incompletely divided. However, below the eye there is a strong, dorsal tendon and medial aponeurosis with a slight separation of the lateral fibres. The muscle insertion covers a long area of the maxilla, being tendinous anteriorly and musculose posteriorly. Muscle A2 is large with a deep concave anterior border.

The *levator arcus palatini* is a small thin element lying posterodorsally to the *adductor*. The *adductor arcus palatini* is divided, the anterior part inserting on the palatine, the posterior on the medial rim of the hyomandibula.

Summary and discussion of the muscles associated with the jaws and suspensorium

Certain features of these muscles are common to all macrouroids, namely:

1. Muscle A1 is never separated by A2, as is the case in other gadiforms and divisions A1α and A1β lie in the same vertical plane.
2. Muscle A1β always lies lateral to the ramus mandibularis of the trigeminal nerve and, because of this relationship, is homologous with that muscle in other gadiforms.

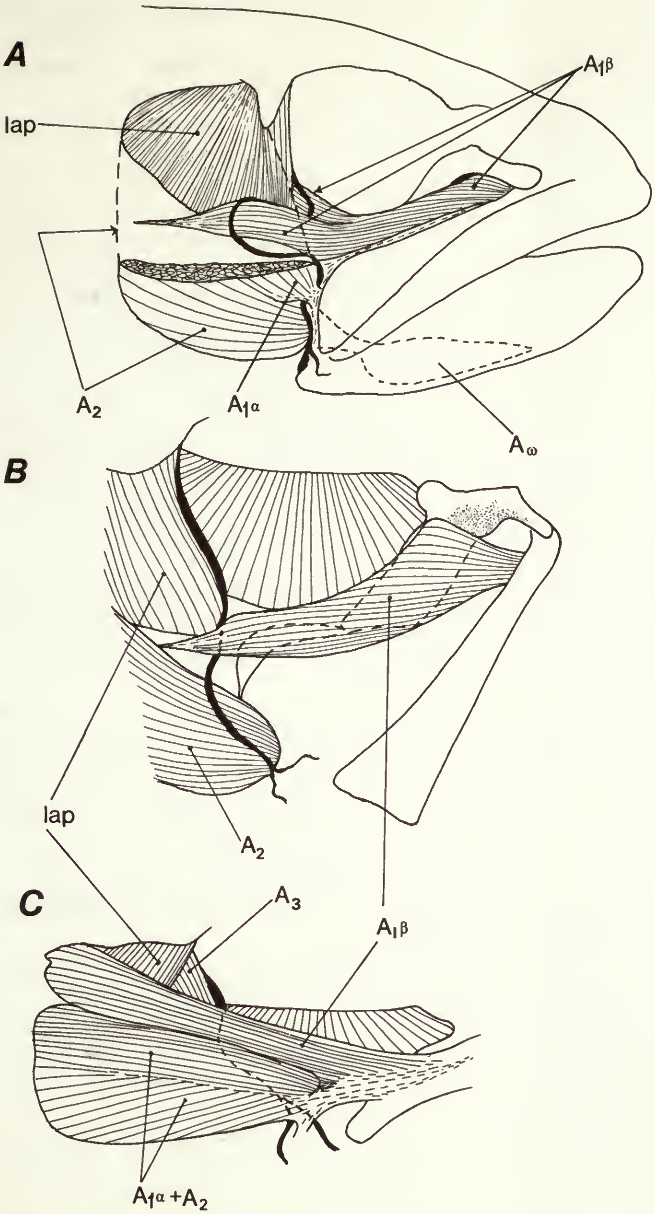

Fig. 23 Muscle $A_1\beta$ and its associations in: A, *Ophidion rochei* (muscle A_1+A_2 cut away, its borders indicated by dashed lines; B, *Glyptophidium macropus*; C, *Lycodes frigidus*.

3. Muscle A1β never originates from the palatine, in contrast to the condition in some gadoids.
4. Muscle A1β in the majority of macrouroids, is not constricted below the orbit, nor has it an anterior expansion.
5. The *adductor arcus palatini* is continuous and never divided as in some gadoids.
6. The *levator arcus palatini* lies lateral to muscle A1 and A2, a feature shared with some gadoids but few other teleosts.
7. Muscle A3 is absent, in contrast to most other gadiforms and acanthopterygians.

Because of the often contrasting conditions in these features between macrouroids and other gadiforms, it is necessary to examine each in detail.

1. *In macrouroids both muscles A1α and A1β always lie lateral to muscle A2 and the division between the A1 element is in the vertical rather than the sagittal plane.*

In the Macrouroidinae (*Macrouroides* and *Squalogadus*) and some genera of Macrourinae (Type II morphotype, see p. 12), A1 is undivided, or incompletely so. Incomplete separation of A1α and A1β occurs in some gadoids (i.e. *Bregmaceros, Euclichthys, Lyconus, Steindachneria, Lepidion*). In other paracanthopterygians (ophidioids, zoarcids and percopsids) there is no A1α, the single muscle inserting on the *lower jaw*. However, it is questionable whether this muscle is the homologue of A2 since the ramus mandibularis of the trigeminal nerve runs medial to it, and in some taxa the upper portion of the muscle has a close association with the maxillo-mandibular ligament. For example, in the ophidiiform *Ophidion rochei* (Fig. 23A) the ramus mandibularis runs medial to the upper part of the muscle, which is attached to the maxillo-mandibular ligament, the nerve then piercing the element and running laterally into the lower jaw. In the zoarcid *Lycodes frigidus* (Fig. 23C) the entire length of the nerve branch runs medial to the outer muscle bloc, but there is a distinct lateral myocomma which marks an abrupt change in fibre direction; the dorsal, parallel fibres insert directly onto the maxillo-mandibular ligament. In the percopsiform *Percopsis* (Fig. 24), although the nerve runs medial to the outer adductor muscle, there is no sign of any fibres running onto the maxillo-mandibular ligament or the upper jaw.

Thus, on the basis of the position of the ramus mandibularis and on what has been said above (p. 16) concerning its topographical position, the outer muscle in the above mentioned ophidioids, zoarcids and percopsids must be construed as the homologue of the element identified as A1 in macrouroids and gadoids (and various other teleosts) despite the fact that in some cases it does not insert on the upper jaw.

Whether the lack of an upper jaw insertion is the plesiomorphic condition or whether attachment of the muscle to the upper jaw has been lost, may only be assessed through congruence with other synapomorphies.

In the majority of acanthopterygians the ramus mandibularis of the trigeminal nerve consistently lies medial to muscle A1 (and so by its position signifies the identity of that element) even though in some taxa it follows the anterior border of A2.

2. *Muscle A1β (and A1γ)*. A brief account was given above (p. 16) of the nomenclatural history of muscle A1β and it is now treated in detail.

Rosen (1973), realised, correctly, that the muscle in question is not the homologue of the *levator maxillaris superioris* of halecomorphs, which muscle comprises several sections having their origins from the infraorbitals and lateral ethmoid as well as from the palatine and hyomandibula.

In macrouroids muscle A1β lies lateral to the ramus mandibularis and in some taxa it is incompletely separated from A1α posteriorly. It always inserts on to the medial face of the maxillary shaft and is never attached to an element of the suspensorium.

In assumed primitive gadoids (Bathygadidae; see Howes, 1988), muscle A1β has a similar morphology to that in macrouroids and similarly lies in the same vertical plane as muscle A1α. However, in progressively more advanced gadoids A1β shifts medially; in *Melanonus* and *Steindachneria* the shift concerns only the anterior part of the muscle, but in the Euclichthyidae and other gadoids (apart from the Bregmacerotidae) the posterior part of A1β also shifts medially so that the entire muscle comes to lie mesiad not only to A1α, but also (in more advanced gadoids) to A2.

In the Trachyrincidae although there is a single adductor muscle, it has a double insertion on the maxilla (p. 17) suggesting that A1α and A1β are fused. According to Casinos (1978) *Trachyrincus* has lost muscle A1α and it has been 'replaced' by a '. . . displacement outwards of the levator maxillae superioris' (i.e. A1β). There is, however, no evidence to suggest that such a loss and subsequent displacement has occurred. On the contrary, I would advocate that the opposite is the case and that muscle A1β has shifted medially in gadoids (see above). The situation in *Trachyrincus* is simply a derived specialisation of that taxon.

Casinos (*op. cit.*) in studying a limited taxonomic range of macrouroids has failed to take into

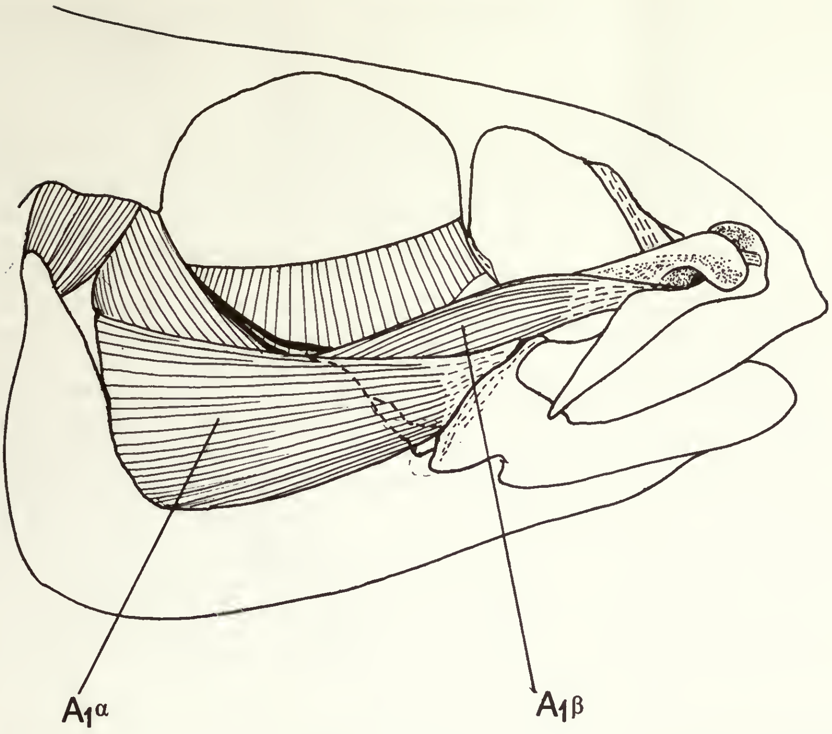

Fig. 24 *Percopsis omiscomayus.* Upper jaw and suspensorial muscles in lateral view. Medial pathway of ramus mandibularis indicated by dashed lines.

account the varying morphology of the adductor muscle. A single element also occurs in the Macrouroidinae and in a group of macrourines (see p. 13), and is probably also the result of fusion between A1α and A1β.

Lauder & Liem (1983: 148) state that it is only in more advanced paracanthopterygians that muscle A1β alone inserts on the maxilla. These authors do not justify that statement by providing examples, nor do they include it as a synapomorphy in their cladogram of paracanthopterygians. Accepting their statement means that no gadiform can be considered 'advanced'. But, on the basis of this character ophidiiforms and percopsiforms must form a monophyletic assemblage. If lophiiforms are taken to be 'advanced paracanthopterygians' then Lauder & Liem's hypothesis is rejected because muscle A1β is absent in these fishes (muscle A1 is a single element inserting on a broad ribbon-like maxillary tendon and posteriorly is undifferentiated from A2).

As noted above, in macrouroids and gadoids muscle A1β lies lateral to the ramus mandibularis of the trigeminal nerve. In other paracanthopterygians, however, the muscle lies medial to the nerve. A variation of this condition is illustrated in the ophidiiform *Ophidion rochei* where the nerve loops medially around the muscle's origin on the hyomandibula (Fig. 23A). In another ophidioid, *Glyptophidium macrops*, the nerve also passes medially to A1β, but A1α is lacking (Fig. 23B). in the neobythitine ophidiiform *Lamprogrammus niger* the ramus mandibularis follows a convoluted path. In this taxon the outer muscle bloc comprises two elements, the dorsal of which inserts on the maxillo-mandibular ligament and the ventral on the mandible. There is a well-developed A1β which is divided posteriorly by the *levator arcus palatini* muscle. The mandibularis nerve passes between the divisions of A1β, then medially to the dorsal adductor element. The nerve then runs laterally across the upper part of the ventral adductor segment, after which it turns inward to course medially to the lower segment. Thus, using the nerve pathway as the criterion of muscle identification, not only is the upper segment A1α, but so is the ventral portion of the lower segment,

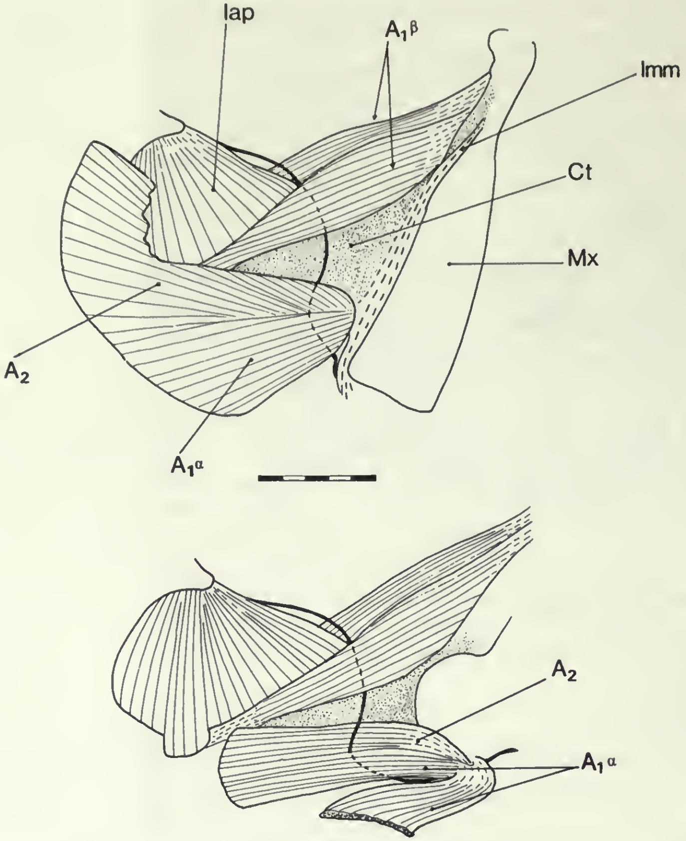

Fig. 25 *Lamprogrammus niger*. Muscle $A_1\beta$ and its associations. In A the upper part of muscle A_2 is cut away, and in B the superficial part is removed with $A_1\alpha$ reflected.

despite its insertion on the lower jaw. Muscle A2 is that small dorsal portion of the lower segment inserting on the mandible (Fig. 25).

Muscle A1β is reported to occur widely in neoteleosts; according to Lauder & Liem (1983: 143) it occurs in stomiiforms, some acanthopterygians, some paracanthopterygians and some aulopiforms but not in atheriniforms or neoscopelids. This statement appears, in part, to be based on the work of Rosen (1973). According to Rosen (*op. cit.*) there is, in stomiiform fishes, an A1β and sometimes an A1α. Fink & Weitzman (1984) maintained that A1β was a neomorphic feature independently derived in stomiiforms, myctophiforms and acanthomorphs (Fig. 26C). I agree that A1β in gadiforms is not homologous with the so-called A1β in stomiiforms or myctophiforms, nor indeed with that in lower groups in which it has been reported (e.g. halosauran elopomorphs; Greenwood, 1977). My reasoning for this assumption is that in those latter groups the muscle in question always lies medial to the ramus mandibularis of the trigeminal nerve (see for example Tchernavin, 1953, fig. 29). In higher neoteleosts an A1β muscle is recorded by Rosen (1973) in some beryciforms. He notes that stephanoberycids have entirely separate internal and external maxillary muscles similar to the gadiform condition. However, I find that in *Stephanoberyx monae*, an example illustrated by Rosen, muscles he labels as A2 and A1β are united at their origin (Fig. 26B). Rosen's A1β, which in his figure appears to have a double insertion on the maxilla, is equivalent to my A1α, and his A1α corresponds to the upper part of what I interpret as muscle A2 since this element inserts on the lower jaw; as shown in Rosen's figure. In the beryciform *Hoplostethes*, muscle A1 lies laterally to A2 (Fig. 26A).

In the myctophiforms examined (*Lampanyctus, Electrona*) and that illustrated by Rosen (1973), (*Protomyctophum*), only an A1β is present and this also lies medial to the ramus mandibularis branch of the trigeminal nerve.

Lauder & Liem's (1983: 143) statement that muscle A1β is absent in atheriniforms needs confirmation. In the small sample examined I find that in some taxa (e.g. *Orestias*) the mandibularis nerve branch passes medially to a segment of adductor muscle which inserts on the lower jaw. This could be muscle A1β having secondarily acquired a mandibular insertion. In *Hemiramphus* muscle A1 appears to be entirely lacking. If the presence of A1β is an acanthomorph synapomorphy then its absence in various atheriniform lineages must be viewed as derived losses.

In *Polymixia* the arrangement of adductor muscles is complex (Fig. 27B). Rosen (1973: 420) suggested that the polymixiid pattern was '. . . transitional between the A1 and A1β systems'. My interpretation is somewhat different, however, since the specimen of *Polymixia nobilis* examined differs from that of *P. japonica* illustrated by Rosen. The principal lateral muscle of *P. nobilis* appears to be a combined A1α and A2 (Rosen's A2) since a group of fibres inserts *via* a narrow tendon on to the posterodorsal part of the maxillo-mandibular ligament and passes laterally to the ramus mandibularis nerve branch. A large anteromedial muscle, corresponding to Rosen's A1β, inserts on to the dorsal surface of the maxilla. Although adhering to the maxillo-mandibular ligament by connective tissue along most of its length, its fibres remain separated from that ligament (Rosen's figure of *P. japonica* shows them inserting on to the maxillo-mandibular ligament). As shown by Rosen, there are two sections of muscle A1β which are separated by the course of the ramus mandibularis branch. The inner section is connected to the outer anteriorly along an internal aponeurosis which is evident laterally as a tendinous band (Ia1b, Fig. 27B). I am unable to locate in *P. nobilis* a muscle corresponding the Rosen's labelled A3 in *P. japonica*.

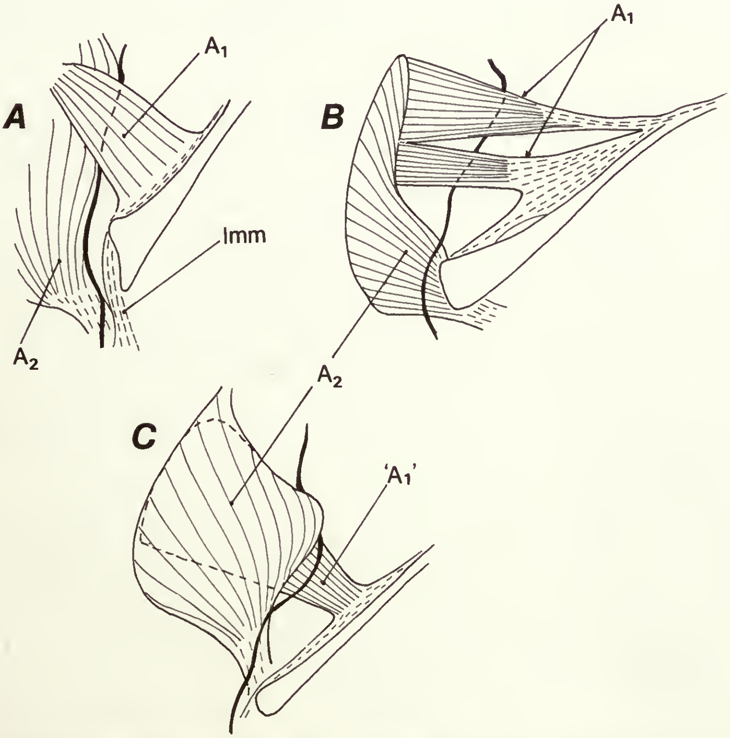

Fig. 26 The superficial upper jaw adductor musculature of the beryciformes: A, *Hoplostethes melanopus*; B, *Stephanoberyx monae*; and the stomiiform, C, *Photichthys argenteus*.

It seems that, at least in *P. nobilis*, muscle A1β is present, although poorly differentiated, and muscle A1β corresponds in topographical position to the so-called A1β in myctophiforms and stomiiforms. This observation supports Stiassny's (1986) phylogenetic positioning of *Polymixia* as the sister-group of the Paracanthopterygii plus Acanthopterygii.

Rather surprisingly, the adductor muscle arrangement in the Sciaenidae (a family currently placed in Acanthopterygii) greatly resembles that of *Polymixia* and certain gadoids. In *Cynoscion* for example (Fig. 27A) muscle A1β is divided as in *Polymixia* by the ramus mandibularis branch of the trigeminal nerve, the outer section running into the maxillo-mandibular ligament; the inner section, which originates from the quadrate and hyomandibula, also joins the maxillo-mandibular ligament for part of its length. The anterior, expanded part of the muscle originates from the palatine as in merlucciid gadoids (see above). Interestingly, Freihofer (1978: 45) draws attention to the resemblances between sciaenid and percopsiform musculature, including the innervation pattern.

One group of macrouroids, designated as morphotype Ia possesses an additional adductor muscle, termed A1γ (p. 12). This muscle is usually a weak spindle-shaped element originating *via* a thin tendon from the medial face of A1β and having a common insertion with that muscle on the maxilla. In *Abyssicola*, the tendon of origin stems from the anterior rim of the hyomandibula and in this respect resembles the condition of A1β in certain gadoids (see above). I have not found a muscle corresponding to A1γ in any other acanthomorph taxon and regard it as synapomorphic for the macourine genera *Coryphaenoides, Abyssicola, Nezumia, Coelorinchus, Lionurus, Nematonurus* and *Chalinura*.

3. *Origin of muscle A1β from the palatine*. Among gadoids this feature occurs in the Merlucciidae (*Merluccius, Macururonus* and *Lyconus*). The anterior part of muscle A1β originates from a lateral palatine cavity (complexly so in *Lyconus*; see p. 26 above). The origin of part of A1β from the palatine also occurs in some sciaenids (see above) in which taxa it is considered to have arisen independently from that in merlucciids (see Howes, 1988 concerning the phylogenetic position of the Merluccidae).

4. *Suborbital constriction of muscle A1*β *and its insertion*. There is no suborbital constriction of muscle A1β in macrouroids. In gadoids, however, a tendinous constriction of the muscle occurs in the Bathygadidae, Moridae, Melanonidae (*sensu* Howes, 1988) and Euclichthyidae. Constriction of the muscle below the orbit leads to an anterior expansion of the muscle.

The occurrence of a suborbital constriction of the dorsal part of A1 in such unrelated groups as Cichlidae (Otten, 1981) and Cyprinidae (Howes, 1984*a*) casts doubt on the feature having any phylogenetic significance; it seems to be a functional means of accommodating the eye. That this is so is indicated bythe long and obliquely angled jaws of the gadoid taxa possessing the constriction, which necessitates a sharp change in angle to pass around the eyeball. In contrast, the jaws of macrouroids are short, so that the fibres of muscle A1β are directed downward and their course is uninterrupted by the eye. The Trachyrincidae are exceptional in that although possessing long jaws they are horizontally aligned and the muscle remains unconstricted (Fig. 7), although the eye is not relatively smaller than that in macrouroids.

Although in primitive gadoids such as *Bathygadus* and *Gadomus* (Figs 9 & 11) the anterior 'expansion' of muscle A1β follows as a consequence of suborbital constriction, in more advanced gadoids this expansion has apparently a functional nature in that it is bulbous and transversely expanded, and fills the palatine cavity; in merlucciids this section of the muscle is even attached to the palatine (see p. 12). Thus, I have considered the anterior development of muscle A1β to be a synapomorphy for gadoids including and above *Bathygadus* (Howes, 1988).

The variability of the site of attachment of muscle A1β to the maxilla demands some comment. In macrouroids the anterior part of the maxilla bears a prominent ventromedial process which contacts the ascending process of the premaxilla (Mvp, Figs 2 & 3). On the inner side of the maxillary ventral process is a small depression into which inserts the tendon of A1β (Fig. 28A). A similar ventromedial process occurs in the Bathygadidae and Moridae but is not so well-developed

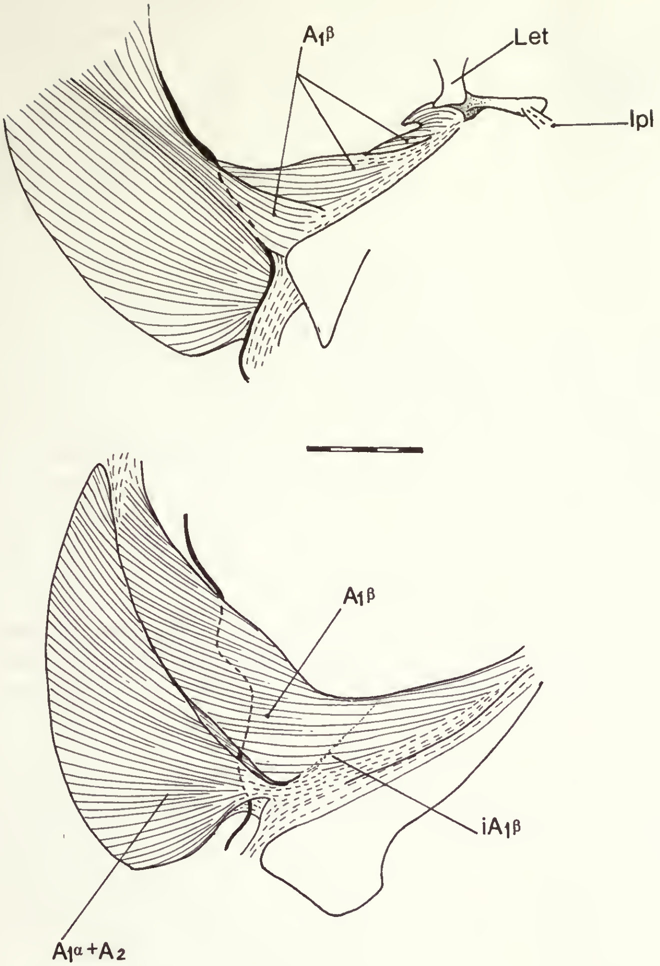

Fig. 27 Jaw adductor muscles in A, a sciaenid *Cynoscion jamaicensis* and B, a polymixiid *Polymixia nobilis*.

as that in macrouroids and the tendon of A1β inserts on the posterior rim of the ventromedial process (Fig. 29A).

In the Trachyrincidae, the inner insertion tendon (presumably representing A1β; see above, p. 17) inserts on the dorsal aspect of a medial maxillary shelf (Fig. 29B). This is similar to the situation in other gadoids where the muscle insertion is shifted forward to insert along the dorsomedial ledge of the maxilla (e.g. Euclichthyidae). In the Melanonidae and Merlucciidae A1β inserts on the medial aspect of the maxillary head (Fig. 29C) whereas in the more advanced gadoids (Gadidae, Lotidae, Phycidae, Ranicepitidae, Muraenolepididae; see Howes, 1988) its insertion is on the ventral limb of the maxillary head (Fig. 29D).

The anterior shift of A1β insertion appears to be correlated with the transverse expansion of that muscle and its shift from a lateral to medial position with respect to the outer adductor muscle (see above). It is supposed that the anterior placement of the muscle's insertion site is a derived condition for those families listed above.

5. The *adductor arcus palatini* is, in some gadoids divided into anterior and posterior parts. According to Winterbottom (1974*a*: 238) the *adductor arcus palatini* in its plesiomorphic state is

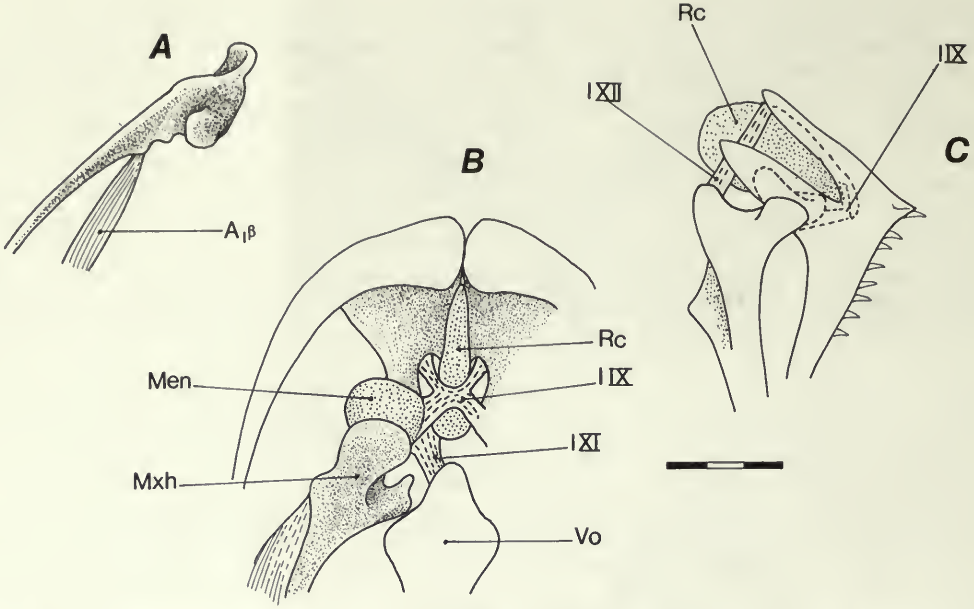

Fig. 28 A, *Nezumia hildebrandi*, insertion of muscle $A_1\beta$ on maxilla (ventral view); B, *Coelorinchus caribbaeus*, ventral view of maxillary and premaxillary ligamentous connections; C, *Ventrifossa occidentalis*, lateral view of maxillary-premaxillary-rostral cartilage associations.

confined to the posterior region of the orbit between the skull and hyomandibula; its derived condition is to floor the orbital cavity and extend posteriorly. Part of the *adductor* in gadoids usually originates from the parasphenoid, only a small portion stemming from the prootic; a separate *adductor hyomandibulae* is not recognisable. The division of the *adductor arcus palatini* in some gadoids (*Bregmaceros, Macruronus*) is, on the basis of in- and out-group distribution, a derived condition and a 'precursor' can be recognised in some morids (p. 20) and *Steindachneria* (p. 22) where the central portion of the muscle is thin and weakly developed.

Apart from *Bathygadus, Gadomus* and *Euclichthys* an anterior insertion of the *adductor arcus palatini* on to the palatine is a feature of all gadiform fishes examined, and is also present in some ophidiiforms. Among acanthopterygians a palatine attachment of the *adductor arcus palatini* is present in Sciaenidae, Eleotridae and some Cichlidae (see, for example, Greenwood, 1985). Of other families checked for this feature, it is lacking in Pomacentridae, Labridae, Atherinidae, Nototheniidae, Stephanoberycidae, Polymixiidae, Scombridae, Sparidae and Lutjanidae. Admittedly this is not an exhaustive survey of acanthopterygian taxa but it does not indicate that a palatine attachment of the *adductor arcus palatini* is an unusual acanthopterygian condition; such an attachment has been treated as derived (Greenwood, 1985: 156; 165). To treat a palatine attachment of the *adductor* as a synapomorphy uniting the majority of gadiforms and some ophidiiforms, would conflict with the pattern of relationships arrived at through other synapomorphies (see Howes, 1988). It is more parsimonious to assume an independent derivation of the feature in the various lineages in which it occurs.

6. In the Trachyrincidae, the *levator arcus palatini* is extensive posteriorly, covering the upper part of the plate-like preoperculum and lying medial to A1 (Fig. 7). In the Melanonidae and Steindachneriidae the *levator* is small, its insertion being high on the preopercular limb (Figs 12 & 13). A similar situation occurs in the Bregmacerotidae, where the *levator* is much reduced and inserts on the dorsal margin of the preoperculum (Fig. 22), a feature also present in the percopsiform *Percopsis* (Fig. 24).

The Euclichthyidae has an autapomorphic arrangement of the *levator arcus palatini*. Although extensive, the muscle does not lie laterally to the superficial adductor musculature as in lower gadoids and macrouroids, but mostly posteromedial. Near its insertion the *levator* is bifurcate, the posterior segment inserting on the preoperculum and just overlapping the posterodorsal edge of A1, the anterior one inserting on the hyomandibula and joining an aponeurosis from which originates muscle A1β (Fig. 14).

The morphology of the *levator* in *Euclichthys* could, in evolutionary terms, be construed as the 'precursor' of the situation found in other gadoids where the entire muscle lies medial to the outer part of the *adductor mandibulae*.

If the acanthomorph condition of the *levator arcus palatini* occurring medially to the outer adductor muscle be regarded as the plesiomorphic condition, then the similarly placed muscle in higher gadoids is a phylogenetic reversal from the laterally placed *levator* which characterises the macrouroids and majority of gadoids. One may then interpret as 'intermediates' between these taxa and higher gadoids the posterior shifts of the levator found in the Melanonidae and Bregmacerotidae and partial lateral overlap of the adductor in the Euclichthyidae.

7. *Muscle A3 is lacking in macrouroids*. This muscle is usually defined as the most medial of the adductor complex, having its insertion in the lower jaw (according to Winterbottom 1974*a*: 234) on the 'medial face of the dentary, in the Meckelian fossa, or both.' Allis (1897: 581) identifies the A3 as that muscle lying medial to the adductor ramus of the maxillaris inferioris nerve.

In most acanthomorphs, the ventral fibres of A3 converge with those of A2 on to a common aponeurosis which attaches to the inner face of the anguloarticular. Dorsally, A2 and A3 are separated by the *levator arcus palatini*. In macrouroids and many gadoids, the *levator* lies outside the adductor complex (see above) and so the medial adductor bloc comprises a single element dorsally. Only in the more advanced gadoids (*Gadus, Lota* etc.) is it possible to distinguish an A3 on the grounds of its dorsal separation from A2 by a *levator arcus palatini*. In macrouroids and lower gadoids, the insertion of the medial adductor element (A2) on the lower jaw is a simple one; all fibres converge into an aponeurosis from which departs a ventrally directed tendon. The tendon inserts on the coronomeckelian bone; no fibres are associated with the tendon.

In advanced gadoids the situation is more complex, with the inner fibres of A2 inserting on the coronomeckelian tendon, while those of A3 cross over to insert on the lateral tendinous sheet.

According to Casinos (1978) muscle A3 in gadoids is homologous with the inner part of the macrouroid adductor complex. Furthermore, Casinos regards the gadoid (= my higher gadoids, e.g. *Gadus, Merluccius, Pollachius*) condition of separate A2 and A3 muscles to be plesiomorphic

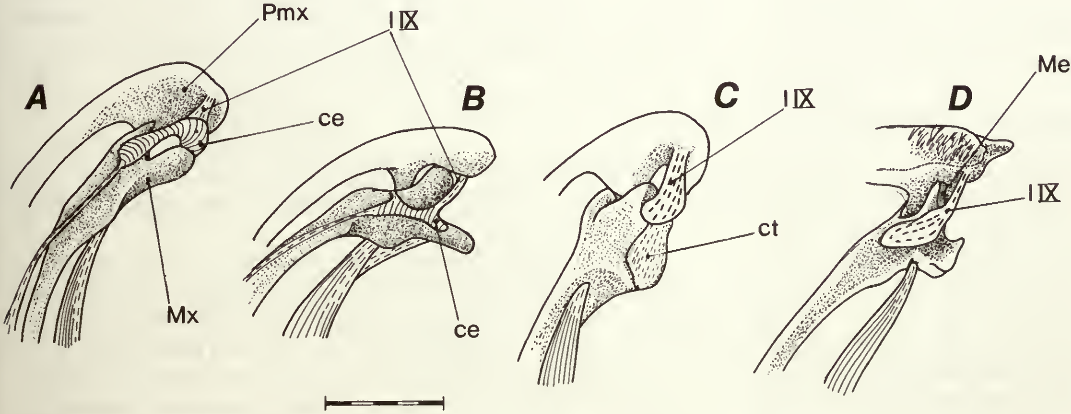

Fig. 29 Maxillary insertion of muscle $A_1\beta$ and the ligamentous connection between the maxilla and premaxilla in: A, Bathygadidae, *Bathygadus favosus*; B, Trachyrincidae, *Trachyrincus trachyrincus*; C, Melanonidae; *Melanonus zugmayeri*; D, Gadidae, *Gadus morhua*.

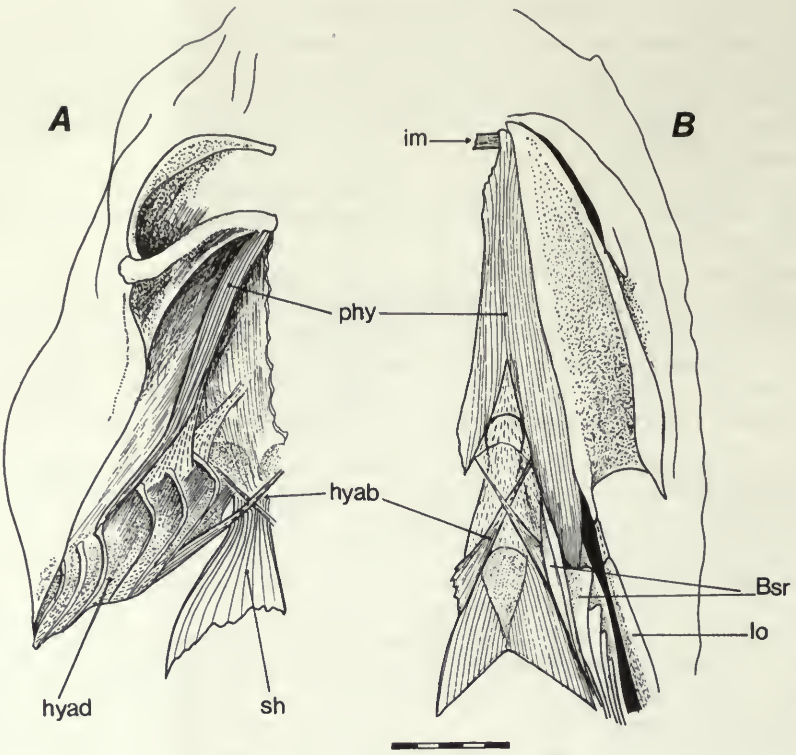

Fig. 30 Hyoid musculature of A, Macrouroidinae: *Squalogadus modificatus*; B, Macrourinae: *Coryphaenoides mexicanus*. Ventral views.

and to have given rise to derived states in macrouroids either by the amalgamation of A2 and A3 or the loss of A2.

Casinos' assumptions are based on the recognition of the gadoids as being plesiomorphic but on the contrary they appear to be the derived sister-group of macrouroids (see Howes, 1988). I would suggest that the 'amalgamation' of A2 and A3 in macrouroids (and in out-groups) is the plesiomorphic state representing an undifferentiated muscle bloc. The differentiation of a medial muscle element (A3) is a derived condition that has undoubtedly occurred independently in several teleostean lineages.

Muscles of the hyoid region

Among macrouroids there is little variability of the hyoid muscles, such variation as does occur concerns the points of attachment of the *protractor hyoidei* and the degree of development of the *hyohyoidei abductores*.

The *protractor hyoidei* originates from the anterohyal at the articulation of, and usually attaching to the 2nd, 3rd or 4th branchiostegal ray. Most frequently the muscle attaches to the proximal stem of the 3rd and 4th rays. Only in *Lionurus* is there a single attachment to the 2nd branchiostegal ray. The *protractor hyoidei* is usually well-developed. In most taxa the left and right parts of the muscle continue forward, narrowly separated from one another in the midline. Anteriorly the parts diverge slightly to insert on their respective dentary. *Echinomacrurus* is unusual among the Macrourinae in having a ribbon-like protractor hyoidei with the right and left parts separated in the midline. In this respect, *Echinomacrurus* resembles taxa of the Macrouroidinae. In both macrouroidine genera the *protractor hyoidei* is a rope-like element extending from the anterohyal anterior to the articulation of the 4th branchiostegal ray; insertion is close to the symphysial tip of the dentary (Fig. 30). The left and right parts of the muscle are separated for their entire lengths. In *Cetonurus* the left and right parts of the *protractor* meet only beneath the ventral hyoids, remaining separated for the remainder of their lengths.

An *intermandibularis* is present in all taxa examined with a single exception, namely the macrouroidine *Squalogadus*. The muscle is a thin, narrow band of fibres with the *protractor hyoidei* inserting below it.

The *hyohyoidei abductores* run from the 1st branchiostegal ray to insert tendinously on the contralateral dorsohyal.

The *hyohyoidei adductores* are weakly developed in all taxa and usually comprise a few widely spaced fibres arranged in narrow bands connecting the branchiostegal rays (Fig. 32). Posteriorly, those fibres connecting the last branchiostegal ray with the suboperculum and operculum are stronger and more numerous.

In gadoids the hyoid musculature is generally more strongly developed than in macrouroids. For example, in the Muraenolepididae (Fig. 31), the *protractor hyoidei* is well-developed, attaching to the base of the 3rd and the upper part of the 2nd branchiostegal ray; an anterior segment of the muscle attaches tendinously to the ventromedial border of the dentary. The parts of either side meet in the midline and run forward as a single muscle inserting at the symphysis beneath a small *intermandibularis*. The *hyohyoidei abductores* and *adductores* are also well-developed.

The morphology of the hyoid muscles in the Gadidae, Lotidae and Phycidae is similar to that in the Muraenolepididae except that the *intermandibularis* is more strongly developed in the former. Holmquist (1911) has described and figured the hyoid musculature of *Gadus* in which he identifies two sections of the *intermandibularis*. Winterbottom (1974*a*: 245) concluded that the anterohyal section should properly be referred to as the *protractor hyoidei*.

The morphology of the hyoid musculature is rather uniform and the often recognised taxonomic grouping of macrouroids based on the number of branchiostegal rays, *viz*. 6 or 7 is not reflected by different muscle morphotypes. The most noticeable differences are those between the Macrouroidinae and Macrourinae where in the former the two parts of the *protractor hyoidei* are ribbon-like and separated in the midline and the *intermandibularis* is absent (at least in *Squalogadus*). A similar separation of the *protractor* also occurs in the macrourine, *Echinomacrurus* (see above). The osteology of *Echinomacrurus* is unknown, but its external morphology would indicate that it is a

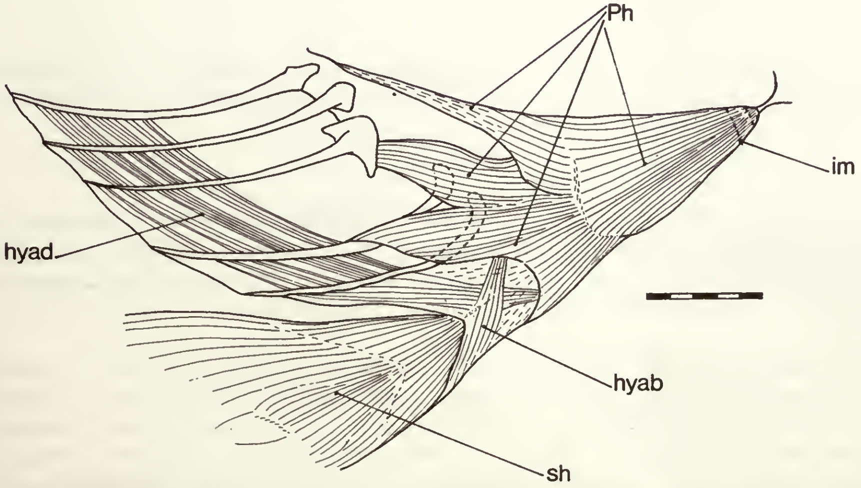

Fig. 31 Hyoid musculature of *Muraenolepis microps*; ventrolateral view, position of *intermandibularis* indicated by dashed lines.

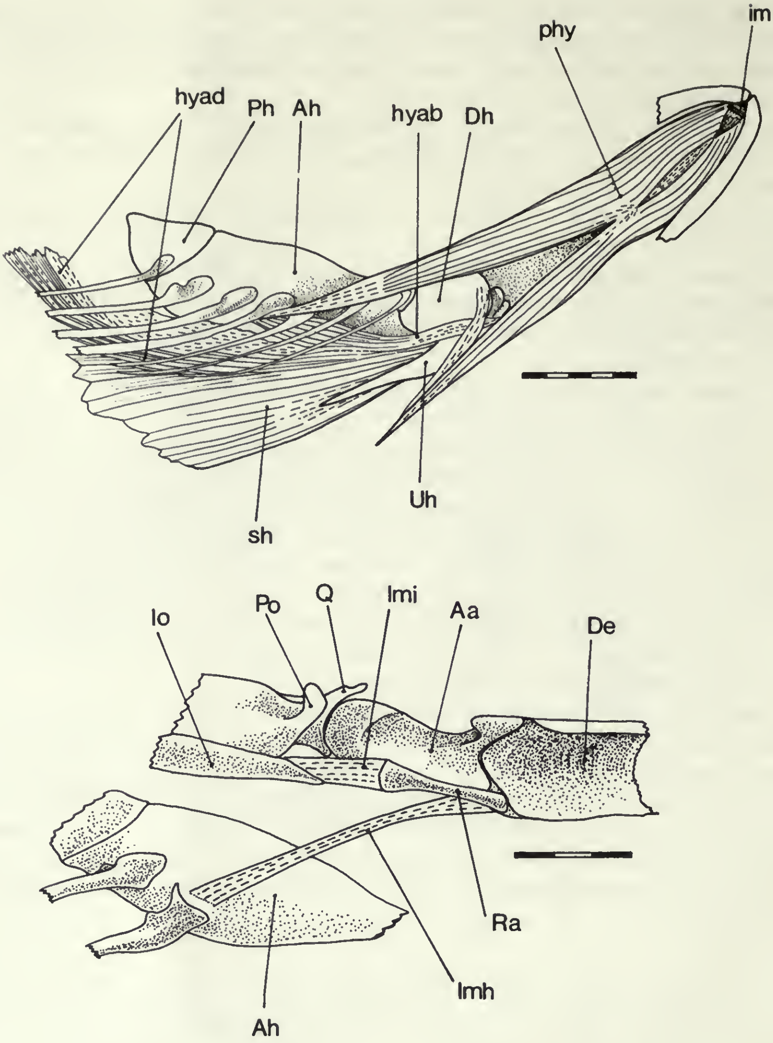

Fig. 32 *Trachyrincus trachyrincus*: above, hyoid musculature seen in oblique ventrolateral view; below, ligamentous connections of the lower jaw and hyoid bar seen in ventral view.

member of the Macrourinae, although a highly derived one. The similarity in the morphology of its hyoid muscles with that of the macrouroidines has possibly been independently derived. The complete separation of the *protractor hyoidei* in the midline is an unusual feature amongst teleosts and is known elsewhere only in the otophysan Loricariidae (Howes, 1983) and the Gyrinocheilidae (pers. obs.).

The *sternohyoideus* muscle, connecting the pectoral girdle with the hyoid bar occurs among gadiforms in two conditions—long and compressed or deep, broad and short. Usually, a long, compressed *sternohyoideus* attaches to a urohyal whose posterior margin is widely separated from the cleithrum, whereas a short, broad *sternohyoideus* is associated with a urohyal whose posterior border is in contact with, or narrowly separated from the cleithrum. The posterior limit of the *sternohyoideus* is usually well-defined ventrally by its attachment to the cleithra, but its lateral fibres are continuous with those of the body musculature (*obliquus inferioris*).

In macrourids a long, compressed *sternohyoideus* occurs in *Odontomacrurus, Hymenocephalus, Chalinura, Echinomacrurus, Cynomacrurus* and *Lionurus*. A stout, broad muscle is present in *Macruorus, Nezumia, Trachonurus, Malacocephalus* and the macrouroidine, *Squalogadus*. The latter is unusual in possessing a stout *sternohyoideus* associated with a urohyal that is widely separated from the pectoral girdle, a feature also possessed by the Trachyrincidae.

Among gadoids, the Bathygadidae and Moridae have a long compressed *sternohyoideus*. However, in bathygadids the tendons of the paired *infracarinalis anterior* stretch forward from the pelvic girdle to attach *via* connective tissue to the ventral tips of the cleithra, and continue forward into the ventral body of the *sternohyoideus*. The tendons of the *infracarinalis* finally insert on either side of the urohyal keel (Fig. 35).

In other gadoids a long compressed *sternohyoideus* is present in the Merlucciidae where there is a well-defined ventral division of the muscle to which the *infracarinalis anterior* is tendinously linked.

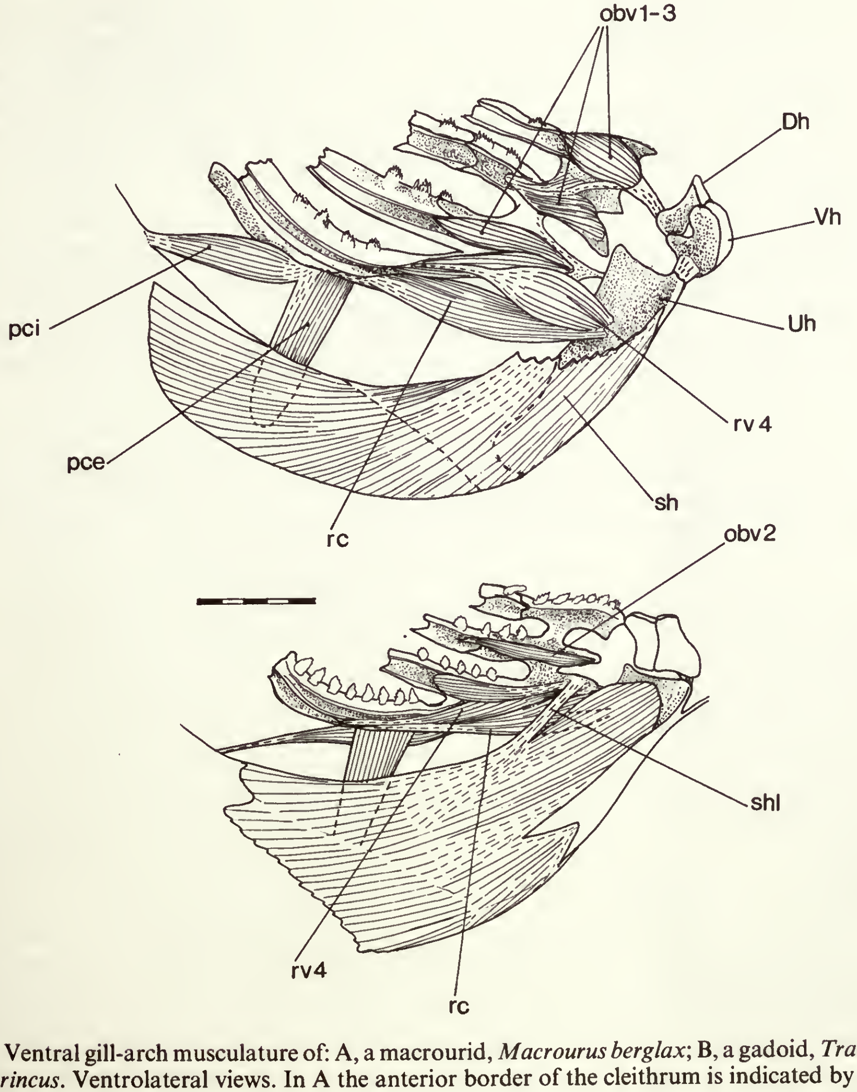

Fig. 33 Ventral gill-arch musculature of: A, a macrourid, *Macrourus berglax*; B, a gadoid, *Trachyrincus trachyrincus*. Ventrolateral views. In A the anterior border of the cleithrum is indicated by a dashed line.

In all gadiforms and other paracanthopterygians examined a dorsolateral segment of the *sternohyoideus* inserts on a stout tendon which runs anterodorsally to insert on the 3rd hypobranchial (see Figs 33–36). In acanthopterygians (?all) a similar tendon runs from the dorsomedial part of the muscle.

Ventral gill-arch muscles

Macrouroids, in common with almost all teleosts possess well-developed *obliqus ventrales* on the 1st through 3rd ventral gill-arches (Fig. 33A; 34). In contrast, gadoids have reduced (or even lack) *obliqus ventrales* on either the 1st or the 1st and 2nd gill-arches (Fig. 35). The Bathygadidae, Steindachneriidae, Melanonidae, Moridae and Trachyrincidae have reduced (or in some bathygadids lack) the muscles from only the 1st arch (Figs 33B; 34); see Howes, 1988. Reduction takes the form of a tendon attaching to the proximal tip of the ceratobranchial and with only a minute muscular element being present. In the Bregmacerotidae, the muscles appear to be lacking entirely on the 1st and 2nd gill-arches.

Winterbottom (1974*a*: 263) notes that there are a variable number of *recti ventrales* in teleosts. The usual acanthomorph condition is for *rectus ventrales* IV to run between the semi-circular ligament connecting the 3rd hypobranchials across the midline, and the 4th ceratobranchial. This is also the condition present in the majority of macrouroids, with the exception of *Hymenocephalus* where the anteroventral part of the muscle inserts on the urohyal and in *Macrourus*, where the entire muscle inserts on the bone. *Squalogadus* is also exceptional in that the *rectus ventrales* IV joins posteriorly to the tendon of the *rectus communis* and so by-passes the 4th ceratobranchial, inserting instead on the 5th.

Among gadoids, the *rectus ventrales* IV attaches to the urohyal in *Lyconus* (Merlucciidae), the Ranicepitidae, Phycidae and Muraenolepididae. In other merlucciids, Bathygadidae, Moridae, Steindachneriidae, Melanonidae and Lotidae, the muscle attaches together with the *rectus communis* to a dorsal aponeurosis of the *sternohyoideus* muscle (Fig. 35). In the merlucciid *Macruronus*, the *rectus ventrales* IV has a long tendon which inserts on the 5th ceratobranchial; the muscle itself is separated from the 4th arch, and anteriorly attaches to a complex aponeurosis of the *sternohyoideus* (Fig. 36).

Table 2 Insertion sites of *rectus communis* and *rectus ventralis* IV muscles in macrouroids and gadoids. Uh = urohyal; Sh = sternohyoideus; 3Hy = third hypobranchial

	Rectus communis		*Rectus ventralis* IV		
	Ur	Sh	3Hy	Sh	Uh
Macrourinae					
(*a*, majority)	*		*		
(*b*, 5 genera)		*	*		
(see Table 1)					
Trachyrincidae		*	*		
Bathygadidae		*	*		
Moridae		*	*		
Euclichthyidae		*	*		
Merluccidae		*		*	*(*Lyconus*)
Melanonidae	* and 3Hy		*		
Steindachneriidae		*		*	
Gadidae		*	*		
Phycidae (part)	*				*
Phycidae (part)		*	*		
Muraenolepididae	*				*
Ranicepitidae	*				*
Lotidae		*		*	

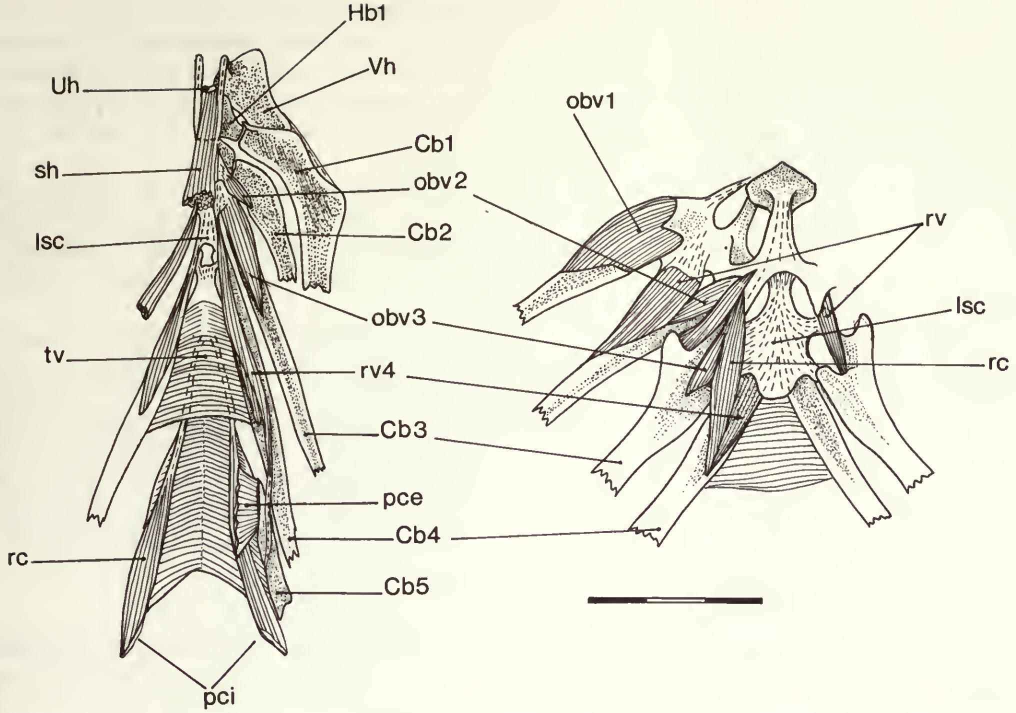

Fig. 34 Ventral gill-arch musculature of: A, a gadoid, *Bathygadus melanobranchus*; B, a macrourid, *Nezumia hildebrandi*. Ventral views.

In other paracanthopterygians examined, *rectus ventrales* IV extends from the 3rd hypobranchial ligament to the 4th ceratobranchial, namely, the plesiomorphic acanthomorph condition.

In nearly all macrouroids, as in the majority of acanthomorphs, the *rectus communis* runs from the urohyal to the 5th ceratobranchial. Exceptional taxa are *Nezumia, Ventrifossa, Hymenocephalus, Odontomacrurus* and *Cynomacrurus,* where the *rectus communis* runs from a dorsal tendon of the *sternohyoideus* to the 5th ceratobranchial.

Among gadoids, the *rectus communis* almost always has a direct attachment to the *sternohyoideus*; in some taxa the *rectus communis* joins a tendinous aponeurosis (Merlucciidae, Fig. 36); in others, the fibres run into the body of the *sternohyoideus* and insert on an internal myocomma (Trachyrincidae, Fig. 33); and yet others, the *rectus communis* attaches directly to the urohyal (some Phycidae, Ranicepitidae, Muraenolepididae and Lotidae). However, unlike the condition in macrouroids and acanthomorphs it attaches to the anterior tip of the bone rather than to the lateral face of the keel. This different insertion site on the urohyal suggests that the attachment has been secondarily derived to that in acanthomorphs rather than representing a plesiomorphic condition (see Howes, 1988).

The various conditions of ventral gill-arch muscles in macrouroids and gadoids are summarised in Table 2.

Lauder (1983) considered a urohyal attachment of the *rectus communis* a synapomorphy for the ctenosquamates (Myctophiformes, Paracanthopterygii and Acanthopterygii). Because of its urohyal attachment, Lauder prefers the term '*pharyngohyoideus*' for ctenosquamates rather than *rectus communis*. I have, however, continued the use of *rectus communis* for gadoids since here there is no, or at best, an indirect urohyal insertion. It could be argued that '*pharyngohyoideus*' should be used for macrouroids, but here too there are exceptions to a urohyal insertion (see above and Table 2).

Following Lauder's assumption that a urohyal attachment for the *rectus communis* is a derived state it would appear that a direct linkage with the *sternohyoideus* represents a further derived condition. If it be assumed that this condition represented a less derived state, i.e. an evolutionary 'intermediate' position between a hypobranchial and urohyal attachment then it must also be assumed that the gadoids are less derived than myctophiforms, a conclusion unjustified on the basis of other synapomorphies (see Lauder & Liem, 1983).

Howes (1987) considered the *rectus communis-sternohyoideus* linkage to be a synapomorphy uniting gadoids. It is now apparent that the feature also occurs in some macrouroids (see above). The possession by macrouroids of other synapomorphies lacking in gadoids makes it reasonable to assume, however, that the *rectus communis-sternohyoideus* linkage in the five macrouroid genera (see p. 47) is homoplastic.

Lauder (1983: 26) notes that in euteleosts a *rectus ventralis* IV commonly originates from the urohyal, but that the muscle is mosaically distributed and has probably evolved independently in several lineages through the subdivision of the *rectus communis*.

The lability of the *rectus ventralis* IV casts doubt upon its usefulness as a phylogenetic indicator and I have preferred to regard its association with the *sternohyoideus* in the Moridae, Merlucciidae and Lotidae as having been derived independently in those lineages; certainly there are no other synapomorphies that would suggest a close relationship of these taxa (see Howes, 1988). Further discussion of functional aspects of the ventral gill-arch musculature is given on pages 54–55.

Dorsal gill-arch muscles

Unlike the ventral gill-arch musculature, there is little variability in the dorsal gill-arch muscles among macrouroids apart from the angles at which the *levatores* are aligned between the gill-arches and the cranium, and in the size differences of some muscles.

The basic pattern present in all macrouroid and gadoid taxa examined is: three *levatores externi*, two attaching to the 1st and 2nd and the third to the 4th epibranchials (*levator* IV crosses the otic region of the cranium anteroventrally, medial to *levatores* I and II); two *levatores interni*, one attaching to the 2nd infraphayngobranchial, the other to the 3rd or 4th (Fig. 37); all these muscles originate from the intercalar and/or the upper part of the prootic.

Transversi dorsales run from the 2nd, 3rd and 4th epibranchials to a midline raphe (that serving the 2nd and 3rd arches is a single element); an *obliqus posterior* connects the postero-medial surface of the 4th epibranchial with the 5th cerato-branchial (pharyngeal tooth-plate).

In macrouroids the *retractor dorsalis* stems from the 3rd and 4th centra to insert tendinously on the medial rim of the 3rd pharyngobranchial. In some taxa, e.g. *Nezumia* (Fig. 38C), a ventral part of the *retractor* inserts on the rim of the 4th pharyngobranchial tooth-plate.

Lauder (1983) noted that in the gadoid *Pollachius*, the *retractor dorsalis* inserts on both pharyngobranchials 3 and 4; I find similar sites of insertion in all 'advanced' gadoids, but in merlucciids, melanonids, morids and bathgadids the muscle inserts, as in most macrouroids on the medial rim of pharyngobranchial 3.

In the Muraenolepididae, the *retractor dorsalis* inserts only on pharyngobranchial 4 (Howes, 1988). Lauder's (1983) and my own observations on acanthopterygians suggest that insertion on pharyngobranchial 3 is the plesiomorphic site of attachment and that one involving the 4th pharyngobranchial is the derived state. In this respect, the Muraenolepididae is the most derived group of gadoid taxa.

Eye muscles

Macrouroids and gadoids lack a posterior myodome, apparently a secondary loss (see Patterson, 1975: 544). The posterior eye muscles originate from a medial septum close to the floor of the parasphenoid and run almost lateral to their insertions on the eyeball. The accompanying figure of *Gadomus* (Fig. 39) exemplifies the condition in all macrouroids and gadoids examined (the eye muscles of *Gadomus* are narrower than in most other taxa). In some gadoids the posterior eye muscles originate from a small ossified protruberance of the parasphenoid. In *Gaidropsarus*, *Merluccius* and *Brosme* the eye muscles pass medial to a vertical parasphenoid-pterosphenoid strut bordering the optic fenestra.

The origin of the posterior eye muscles from the centre of the parasphenoid and their transverse orientation is considered a further synapomorphy uniting the Macrouroidei and Gadoidei (see Howes, 1988).

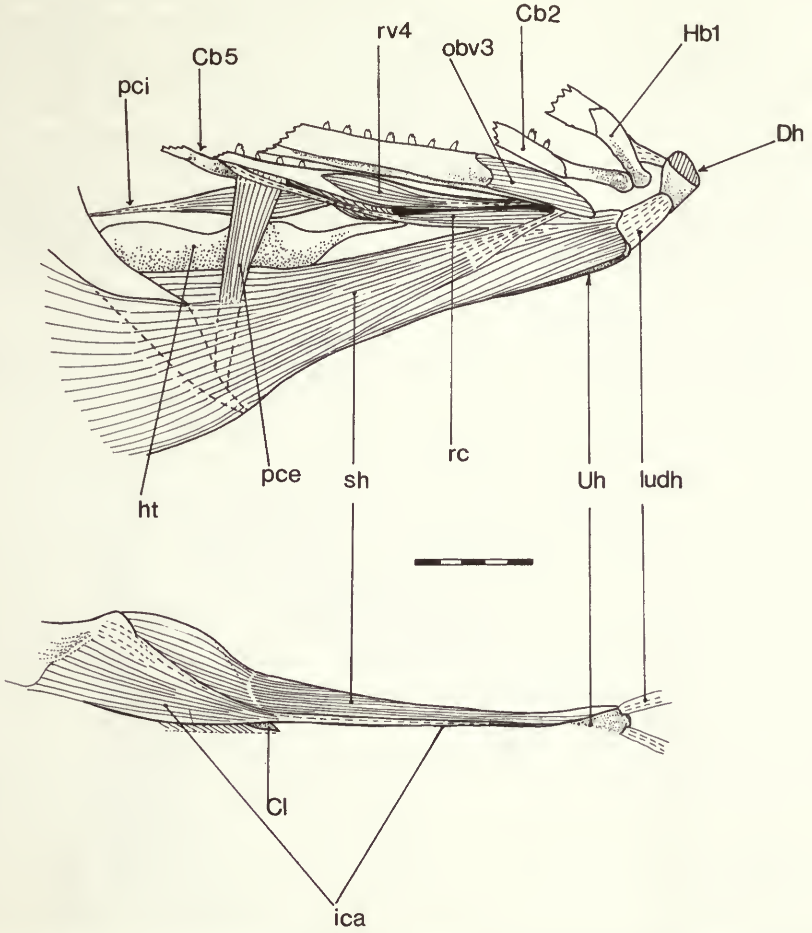

Fig. 35 Ventral gill-arch and hyoid muscles of a gadoid, *Gadomus longifilis*. Above, lateral; below, ventral view.

Functional and ecological inferences

Jaw protrusion mechanisms

Recent recoveries of live macrouroids (Wilson & Smith, 1985) while encouraging, also indicate the difficulties of maintaining these fishes under laboratory conditions. Results so far discount the possibility of obtaining direct experimental data on jaw function. One is therefore obliged to derive hypotheses of functional mechanisms from morbid anatomical investigation.

Those who have studied macrouroid anatomy are agreed that the jaws of most taxa are highly protrusible, the degree of protrusibility being a corollary of the length of the premaxillary ascending process (Okamura, 1970*a*,*b*; Marshall & Iwamoto, 1973: 479; Geistdorfer, 1975; McLellan, 1977;

Casinos, 1978; 1981). Several models of acanthomorph upper jaw protrusion mechanisms have been proposed, but most authors are in agreement that muscle A1 plays a predominant part in this function (see Lauder, 1982: 280; Motta, 1984 for references to, and review of previous literature). Rosen (1973) disagrees, however, believing that the development of an A1α or A1β division of the *adductor mandibulae* '. . . is not dependent on, or even correlated with, the existence of a protrusible jaw mechanism . . .'.

According to Anker (1974) muscle A1 serves not only to keep the mouth closed but possibly forces protrusion of the premaxilla. Gosline (1981: 15) thought the most likely cause of jaw protrusion in acanthomorph fishes is ligament IX, *viz.* that connecting the rostral cartilage with the maxilla. He hypothesised that as the maxilla twists around its articulation with the cranium, it pulls ligament IX anteroventrally, thus protruding the premaxilla which is attached to the rostral cartilage. This idea does not entirely explain protrusion, however, since the initial twisting of the maxilla must be explained in terms of muscular control. Is the maxilla pulled downward and inward passively by abduction of the lower jaw, or through direct action of muscles A1α and A1β?

McLellan (1977) accounted for upper jaw protrusion in macrouroids by the action of muscle A1, since she found that pulling on the maxillo-mandibular ligament along the line of force exerted by

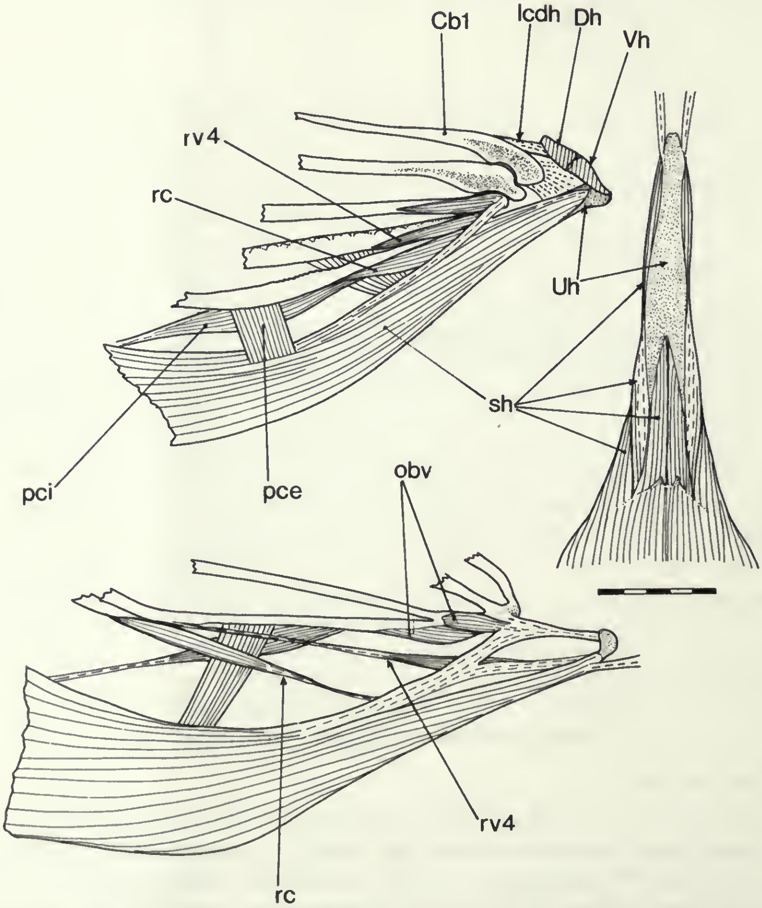

Fig. 36 Merlucciidae; ventral gill-arch and sternohyoid muscles of *Merluccius merluccius* in A, lateral and B, ventral views; the latter showing the partitions of the *sternohyoideus*. C, *Macruronus magellanicus* in lateral view.

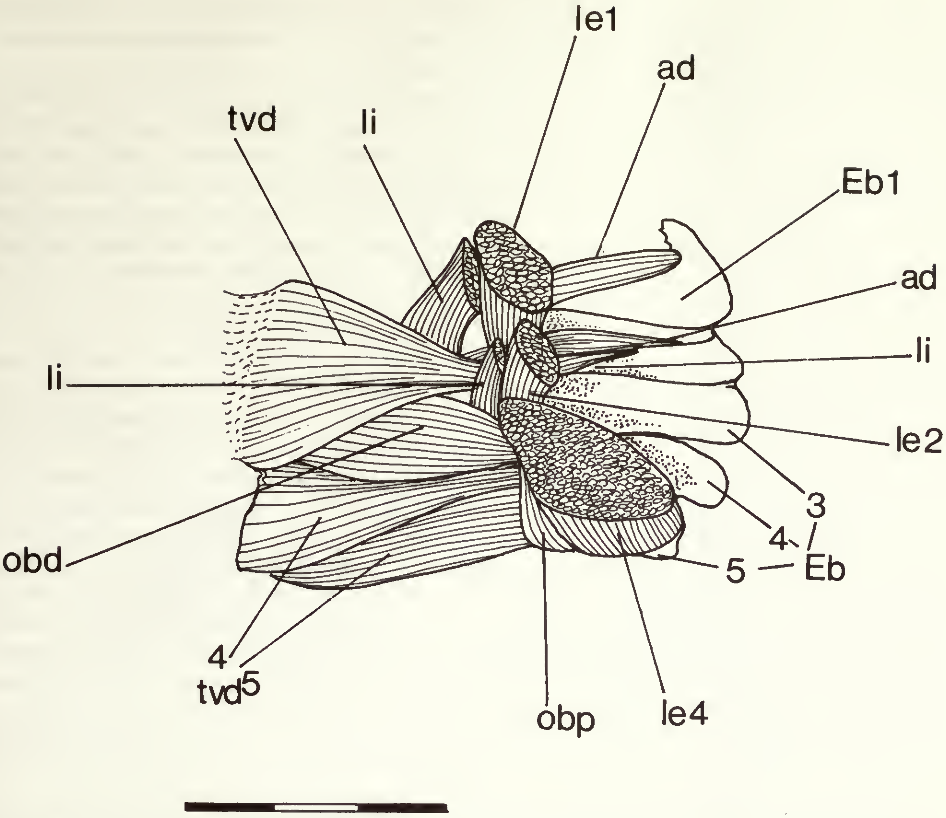

Fig. 37 Dorsal gill-arch muscles of a macrourid, *Coelorinchus caribbaeus* (dorsal view).

the fibres of A1 produced premaxillary protrusion. However, McLellan hypothesised that the macrouroid type of mechanism was '. . . a fundamentally different means of protruding the upper jaw from that of *Bathygadus*', which she supposed to be produced by rotation of the maxillary head (i.e. as in Gosline's hypothesis).

Geistdorfer (1975) gave a theoretical account of jaw movements in the macourine *Ventrifossa occidentalis*. For the most part, he considered jaw action to be similar to that in acanthopterygians and although stating that protrusion is limited by ligaments, he gave no account of arthrology.

Casinos (1981) attempted an explanation of jaw protrusion in gadids (Gadidae) based on observation by high-speed cinematography, and in macrouroids by the extrapolation of these data. According to Casinos, there is no or little jaw protrusion in gadids, except *Pollachius*, whereas there is pronounced protrusion in macrouroids.

Casinos devised a protrusion index (not to be confused with the protrusion index of Okamura, 1970*b*; see below) which showed that although the gadid *Pollachius* has a high degree of protrusion, comparable with that of macrouroids, the 'macrouroid' *Trachyrincus* has a low protrusion index comparable with that of the gadids.

Casinos' explanations of these apparent anomalies are confusing and rely on different sizes and moments of muscle A1β, and are also based on incorrect anatomical data. For example, Casinos explains the higher degree of protrusibility in macrouroids as due to an 'additional' rostro-maxillary ligament. However, a rostro-maxillary ligament (ligament VII, see p. 6) is present in *all* gadiforms and indeed all acanthomorphs (Stiassny, 1986).

I would agree with Casinos (1981) that the restriction of muscle A1β to the same vertical plane as A1α gives the macrouroid upper jaw a degree of freedom greater than that of gadoids where the vertical movement of the maxilla appears to be restricted by the obliquely and transversely angled A1β (particularly so in merlucciids where a short-fibred A1β runs from the palatine to the maxillary head thus affording the maxilla little downward movement).

As noted above (p. 38) in some gadoids, seemingly those with restricted jaw protrusibility, the insertion of A1β is sited further anteriorly on the maxilla than in those with a greater degree of jaw freedom. In macrouroids the insertion of muscle A1β is on the ventromedial prominence posterior to the maxillary head. As noted above (p. 39) in gadoids the ventromedial process is less prominent and in more advanced taxa is reduced to a medial shelf, with the insertion of A1β shifted anteriorly to what is regarded as the most derived situation, namely to the symphysial border of the maxillary head. It was also noted above (p. 39) that the anterior insertion of A1β is correlated with the medial shift and enlargement of the entire muscle.

What is possibly an important factor concerning differences in protrusion between macrouroids and gadoids is that in macrouroids muscle A1α is attached to the maxilla *via* the maxillo-mandibular ligament (Figs 1–4), whereas in gadoids A1α, although often associated with the maxillo-mandibular ligament is fastened to the jaw independently by its own tendon (Figs 9–20).

Another factor which may affect the degree of protrusibility is the ligamentous connection between the maxillary head and the premaxillary ascending process. It was noted above (p. 7) that there are different forms of attachment between these bones in gadoids. The ligament (lig. XI) either attaches directly to the bone or *via* a cylindrical chondroid or fibrous element. The latter form of attachment (confined to the more plesiomorphic gadoids) suggests a greater degree of separation between the bones. In macrouroids the meniscus is a thick disc, loosely interposed between the maxillary head and the premaxilla, with ligament IX also attaching to the rostral cartilage (Fig. 28B & C). Thus, the only check on a total downward release of the premaxilla is ligament XI, which connects the maxilla to the ethmoid. If this ligament is cut in preserved specimens, there is a dramatic and passive jaw protrusion. Such is not the case in gadoids where muscle A1β runs obliquely from the suspensorium to the maxilla and acts as a brake, but there is a pronounced protrusion in those gadoids where A1β, like the macrouroids, lies in the same vertical plane as A1α (e.g. *Bathygadus, Gadomus*). Thus, it is suggested that muscle A1β plays an active role in both holding and rotating the maxilla and so effecting protrusion of the premaxilla as hypothesised by Alexander (1963) and Gosline (1981).

A further point to be considered is that suggested by Casinos (1981) concerning the role of the labial 'ligament' (see p. 8). In Casinos' view in macrouroids the '. . . depression of the lower jaw transmits the force by means of the circumbuccal ligament' (= labial ligament). Since a labial ligament is also highly developed in some gadoids (*Bathygadus, Melanonus, Merluccius*) presumably the same function applies in these taxa. Casinos' statement is somewhat ambiguous, however, particularly as he regards the ligament as extending around the mandibles whereas in fact, there is a separate ligament attached to each dentary (see Fig. 9). Nonetheless, the idea that the ligament plays a role in protruding the upper jaw appears valid when one considers the direct linkage of the ligament from the mandible to the premaxilla and maxilla and that it appears to be a contractile element (see p. 8). In this regard, some attention should be paid to the work of Otten (1983) who points out the importance of the maxillo-dentary, and the posterior premaxillary-maxillary ligaments in jaw protrusion.

Otten (1983) recognised two groups of acanthopterygian fishes on the basis of jaw protrusion morphotypes:

1. in which the maxilla rotates about its long axis and pushes the premaxilla anteriorly (exemplified by *Perca*).
2. in which the maxilla pushes, pulls and retains the premaxilla in protruded position (occurs in cichlids). He notes, however, that these two groups show some degree of overlap.

Otten also makes the point that a shortening and steepening of the premaxillary ascending process coupled with a caudo-ventral shift in the insertion of muscle A1 are factors responsible for increased biting force. Although Otten's hypotheses were directed toward cichlid jaw mechanisms, these principles also apply to macrouroids. Most macrouroids differ noticeably from gadoids in their long, steep premaxillary ascending processes and posterior insertion of A1β (see p. 38).

Motta (1984) reviewed the history of ideas concerning the mechanics of teleost jaw protrusion and presented a classification of protrusion types but unfortunately disregarded paracanthopterygians in his account. Following Motta's classification the macrouroids and gadoids would seem to fall into three of his four categories, namely, type A: protrusion as a result of mandibular depression; type B: as a result of maxillary twist, and type C: as a result of neurocranial elevation (the degree of development of *epaxialis* musculature in many gadoids suggest this).

Motta also believes that the 'twisting maxilla model' has been overemphasised and that the 'mandible depression model' of jaw protrusion is probably the dominant type. Motta emphasised that the protruded mouth forms a circular orifice which is the most efficient configuration for employing suction feeding (see also Osse & Muller, 1980). A circular, protruded mouth profile is probably produced by all macrouroids and plesiomorphic gadoids (i.e. *Bathygadus, Gadomus*).

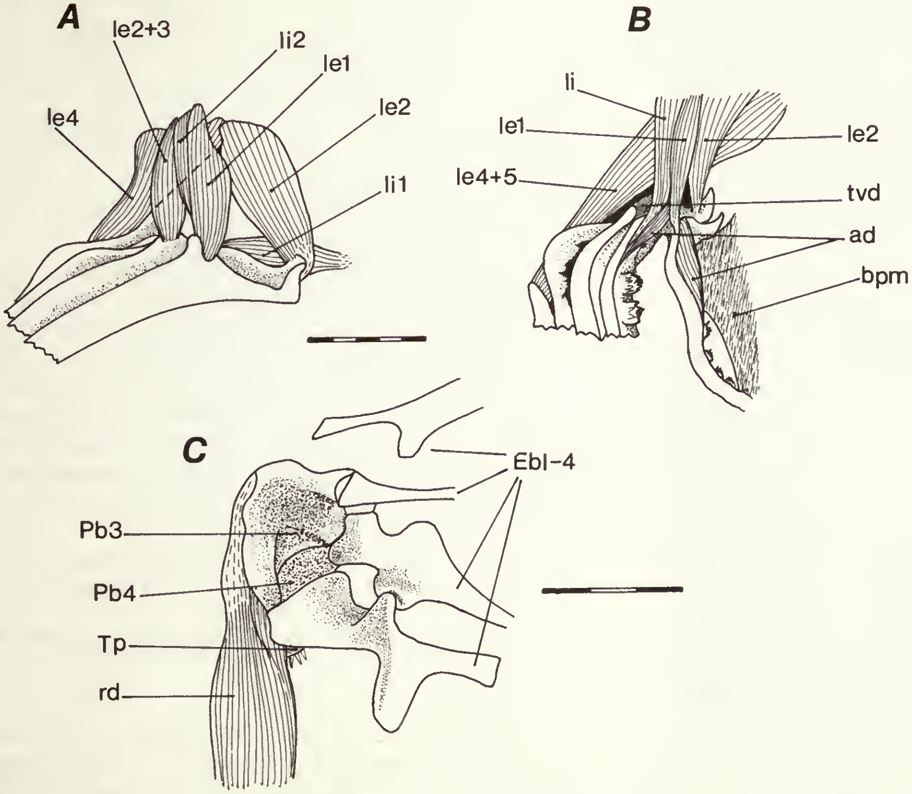

Fig. 38 Dorsal gill-arch muscles of: A, a gadoid, *Gadomus longifilis*; B, a macrourid, *Nezumia hildebrandi* (lateral views); C, *Nezumia hildebrandi* showing *retractor dorsalis* insertion (dorsal view).

Hyoid-opercular mechanisms

In discussing *Bathygadus*, McLellan (1977: 1026–7) states that '. . . the motion of the maxilla is mediated through a ligament of the interopercle . . .' and '. . . ligamentous connections between the interopercle, subopercle and opercle, and the contraction of the levator operculi muscle which runs from the cranium to the opercle.'

Although the opercular series-jaw linkage serves to depress the mandible, its effect on moving the maxilla is doubtful. Furthermore, McLellan has overlooked the fact that *Bathygadus*, in common with other gadoids, possesses a different jaw-opercular linkage system from that in other acanthomorphs (see p. 9). The interoperculum, instead of being the mediator between the mandible and suboperculum as in most acanthomorphs mediates between the mandible and preoperculum/hyomandibula. It should be noted that in most macrouroids and all gadoids the *adductor operculi* muscle inserts principally or entirely on the horizontal, opercular process of the hyomandibula; although the *levator* retains some attachment to the operculum, often its area of insertion is small and confined to the anterodorsal margin of the bone.

The *adductor operculi* normally acts as an antagonist to the *dilatator operculi* and together they elevate the operculum. The consequences of the redirection of the *adductor* force to the hyomandibula are difficult to evaluate, but a rotational component directly coupled *via* the hyomandibular-interopercular ligament to the lower jaw is suggested. Another feature to note is that because of the anterior shift of the *adductor operculi* and the reduced insertion area of the *levator operculi*, there is a greater medial surface area available for the insertion of the *hyohyoidei adductores,* and in the Phycidae, Lotidae and Muraenolepididae, for epaxial muscle as well (see p. 32).

The presence in the Trachyrincidae of a mandibulohyoid ligament (Fig. 32) may be another indication of this taxon's closer relationships with gadoids than macrouroids (see Howes, 1987). However, as yet, too few comparative data exist on the distribution of a mandibulohyoid ligament to comment on its phylogenetic value. It is certainly present in most, if not all basal euteleosts and has been reported in clupeomorphs, stomiiforms and percomorphs (see Verraes, 1977; Otten, 1982 for specific examples). The ligament has also been reported by Holmquist (1911) in the gadoid *Gadus*, a condition which I can confirm. Furthermore, the ligament is also present in other Gadidae examined and the Lotidae and Phycidae, but not in the Muraenolepididae.

According to Verraes (1977) a mandibulohyoid ligament is a feature of fishes having a long lower jaw and short interoperculum. In *Trachyrincus* the ligament attaches to the central part of the anterorhyal (Fig. 32) but in other gadoids it attaches to the posterior part of the anterohyal as in the percomorph *Perca* (see Verraes *op. cit.*). According to Lauder & Liem (1980: 389) in the salmonid *Salvelinus* the presence of the mandibulohyoid ligament possibly allows for another coupling to depress the lower jaw. Such may also be the case in *Trachyrincus* and other gadoids where it is present. Otten (1982: 47) believes that the occurrence of the mandibulohyoid ligament in various teleosts is homoplastic. 'Undoubtedly, ligaments are products of evolutionary pathways. Theoretically, redundancies may occur along these pathways, but it is more likely that ligaments evolve together with the whole apparatus in which they are functional . . .'.

Finally, it should be noted that macrouroids and gadoids possess an elongate interhyal. Lauder & Liem (1980) drew attention to two functional roles of the interhyal in feeding mechanics, namely:

> giving the hyoid an increased dorsoventral rotation and so providing greater orobranchial expansion
> giving the hyoid a posterodorsal movement.

Although the above discussion has concentrated on the jaw mechanism in terms of feeding, the various modifications of the jaws and their couplings in gadoids possibly have a greater significance in respiratory function. After all, Smith & Hessler (1974) have pointed out that the respiratory rate for cod (*Gadus*) is over twenty times greater than that for a macrourid (*Coryphaenoides*). Experimental and functional analytic data are needed to assess the significance of the gadoid type of lower jaw coupling in which an interopercular-preopercular-hyomandibular ligament is introduced.

Pharyngeal mechanisms

Geistdorfer (1975) described and commented on the pharyngeal dentition of various macrouroid genera but paid no attention to the pharyngeal musculature. There is little variation in both the upper and lower pharyngeal muscles in the taxa examined (see p. 48). In general the *posterior levatores* are long, deep and angled at 45°, suggesting a high degree of forward movement of the upper pharyngeal apparatus.

The functional significance of a *sternohyoideus* link with the *rectus communis* and *recti ventrales*

IV muscles is speculative. According to Lauder (1983: 25) the shift of the anterior attachment of the *rectus communis* from hypobranchial 3 to the urohyal is a key specialisation in the evolution of euteleostean pharyngeal manipulation. A urohyal attachment of the muscle provides an axial rotation to the pharyngeal tooth plates. In gadoids the degree of axial rotation allowed by a direct *sternohyoideus-rectus communis* link would seem to be minimal but might facilitate asymmetrical activity of the lower pharyngeal tooth-plates.

The reduction or absence of *obliqus ventrales* muscles associated with the 1st and/or 2nd gill arch is probably correlated with a strong ligamentous attachment of the 1st gill-arch to the hyoid bar.

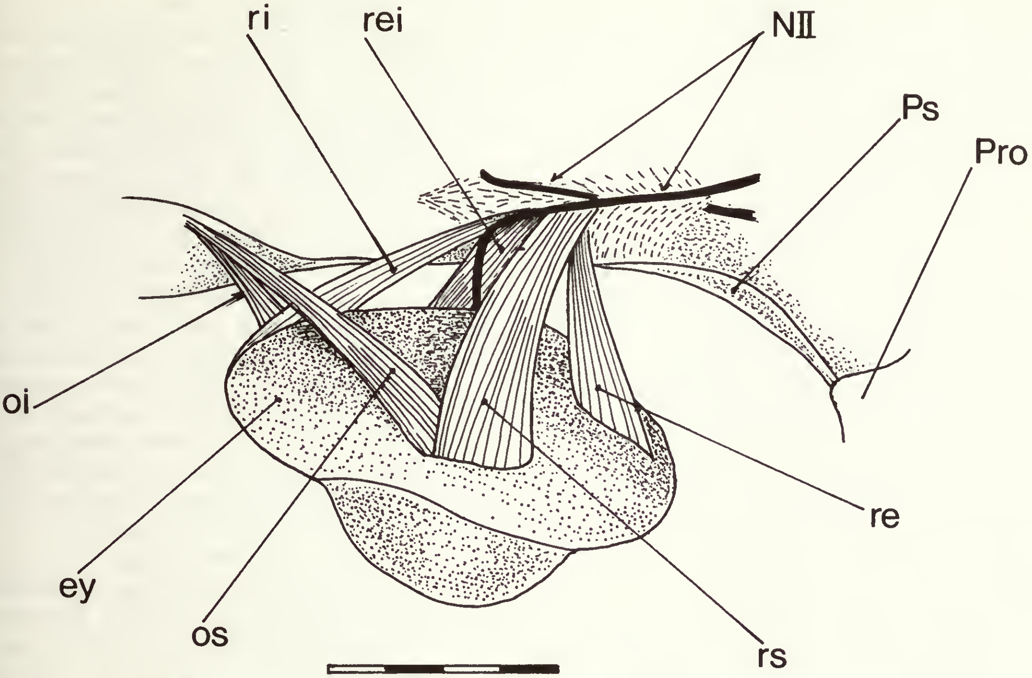

Fig. 39 Eye muscles of a gadoid, *Gadomus longifilis*. Dorsal view of left eye.

Trophic strategies

The trophic ecology of macrouroids is poorly known, but it would seem that the majority of taxa feed on a broad spectrum of organisms (see Mauchline & Gordon, 1985). This trophic diversity is a consequence of the rather unspecialised organisation of the adductor and ventral gill-arch musculature described in this text.

Okamura (1970*b*) classified macrouroids into four groups according to their jaw and mouth type and devised a protrusion index (a percentage ratio of premaxillary ascending process length to that of the ramus), the application of which gives a higher figure to the smaller mouth. Okamura attempted to relate the index to ecological categories, those taxa with a low index being predominantly nekton feeders, those with a high index being mostly benthic feeders. Okamura's groupings included *Bathygadus* and *Gadomus*, which are here considered to be gadoids and which according to his formula have a low protrusion index. *Trachyrincus* was not studied by Okamura, but application of his formula to this taxon gives it a protrusion index closer to *Bathygadus* and *Gadomus* than to any macrouroid.

McLellan (1977) also attempted to correlate head shape with trophic specialisations and believed she could match those taxa with long rostra (i.e. elongate nasals) to benthic habitats, whereas taxa with large, terminal mouths were associated with benthopelagic feeding. In McLellan's view *Bathygadus* and *Coelorinchus* represent two extremes of the Macrouridae with regard to ratio of mouth to head length, degree of jaw movement and expansion of orobranchial cavity. She considered *Bathygadus* to possess a prey-capture activity similar to that of 'other teleosts' with large, terminal mouths. However, as Lauder & Liem (1980: 387) point out, the feeding mechanisms of acanthopterygians (e.g. *Perca*) and basal euteleosts (e.g. *Salvelinus*) are quite different, involving different patterns of muscle activity. McLellan's reference to 'other teleosts' presumably refers to acanthopterygians, but the anatomical observations made in this text on the mode of jaw coupling in gadoids suggest that a somewhat different type of feeding pattern to that in other paracanthopterygians and in acanthopterygians might be operating.

McLellan (1977: 1034) hypothesised that *Coelorinchus* and taxa with a protracted rostrum feed by using the rostrum as a sediment probe, as did Casinos (1978) for *Trachyrincus*. McLellan argues that this method of feeding prevents rapid forward swimming necessary for creating suction. As such she sees a high degree of muscular control in varying the protrusion angle of the upper jaw (elsewhere, however, she noted that *Coelorinchus* has 'weak musculature'). McLellan's assumption that rapid swimming is the only means of generating suction is not entirely correct, however, and she seems to be confusing inertial suction and ram feeding. For example, Lauder & Liem (1980) in their study of the salmonid *Salvelinus* note that although this fish is not *primarily* a suction feeder, inertial suction *is* created by varying the sequence of muscle activity, i.e. the activation of the *levator arcus palatini* prior to that of the *levator operculi* and the hyoid musculature. McLellan appears to be working from similar assumptions made by Weihs (1980) that higher swimming speeds extend the suction field further forward. However, this strategy would seem applicable only to predatory fish using strike tactics rather than hovering fish sucking food from the substrate whose principal feeding method would seem more likely to be inertial suction (see Liem, 1980).

Both McLellan (1977) and Casinos (1978) have hypothesised that the rostrum of macrouroids and trachyrincids is used as a probe. Both authors have based their assumptions on the characteristic swimming mode of macrourids, shown in Marshall & Bourne (1964) to be head down and forming an angle of approximately 45° with the substrate. Isaacs & Schwartzlose (1975) have reported, from cinematographic evidence, macrouroids thrusting into the sediment and 'throwing a cloud of sediment through the gills'. Marshall (1979) believes this method of feeding enables macrourids to screen ooze-laden water by forcing it through the restricted first gill-slit. McLellan also supposed that the shorter snout of some species is probably more a sensory device than a mechanical probe. It should be emphasised that the rostrum is not part of the snout (i.e. ethmoid) but comprises the medially joined nasal bones which are trough-like, house many neuromasts and are fluid filled in life. Thus, a sensory function of the 'rostrum' seems a feasible idea. Casinos (1978) in his reconstruction of *Trachyrincus* probing and feeding from the substrate appears to overlook the fact that although the mouth may appear to be inferior in relation to the extended nasals, it is, in relation to the ethmoid, terminal. Furthermore, the lack of extended premaxillary ascending processes, the elongate jaws and the wide gape of the mouth (see p. 17) all point to *Trachyrincus* being benthopelagic rather than benthic in its feeding habits. Marshall & Merrett (1977: 489) point out that *Trachyrincus* '... has a marked preference for pelagic food'.

As mentioned above, macrouroids display little morphological specialisation in their jaw musculature but from their trophic diversification (see Mauchine & Gordon, 1985) it would seem that they are capable of employing some specialised feeding habits. In this respect their feeding mechanisms resemble those of cichlids recognised by Liem (1980) as being suboptimilised.

The hypothesis presented here and in Howes (1988) that *Bathygadus, Gadomus* and *Trachyrincus* are not members of the Macrouroidei, but represent clades within the Gadoidei, negates to a certain degree the functional hypotheses advanced by McLellan (1977) and Casinos (1978; 1981). To those authors, the Macrouroidei was unquestionably a monophyletic group and so functional mechanisms identified among any of the included taxa would be considered homologous. The identification of a different jaw coupling in *Bathygadus, Gadomus* and *Trachyrincus* that is shared with gadoids necessitates a reappraisal of macrouroid trophic strategies.

Taxonomic and phylogenetic inferences

The results of the character analyses in this study have already been utilised in another paper (Howes, 1988) to demonstrate the paraphyletic nature of the Macrouroidei. It has been established here and in Howes (1987) that four taxa formerly recognised as macrouroids, namely, *Euclichthys, Bathygadus, Gadomus,* and *Trachyrincus* share myological and arthrological synapomorphies with the Gadoidei, *viz.*:

anterior expansion of the jaw adductor muscle A1
reduction of *obliqui ventrales* on the 1st and 2nd gill-arches
rectus communis attaching aponeurotically to the *sternohyoideus* muscle
possession of an interopercular-hyomandibular-preopercular ligament.

As yet, there exists no comprehensive osteological account of *Bathygadus* and *Gadomus*, and their close affinities among gadoids are obscure. Howes (1988) tentatively recognised the Bathygadidae as the sister-group to the Moridae. The basis for this arrangement is the scale pattern shared between the two families. The scales are cycloid, with a *reticulate pattern of sulci.* According to Peabody (1931) the scale pattern of *Bathygadus* '. . . show no affinity for the Macrouridae and could easily be classified with either or both of the other families' (i.e. Gadidae and Bregmacerotidae). In Okamura's (1970*b*) opinion, the 'bathygadine' scales are not secondarily derived from the ctenoid scales present in macrourids but are 'essentially primitive' and he draws attention to the '. . . striking resemblance to morids . . . which are characterised by the reticulate structure of ridges on the exposed area'. There are, regrettably, no derived myological features shared between the Bathygadidae and Moridae, the shared myomorphology being plesiomorphic for gadoids.

The Bathygadidae was considered by Howes (1988) to represent a plesiomorphic lineage of gadoids. Work in progress has identified further synapomorphies that support the sister-group relationship of *Bathygadus* and *Gadomus* and the distinctiveness of the family (see also p. 18), but no further evidence has come to light which would suggest that the family is anything but plesiomorphic.

Trachyrincus and *Euclichthys* each represent gadoid lineages, the former being recognised as the sister-group to all other gadoids, the latter as the sister-taxon of more advanced gadoid families (Howes, 1988).

Intrarelationships of the Macrouroidei

The attrition of the Macrouroidei by the removal of the Euclichthyidae leaves a single family in the suborder, the Macrouridae. In turn, this family has been reduced by the removal of the 'Bathygadinae' and 'Trachyrincinae' to two subfamilies, the Macrouroidinae and Macrourinae. The former contains two genera, *Macrouroides* and *Squalogadus*, the latter some 30 genera of diverse external morphology.

The monophyly of the Macrouridae has been discussed by Howes (1988) and is supported by three derived characters; *levator arcus palatini* muscle enlarged and lying lateral to the jaw adductor musculature; trough-like nasal bones meeting in the midline; compressed, plate-like ethmoid.

The laterally placed *levator arcus palatini* is a feature shared with the gadoids and is discussed in Howes (1988).

The nasals of macrouroids are large, with a noticeable anteroventral curvature, the anterior border is often notched and the medial surface raised, contacting its partner along the midline. Enlarged, medially united nasals also occur in the gadoid family Trachyrincidae. Arguments for recognising the macrouroid and trachyrincid conditions as homoplastic are given in Howes (1988).

The ethmoid region of macrouroid taxa comprises a deep, vertical, plate-like bone with an expanded base capping a cartilaginous bloc. The plate-like part of the ethmoid divides the posterior borders of the nasals and the anterior borders of the frontals. The dorsal margin of the ethmoid is confluent with the dorsomedial margin of the nasals, thus forming a long crest. The identity of the ossified crest-like cap of the ethmoid is doubtful, but it is easily detached from the ethmoid (mesethmoid) cartilage and, as there is no sign of perichondral ossification, it would appear to be a rostrodermosupraethmoid.

Apart from the derived nature of the *levator arcus palatini*, which is also shared with the Gadoidei, no myological synapomorphies have been identified which corroborate the monophyly of the Macrouridae.

MACROUROIDINAE

Three myological apomorphies have been identified in *Squalogadus*, one is also known to occur in *Macrouroides* but it has not been possible, with the nature of the material available (see p. 15), to observe the other two features. These characters are:

> *protractor hyoidei* entirely separated in the midline (present in *Squalogadus* and *Macrouroides*)
> *intermandibularis* lacking
> *rectus ventralis* IV joins *rectus communis*, by-passes and inserts on ceratobranchial 5.

Okamura (1970*b*) treated the group as a family on the basis of '. . . notable differences from other macrouroids'. Indeed, from the characters he enumerates there is little doubt that the Macrouroidinae possess a number of uniquely derived features, e.g. anterior and posterior ascending processes of the ethmoid (? rostrodermethmoid); division of the orbital fontanel; reduced, filamentous lateral ethmoid; deep 1st infraorbital; enlarged 5th infraorbital. Other features listed by Okamura (*op. cit.*) as defining the group, however, appear to be plesiomorphic, *viz.*: unmodified gill-rakers, unrestricted buccobranchial aperture, dorsal fin lacking spinous rays, flattened parietal, bar-like parasphenoid. It is more difficult to ascribe polarity to certain other characters, e.g. 'rostral' cartilage between ethmoid and parasphenoid (Okamura appears to confuse the rostral and mesethmoidal cartilages); lachrymal lacking ascending process (this could be a plesiomorphic condition or a reversal).

MACROURINAE

The characters given by Okamura (1970*a,b*) and Marshall (1973) as defining macrourines are, for the most part synapomorphic; they are:

> aperture between operculum and 1st gill-arch restricted by bucco-pharyngeal lining (Fig. 38B).
> olfactory bulbs lying close to nasal sac and within the nasal cavity
> spinule-bearing scales
> swimbladder (often) with drumming muscles and high number of retia mirabilia
> presence of light organs (in some taxa).

The first three characters are common to all genera, but the other two only to some (see Fahay & Markle, 1984 for generic distribution of the light organs). No myological synapomorphies have been identified that support monophyly of the group.

Within the Macrourinae three groups of genera can be distinguished on the basis of their jaw adductor muscle morphology; see pp. 12–13. These groups largely correspond with Okamura's (1970*b*) scheme of generic relationships. Okamura's *Coelorinchus* group includes *Coelorinchus, Coryphaenoides* and *Abyssicola* and thus corresponds to my group Ia (p. 12). He also relates the genera *Ventrifossa* and *Malacocephalus*; *Odontomacrurus* and *Cynomacrurus*, and *Echinomacrurus*, *Cetonurus* and *Sphagemacrurus*; groupings which correspond with my group II (Table I). This group, however, is probably based on symplesiomorphies.

Two groups of genera can be distinguished on the basis of their ventral gill-arch musculature, namely those where the *rectus communis* has an aponeurotic attachment to the *sterno-hyoideus* (as in gadoids) and where the muscle inserts on the urohyal. The latter group comprising the majority of macrourine taxa, the former includes *Nezumia, Ventrifossa, Hymenocephalus, Odontomacrurus* and *Cynomacrurus*. All these genera except for one (*Nezumia*) belong to the jaw muscle morphotype II.

Conclusions

The salient points to emerge from this study of macrouroid and gadoid cranial muscles are:

Anatomical

The jaw adductor muscles of macrouroids are, in comparison with those of other 'paracanthopterygians', unspecialised. Muscle A1β is homologous with that so-called element in other acanthomorphs. Muscles A1α and A1β lie in the same vertical plane, an arrangement which seems to afford a large degree of jaw protrusion.

The arrangement of macrouroid hyoid muscles are typically those of acanthopterygians, *viz.*: anterior attachment of the *rectus communis* to the urohyal (with the exception of five genera), *rectus ventralis* IV to the 3rd hypobranchial, and a well-developed complement of *obliqui ventrales* muscles. In gadoids, the *rectus communis* and *rectus ventralis* IV attach directly to the *sternohyoideus* and the *obliqui ventrales* are reduced on the 1st or 1st and 2nd gill-arches (in some bathygadids they are absent from the 1st arch).

In common with acanthopterygians, macrouroids possess a mandibular-interopercular-subopercular ligamentous connection. In gadoids the linkage runs from the interoperculum to the hyomandibula, preoperculum or both. In both macrouroids and gadoids the *adductor operculi* muscle inserts wholly, or principally on the opercular process of the hyomandibula.

Macrouroids, in common with 'lower' gadoids have the *levator arcus palatini* situated posterolateral to the jaw adductor muscles. This is considered a derived condition and one allowing for a high degree of orobranchial expansion.

Taxonomic and phylogenetic

The Macrouroidei comprises a single family, the Macrouridae and two subfamilies, Macrourinae and Macrouroidinae. Although the monophyly of the Macrouridae is unsupported by myological characters, the presence of a maxillary-nasal ligament and a rostral cartilage attachment of ligament IX corroborates other synapomorphies.

Monophyly of the Macrouroidinae is attested by ventral gill-arch and hyoid muscle synapomorphies (pp. 43; 46). No myological characters have been identified as synapomorphic for the Macrourinae, although two jaw adductor muscle morphotypes are identified, one of which, possessed by the genera *Coelorinchus, Coryphaenoides, Abyssicola, Nezumia, Lionurus, Nematonurus* and *Chalinura* is considered to be derived.

Functional

Previous functional hypothesis of macrouroid feeding mechanisms were based on the assumption that the group is monophyletic. The studies of McLellan (1977) and Casinos (1978; 1981) included taxa which properly belong to the Gadoidei. Indications from jaw-opercular linkages and muscle insertions are that gadoids employ a different feeding mechanism from that of macrouroids. The extrapolation of data gleaned from functional studies of acanthopterygian fishes to 'paracanthopterygians' is a flawed approach.

Ecological

Hypotheses of trophic strategies have also suffered by the tacit assumption of macrouroid monophyly. The ecological and evolutionary scenarios of McLellan (1977) and Casinos (1978) must be reassessed in the light of the revised classification of macrouroids and gadoids (Howes, 1988; Howes & Crimmen, in prep.).

That the monophyly of a group so seemingly highly characterised as the Macrouroidei should be questioned is a warning that functional and ecological hypotheses must be used guardedly and are valid only for groups whose monophyly is well corroborated.

According to Lauder's (1981) 'decoupling hypothesis' there is a phylogenetic increase in the number of biomechanical components and their pathways. Thus the derived sister taxon of a group displays greater diversity and 'constructional flexibility' than its plesiomorphic sister taxon. The Gadoidei are hypothesised to be the derived sister group of the Macrouroidei (see Howes, 1988), and as such Lauder's hypothesis is borne out (in part) since the macrouroids lack what might be the more manipulative functions of the upper jaws possessed by gadoids. There is also a more complex arrangement of the hyoid and ventral gill-arch musculature in gadoids, although it is arguable whether a greater range of function is achieved (see p. 54). Only a complete comparative functional analysis of feeding mechanisms of taxa in the two groups will support Lauder's claim.

The intrarelationships of the morphologically diverse genera assigned to the Macrourinae have yet to be worked out cladistically. Myological characters have not been rewarding in this regard, and synapomorphies must be sought in other soft-anatomical (particularly in the structure of the light organs) and skeletal features.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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A review of the Macrochelidae (Acari: Mesostigmata) of the British Isles. By Keith H. Hyatt & Rowan M. Emberson

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A review of the Macrochelidae (Acari: Mesostigmata) of the British Isles

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This paper is dedicated to Ernest Browning, M.B.E., who died on the 1st September 1987, aged 91

Contents

Synopsis

Thirty-two species of mites of the family Macrochelidae are now known to occur in the British Isles. Descriptions are given for the nine species, including one new to science, recorded for the first time, and for other selected species. Habitat and distributional data are given and keys to the genera and species for adults are provided. Two neotypes and four lectotypes are newly designated. The genus *Dissoloncha* Falconer, 1923 is resurrected and four specific names are newly synonymized.

Introduction

It is over thirty years since the publication by Evans & Browning (1956) of their work on the British Macrochelinae (now generally treated as the family Macrochelidae). This work was a turning point in the taxonomic study of the Macrochelidae. For the first time it was relatively easy to identify many of the common macrochelids, not only of the British Isles but also of northern Europe and to some extent further afield. It was also the first substantial revisionary work on European macrochelids since that of Berlese (1918).

In the intervening time our knowledge of all aspects of macrochelids has increased rapidly. Their role as predators of the eggs and larvae of synanthropic flies has been fully realised, and steps taken to make practical use of this knowledge. In connection with this, detailed studies of the biology of

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*The first part of this work was done whilst on leave based at the British Museum (Natural History).

Bull. Br. Mus. nat. Hist. (Zool.) **54** (2): 63–125   Issued 28 April 1988

some species have been undertaken. Taxonomic work has proceeded at all levels within the family both in Europe and elsewhere. Generic concepts have changed, many new species have been described and the type specimens of old species re-examined. Groups of closely related species have been recognised and in some cases distinguished with the help of breeding experiments.

It therefore seems appropriate to apply this new understanding of the group to the fauna of the British Isles, particularly as part of the acarine collection of the Rev. J. E. Hull, containing some of his type material of British macrochelids, has been found and is now housed in the Arachnida collections of the British Museum (Natural History).

Evans & Browning (1956) recorded and gave descriptions of twenty-three species of Macrochelidae. It now seems likely that at least one and probably two of the species recorded by them are not members of the British fauna. The inclusion of these species was based on old records and no British material was seen by Evans & Browning or in the extensive collections examined in the present study. The names of seven previously recorded species must be changed. In all, nine species, one previously undescribed, are reported from the British Isles for the first time.

Since the main purpose of this work is to bring our knowledge of the British Macrochelidae up to date, species described in detail by Evans & Browning are not redescribed here although amendments are made where necessary. However, species not previously recorded are described fully. All the species are figured; those previously recorded are illustrated, with some minor amendments, from the original figures of Evans & Browning, since that paper has been out of print for many years, whilst those recorded for the first time are newly illustrated. Notes on morphology and classification are included and keys to genera, species groups and species are provided.

Material examined

The primary source of material on which this study is based is the large collection of Macrochelidae preserved in the collections of the British Museum (Natural History). Over five and a half thousand specimens have been examined. All the locality information for the British Isles is based on this material, except where otherwise noted.

In addition, macrochelid material in the Berlese Collection, Istituto Sperimentale per la Zoologia Agraria, Firenze, was examined. This was mainly for type material of species occurring in the British Isles, but much other material, particularly of European species, was also examined.

Type material of species described by Bregetova & Koroleva (1960) was borrowed from the Institute of Zoology of the Academy of Sciences, in Leningrad and parts of the extensive collection of North American and tropical macrochelids in the Department of Entomology, Oregon State University, Corvallis, were also examined.

The following abbreviations appear in the text:

BMNH:	British Museum (Natural History)
ISZA:	Berlese Collection, Istituto Sperimentale per la Zoologia Agraria, Firenze, Italy.
ZINL:	Institute of Zoology, Academy of Sciences, Leningrad, U.S.S.R.
OSUC:	Entomology Department, Oregon State University, Corvallis, U.S.A.

Morphology

A detailed study of the morphology of *Glyptholaspis confusa* (Foà) has been published by van der Hammen (1964), but not all of his interpretations would be accepted by all workers on Mesostigmata (Evans & Till, 1965). In general the terminology used here follows Evans & Till (1979).

Idiosoma

Dorsum

The system of setal nomenclature used here was first developed by Lindquist & Evans (1965) for the Ascidae and has since been widely applied to other groups of gamasine Mesostigmata. The relationships between the setal nomenclature used by Evans & Browning (1956) and that used here are shown in Figure 1A and further compared in Table 1 with those of Bregetova & Koroleva (1960) and Hirschmann (1957), both of which have been used by various authors. More recently Halliday (1986) has compared in detail the various systems of dorsal setal nomenclature used in the Macrochelidae and has advocated that of Lindquist & Evans (1965) for general application in this family.

The number of setae on the dorsal shield in British species is remarkably constant, varying from 56–60, but usually expressed as 28 regularly arranged pairs (Fig. 1A). The major exception to this arrangement is in the *opacus* species group of *Macrocheles* (the former genus *Macrholaspis* Oudemans) which always have setae *J3* present instead of *J2* and, in addition have 1–4 setae, often asymmetrically arranged between *j6* and *J3*. *M. montanus* (Willman) has both *J2* and *J3* present giving 29 pairs and *Glyptholaspis confusa* typically has one or two small asymmetric setae between *j6* and *J2*. The situation in *Geholaspis* Berlese is more difficult to interpret. It has the usual 28 pairs of setae but *j5* and *j6* appear to have migrated posteriorly from their usual positions.

Venter

The form and ornamentation of the sternal shield have been used as one of the main characters to distinguish the genus *Glyptholaspis* Fillipponi & Pegazzano from *Macrocheles*, whilst the pattern of lines described by Berlese (1918) is very useful in distinguishing species and species groups of *Macrocheles* (Fig. 1B).

The setal nomenclature system of Lindquist & Evans (1965) is used for the opisthogaster. The setation of the ventrianal shield is now known to be more variable than previously realised. *Holostaspella* Berlese may have three or four pairs of setae, *Zv1* lying either on or off the ventrianal shield. In all British species it is on the shield (Fig. 22D). The *opacus* species group of *Macrocheles*, previously recognised as a separate genus, *Macrholaspis*, largely on the basis of only having *Jv2*

Table 1 Chaetotaxy of the dorsal shield.

Dorsocentral series				Mediolateral series				Lateral series				Marginal series			
L & E	E & B	B & K	H	L & E	E & B	B & K	H	L & E	E & B	B & K	H	L & E	E & B	B & K	H
Anterior region (podonotum)															
j1	*D1*	*F1*	*i1*	*z1*	*M1*	*F2*	*r1*	—	—	—	—	—	—	—	—
j2	*D2*	*F3*	*s1*	*z2*	*M2*	*T1*	*s2*	*s2*	*L1*	*S1*	*r3*	*r2*	*Mg1*	*M1*	*r4*
j3	*D3*	*V*	*i2*	—	—	—	—	—	—	—	—	*r3*	*Mg2*	*M2*	*r5*
j4	*D4*	*D1*	*i3*	*z4*	*L2*	*Sc*	*z1*	*s4*	*Mg3*	*S2*	*s5*	*r4*	*Mg4*	*M3*	*r7*
j5	*D5*	*D2*	*i4*	*z5*	*M3*	*D3*	*z2*	*s5*	*L3*	*S3*	*s6*	—	—	—	—
j6	*D6*	*D4*	*i5*	*z6*	*M4*	*I1*	*z3*	*s6*	*Mg5*	*M4*	*s7*	—	—	—	—
Posterior region (opisthonotum)															
—	—	—	—	*Z1*	*L4*	*S4*	*Z1*	*S1*	*Mg6*	*M6*	*S1*				
J2	*D7*	*D6*	*J1*	*Z2*	*L5*	*S6*	*Z2*	*S2*	*Mg7*	*M8*	*S2*				
J3	—	*D7*	*J2*	—	—	—	—	—	—	—	—				
—	—	—	—	*Z4*	*L6*	*S7*	*Z3*	*S4*	*Mg8*	*M9*	*S3*				
J5	*D8*	*S8*	*J5*	*Z5*	*Mg10*	*M11*	*S5*	*S5*	*Mg9*	*M10*	*S4*				

L & E = Lindquist & Evans (1965)
E & B = Evans & Browning (1956)
B & K = Bregetova & Koroleva (1960)
H = Hirschmann (1957)

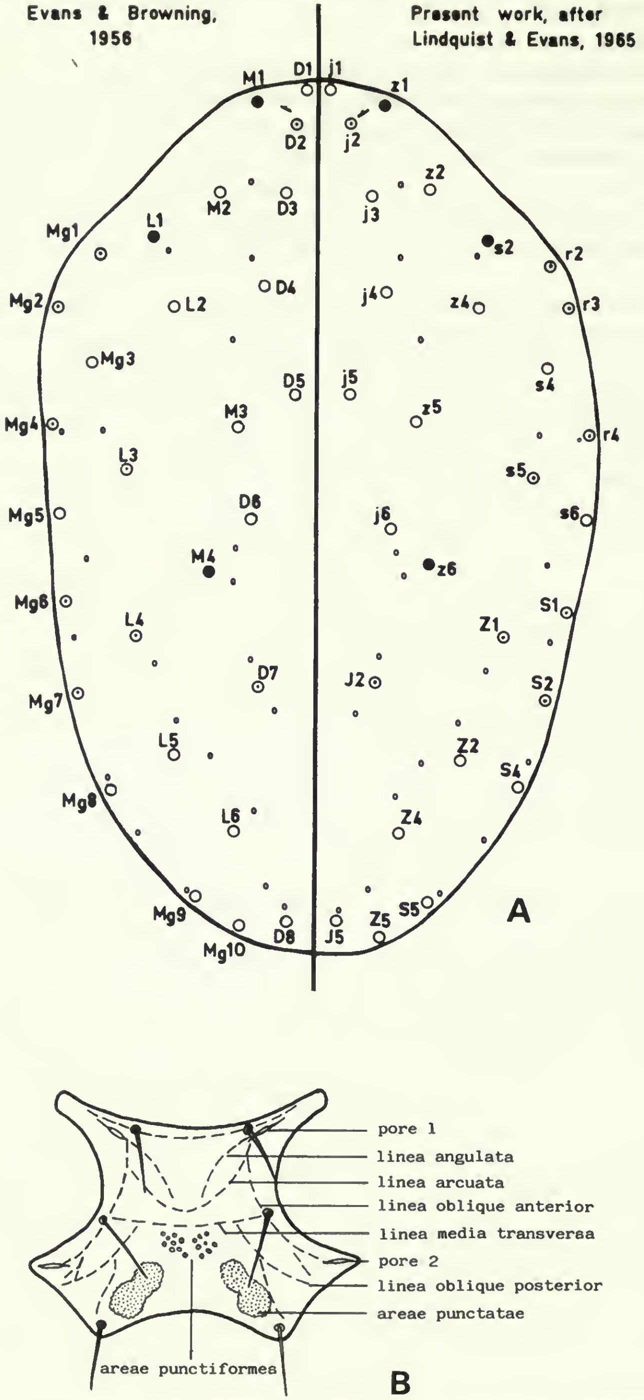

Fig. 1 A dorsal chaetotaxy of *Macrocheles* sp. comparing the systems of Evans & Browning (1956) and the present work, after Lindquist & Evans (1965); B structure and ornamentation of the sternal shield in the Macrochelidae, based on Berlese (1918).

and *Jv3* on the ventrianal shield, has been found to be much more variable. Species exist without any of the *Jv* series on the sclerotised part of the venter (Fig. 13B) and others with *Jv3*, or *Jv2* and *3* or *Jv1–3* on the ventrianal shield (Fig. 3B).

The distribution and type of pore-like structures in the Gamasina has been studied by Athias-Henriot (1969). The inguinal pores occur in the anterolateral corners of the ventrianal shield in *Geholaspis* and *Dissoloncha* Falconer, but are free on the membrane in *Macrocheles, Glyptholaspis* and *Holostaspella.*

In the genus *Glyptholaspis* all males have holoventral shields, whilst in *Dissoloncha* the males have separate sternogenital and ventrianal shields. In *Macrocheles* and *Holostaspella* the males have either separate sternogenital and ventrianal shields or holoventral shields.

Gnathosoma

The terminology used is that of Evans & Till (1979). The chaetotaxy of the pedipalps has been investigated by Evans (1964). The numbers and positions of setae in the Macrochelidae are quite typical for the free-living Gamasina having 2–5–6–15–15 setae on the trochanter, femur, genu, tibia and tarsus respectively.

The form and length of the brush-like outgrowths of the cheliceral arthrodial membrane are important at the generic level, although they do not vary much in the British species. The form of the cheliceral dorsal seta is of use in distinguishing species groups in *Macrocheles.* The shape of the gnathotectum is of importance at the generic level and for species groups in *Macrocheles* (Figs 2B, 7B, 13B).

Legs

Leg I is without ambulacral apparatus in all British species although species with pulvilli in the adults and pulvilli and claws in the immature stages have been assigned to the macrochelid genus *Neopodocinum* Oudemans by Krantz (1965).

The leg setation of the Gamasina has been studied by Evans (1963). Macrochelids have a remarkably constant pattern of leg setation (Table 2). The only variation known in species from the

Table 2 Numbers of setae on leg segments in the Macrochelidae.

legs	I	II	III	IV
coxa	2	2	2	1
trochanter	$1\text{-}\frac{0}{3}\text{-}1$	$1\text{-}\frac{0}{3}\text{-}1$	$1\text{-}\frac{0}{3}\text{-}1$ or $1\text{-}\frac{0}{2}\text{-}1$	$1\text{-}\frac{0}{3}\text{-}1$
femur	$2\text{-}\frac{5}{4}\text{-}2$	$2\text{-}\frac{5}{3}\text{-}1$	$1\text{-}\frac{0}{2}\text{-}1$	$1\text{-}\frac{3}{1}\text{-}1$
genu	$2\text{-}\frac{3}{1},\frac{2}{1}\text{-}2$	$2\text{-}\frac{3}{1},\frac{2}{1}\text{-}2$	$1\text{-}\frac{2}{1},\frac{2}{0}\text{-}1$	$1\text{-}\frac{2}{1},\frac{2}{0}\text{-}0$ or $1\text{-}\frac{2}{1},\frac{2}{0}\text{-}1$
tibia	$2\text{-}\frac{3}{2},\frac{2}{1}\text{-}2$	$2\text{-}\frac{2}{1},\frac{2}{1}\text{-}2$	$1\text{-}\frac{1}{1},\frac{2}{1}\text{-}1$	$1\text{-}\frac{1}{1},\frac{2}{1}\text{-}1$
tarsus	—	18	18	18

British Isles is in genu IV which has seven setae in *M. subbadius*, seta pl_1 being present, instead of the usual six setae. This condition is also found in a few other species of *Macrocheles* and in the mainly tropical genera *Holocelaeno* Berlese and *Neopodocinum*. The genus *Neopodocinum* also has only four setae on trochanter III instead of the usual five due to the absence of one of the ventral setae.

The distribution of spurs on the legs of male macrochelids is useful at the generic level; *Glyptholaspis* having spurs on legs II, III and IV, *Macrocheles* on legs II and often on legs IV and *Holostaspella* only on femur II, if at all. The form and precise distribution of these spurs is also useful in distinguishing closely related species, as are the spurs on leg II of female *Holostaspella*.

Spermathecal structures

Recently there have been a number of studies on the method of insemination of gamasine mites and of the spermathecal structures. The information derived from this work has proved to be useful at all levels of classification in the Gamasina.

There appear to be two basic types of insemination (Athias-Henriot, 1968), vaginal, or tocospermic, in which insemination is via a median endogynal, cuticular sac and podospermic where it is via tubular cuticular invaginations associated with the bases of legs III or IV. In the British Gamasina, tocospermic insemination is found only in the families Parasitidae, Epicriidae and Zerconidae. Podospermic insemination is characteristic of other gamasine groups.

Within the podospermic group two main variations of the spermathecal structures (Michael's organ) are found, the tubular cuticular invaginations may lead either to paired terminal organs (phytoseiid type) or to a single median organ (laelapid type). Paired spermathecal structures are found in the Phytoseiidae and some genera of the Ascidae (*sensu* Lindquist & Evans, 1965), median spermathecal structures are found in most other families of the Gamasina, including the Macrochelidae.

The spermathecal complex has been described for a number of species of European Macrochelidae (Petrova, 1960; Costa, 1966*a*, 1967; Athias-Henriot, 1968) and provides good taxonomic characters at the generic and species level.

The opening, or solenostome, of the *tubulus annulatus*, is always on the posterior basal margin of coxa III. In *Macrocheles* the infundibulum is well developed, the rami are usually short and the sacculus generally consists of two, more or less, spherical lobes broadly joined by a tubular section which gives rise to the corniculum posteriorly (Fig. 14F). In a few species the sacculus is unlobed, spherical and merges into the corniculum to give an overall pear-shaped median organ (Costa, 1967). *Dissoloncha superbus* has a very different sacculus from all other species of Macrochelidae: it is large, more or less spherical and strongly convoluted.

Classification

Evans & Browning (1956) recognised two subfamilies of Macrochelidae, the Macrochelinae Trägårdh, 1949 (*sic*) and the Areolaspinae Trägårdh, 1952, based mainly on the patterns of fusion of the ventral shields. Subsequently Evans (1956), in a radical reappraisal of the classification, taking into account the great variation shown in the ventral shields, proposed a new classification based on characters of the peritreme, gnathotectum, genital sclerotisation and gnathosoma. In this classification the family was split into the Macrochelinae Trägårdh (*sic*) and the Parholaspinae Evans 1956 (*Areolaspis* having been shown to be closely allied to other macrocheline genera).

Krantz (1969) regarded the two groups as distinct families, as have most subsequent authors, but see Karg (1971) and Krauss (1970). Evans' (1956) definition of the group, however, remains almost unchanged.

About sixteen genera of Macrochelidae are distinguished at present, of which only five occur in the British Isles. There has been some change in generic limits affecting these genera during the last thirty years.

Macrholaspis is now generally regarded as a synonym of *Macrocheles* (Krantz, 1962) following recognition of species closely related to the type species, *Gamasus opacus* C. L. Koch, with three pairs of setae on the ventrianal shield and lacking denticulate margins to the dorsal shield.

The genus *Glyptholaspis* has been split off from *Macrocheles* to contain several species, including two formerly confused under the name *M. plumiventris* Hull, in the British fauna. The main distinguishing features of the genus are the posterior extension of the sternal shields, the crenulate reticular pattern of the main shields and the presence of spurs on legs II, III and IV in the male. The genus *Dissoloncha* Falconer is here resurrected for *M. superbus* Hull, which is shown to share characters of the gnathosoma and other features with *Geholaspis* and to be isolated from *Macrocheles* s. str.

The generic limits of *Holastaspella* have been widened to include species without seta *Zv1* on the ventrianal shield* and a greater range of variation in the form of the ventral sclerotisation.

Geholaspis remains essentially unchanged although some authors give the subgenus *Longicheles* Valle full generic status (Athias-Henriot, 1968).

A number of species groups have been distinguished in the genus *Macrocheles* following the work of Filipponi & Pegazzano (1962, 1963) on closely related species. This concept has been extended by Krantz (1972) and is also used here.

Key to the genera of Macrochelidae occurring in the British Isles

1 Femur II armed with a sclerotised spur in the female, seta *mv* of tarsus II modified into a thick spine (Fig. 22B); vertical setae inserted on an anterior projection of the dorsal shield (Fig. 22A). British species with four pairs of preanal setae on the female ventrianal shield . . . . . .
HOLOSTASPELLA Berlese (p. 118)

– Femur II unarmed in the female, seta *mv* of tarsus II unmodified; without anterior projection of the dorsal shield. British species never with four pairs of preanal setae 2

2 Ventrianal shield with inguinal pores on anterolateral corners; gnathotectum lacking lateral processes (Figs 2B, 4E); corniculi three or more time longer than broad (Fig. 3C) 3

– Inguinal pores free on post-coxal membrane; gnathotectum with free or fused lateral processes (Fig. 7B, D); corniculi no more than twice as long as broad, or if gnathotectum without lateral processes and corniculi elongate then with anal shield only (Fig. 13B). 4

3 Ventrianal shield with five pairs of preanal setae; terrestrial litter species . . . . . .
GEHOLASPIS Berlese (p. 69)

– Ventrianal shield with three pairs of preanal setae; seashore species . . . .
DISSOLONCHA Falconer (p. 76)

4 Sternal shield with characteristic reticulate pattern (Pl. 3C), extending posterolaterally to level of posterior margins of coxae III; legs II–IV of males armed with spurs . . . .
GLYPTHOLASPIS Filipponi & Pegazzano (p. 114)

– Sternal shield variously ornamented but never similar to the above, not produced posterolaterally beyond the middle of coxae III; legs II and sometimes IV, but not III, armed with spurs and tubercles in the male . . . . ***MACROCHELES*** Latreille (p. 78)

Genus *GEHOLASPIS* Berlese

Geholaspis Berlese, 1918. *Redia* **13**: 145.

TYPE SPECIES. *Gamasus longispinosus* Kramer, 1876.

The dorsal shield has 28 pairs of setae which are mostly pilose or plumose distally. The ventral setae are mostly simple except towards the posterior lateral margins. The sternal and genital shields are similar to those of *Macrocheles*, but the metasternal plates may be free or fused to the endopodal shields (subgenus *Cyrtocheles* Valle). The ventrianal shield has five pairs of preanal setae and bears the inguinal pores (Athias-Henriot, 1969) in the anterolateral corners. Males, where known, have

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*It should be noted that contrary to the statement and figures of Krantz (1967), *H. sculpta* Berlese, the type species of *Holostaspella*, in fact lacks setae *Zv1* on the ventrianal shield (Filipponi & Pegazzano, 1967, and personal observation of R.M.E.).

holoventral shields. The gnathotectum has an elongate median process that may be toothed or bifurcate distally and dentate laterally. The chelicerae may be either short (*Geholaspis* s. str. and *Cyrtocheles*) with basically tridentate fixed chelae and bidentate movable chelae, or very elongate (*Longicheles* Valle) and multidentate. The spermatodactyl is short and dorsally directed. The corniculi are elongate, more than three times as long as broad and the external hypostomal setae are anterior to the internals. The males have a small spur on femur II.

The setation of the dorsum varies from the usual condition as seen in *Macrocheles* (Fig. 1A) in that setae *j5* are displaced posteriorly, so as to lie mesad and only slightly anterior of *j6* in subgenera *Geholaspis* s. str. (Figs 2A, 3A) and *Cyrtocheles* and considerably posterior to setae *j6* in subgenus *Longicheles* (Figs 4A, 5A). This latter position is associated with a posterior projection of the podonotal shield in the protonymphs and is no doubt a consequence of a posterior migration of the cheliceral retractor muscles, associated with the massive development of the chelicerae in this subgenus.

Key to subgenera and species of *Geholaspis* s. lat. recorded from the British Isles

1 Cheliceral digits short, with not more than 5 teeth (Fig. 2C); gnathotectum more or less triangular, median process with prominent lateral projections (Fig. 2B) Subgenus ***GEHOLASPIS*** s. str. 2

– Cheliceral digits prominently elongate, multidentate, movable digit with 10 or more teeth (Fig. 4F); gnathotectum with median process parallel sided, bifurcate distally (Fig. 4E) . . . . Subgenus ***LONGICHELES*** Valle 3

2 Dorsal setae less than 100 μm in length; ventrianal shield only slightly wider than long (Pl. 4A). . . . . ***Geholaspis (G.) longispinosus*** (Kramer) (p. 70)

– Dorsal setae generally exceeding 150 μm in length; ventrianal shield conspicuously wider than long (Fig. 3B) . . . . ***Geholaspis (G.) aeneus*** Krauss (p. 71)

3 Setae *z5* simple (Fig. 4A); median process of gnathotectum smooth or minutely denticulate behind terminal bifurcation (Fig. 4E); ventrianal shield almost as broad as or broader than long (Fig. 4B–D) . . . . ***Geholaspis (L.) mandibularis*** (Berlese) (p. 74)

– Setae *z5* plumose, *j6* serrate or simple (Fig. 5A); median process of tectum strongly toothed behind terminal bifurcation (Fig. 5C); ventrianal shield noticeably longer than broad (Fig. 5B) . . . . ***Geholaspis (L.) hortorum*** (Berlese) (p. 74)

Geholaspis (Geholaspis) longispinosus (Kramer)
(Fig. 2A–C, Pl. 4A)

The description and synonymy given by Evans & Browning (1956) are unchanged.

MATERIAL EXAMINED. 127 collections—4 PNN, 16 DNN, numerous ♀♀.

ENGLAND: Isles of Scilly, Cornwall, Devon, Somerset, Dorset, Gloucestershire, Hampshire, Sussex, Surrey, London, Kent, Essex, Cambridgeshire (including Huntingdonshire), Norfolk, Suffolk, Hertfordshire, Berkshire, Buckinghamshire, Worcestershire, Warwickshire, Lincolnshire, Yorkshire, Cumbria (Cumberland and Westmorland), Northumberland.

SCOTLAND: Strathclyde (Argyllshire), Dumfries & Galloway (Wigtownshire), Tayside (Perthshire), Highland (Inverness-shire, Wester Ross), Inner Hebrides (Mull, Ulva), Shetland.

WALES: Glamorgan, Gwent, Gwynedd (Merionethshire and Caernarvonshire), Clwyd (Denbighshire).

IRELAND: Clare, Westmeath, Galway, Mayo, Leitrim.

CHANNEL ISLANDS: Jersey.

HABITATS. Found in all sorts of forest leaf litter, among dead grass and other decaying vegetation, also in moss. Bregetova & Koroleva (1960) also have records from small mammal nests.

DISTRIBUTION. One of the commonest European macrochelids, found throughout the British Isles and Europe generally (Valle, 1953; Balogh, 1958; Bregetova & Koroleva, 1960; Halaskova & Kunst, 1960; Johnston, 1970; Krantz, 1972). Emberson (1973*a*) has reported the species from New Zealand where it is presumably adventive.

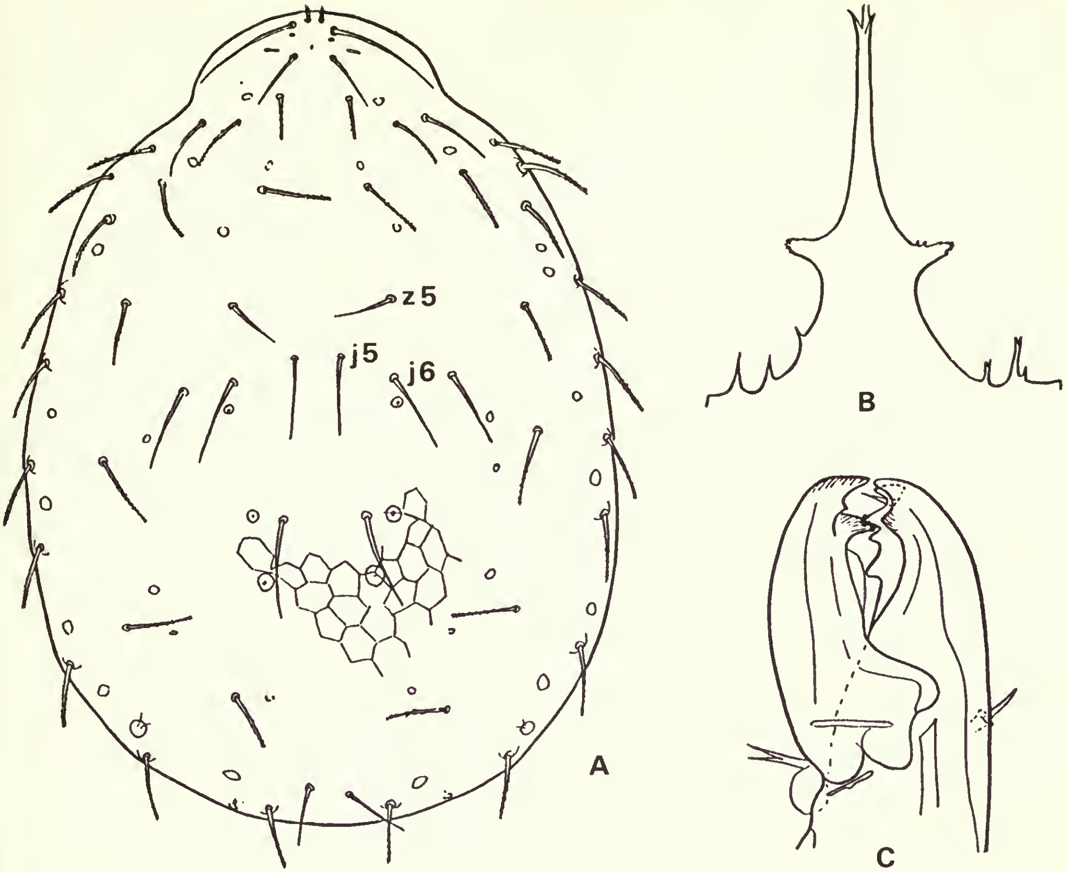

Fig. 2 *Geholaspis (G.) longispinosus* (Kramer): **female**—A dorsal shield; B gnathotectum; C chelicera. After Evans & Browning (1956).

Geholaspis (Geholaspis) aeneus Krauss
(Fig. 3A–C)

Geholaspis (Geholaspis) aeneus Krauss, 1970. *Acarologie* **14:** 38.

FEMALE. The dorsal shield (Fig. 3A) measures 1130 µm long × 840 µm wide (Krauss gives 1050 µm × 750 µm) and is finely granular. The posterior half is covered by a finely regular reticulated pattern, whilst anteriorly it is punctate-reticulate towards the lateral margins. There are 28 pairs of setae. With the exception of setae *j1, z1* and *J5*, all exceed 150 µm in length. The majority are finely pilose, at least in their distal halves. The dorsal pores are conspicuous.

The ventral ornamentation and chaetotaxy are shown in figure 3B. The sternal shield has a characteristic reticulate pattern. The metasternal plates are free. The genital and ventrianal shields have strong reticulate ornamentation. The ventrianal shield (460 µm long × 630 µm wide) is conspicuously wider than long and the preanal setae appear to be simple.

The venter of the gnathosoma is shown in figure 3C. The corniculi measure *c.* 140 µm in length, and the setae appear simple. The chelicerae and gnathotectum are not visible in the only specimen available for study. The leg setae are normal for the genus. The majority are pilose, whilst those on tarsus I and distally on the remaining tarsi are simple.

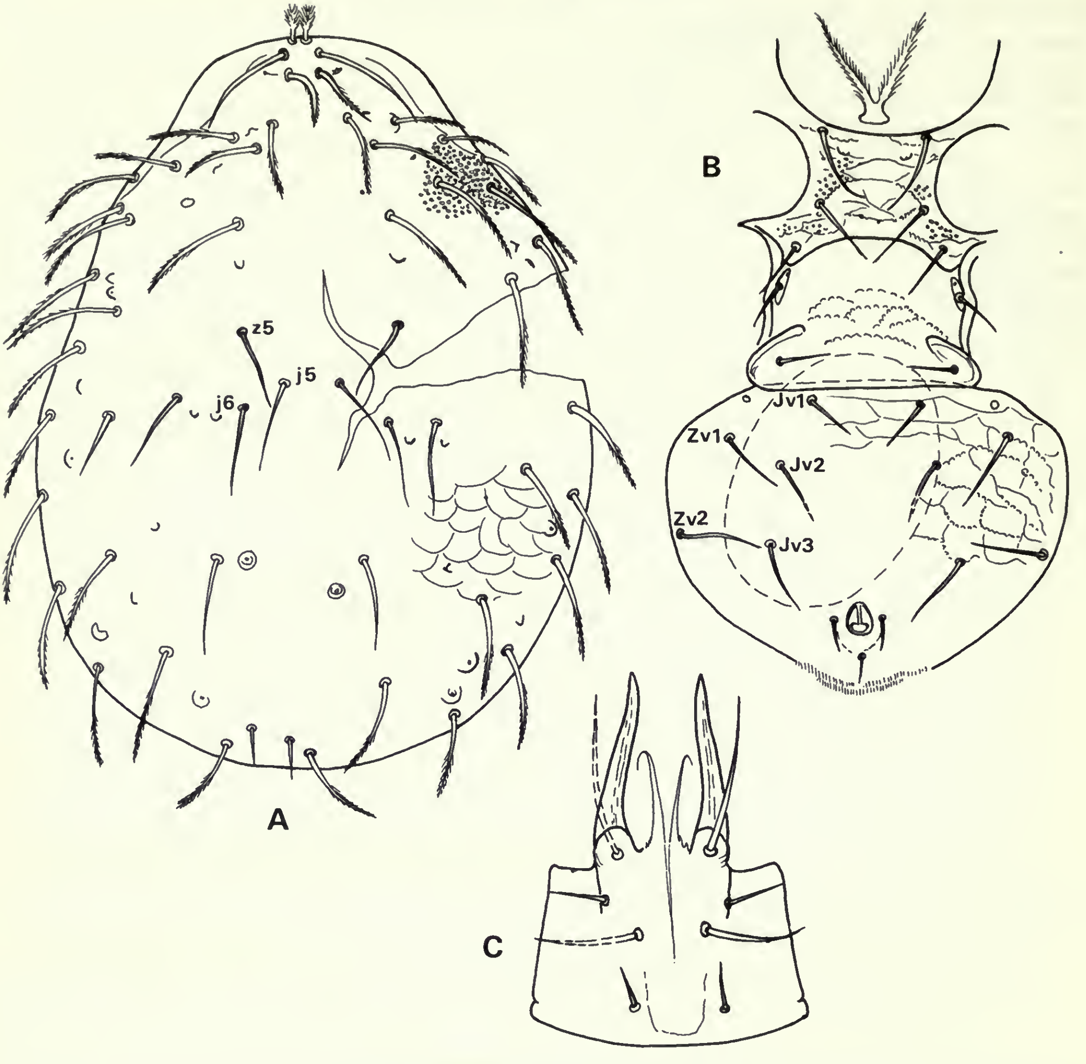

Fig. 3 *Geholaspis (G.) aeneus* Krauss: **female**—A dorsal shield; B ventral sclerotisation; C venter of gnathosoma.

MATERIAL EXAMINED. 1 collection—1♀, in moss.
IRELAND: Mayo. See below.
This is the first British record.

REMARKS. This species was described from protonymph, deutonymph and female stages collected at Valle de Lozera, Puento de Lozera (600 m), Lugo Province, in northwest Spain (Krauss, 1970). The habitat is given as the foot of an old sweet chestnut *Castanea sativa* tree and an oak *Quercus toza* tree in a dry river-bed. We have tried to obtain specimens, but have been informed by Dr W. Hirschmann that Dr Krauss (pers. comm.) has no specimens in his possession.

The Halbert collection contains a single slide preparation labelled '*Holostaspis longispinosus* (Kram.), 1♀, Clare Island, in moss, III/1910'. The idiosoma of this specimen has been damaged on the slide and it is felt at present inadvisable to dismount it. However, the dorsal and ventral chaetotaxy and the venter of the gnathosoma are clearly discernible.

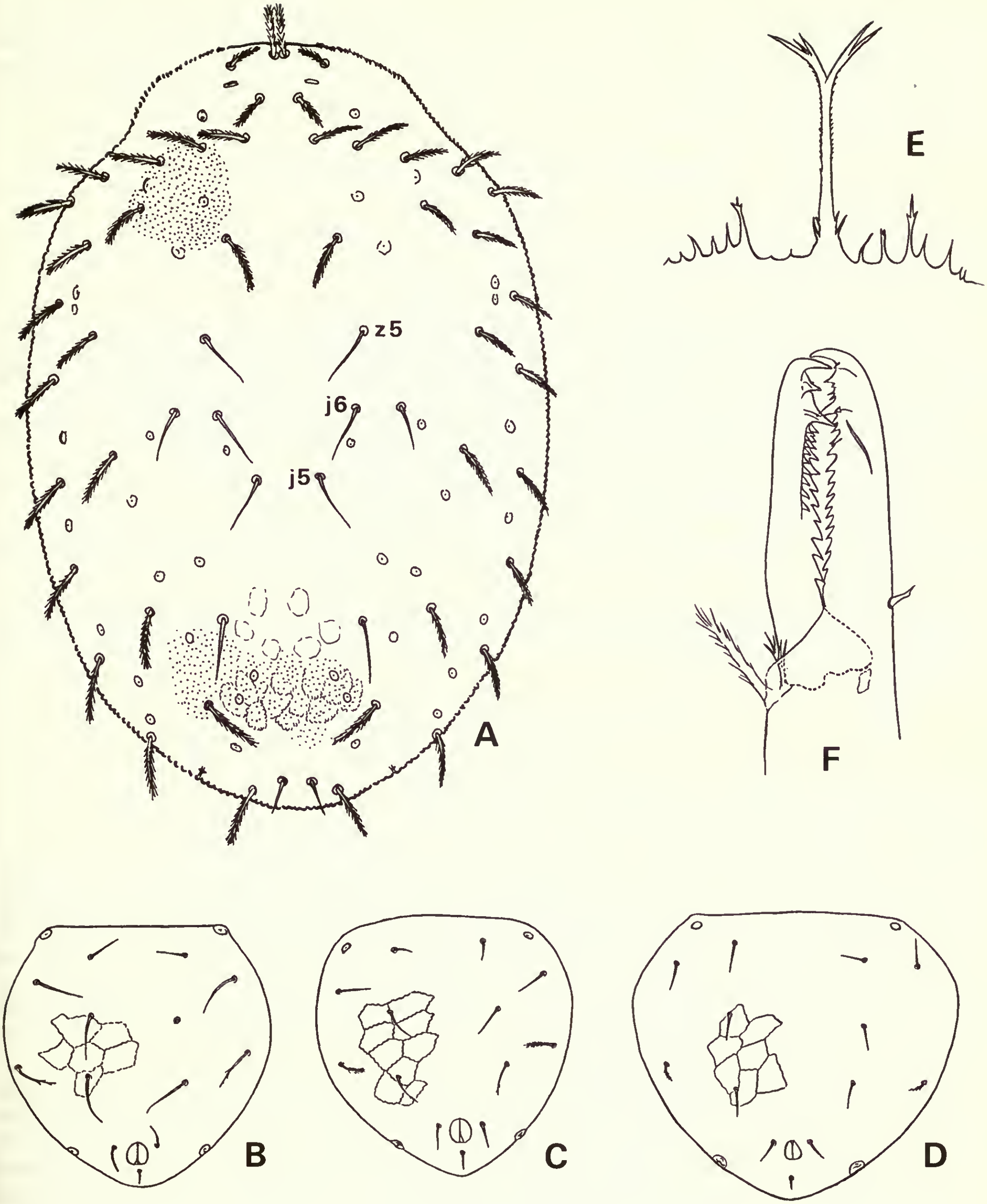

Fig. 4 *Geholaspis (Longicheles) mandibularis* (Berlese): **female**—A dorsal shield; B–D variation in the form of the ventrianal shield; E gnathotectum, F chelicera. After Evans & Browning (1956).

Geholaspis (Longicheles) longulus (Berlese)

The presence of this species in the British Isles is now doubtful. The discovery of a specimen in the Hull Collection with the data '*Macrocheles longulus* dead fowl' is probably the one mentioned (Hull, 1918) as being caught 'at one of my carrion traps'. This is a specimen of *G. longispinosus*. The specimens recorded by Halbert (1915) from Clare Island, Mulranny and Castlebar, all in Co. Mayo, have been examined and are *G. mandibularis*.

Geholaspis (Longicheles) mandibularis (Berlese)

(Fig. 4A–F)

The description and synonymy given by Evans & Browning (1956) do not require amendment.

TYPE MATERIAL. **Holotype** ♀, Cansiglio. Slide 2/34 [ISZA].

MATERIAL EXAMINED. 114 collections—3 PNN, 29 DNN, many ♀♀.

ENGLAND: Isles of Scilly, Cornwall, Somerset, Dorset, Gloucestershire, Hampshire, Surrey, Sussex, London, Kent, Middlesex, Hertfordshire, Suffolk, Cambridgeshire (including Huntingdonshire), Berkshire, Lancashire, Cumbria (Westmorland), Northumberland.

SCOTLAND: Strathclyde (Argyllshire), Dumfries & Galloway (Wigtownshire), Inner Hebrides (Mull, Ulva, Iona), Highland (Ross & Cromarty), Shetland.

WALES: Glamorgan, Gwent, Gwynedd (Merionethshire and Caernarvonshire).

IRELAND: Clare, Sligo, Galway, Mayo, Leitrim, Westmeath.

HABITATS. A wide variety of litter habitats, also turf, soil, moss, ants' nests and nests of small mammals.

DISTRIBUTION. Found throughout the British Isles and widespread in Europe (Valle, 1953). The specimens recorded by Halbert (1915) from Co. Mayo, as *Holostaspis longulus* Berlese, have been examined and are *G. mandibularis*.

Geholaspis (Longicheles) hortorum (Berlese)

(Fig. 5A–D, Pl. 5A)

Holostaspis longulus var. *hortorum* Berlese, 1904. *Redia* **1**: 265.
Macrocheles (Geholaspis) hortorum: Berlese, 1918. *Redia* **13**: 145.
Geholaspis (Longicheles) mandibularis hortorum: Valle, 1953. *Redia* **38**: 349.

FEMALE. Generally very similar to *G. mandibularis* but differing in numerous details. The dorsal shield (Fig. 5A), which measures 770–880 μm long × 440–500 μm wide, is more tapered posteriorly than in *G. mandibularis*. The setae are arranged as in *G. mandibularis*, except that *z5* is plumose and *z6* is occasionally dentate; these setae are simple in *G. mandibularis*. Setae *j5, j6, J2* and *J5* are simple, all other dorsal setae are plumose. In the figured specimen there is, on the left side, an additional seta between and slightly below *S1* and *Z1*. The dorsal shield is ornamented with conspicuous, dense, small denticles which diminish towards the centre of the shield, becoming fine granulation. The lateral margins are crenate.

With the exception of setae *Zv1* and *Zv2* the setae of the ventral shields are simple. The sternal shield has a characteristic reticulate pattern with fine punctures (Pl. 5A). The metasternal platelets are free and ovate. The genital and ventrianal shields have reticulate ornamentation. The ventrianal shield (Fig. 5B) is longer than broad (290–360 μm long × 260–305 μm wide) and has prominent pores at its anterolateral corners and on its posterolateral margin. The ventrianal setae are noticeably shorter than in *G. mandibularis*. Setae *Zv1* are pilose and *Zv2* are plumose. The shield is ornamented with clear reticulation. Only the tubuli and rami of the spermathecal apparatus are normally visible.

The gnathotectum (Fig. 5C) has the median process bifurcate and almost fimbriate distally; posterior to the bifurcation the process is distinctly toothed while basally there is a series of irregular lateral teeth. The cheliceral dorsal seta is simple. The chelae are elongate and multidentate (Fig. 5D). The fixed chela has a main row of about 10–15 teeth with the third or fourth tooth from

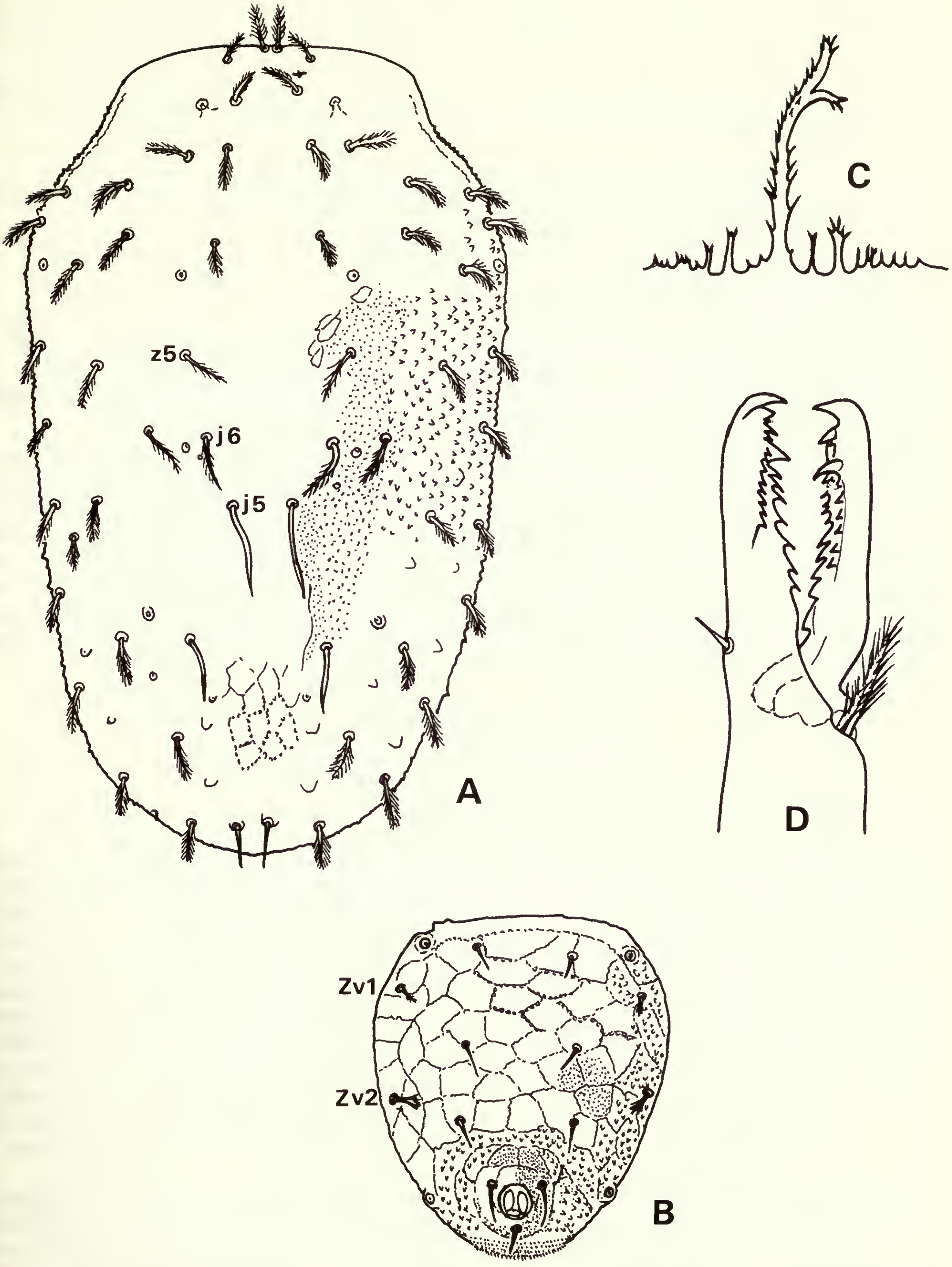

Fig. 5 *Geholaspis (Longicheles) hortorum* (Berlese): **female**—A dorsal shield; B ventrianal shield; C gnathotectum; D chelicera.

the distal end noticeably larger than the others and a subsidiary row of 6 or 8 teeth on the exterior face extending posteriorly from the large tooth. The movable chela (*c.* 198 μm) has a main row of about nine teeth with the second noticeably larger, whilst there is a subsidiary outer row of about 5–6 teeth.

Most leg setae are pilose, except for those on tarsus I, the distal part of tarsi II–IV, and the setae on coxae I and II, trochanters I and II and ventrally on femora I and II.

MALE. Unknown.

TYPE MATERIAL. Not seen, identification based on Valle's (1953) redescription of Berlese's type material.

MATERIAL EXAMINED. 8 collections—1 PN, 1 DN, 13 ♀♀.
ENGLAND: Yorkshire.

HABITAT. The first British record. From semi-natural grasslands in the Yorkshire Wolds.

DISTRIBUTION. Valle (1953) lists material from Italy, Switzerland, Austria, Belgium, Iceland and Germany, however it was not reported from Germany by Karg (1971) or Krauss (1970).

REMARKS. This species is most clearly separated from *G. mandibularis* on the setation of the dorsal shield, the longer than broad ventrianal shield, details of the gnathotectum and the dentition of the chelicerae, which in British specimens of *G. mandibularis* are characterised by more numerous (fixed chela 18–20 teeth, movable chela 14–15 teeth) and smaller teeth, the fixed chela also lacks the clear subsidiary row of teeth found in *G. hortorum*. There seems to be considerable variation in the cheliceral dentition in continental specimens of both species and a complex of forms could be involved. Since *G. hortorum* and *G. mandibularis* occur together in Yorkshire, and appear to overlap in much of their continental ranges, they must be regarded as distinct species rather than subspecies as suggested by Valle (1953).

Genus ***DISSOLONCHA*** Falconer

Dissoloncha Falconer, 1923. *Naturalist, Hull* 1923: 151.

TYPE SPECIES. *Macrocheles superbus* Hull, 1918.

The dorsal shield has 28 pairs of setae which are mainly pilose distally; it has a distinct border and crenulate lateral margins. The ventral setae are all pilose distally with the exception of the paranals. The sternal and genital shields are similar to those of *Macrocheles*, but have distinctive patterns. The ventrianal shield has three pairs of preanal setae and bears the inguinal pores (Athias, 1969) in the anterolateral corners. There may be up to three pairs of muscle apodomes between the ventrianal and genital shields, usually two pairs of these adjoin the ventrianal shield. Males have separate sternogenital and ventrianal shields. The gnathotectum tapers into an elongate median process, dentate laterally and bifurcate distally. The female chelae are elongate and basically bidentate; the male chelae are shorter, the fixed chela has four to five teeth and the movable chela is unidentate, the spermatodactyl is short, blunt and dorsally directed. The corniculi are elongate, more than three times as long as broad at the base and the external hypostomal setae are anterior to the internals. The males have major spurs on legs II and IV. The spermathecal sacculus is large, spherical and strongly convoluted, its diameter is greater than the distance between coxae IV.

The most distinctive features of *Dissoloncha* are the shape of the gnathotectum, the elongate corniculi and the more distally placed external hypostomal setae, characters which are all shared with *Geholaspis* s. lat. The placement of the inguinal pores on the anterior lateral corners of the ventrianal shield, a feature also found in *Geholaspis*, is not simply a reflection of the lateral expansion of the ventrianal shield as species of *Macrocheles* in which the shield is strongly expanded still have the inguinal pores free on the membrane. The structure of the sacculus is unique within the Macrochelidae, as is the habitat of rotting seaweed and tidal wrack.

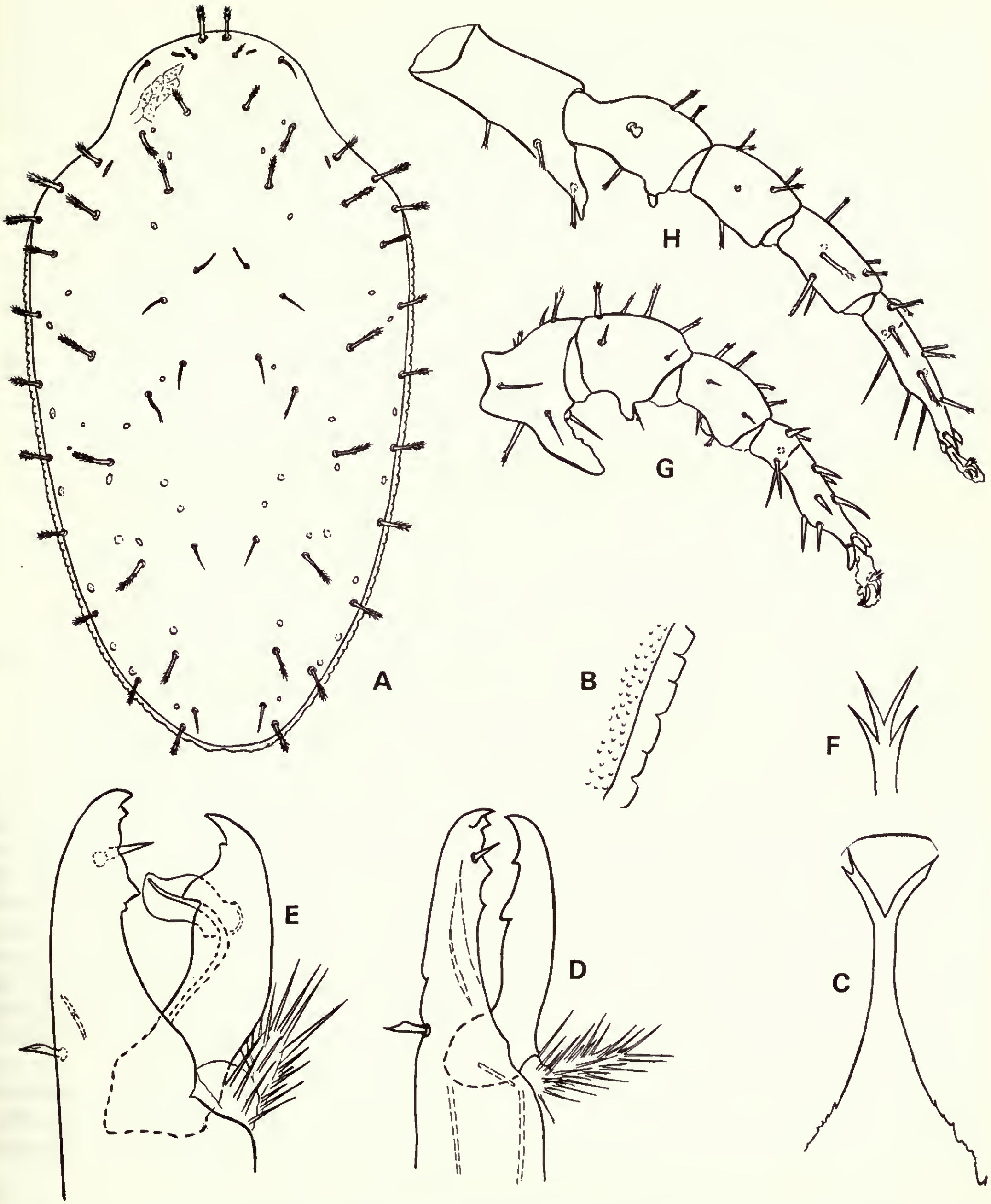

Fig. 6 *Dissoloncha superbus* (Hull): **female**—A dorsal shield; B lateral margin of dorsal shield; C gnathotectum; D chelicera: **male**—E chelicera; F distal end of gnathotectum; G leg II; H leg IV. After Evans & Browning (1956).

Dissoloncha superbus (Hull)
(Fig. 6A–H, Pl. 3D)

Macrocheles superbus Hull, 1918. *Trans. nat. Hist. Soc. Northumb.* **5,** 1: 71.
Dissoloncha superbus: Falconer, 1923. *Naturalist, Hull* 1923: 151.
Macrocheles superbus: Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 38.

The description of this species given by Evans & Browning (1956) remains adequate.

MATERIAL EXAMINED. 25 collections—3 PNN, approximately 45 DNN, 28 ♂♂ and 200 ♀♀.
ENGLAND: Cornwall, Dorset, Kent, Essex, Yorkshire, Northumberland, Durham.
SCOTLAND: Highland (Inverness-shire), Outer Hebrides (Lewis), Fife, Shetland, Fair Isle, Dumfries & Galloway (Wigtownshire).
WALES: Menai Straits, Milford Haven.

HABITATS. Common in rotting seaweed on beaches, also found in a salt marsh and in rotten grass on a beach. Bregetova & Koroleva (1960) reported it from gulls' nests.

DISTRIBUTION. Probably around the entire coast of the British Isles; also northern Europe, Germany (Krantz, 1972), N. America (Krantz, 1972) and Kuril Islands (Bregetova & Koroleva, 1960). This is quite possibly a holarctic seashore species.

Genus *MACROCHELES* Latreille

Macrocheles Latreille, 1829. In Cuvier, *Règne animalium* 2nd ed. **4**: 282. Type species: *Acarus marginatus* Hermann, 1804 = *Acarus muscae domesticae* Scopoli, 1772.
Coprholaspis Berlese, 1918. *Redia* **13**: 146. Type species: *Holostaspis glabra* Müller, 1860.
Nothrholaspis Berlese, 1918. *Redia* **13**: 169. Type species: *Holostaspis tridentinus* G. & R. Canestrini, 1882.
Monoplites Hull, 1925. *Ann. Mag. nat. Hist.* (9) **15**: 215. Type species: *Macrocheles (Monoplites) oudemansii* Hull, 1925 = *Macrocheles marginatus* Oudemans, 1901 *nec* Hermann, 1804.
Macrholaspis Oudemans, 1931. *Ent. Ber.* **8** No. 180: 272. Type species: *Gamasus opacus* C. L. Koch, 1839.
Andrholaspis Turk, 1948. *Proc. zool. Soc. Lond.* **118**: 103. Type species: *Andrholaspis trinitatus* Turk, 1948.

The dorsal shield has 28–30 pairs of setae and smooth or dentate lateral margins; the dorsum lacks an anterior extension bearing setae *j1*. The sternal shield does not extend posteriorly beyond the middle of coxae III. The metasternal platelets are free, usually small, rounded and bear the metasternal setae. The ventrianal shield has 0–3 pairs of preanal setae, depending on the extent to which it is reduced. If it is reduced there are 1–3 pairs of platelets (muscle apodemes) between it and the genital shield. The peritrematic shield is not fused to the expodal shields. The males either have holoventral shields or separate sternogenital and ventrianal shields. The gnathotectum is usually tripartite, the lateral processes may be free, fused basally or strongly reduced. The chelicerae are strong, the dentition is variable, the cheliceral brushes are shorter than the movable digit, the dorsal seta may be simple, spatulate or pectinate. The leg chaetotaxy is normal for the family (except *M. subbadius* Berlese which has seta pl_1 present on genua IV). The legs of the females are without spurs, the males have spurs on leg II and often on leg IV.

The main change to the definition of Evans & Browning (1956) has been its widening to include species formerly placed in *Macrholaspis* Oudemans (Krantz, 1962) following the realisation that there are species closely related to *M. opacus* (C. L. Koch), its type, with three pairs of preanal ventrianal setae.

Ecological and morphological grouping of the species of *Macrocheles*

The species of the genus *Macrocheles* fall into two broad categories on ecological grounds which correlate with certain morphological features. There are those species that are usually found in leaf litter, moss, nests of birds and small mammals and other habitats not predominantly associated with coprophilic insects, and there are those species that are usually coprophilic, but also found in compost heaps, rotting grass clippings, carrion and similar habitats, generally favoured as breeding grounds by synanthropic muscoid flies.

Species of the latter grouping are often found phoretic, as females, on coprophilic and necrophilic insects, for instance dung beetles, burying beetles and synanthropic flies. Males of these species are rarely found, but when they are, they are usually strongly dimorphic in the shape of the dorsal shield and in the number of pilose dorsal setae, which tends to increase. Well developed spurs are usually found on legs IV of the males of this group as well as on legs II. In the European fauna species of this group tend to have a preponderance of simple setae that are only faintly pilose, but this feature is not constant, particularly in the tropical macrochelid fauna.

Species of the former grouping are generally not phoretic on coprophilic insects, and in some, males are commonly found. The males are not strongly dimorphic, although smaller and with a more tapered dorsal shield. The number of pilose setae remains approximately the same in the males. Well developed spurs are usually only found on legs II although there may be minor tubercles and ridges on legs IV. There tends to be a greater number of strongly pilose setae than in the former grouping.

A few species combine the characters of both these categories, *M. penicilliger* is found phoretic on insects, is not strongly dimorphic and has well-developed spurs on legs IV of the male. *M. matrius* is very often associated with chicken manure and compost heaps, but is not usually phoretic on coprophilic insects; it is not strongly dimorphic but has well developed spurs on legs IV of the male. Both these species have a preponderance of strongly pilose setae.

The species of *Macrocheles* found in the British Isles may therefore be grouped as follows:

Leaf-litter species

M. decoloratus
M. punctoscutatus
M. rotundiscutis
carinatus species group
opacus species group

Coprophilic species

M. muscaedomesticae
M. robustulus
glaber species group
subbadius species group

Intermediate species

M. matrius
M. penicilliger

It is interesting to note that Krantz (1981) has shown that the *glaber* species group, the *subbadius* species group, and *M. robustulus*, share characters of the ambulacra in the immature stages not found in other species of *Macrocheles*, and that *M. penicilliger* is intermediate between the two main types of ambulacral structures.

Most of the coprophilic species have been shown to be specialised predators on eggs and young larvae of muscid flies and also on the nematodes and small enchytraeid worms found in their habitat. The leaf-litter group are more likely to be general predators on small anthropods and other animals in their habitat, although biological data are much more fragmentary for these species.

The coprophilic way of life and the characters associated with it are probably derived from the more generalised leaf-litter species. This is supported by comparison with the genus *Geholaspis* which is all litter dwelling and is the most plesiomorphic group of macrochelids. However, males are very rare or unknown in most species of the genus *Geholaspis* and in the *opacus* species group which makes it difficult to draw positive conclusions about their relationships.

Key to the females of the species of *Macrocheles* occurring in the British Isles

1 All setae on dorsal shield simple, needle-like, setae *j1* short, spine-like; sternal shield with *lineae oblique anteriores* joined by four or five transverse lines, the most posterior of which is the *linea media transversa* (Pl. 1F) . . . . **subbadius** species group 2

– Some dorsal setae, always including *j1*, pilose, at least distally; sternal shield variously ornamented, sometimes without regular lines and never as above 4

2 Sternal shield with *lineae oblique anteriores* connected by five lines (Pl. 2A), *linea media transversa* straight or slightly curved posteriorly; genu IV with six or seven setae. 3

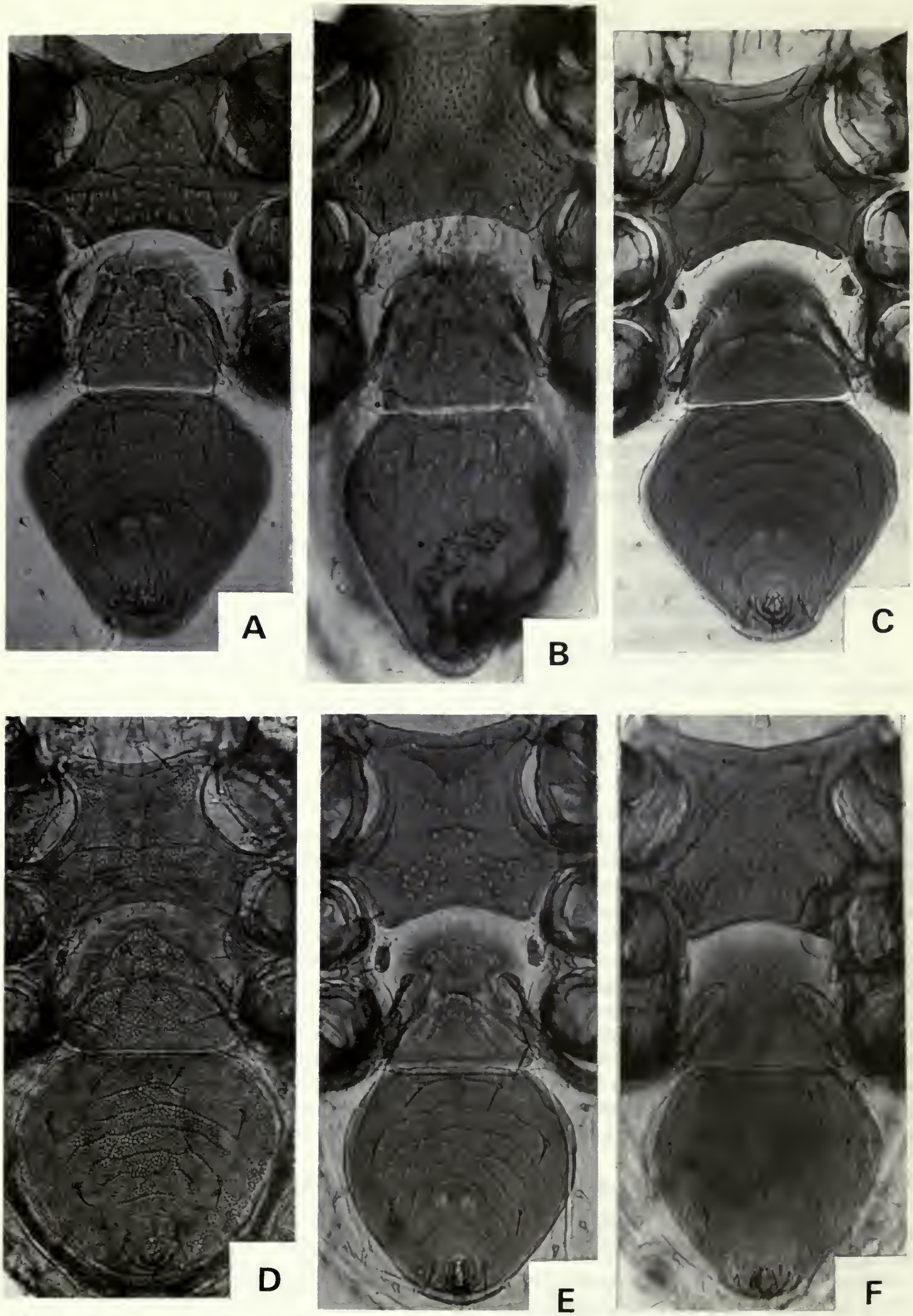

Plate 1 Sternal, genital and ventrianal shields of the females of: A *Macrocheles muscaedomesticae* (Scopoli); B *M. robustulus* (Berlese); C *M. glaber* (Müller); D *M. punctoscutatus* Evans & Browning; E *M. scutatus* (Berlese); F *M. insignitus* Berlese. After Evans & Browning (1956).

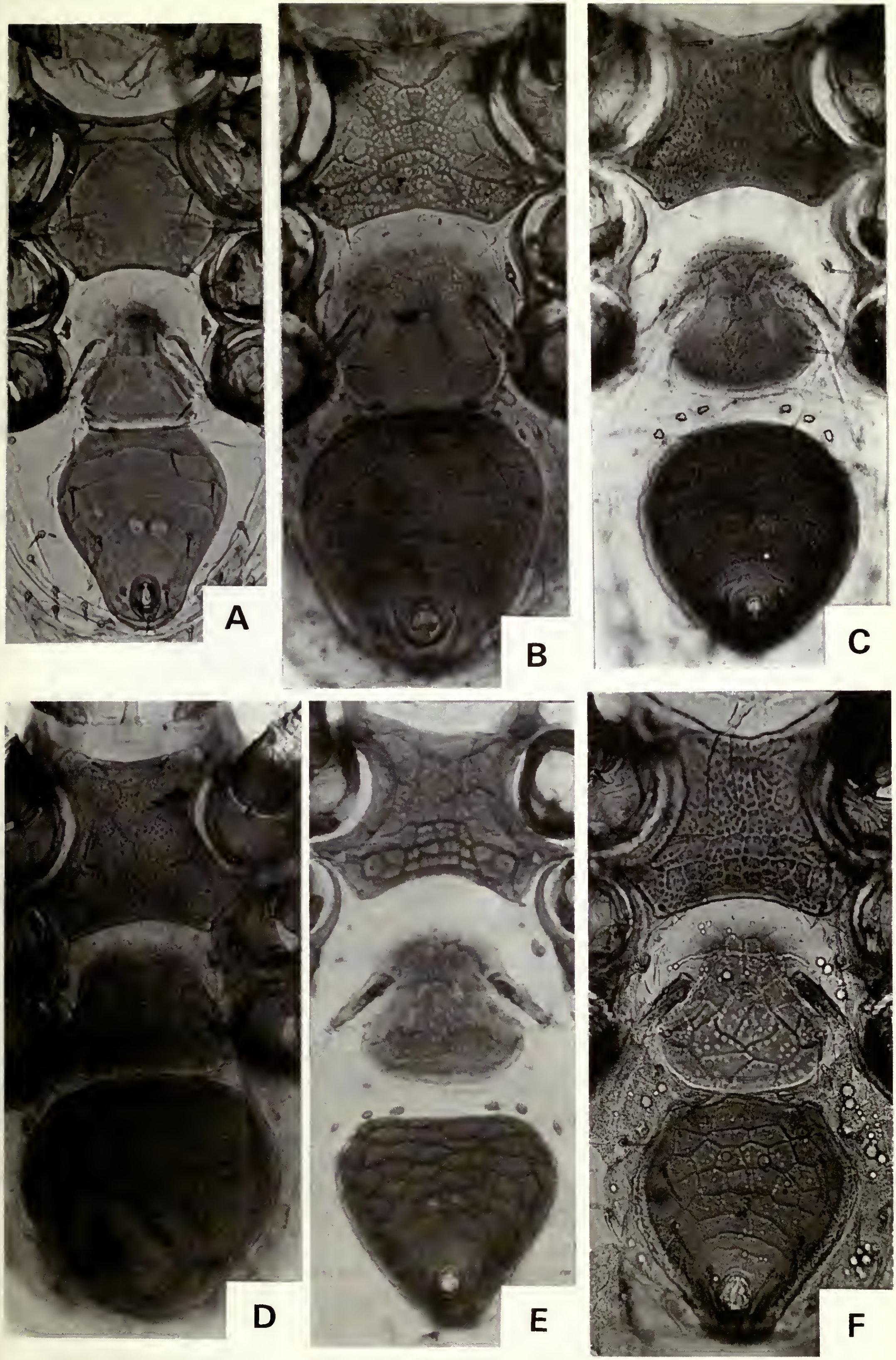

Plate 2 Sternal, genital and ventrianal shields of the females of: A *Macrocheles merdarius* (Berlese); B *M. montanus* (Willmann); C *M. carinatus* (C. L. Koch); D *M. penicilliger* (Berlese); E *M. submotus* Falconer; F *M. tardus* (C. L. Koch). After Evans & Browning (1956).

– Sternal shield with *lineae oblique anteriores* connected by four lines (Pl. 1F), *linea media transversa* arched forwards, all sternal shield lines with a strong edging of punctures; genu IV with six setae, pl_1 absent . . . . **M. insignitus** Berlese (p. 113)

3 All lines of the sternal shield with a strong edging of punctures (Pl. 6E); reticulations of dorsal shield densely covered with minute punctures (Fig. 19A); genu IV with seven setae, pl_1 present . . . . **M. subbadius** (Berlese) (p. 110)

– Transverse lines of sternal shield poorly marked and punctured (Pl. 2A); dorsal shield reticulations more or less unmarked with punctures; genu IV with six setae, pl_1 absent . . . . **M. merdarius** (Berlese) (p. 113)

4 With 1–3 pairs of postgenital platelets or apodemes; ventrianal shield sometimes reduced in size, sometimes with less than three pairs of preanal setae (Pl. 4B) 5

– Without separate postgenital platelets, muscle attachments on ventrianal shield; ventrianal shield of normal size, always with three pairs of preanal setae 12

5 All dorsal setae strongly pilose throughout their entire length, setae *J3* always present, either with *J2* also present or with unpaired setae between *j6* and *J3*; ventrianal shield with two or three pairs of setae, or reduced to an anal shield (Pl. 4B); lateral elements of gnathotectum free (Fig. 12D), reduced in size or absent (Fig. 13D) . . . . . . **opacus** species group (*partim*) 6

– Some dorsal setae, including *j6, z5, z6, J2* and *J5*, simple, others only pilose in their distal half or two thirds, setae *J3* absent (except *M. montanus* (Willmann)); ventrianal shield always with three pairs of preanal setae; lateral elements of gnathotectum fused basally (Fig. 11B) . . . . **carinatus** species group 9

6 Opisthogastric sclerotisation reduced to an anal shield, without preanal setae (Fig. 13B); lateral elements of gnathotectum absent, with single median process bifurcate distally (Fig. 13D) . . . . **M. analis** sp. nov. (p. 96)

– Opisthogaster with a ventrianal shield with two or three pairs of preanal setae; gnathotectum with reduced lateral elements present (Fig. 12D) 7

7 Ventrianal shield with two pairs of preanal setae 8

– Ventrianal shield with three pairs of preanal setae **M. terreus** (Canestrini & Fanzago) (p. 103)

8 Anterior portion of dorsal shield with a network of minute spicules (Fig. 12B), lateral margins with small rounded serrations (Fig. 12C), with a pair of setae in the *J2* position (Fig. 12A) . . . . **M. opacus** (C. L. Koch) (p. 96)

– Anterior portion of dorsal shield without spicules (Fig. 14B), lateral margins with sharp pointed serrations (Fig. 14C), with three or four unpaired median setae between *j6* and *J3* (Fig. 14A) . . . . **M. dentatus** (Evans & Browning) (p. 101)

9 Dorsal setae *z1* smooth, nearly as long as or longer than setae *j1*, and always extending beyond the bases of setae *j2* (Fig. 11A, E) 10

– Dorsal setae *z1* smooth or pilose, much shorter than setae *j1* and never reaching the bases of setae *j2* (Fig. 10A, E) 11

10 Dorsal shield never with more than six pairs of smooth setae (*j6, z1, z5, z6, J2, J5*), setae *j5* as long as setae *j4* and lightly pilose . . . . **M. tardus** (C. L. Koch) (p. 94)

— Dorsal shield with more than six pairs of smooth setae, setae *j2, j5, s2, r3, r4* in addition also smooth (Fig. 11A) . . . . **M. submotus** Falconer (p. 92)

11 Dorsal shield with 29 pairs of setae, *J3* present (Fig. 10E) . **M. montanus** (Willmann) (p. 92)

— Dorsal shield with 28 pairs of setae, *J3* absent, setae *j5* shorter than setae *j4* . . . . **M. carinatus** (C. L. Koch) (p. 90)

12 Some dorsal setae, at least a group in the middle of the dorsal shield, including setae *j6, z5, z6* and *J2*, simple needle-like, not pilose (Fig. 9) 13

— All dorsal setae pilose (Fig. 14A) 20

13 Most setae on the dorsal shield simple, setae *s6, S1* and *S2* and usually others on the shield margin simple 14

— All setae on the dorsal shield margins, including all the *s-S* series, pilose (Fig. 15C). 19

14 Dorsal setae generally long, curved or wavy, setae *Z4* reaching beyond bases of setae *J5*, setae *j4, z2, z4, s2, r2, r3* pilose (Fig. 9); ventrianal shield subcircular, slightly truncate anteriorly, ornamented with lines and punctures . **M. rotundiscutis** Bregetova & Koroleva (p. 88)

— Dorsal setae generally short, straight or slightly curved; distal ends of setae *Z4* fall well short of bases of setae *J5* (Fig. 16A); ventrianal shield usually pentagonal, truncate anteriorly (Pl. 1B), if strongly rounded then densely covered with minute punctations (Pl. 1D) and with only setae *j1* and *r3* pilose on anterior part of dorsal shield (Fig. 8G) 15

15 Setae *j1* elongate, over twice as long as setae *j2* and noticeably longer than setae *j3*, minutely pilose

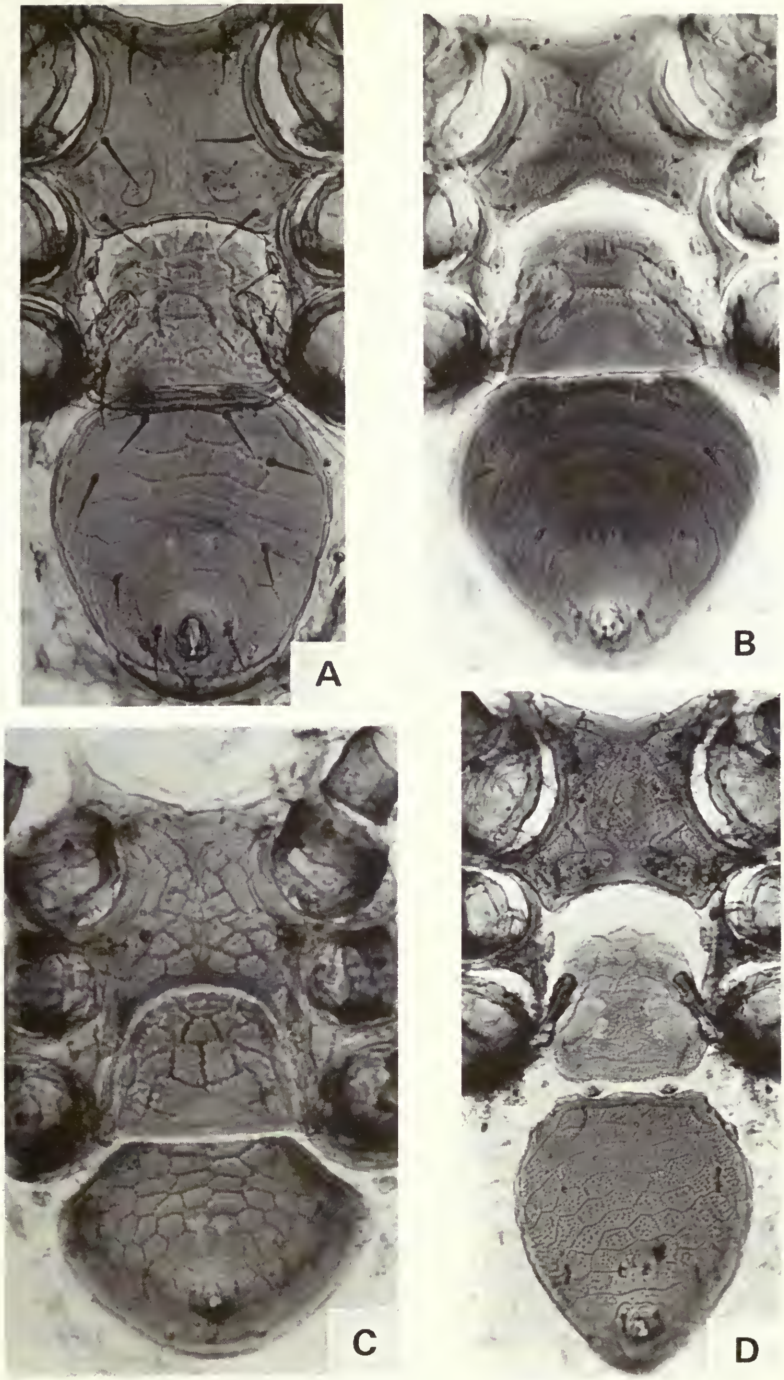

Plate 3 Sternal, genital and ventrianal shields of the females of: A *Macrocheles decoloratus* (C. L. Koch); B *M. matrius* (Hull); C *Glyptholaspis confusa* (Foà); D *Dissoloncha superbus* (Hull). After Evans & Browning (1956).

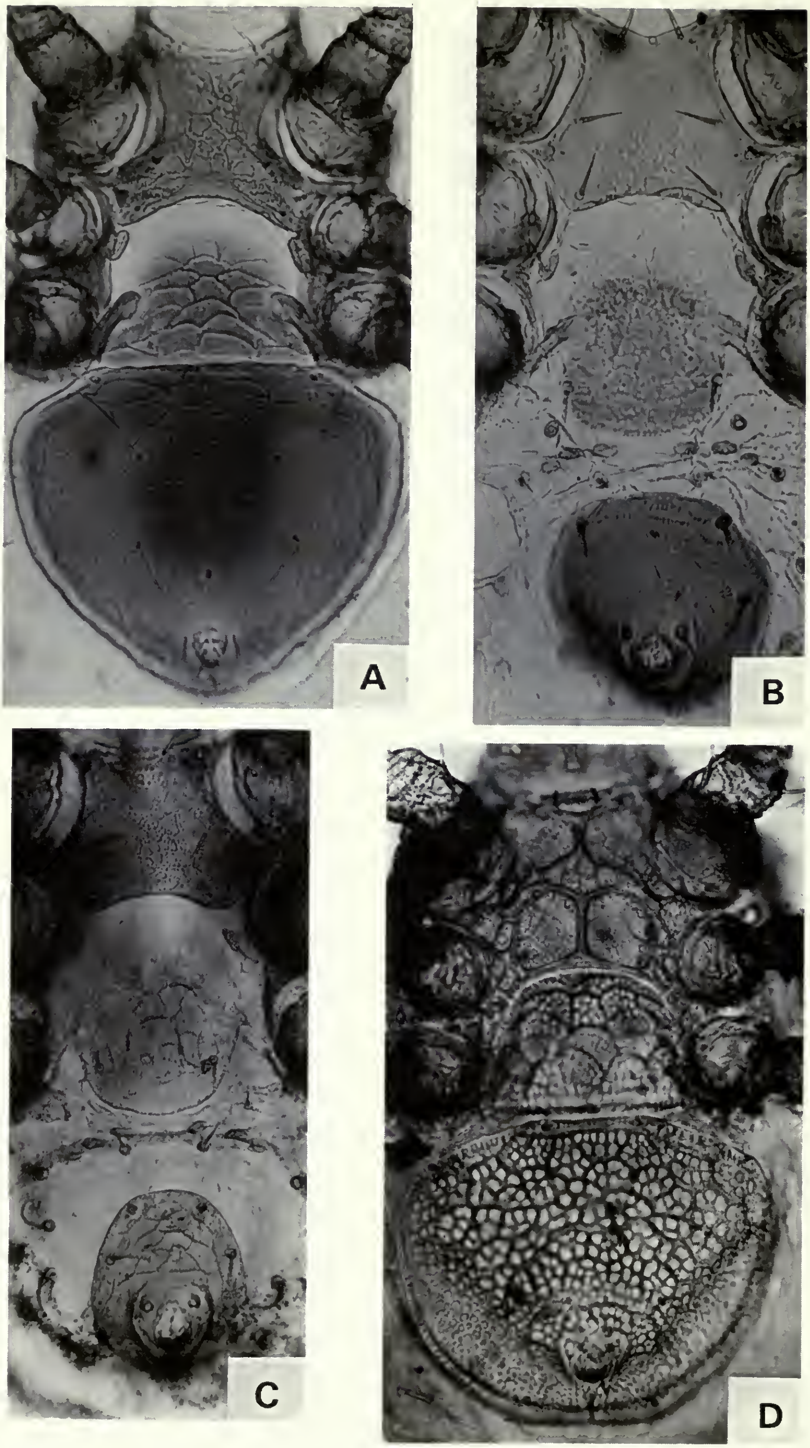

Plate 4 Sternal, genital and ventrianal shields of the females of: A *Geholaspis (G.) longispinosus* (Kramer); B *Macrocheles opacus* (C. L. Koch); C *M. dentatus* Evans & Browning; D *Holostaspella ornata* (Berlese). After Evans & Browning (1956).

distally (Fig. 16B), setae *J5* simple, about half as long as setae *Z5* (Fig. 16A); sternal shield without distinct lines but with a more or less symmetrical pattern of punctures some of which may be linearly arranged (Pl. 1B) . . . . **M. robustulus** (Berlese) (p. 106)

— Setae *j1* short and stout, little longer than setae *j2* and *j3*, distinctly pilose in distal third to half, setae *J5* simple or pilose, as long as or little shorter than setae *Z5* (Fig. 8D); sternal shield with a distinct pattern of lines (Pl. 1D) 16

16 All sclerotised regions densely covered with minute punctations (Fig. 8D); ventrianal shield strongly rounded, almost subcircular in outline (Pl. 1D). . . . . **M. punctoscutatus** Evans & Browning (p. 88)

— Sclerotised regions not densely punctate as above; ventrianal shield pentagonal in outline (Pl. 1C) . . . . **glaber** species group 17

17 Posterior series of dorsal setae with five pairs (*J5, Z4, Z5, S4, S5*) of setae on the dorsal shield pilose, at least distally (Fig. 17E); sternal shield with *linea arcuata* faintly impressed impunctate, all sternal shield punctures minute (Pl. 6D) . . **M. nataliae** Bregetova & Koroleva (p. 109)

— Posterior series of dorsal setae with only one pair of pilose setae (*J5*) on the dorsal shield (Fig. 17A); sternal shield with several well developed punctures along *linea arcuata* (Pl. 1C), sternal shield punctures of different sizes, some minute, some larger 18

18 *Linea arcuata* on sternal shield more or less straight but having its ends directed posteriorly, all lines on sternal shield well developed, not strongly punctured (Pl. 1C) . . . . **M. glaber** (Müller) (p. 107)

— *Linea arcuata* strongly concave, having its ends directed anteriorly, lines on sternal shield not strongly impressed, punctures well developed (Pl. 1E) . **M. scutatus** (Berlese) (p. 110)

19 Dorsal setae only pilose in their distal third; setae *J5* pilose (Fig. 15C); lateral elements of gnathotectum free (Fig. 15D) . . . . **M. muscaedomesticae** (Scopoli) (p. 105)

— Dorsal setae pilose in their distal half to two thirds, setae *J5* simple (Fig. 7C); lateral elements of gnathotectum fused basally (Fig. 7D) . . . . . **M. penicilliger** (Berlese) (p. 86)

20 Dorsal setae pilose along their entire length, with an extra unpaired median seta present in the *J2* position between *j6* and *J3* (Fig. 14E); sternal shield densely covered with punctures (Pl. 6B) . . . . **M. punctatissimus** Berlese (**opacus** species group) (p. 101)

— Dorsal setae only pilose in their distal halves, setae *J2* paired, setae *J3* absent, i.e. with 28 pairs of setae (Fig. 8A); sternal shield with a pattern of lines and small areas of punctures (Pl. 3A) . . 21

21 Setae *J5* approximately equal in length to setae *Z5* and little more than half as long as setae *S5* (Fig. 8A); outer margins of lateral elements of gnathotectum smooth (Fig. 8B) . . . . **M. decoloratus** (C. L. Koch) (p. 88)

— Setae *J5* shorter than setae *Z5*, setae *Z5* approximately equal in length to setae *S5* (Fig. 7A); outer margins of lateral elements of gnathotectum serrated (Fig. 7B) . **M. matrius** (Hull) (p. 85)

Macrocheles matrius (Hull)
(Fig. 7A, B, Pl. 3B)

The description of Evans & Browning (1956) requires no amendment.

TYPE MATERIAL. **Lectotype** ♀ 'n.v.' [? Ninebanks vicarage, Northumberland]. poultry manure, Hull collection. Here designated. **Paralectotypes** 18 ♀♀, same data as lectotype [BMNH].

MATERIAL EXAMINED. 11 collections—4 ♂♂, 194 ♀♀.

ENGLAND: Gloucestershire, Surrey, Cambridgeshire (Huntingdonshire), Worcestershire, Staffordshire, Derbyshire, Northumberland.

SCOTLAND: Grampian (Aberdeenshire), Inner Hebrides (Pabay).

HABITATS. Four collections associated with poultry, also with mink *Mustela vison*, water shrews *Neomys fodiens*, in a canary cage and from grass clippings and compost.

DISTRIBUTION. Widespread in Europe; Germany (Krantz, 1972), Austria (Johnston, 1970), Bulgaria (Balogh, 1958), U.S.S.R. (Bregetova & Koroleva, 1960). Also known from the U.S.A. (Axtell, 1963), Israel (Costa, 1966*b*) and New Zealand (Emberson, 1973*a*).

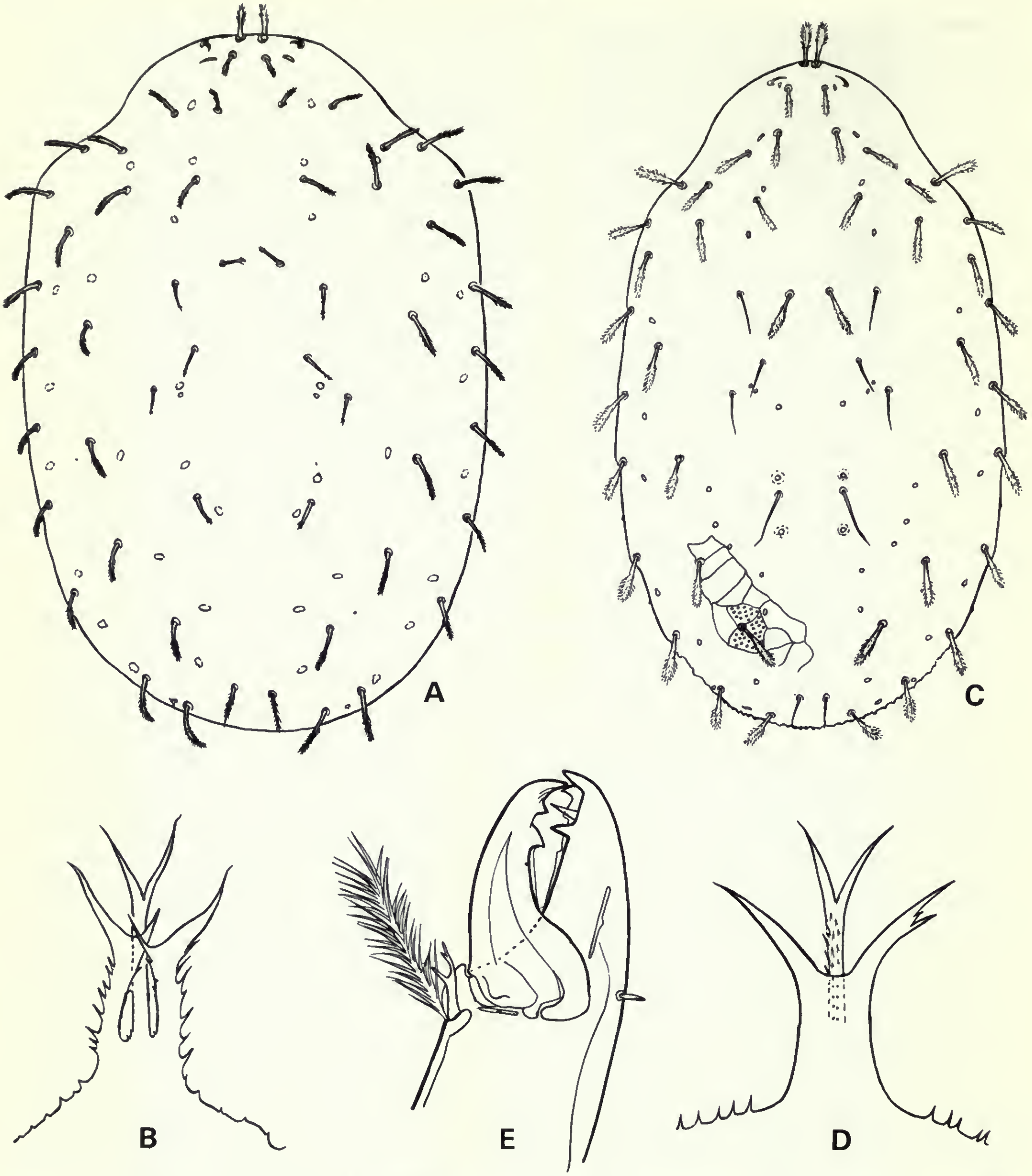

Fig. 7 *Macrocheles matrius* (Hull): **female**—A dorsal shield; B gnathotectum. *Macrocheles penicilliger* (Berlese): **female**—C dorsal shield; D gnathotectum; E chelicera. After Evans & Browning (1956).

Macrocheles penicilliger (Berlese)

(Fig. 7C–E, Pl. 2D)

The description of Evans & Browning (1956) requires no amendment.

TYPE MATERIAL. **Syntypes** 2 ♀♀ only, Italy, Cison di Valmarino, Treviso, sotto legni [under wood] slide 3/38 [ISZA].

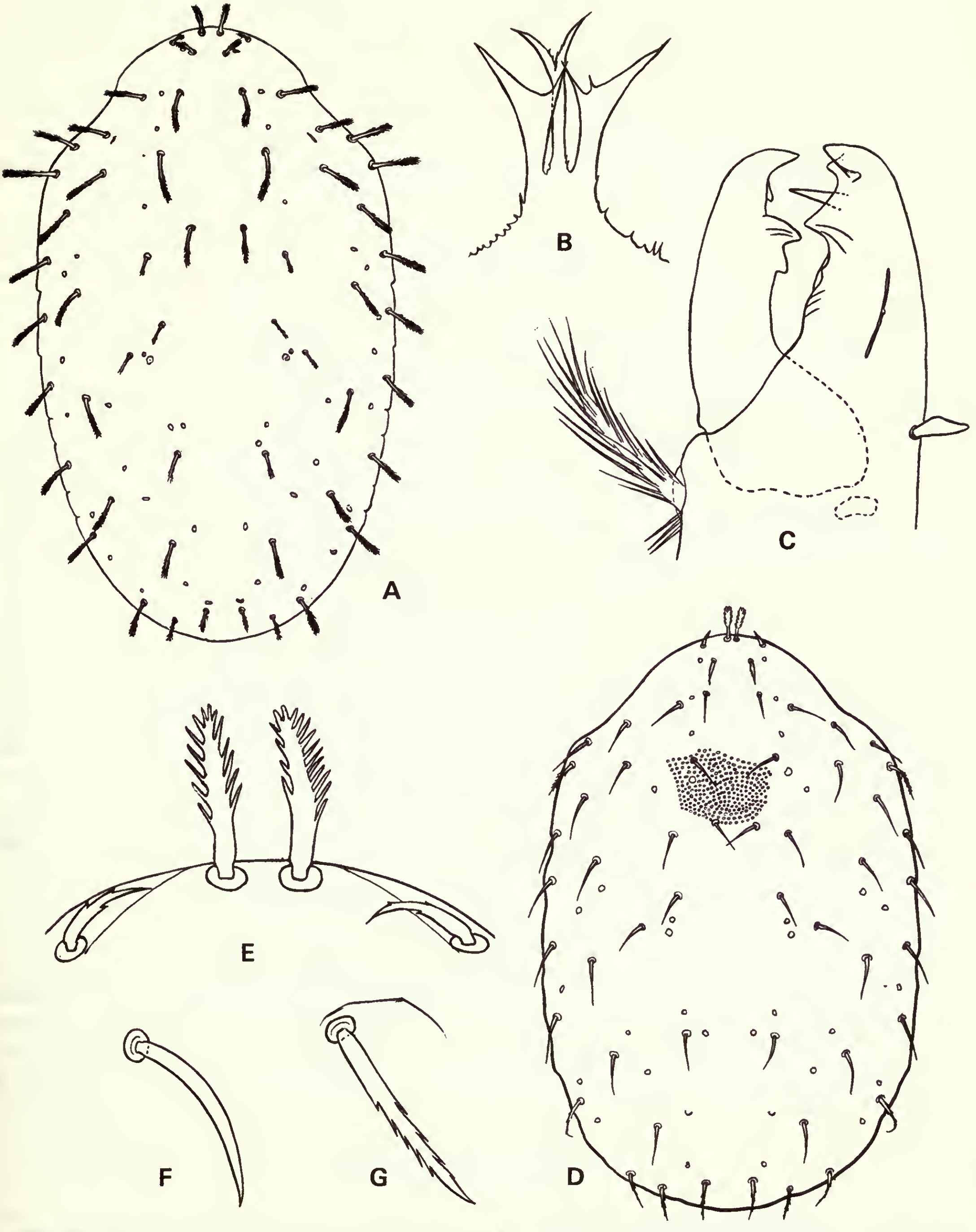

Fig. 8 *Macrocheles decoloratus* (C. L. Koch): **female**—A dorsal shield; B gnathotectum; C chelicera. *Macrocheles punctoscutatus* Evans & Browning: **female**—D dorsal shield; E anterior margin of dorsal shield; F seta *s2*; G seta *r3*. After Evans & Browning (1956).

Material examined. 13 collections—3 DNN, 1 ♂, 125 ♀♀.
ENGLAND: Cornwall, Surrey, Kent, London, Middlesex, Essex, Bucks, Oxfordshire, Cheshire.
WALES: Gwynedd (Caernarvonshire).
IRELAND: Clare.
CHANNEL ISLANDS: Jersey.

Habitats. Three collections associated with *Trox scaber* (L.), also found in insect cultures, decaying leaves, compost and sewage culture.

Distribution. Apparently widespread in Europe; Germany (Karg, 1970), U.S.S.R. (Bregetova & Koroleva, 1960), also known from New Zealand (Emberson, 1973*a*).

Macrocheles decoloratus (C. L. Koch)
(Fig. 8A–C, Pl. 3A)

Evans & Browning's (1956) description and synonymy remain unchanged

Material examined. 8 collections—1 ♂, 60 ♀♀.
ENGLAND: Gloucestershire, Kent.
SCOTLAND: Tayside (Perthshire), Fife, Highland (Inverness-shire).
IRELAND: Cork.

Habitats. Six out of eight collections are from sand martin *Riparia riparia* nests, also collected from cow dung and moss and known from small mammal nests in U.S.S.R.

Distribution. Widespread in the British Isles and Europe; Germany (Karg, 1970), U.S.S.R., (Bregetova & Koroleva, 1960).

Macrocheles punctoscutatus Evans & Browning
(Fig. 8D–G, Pl. 1D)

Macrocheles punctoscutatus Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 18.

The description of this species remains adequate. Bregetova & Koroleva (1960) have published a description of a male reputed to be this species. It appears to be very different from the female having only setae *J5* on the dorsal shield pilose, also the complete covering of fine punctures appears to be lacking. The male has a holoventral shield, leg II is armed with a strong spur on the femur, small tubercles are present on other segments and on leg IV.

Type material. **Holotype** ♀, England, Glos., Churcham, from nest of mole *Talpa europaea*, 16.v.1954. R. S. George. [BMNH].

Material examined. 4 collections—12 ♀♀.
ENGLAND: Gloucestershire, Wiltshire, Oxfordshire.
SCOTLAND: Inner Hebrides (Eigg).

Habitats. Associated with small mammals; three collections from nests of moles *Talpa europaea*, one collection from *Microtus agrestis*. Bregetova & Koroleva (1960) record this species from a variety of small mammals.

Distribution. Probably throughout the British Isles. Widespread in U.S.S.R. (Bregetova & Koroleva, 1960), Germany (Karg, 1970).

Macrocheles rotundiscutis Bregetova & Koroleva
(Fig. 9, Pl. 6A)

Macrocheles rotundiscutis Bregetova & Koroleva, 1960. *Parazit. Sb.* **19**: 116.
Macrocheles bombophilus Götz, in Krauss, 1970. *Acarologie* **14**: 28, **Syn. nov.**

Female. The dorsal shield has 28 pairs of setae, most of which are long and curved or slightly wavy (Fig. 9). Setae *j1* are short, broad and pilose; eight pairs of setae (*j4, z2, z4, s2, r2, J5, Z5, S5*) are long and strongly pilose over most of their length, setae *r3* are faintly pilose and the other setae are simple. The setae on the dorsal shield are much longer than those off the shield. The dorsal shield

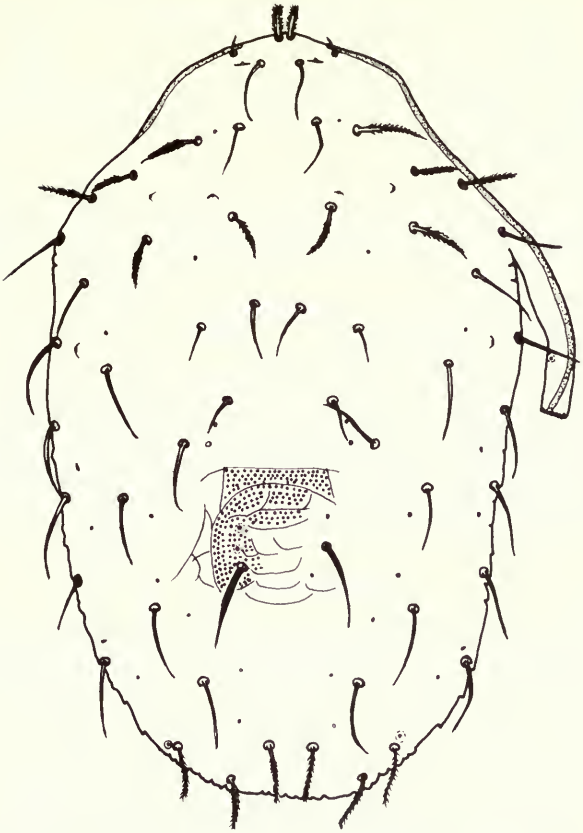

Fig. 9 *Macrocheles rotundiscutis* Bregetova & Koroleva: **female**—dorsal shield.

is ornamented with reticulations and fine dense punctation, the lateral margins are irregularly serrate.

With the exception of the postanal setae, the setae on the ventral shields are simple. The sternal shield has a characteristic reticulate pattern (Pl. 6A) of ridges and punctures within the reticulations. The metasternal plates are rounded ovate. The genital shield is well marked with fine ridges and punctures. The ventrianal shield is broader than long and subcircular in outline, truncate anteriorly and only slightly angled laterally. The ornamentation is characteristic, consisting of curved transverse lines with a broad band of punctuation along the posterior edge of each line, and the punctures in each band decreasing in size posteriorly. The spermathecal apparatus has the normal two-lobed sacculus with the lobes widely separated, the corniculum is small and narrow.

The gnathotectum has free lateral processes, the bifurcate median process is spiculate basally. The fixed chela is bidentate and the movable chela tridentate. The cheliceral dorsal seta is simple or faintly serrate distally.

The setae on coxae III and IV are pilose; those on coxa, tibia and tarsus I are simple; other leg segments have a mixture of pilose and simple setae.

MALE. The male is unknown in the British Isles and was not known to Bregetova & Koroleva (1960). However, Götz (in Krauss, 1970), described the male from Germany (as *M. bombophilus*).

The distribution of pilose dorsal setae is similar to the female. There is a holoventral shield. The fixed chela is bidentate and the movable chela unidentate; the spermatodactyl is about one-and-a-half times the length of the movable chela and has an anteriorly projecting basal tubercle. Leg II is armed with a spur on the femur and leg IV with tubercles and ridges on the trochanter and femur.

TYPE MATERIAL. *M. rotundiscutis*: 10 ♀♀ **syntypes**, Lithuanian S.S.R., Ventes-ragas, litter under leaves in cemetery, 27.vii.1957, Ivanov [ZINL].

The type material of *M. bombophilus* was not available for study, but there can be little doubt of the synonymy based on the description and drawings of Götz (in Krauss, 1970).

MATERIAL EXAMINED. 1 collection—1 ♀.

ENGLAND: Surrey.

HABITAT. A single female in leaf litter at Kew Gardens, Surrey is the first British record. Bregetova & Koroleva (1960) record this species from leaf litter, hay and compost, and Götz (in Krauss, 1970) records it from bumble-bee nests.

DISTRIBUTION. Germany (Götz in Krauss, 1970); U.S.S.R., Leningrad region, Lithuanian S.S.R. and Caucasus (Bregetova & Koroleva, 1960).

REMARKS. There are slight variations between the British specimen and the Lithuanian syntypes, the sternal shield pattern is slightly more complex and the punctate bands on the ventrianal shield wider in the British specimen. Setae *J5* are longer than shown in Bregetova & Koroleva's drawing, both in the British and Lithuanian material examined, almost reaching the posterior margin of the dorsal shield. Also setae *z2* are pilose in all the material examined and are shown in Bregetova & Koroleva's drawing, but said to be simple by Götz.

carinatus group

Krantz (1972) intimated that *M. carinatus* and other similar species formed a species group, although the existence of a group of very similar species was implicitly recognised by Bregetova & Koroleva (1960) and others. The members are medium to large sized (females 1000–1500 µm in length) heavily sclerotized, litter-dwelling species of *Macrocheles*. The dorsal shield has 28–29 pairs of setae, *J3* being present in addition to *J2* in some species. Most of the dorsal setae are pilose in their distal half to two thirds. There is always a group of more or less simple setae in the middle of the dorsal shield that includes *j6, z5, z6, J2* and *J3* if present. In addition other setae, including *j2, j5, z1, s2, r3, r4* and *J5*, are simple in some species. The dorsal shield is generally ornamented with a reticulate pattern and sometimes with a punctate microsculpture. The posterior and lateral margins may be irregularly crenulate or smooth. The setae on the ventral shields may be simple or pilose. The sternal shield pattern consists of a reticulate-punctate network which is more pronounced and more punctate in the posterior third. The metasternal plates are small and oval with both seta and pore. The genital shield is ornamented with a punctate lineal pattern. It is generally rounded posteriorly and the associated pores are free on the membrane. The ventrianal shield is reduced, subtriangular or rounded and has a pattern of punctate lines. There are three pairs of free postepigynal apodemes in the membranous cuticle. Males have separate sternogenital and ventrianal shields. The gnathotectum has the lateral processes fused and the stem of the median process strongly spiculate. The dentition of the chelae varies from species to species, but the spermatodactyl is short, about half the length of the movable chela, strongly tapered and directed postero-dorsally; the dorsal seta is pectinate latero-distally. The leg setation is normal for the genus and is a mixture of simple and pilose setae. In the male leg II is armed with a simple spur on the femur and small tubercles on the genu and tibia. The spermathecal structures are indistinct.

INCLUDED SPECIES: *M. carinatus* (C. L. Koch), *M. montanus* (Willmann), *M. submotus* Falconer, *M. tardus* (C. L. Koch).

Macrocheles carinatus (C. L. Koch)
(Fig. 10A–D, Pl. 2C)

The description and synonymy given by Evans & Browning (1956) need no amendment.

MATERIAL EXAMINED. 53 collections—several DNN, 49 ♂♂, 90 ♀♀.

ENGLAND: Isles of Scilly, Cornwall, Somerset, Dorset, Surrey, London, Kent, Hertfordshire, Berkshire, Buckinghamshire, Cambridgeshire, Leicestershire, Nottinghamshire, Yorkshire, Cumbria (Westmorland), Northumberland.

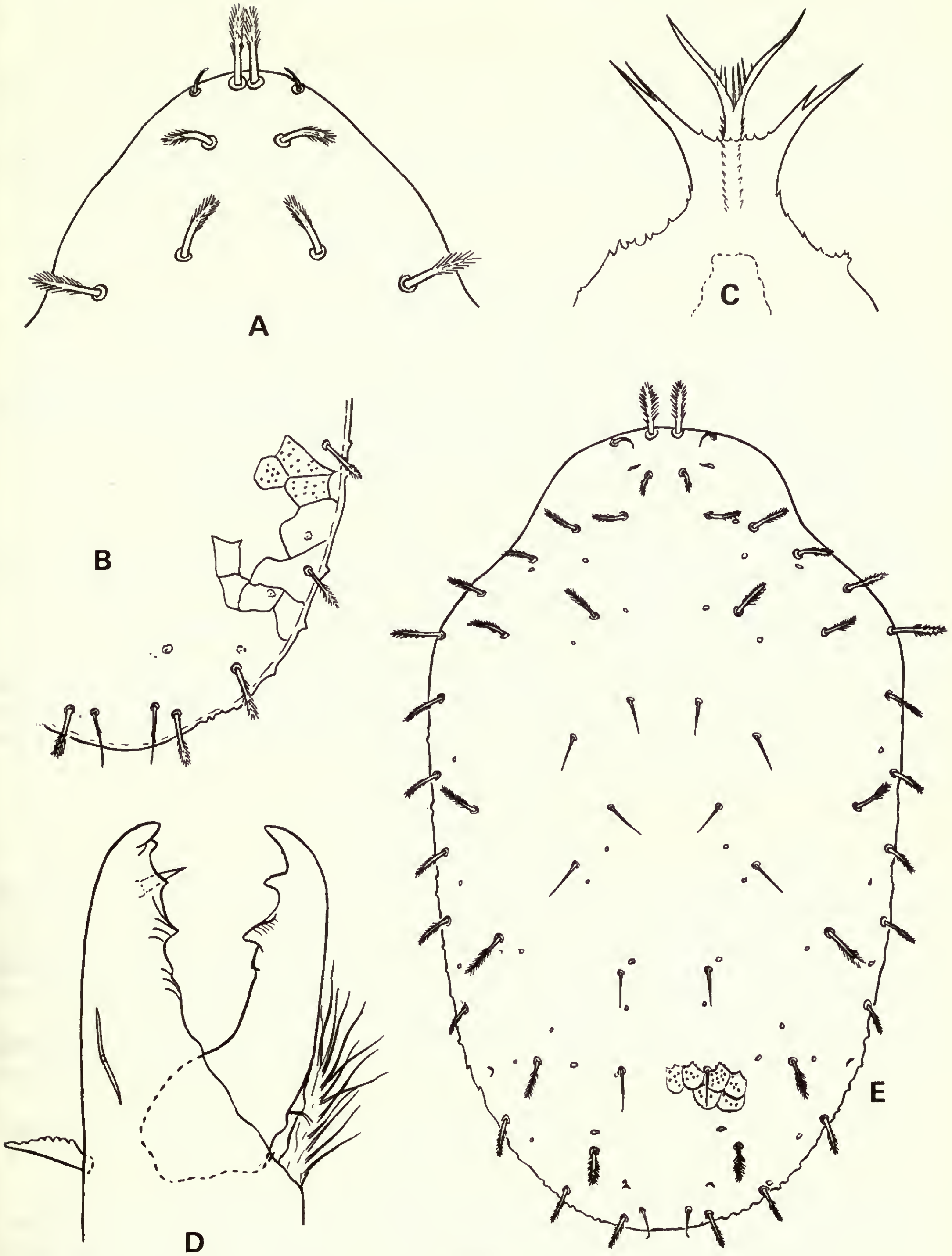

Fig. 10 *Macrocheles carinatus* (C. L. Koch): **female**—A anterior region of dorsal shield; B postero-lateral margin of dorsal shield; C gnathotectum; D chelicera. *Macrocheles montanus* (Willmann): **female**—E dorsal shield. After Evans & Browning (1956).

SCOTLAND: Tayside (Perthshire), Inner Hebrides (Mull), Shetland.
WALES: Dyfed (Pembrokeshire), Glamorgan, Gwent, Gwynedd (Caernarvonshire).
IRELAND: Clare, Westmeath, Leitrim.

HABITATS. A variety of litter habitats including flood debris, dead grass, seaweed, moss, etc., also from *Microtus agrestis*. Probably mainly found in damp places.

DISTRIBUTION. Throughout the British Isles, widespread in Europe, recent records include: U.S.S.R. (Bregetova & Koroleva, 1960), Germany (Krantz, 1972), Austria (Johnston, 1970), Bulgaria (Balogh, 1958).

Macrocheles montanus (Willmann)

(Fig. 10E, Pl. 2B)

The description and synonymy given by Evans & Browning (1956) remain unaltered.

MATERIAL EXAMINED. 40 collections—1 ♂, 82 ♀♀.
ENGLAND: Cornwall, Somerset, Dorset, Sussex, Surrey, London, Kent, Hertfordshire, Berkshire, Buckinghamshire, Cambridgeshire (including Huntingdonshire), Northamptonshire, Lancashire, Durham, Northumberland, Cumbria (Cumberland).
SCOTLAND: Tayside (Angus, Perthshire), Inner Hebrides (Mull).
WALES: Gwent.
IRELAND: Westmeath.

HABITATS. Mainly leaf litter, also cow dung and under wet oak bark. Three collections from small mammals (*Sorex araneus* and *Microtus agrestis*).

DISTRIBUTION. Similar to *M. carinatus*, recent records include U.S.S.R. (Bregetova & Koroleva, 1960), and Germany (Krantz, 1972).

REMARKS. A very similar species, also with setae *J3* present, has been described by Bregetova & Koroleva (1960) from the Caucasus region of the U.S.S.R. One of us (R.M.E.), having examined the types of *M. montivagus* Berlese, follows Krantz (1972) in rejecting the synonymy of *M. montanus* with that species as proposed by Krauss (1970).

Macrocheles submotus Falconer

(Fig. 11A–D, Pl. 2E)

The description of this species in Evans & Browning (1956) is satisfactory, except that *j3* (*D3*) and *z2* (*M2*) are usually less pilose than described and figured.

It is evident that Falconer had several collections before him when he described this species as *M. cognatus*, a junior homonym of *M. cognatus* Berlese 1918. He states (Falconer, 1923: 152) 'Found amongst dead leaves, sphagnum and heaps of cut grass in a field at Slaithwaite, *first examples* [our italics] May, 1919'. He also mentions both males and females. No type was designated.

The only material of these collections now known to exist is two females and two males labelled '2nd lot' from the Falconer collection and now housed in the Arachnida collection of the British Museum (Natural History).

TYPE MATERIAL. **Lectotype** ♀, here designated, [England, ? Slaithwaite, Yorkshire] '2nd lot', Falconer coll. [BMNH]. **Paralectotypes**, 1 ♀, 2 ♂♂, same data as lectotype, [BMNH].

MATERIAL EXAMINED. 122 collections—*c*. 26 PNN, 44 DNN, 134 ♂♂, 225 ♀♀.
ENGLAND: Devon, Somerset, Gloucestershire, Dorset, Hampshire, Surrey, Sussex, Kent, London, Essex, Middlesex, Berkshire, Leicestershire, Lancashire, Yorkshire, Durham, Northumberland, Cumbria (Westmorland).
SCOTLAND: Strathclyde (Argyllshire), Tayside (Perthshire), Dumfries & Galloway (Wigtownshire), Highland (Inverness-shire, Ross & Cromarty), Inner Hebrides (Skye, Scalpay, Mull, Ulva), Shetland.

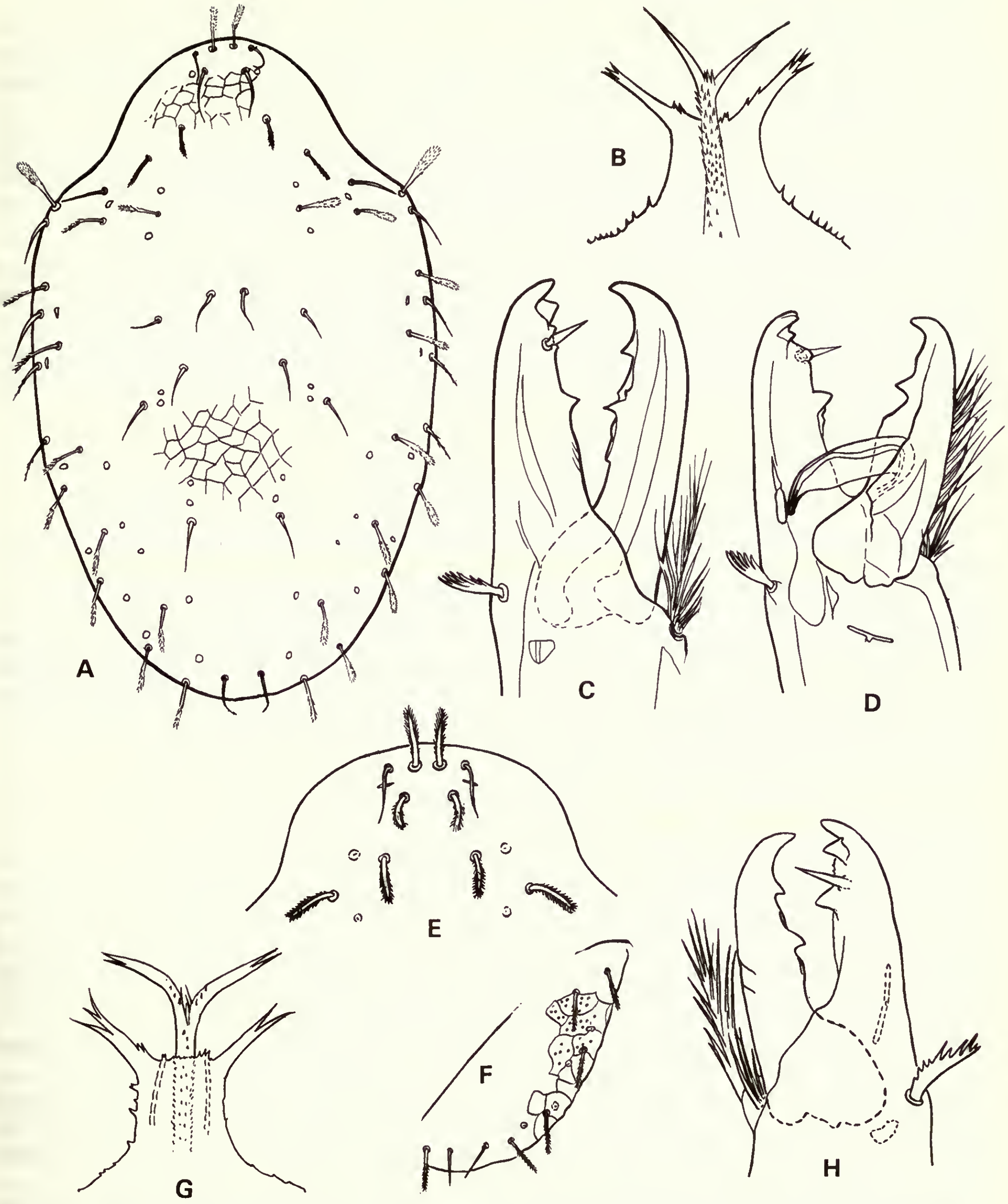

Fig. 11 *Macrocheles submotus* Falconer: **female**—A dorsal shield; B gnathotectum; C chelicera: **male**—D chelicera. *Macrocheles tardus* (C. L. Koch): **female**—E anterior region of dorsal shield; F posterolateral margin of dorsal shield; G gnathotectum; H chelicera. After Evans & Browning (1956).

WALES: Glamorgan, Gwent, Gwynedd (Merionethshire, Caernarvonshire), Clwyd (Denbighshire).

IRELAND: Clare, Mayo, Galway, Sligo, Leitrim, Westmeath.

CHANNEL ISLANDS: Jersey.

HABITATS. A wide variety of leaf litter habitats, also mosses; some evidence of association with damp habitats, i.e. *Sphagnum*, flood debris, saltwater marsh, etc. Twelve collections from small mammals (*Sorex minutus, S. araneus* and *Microtus agrestis*).

DISTRIBUTION. Common throughout the British Isles. No positive records for this species outside the British Isles are known to the authors. The records by Halbert (1915) of *Holostaspis tridentinus* G. & R. Can. refer to this species, but other records, where it has been possible to check, refer to other species of the *carinatus* group.

REMARKS. As mentioned above, the correct name for this species has been very confused in the European literature. The situation has not been helped by Krauss (1970) who synonymizes *M. submotus* Falconer and *M. tardus, sensu* Evans & Browning, with *M. tridentinus* (G. & R. Canestrini). Whatever decision is made as to the status of *M. tardus* (Koch) the fact remains that *M. submotus* is a very different species from that described and illustrated by Krauss (1970) as *M. tridentinus*.

Macrocheles tardus (C. L. Koch)
(Fig. 11E–H, Pl. 2F)

Gamasus tardus C. L. Koch, 1841. *Deutschlands Crustaceen, Myriapoden und Arachniden.* Regensburg, Heft 39, no. 14.

Holostaspis tridentinus G. & R. Canestrini, 1882. *Atti Soc. ven.-trent. sci.* **8**: 28.

The treatment of this species by Evans & Browning (1956) remains adequate.

TYPE MATERIAL. *M. tridentinus*: **Neotype** ♂, here designated. Labelled as follows: yellow-bordered printed label, Coll. Berlese. *Macrocheles tridentinus* (G. & R. Can.), ♂ Tiarno (Trentino) musco [moss], slide 187/43 [ISZA].

MATERIAL EXAMINED. 18 collections—9 ♂♂, 29 ♀♀.

ENGLAND: Gloucestershire, Cambridgeshire (including Huntingdonshire), Yorkshire, Cumbria (Westmorland).

WALES: Glamorgan.

IRELAND: Leitrim, Westmeath.

HABITAT. A variety of habitats with a tendency towards damp situations, i.e. flood debris, moss, peat and *Molinia* tussocks in the fens.

DISTRIBUTION. A widespread species in the British Isles and Europe. Recent records include: U.S.S.R. (Bregetova & Koroleva, 1960), Germany (Krantz, 1972).

REMARKS. The present authors agree with Krantz (1972) that the name *M. tardus* Koch is best used for this species rather than for species of *Glyptholaspis* as proposed by Krauss (1970).

The identity of *M. tridentinus* has long remained a problem because of the inadequate original description and figures (G. & R. Canestrini, 1882). One of us (R.M.E.) has recently had the opportunity to examine parts of the Canestrini Collection in Padova and hopes that the problem may here be resolved.

The original description was based mainly on a male specimen, and, to a lesser extent, on what the Canestrini brothers referred to as juvenile females. These latter were probably specimens of an unrelated and now entirely unrecognisable species. No types were specifically designated but Trentino was mentioned as the locality from which the material came. In the Canestrini Collection there is a tube (jar no. XX, vial no. 556) labelled *Holostaspis tridentinus* Can., Trentino, which could be taken as containing the type series of *M. tridentinus*. This material was evidently seen by Valle (1955). Unfortunately this tube, together with several others examined, was empty. The late Dr A. Filipponi also encountered this problem when he examined parts of the Canestrini Collection (Pegazzano, personal communication).

The only other material in the Collection labelled as *H. tridentinus* is a badly damaged, over-cleared, transparent male of *M. carinatus* (jar no. XX, vial no. 604) from an unknown locality.

H. tridentinus appears to be conspecific with either *M. tardus* or *M. carinatus* as understood here and interpreted by Evans & Browning (1956). For reasons given below synonymy with the former species is favoured. *M. submotus* can be almost totally discounted from consideration in spite of its frequent synonymisation with *tridentinus* on the grounds that no authentic material of *M. submotus* is known to exist in central or southern Europe.

In the Berlese collection there are two specimens identified as *M. tridentinus* from Tiarno (Trentino) which can be considered topotypical. They date from Berlese's Padova period (slide labels with yellow borders) and may have been collected when Berlese was a student of G. Canestrini. These specimens are both *M. tardus* as here understood. One of these (187/43) has been selected as a neotype of *M. tridentinus*.

The only discrepancy between the neotype and the original description of *tridentinus* is the length of the body. The following are measurements based on G. & R. Canestrinis' (1882) description, the neotype, and typical values for *M. carinatus* and also ratios of body length to the other values:

		Canestrini *tridentinus*	**neotype** *tridentinus*	**typical values** *carinatus*
Body length	µm	860	1050	870–910
Body width	µm	640 (1 : 0.74)	660 (1 : 0.63)	500–540 (1 : 0.58)
Leg IV length	µm	1250 (1 : 1.45)	1300 (1 : 1.24)	980–1000 (1 : 1.11)

It is apparent that there is good agreement in body width and leg length with the neotype and that these measurements fall outside the normal range for *M. carinatus*. Also the ratios of body length to body width and body length to length of leg IV derived from the Canestrini measurements would be abnormal for this type of mite.

The most likely explanation for these inconsistencies is that there is an error in the body length measurement in the original description, and that the Canestrinis had before them a specimen of *M. tardus*. For these reasons synonymy with *M. tardus* is favoured and a suitable neotype chosen.

opacus group

The *opacus* species group was distinguished by Johnston (1970) for a characteristic group of litter- and soil-dwelling *Macrocheles*. The dorsal shield has a basic complement of twenty-eight pairs of setae plus an additional one to four setae that may be paired or unpaired. Setae *J3* are always present (absent in most other *Macrocheles*) and between setae *j6* and *J3* there may be a single seta, a pair of setae or three or four unpaired setae. Setae *j1* are short and laterally expanded, other setae are usually long, tapered and pilose along their entire length; setae *z1* and *J5* may be considerably shorter than the others. The dorsal shield usually tapers from the shoulders and often does not cover the entire dorsum. The lateral and posterior margins are often finely dentate or crenulate. The sternal shield is reticulate-punctate without a strong pattern of lines. The genital shield is usually reduced and rounded posteriorly. The ventrianal shield is reduced to a greater or lesser extent so that three pairs of apodemes are usually exposed; the number of ventrianal shield setae may be reduced to two, one, or no preanal pairs. Males have separate sternogenital and ventrianal shields, which may also be reduced. The lateral processes of the gnathotectum are usually reduced to narrow spikes and the median bifurcate process may be dissected distally. The fixed chela has an offset subterminal tooth and a central tooth, whilst the movable chela of the female has two central teeth; the male has a unidentate movable chela and a short, strongly tapered, posterodorsally directed spermatodactyl. The cheliceral dorsal seta is pectinate distally. The legs are highly rugose and have mainly pilose setae on most segments except coxa and tarsus I. The form of the spermathecal complex varies from the typical bilobed *Macrocheles* type through a stage with slightly enlarged rami and increasingly delicate membranous median organs to an extreme form with very elongate rami and indiscernible median organs similar to *Geholaspis* (*Longicheles*).

INCLUDED SPECIES. *M. opacus* (C. L. Koch), *M. analis* sp. nov., *M. dentatus* (Evans & Browning), *M. punctatissimus* Berlese, *M. terreus* (Canestrini & Fanzago).

The inclusion of *M. punctatissimus* in this species group is provisional. The group includes a series of species increasingly specialised by reduction of sclerotization and gnathotectal form, of which *M. punctatissimus* appears to represent the least specialised end. It shows little evidence of reduction of sclerotization except that the ventrianal shield is rather small and rounded. However, the dorsal chaetotaxy is the same as other members of the group and the chelicerae are of the *opacus* type.

Macrocheles opacus (C. L. Koch)
(Fig. 12A–E, Pl. 4B)

Macrholaspis opacus (C. L. Koch): Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 46.
Macrocheles (M.) opacus var. *aciculatus*: Krauss, 1970. *Acarologie* **14**: 23.

Evans & Browning placed this species in the genus *Macrholaspis* Oudemans, mainly on account of it having only two pairs of preanal setae on the ventrianal shield and crenulate margins to the dorsal shield. Krantz (1962) showed that there are closely related species having three pairs of preanal ventrianal setae and synonymised *Macrolaspis* with *Macrocheles*. The present authors also follow Krantz (1972) in synonymising *M. opacus* var. *aciculatus*, Krauss with *M. opacus*.

MATERIAL EXAMINED. 47 collections—7 PNN, 17 DNN, 88 ♀♀.

ENGLAND: Dorset, Gloucestershire, Berkshire, Surrey, Kent, Hertfordshire, Suffolk, Warwickshire, Worcestershire, Cumbria (Westmorland), Northumberland.

SCOTLAND: Strathclyde (Argyllshire), Dumfries & Galloway (Wigtownshire), Highland (Ross & Cromarty), Inner Hebrides (Mull, Ulva).

WALES: Glamorgan, Gwent, Gwynedd (Caernarvonshire), Clwyd (Denbighshire).

IRELAND: Clare, Galway, Mayo, Westmeath.

HABITATS. Collected in a variety of litter and soil habitats, but mainly in moss. Also found in rotten wood and an ants' nest.

DISTRIBUTION. Widespread in Europe, recent records include Germany (Krantz, 1973) and Spain (Athias-Henriot, 1968).

Macrocheles analis sp. nov.
(Fig. 13A–F, Pl. 5B)

FEMALE. The dorsal shield tapers from the shoulders posteriorly (Fig. 13A). It is ornamented with a raised polygonal reticular network which breaks up into small blunt tubercles anteriorly. The ornamentation is more rugose towards the shoulders. Between the main ornamentation there is fine granular microsculpture. The edges of the shield are smooth. There are twenty-nine pairs of pilose setae on the dorsal shield including both *J2* and *J3*.

The shields of the ventral surface are weakly sclerotized and reduced in size. The sternal shield has a fine granular texture and distinct reticulations posteriorly (Pl. 5B). The sternal and genital setae are pilose. The metasternal plates are small and round, only just large enough for the setae; the pores are separate in the unsclerotized membrane. The genital shield has a porous surface without reticulation. It is almost semicircular posteriorly and the genital pores are on the unsclerotized membrane. The postgenital apodemes are weakly sclerotized, barely discernible. The opisthogastric sclerotization is reduced to a small subcircular shield bearing the anal setae (Fig. 13B). The adanal setae are simple, longer than the postanal which is pilose. The *Jv* setae are simple, the other opisthogastric setae are strongly pilose. The spermathecal apparatus has elongate rami and indistinct median organs (Fig. 13C).

The gnathotectum has a bifid median process with the arms dissected and the lateral processes absent, the anterior edge is dentate (Fig. 13D). The fixed chela is basically bidentate with a central tooth and an offset subterminal tooth, it is truncate distally; the movable chela is bidentate (Fig. 13E). The dorsal seta is pectinate laterodistally. The corniculi are elongate (Fig. 13F), one-and-a-

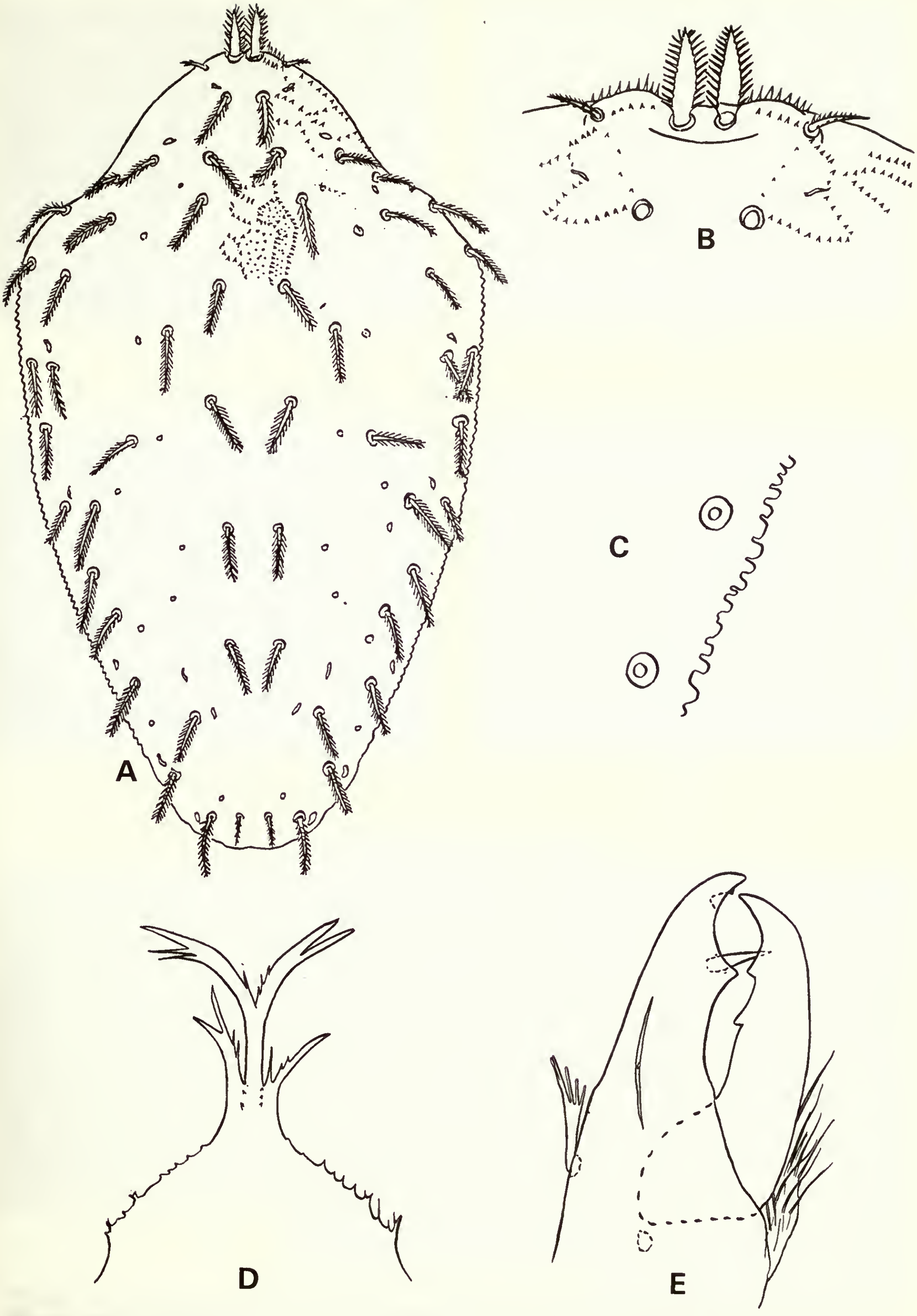

Fig. 12 *Macrocheles opacus* (C. L. Koch): **female**—A dorsal shield; B anterior region of dorsal shield; C lateral margin of dorsal shield; D gnathotectum; E chelicera. After Evans & Browning (1956).

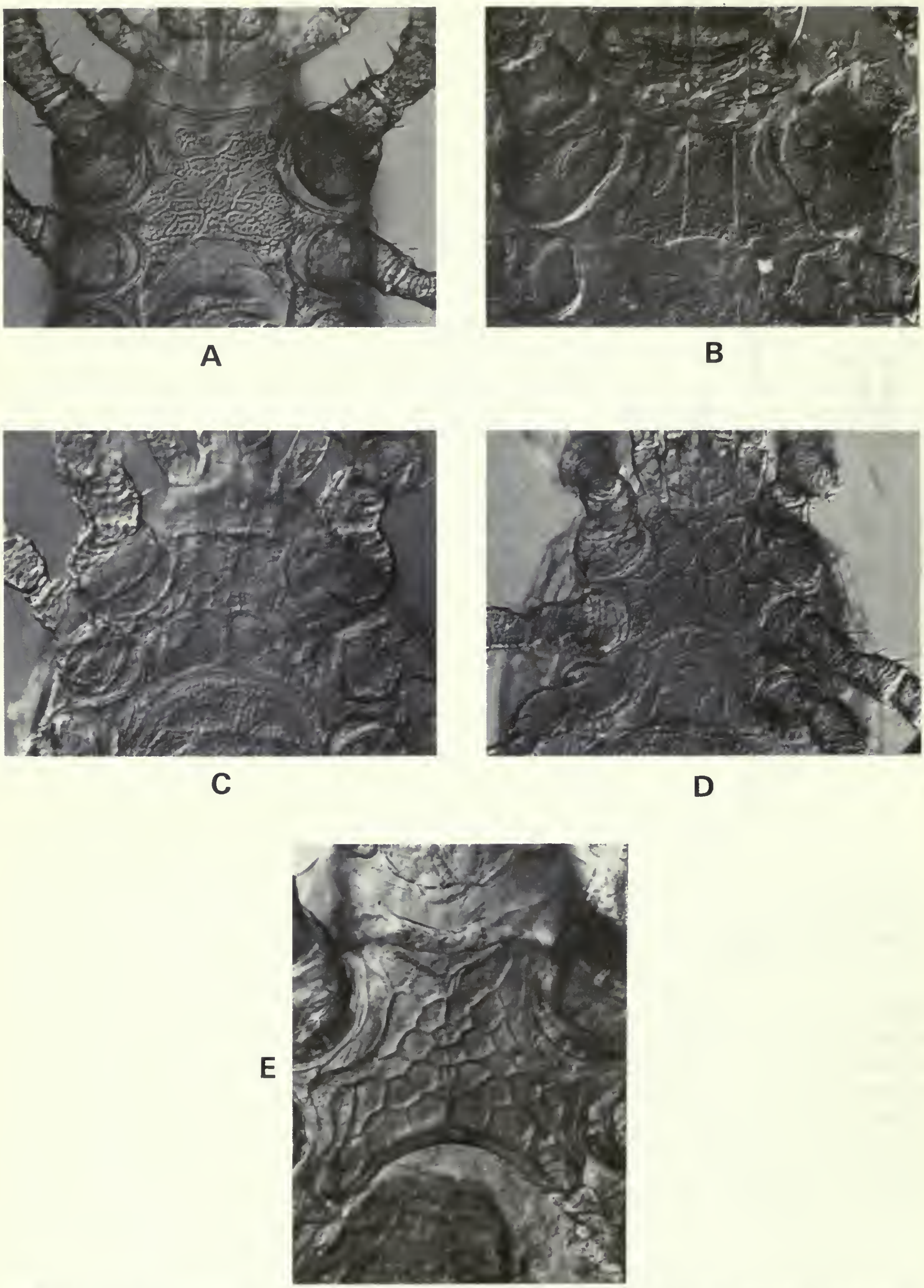

Plate 5 Sternal shields of the females of: A *Geholaspis (Longicheles) hortorum* (Berlese); B *Macrocheles analis* sp. nov.; C *Holostaspella ornata* (Berlese); D *H. exornata* Filipponi & Pegazzano; E *Glyptholaspis fimicola* (Berlese).

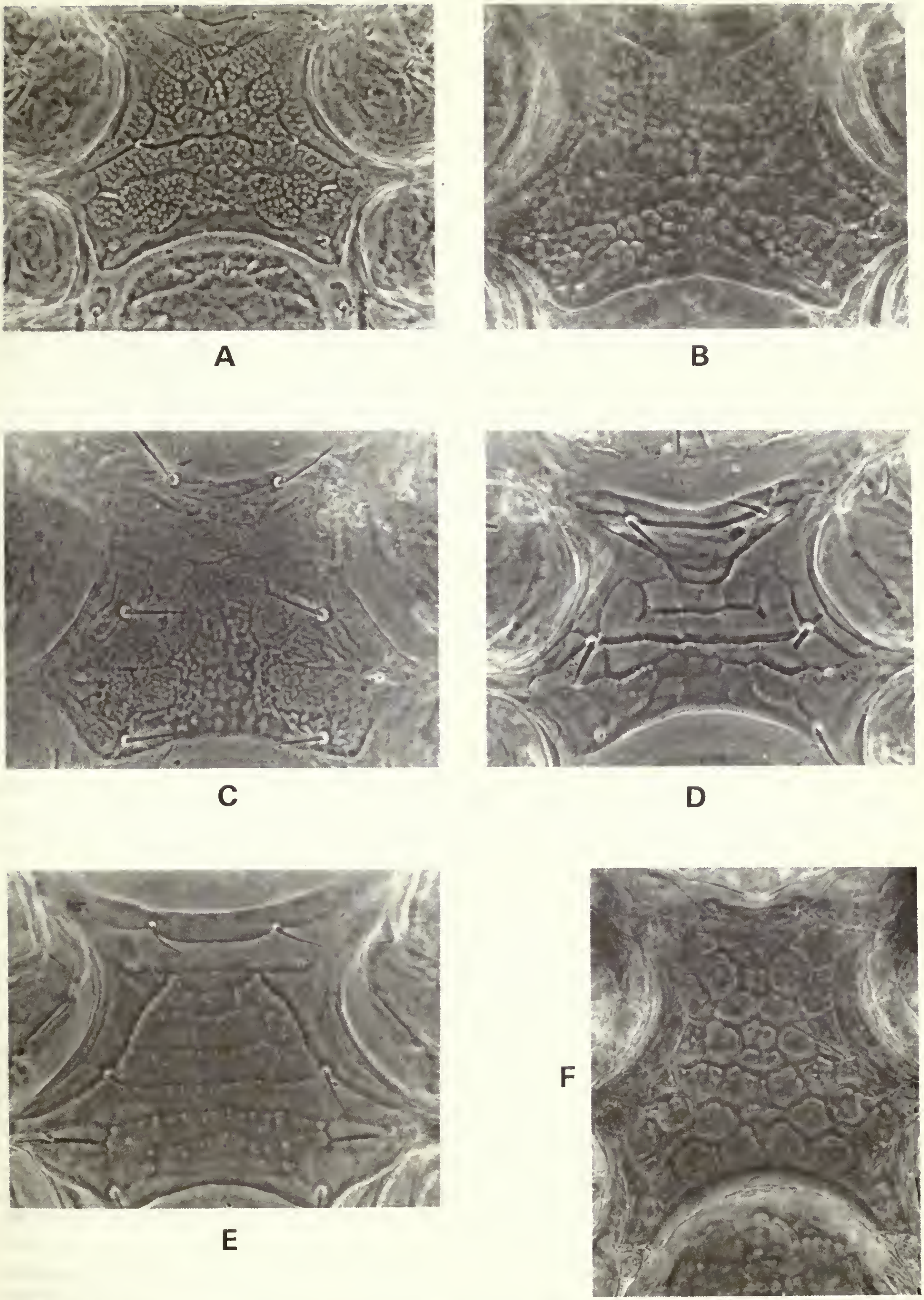

Plate 6 Sternal shields of the females of: A *Macrocheles rotundiscutis* Bregetova & Koroleva; B *M. punctatissimus* Berlese; C *M. terreus* (Canestrini & Fanzago); D *M. nataliae* Bregetova & Koroleva; E *M. subbadius* (Berlese); F *Glyptholaspis americana* (Berlese).

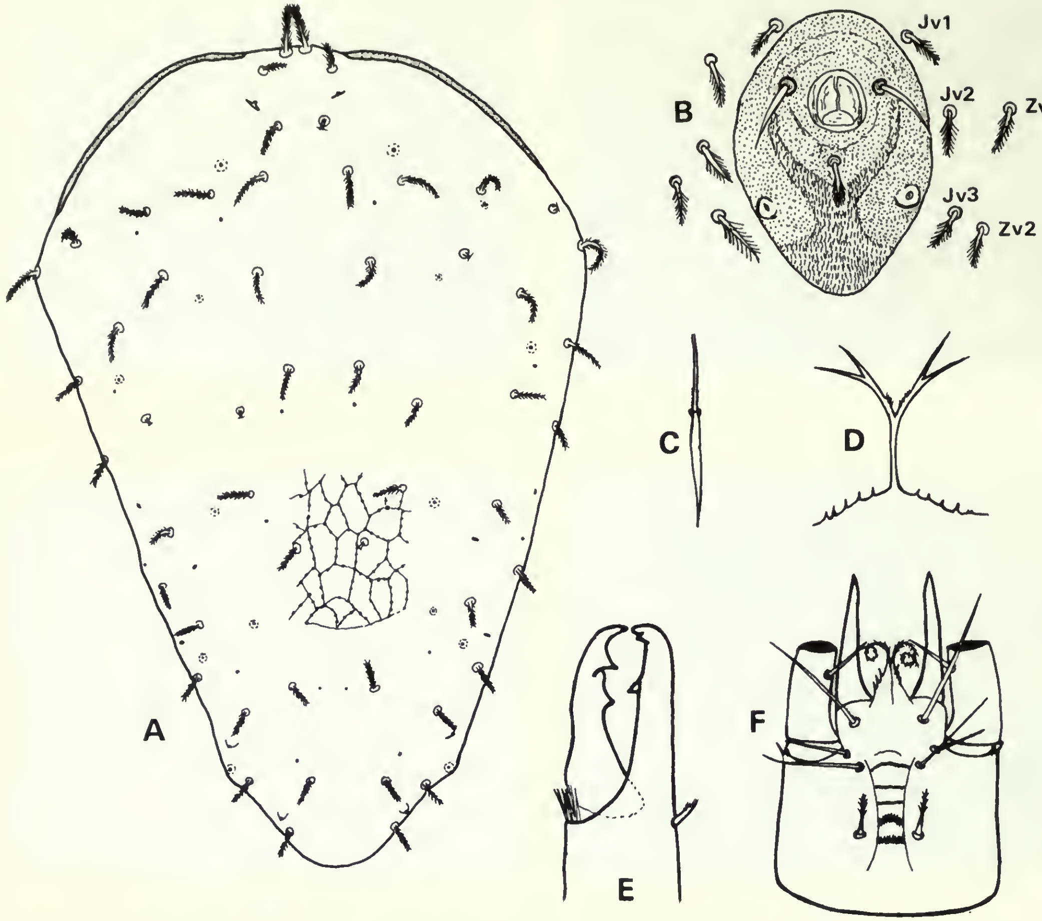

Fig. 13 *Macrocheles analis* sp. n.: **female**—A dorsal shield; B anal shield; C tubulus and ramus of spermathecal apparatus; D gnathotectum; E chelicera; F venter of gnathosoma.

half times as long as the pedipalp trochanter. The internal hypostomal setae are posterior to the external hypostomal setae. The hypognathal groove has two rows of strong denticles (*G5* and *G6* in Hirschmann's notation) and three fine rows (*G2, G3, G4*). The hollow seta on the external part of the palp tarsus, which is elongate in all known species of *Macrocheles*, is barely longer than the surrounding setae.

The legs have mainly pilose setae on all segments except coxa and tarsus I which have all setae simple.

TYPE MATERIAL. **Holotype** ♀, England, Berks, Silwood Park, 'light sandy loam with winter wheat', 23.xi.1963. [BMNH].

MATERIAL EXAMINED. Known only from the holotype in the British Isles, but two specimens from the U.S.A., apparently referrable to this species, have been seen; 1 ♀, Corvallis, Oregon, rotten bulb [OSUC] and 1 ♀, Lexington, Kentucky, duff.

REMARKS. This species represents the end of a series of species showing increasing reduction of the ventral shields and increasing specialisation of the gnathosoma and spermathecal apparatus in the direction of the condition found in *Geholaspis (Longicheles)*. It is probable that the reduction of sclerotization is an adaption to life in deeper soil layers.

Macrocheles dentatus (Evans & Browning)
(Fig. 14A–D, Pl. 4C)

Macrholaspis dentatus Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 49.
Macrocheles (M.) multisetosus Götz in Krauss, 1970. *Acarologie* **14**: 29. **Syn. nov.**

Evans & Browning (1956) described this species in the genus *Macrholaspis*, which was synonymised by Krantz (1962) with *Macrocheles*.

The type material of *M. multisetosus* Götz has not been examined, but the description and illustrations fail to show any significant difference between it and the holotype of *M. dentatus*, with the exception of four rather than three unpaired median dorsal setae. This character has been found to vary in material from collections in the British Isles and is not correlated with other characters. However, the original description of *M. dentatus* is misleading in that the setae on the membrane between the genital and ventrianal shields are stated to be plumose when in fact there are two pairs of simple setae, *Jv1* and *Zv1* (*V1* and *V5* in Hirschmann's notation), in this position in all specimens examined, including the holotype.

In their key to species of *Macrholaspis* Evans & Browning (1956) state that there is a strong tubercle on the posterior margin of trochanter IV. This is an error for femur III.

The Hull Collection includes a specimen labelled '*Macrocheles pannosus* 9 Bks.' [Ninebanks, Northumberland], which is a specimen of *M. dentatus*. Reluctantly the present authors have concluded that this cannot be the type of *M. pannosus* Hull, 1925, described from West Allendale, as it does not agree with the description either as to size or in the characters described.

TYPE MATERIAL. *M. dentatus*; **holotype** ♀, Wales, Cardiganshire, Dolybont, Leri Valley, in litter under bracken, viii.1954, G. O. Evans. [BMNH].

MATERIAL EXAMINED. 19 collections—2 DNN, 22 ♀♀.

ENGLAND: Cornwall, Devon, Somerset, Surrey, Kent, Cambridgeshire, Yorkshire, Northumberland.
SCOTLAND: Tayside (Perthshire).
WALES: Gwent, Dyfed (Cardiganshire).
IRELAND: Clare, Galway, Westmeath.

HABITATS. Bryophytes, leaf litter and grassland soil, also one collection from *Microtus agrestis*.

DISTRIBUTION. Evidently widespread but rarely collected in the British Isles; also known from Germany (Götz in Krauss, 1970, as *M. multisetosus*).

Macrocheles punctatissimus Berlese
(Fig. 14E–G, Pl. 6B)

Macrocheles (Nothrholaspis) punctatissimus Berlese, 1918. *Redia* **13**: 171.
Nothrholaspis pulcherrimus Willmann, 1951. *Sber. Akad. Wiss. Wien.* **160**: 104.

FEMALE. The dorsal shield (Fig. 14E) completely covers the dorsal surface. It is strongly ornamented with reticulations, the sides of the reticulations are crenate and within them there is a porose microsculpture. There are twenty-eight pairs of setae plus an unpaired median seta between *j6* and *J3* on the dorsal shield. Setae *j1* are slightly flattened, all other setae are of the usual tapering pilose variety. The lateral margins of the dorsal shield are smooth.

The sternal shield is strongly punctured all over; the punctures are arranged in groups to form a symmetrical pattern (Pl. 6B). The metasternal plates are rounded and include the pore. The genital shield is truncate posteriorly and not noticeably reduced. It is ornamented with a series of minute tubercles arranged in rows. The sternal and genital setae are simple. The ventrianal shield is rounded and closely abuts the genital, it bears three pairs of simple preanal setae. The postanal seta is pilose. The spermathecal complex is of the normal type within the genus *Macrocheles* with short rami joining a two-lobed sacculus (Fig. 14F).

The gnathosomal structures are typical of the genus *Macrocheles*. The gnathotectum has a median bifid process (Fig. 14G) and free lateral processes expanded and serrate at the distal end.

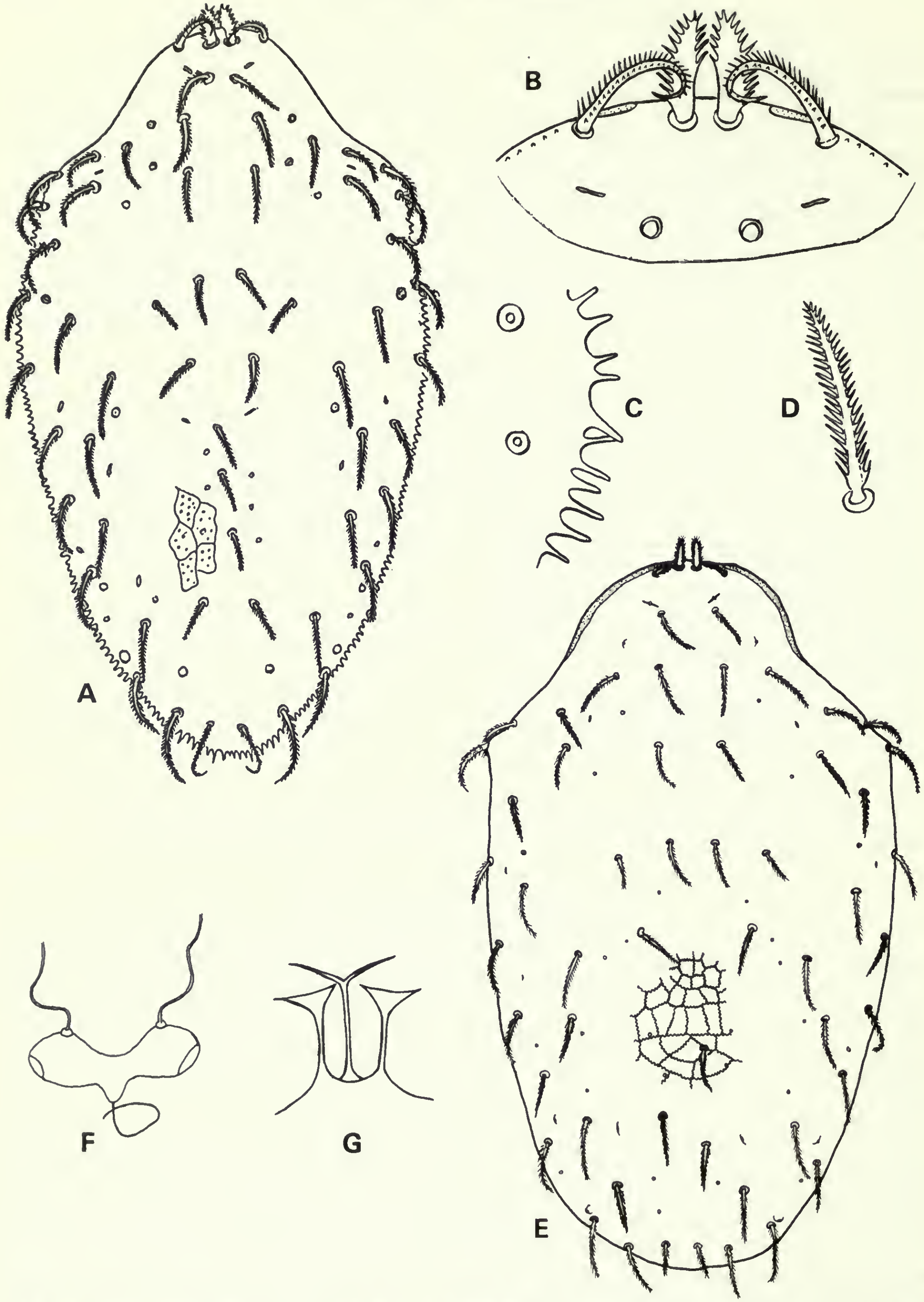

Fig. 14 *Macrocheles dentatus* Evans & Browning: **female**—A dorsal shield; B anterior region of dorsal shield; C lateral margin of dorsal shield; D dorsal seta *z4*. After Evans & Browning (1956). *Macrocheles punctatissimus* Berlese: **female**—E dorsal shield; F spermathecal apparatus; G gnathotectum.

The fixed chela is basically bidentate, including an offset terminal tooth. The movable chela is bidentate and the dorsal seta is slightly pectinate distally. The hypognathal groove has the usual five rows of denticles and hypostomal setae 2 and 3 are opposite each other.

The legs are normal for the species group, rugose and with the usual mixture of pilose and simple setae on most segments. Seta pl_1 on femur III is conspicuous and blade shaped.

TYPE MATERIAL. *Macrocheles punctatissimus*: **Syntypes** 2 ♀♀ 'Castions distruda (Udine), musco [moss]', slide 131/46 [ISZA].

MATERIAL EXAMINED. 2 collections—3 ♀♀.
ENGLAND: Cambridgeshire.

HABITATS. The first British record. From the bases of *Molinia* tussocks in Wicken Fen. Apparently found in similar places in Austria (as *pulcherrimus*).

DISTRIBUTION. Germany (Krauss, 1970), Austria (Willmann, 1951 as *pulcherrimus*).

REMARKS. No type material of *Nothrholaspis pulcherrimus* has been examined so the synonymy follows Krauss (1970). The species present in Britain is clearly conspecific with that described by Krauss (1970) and probably with that described by Willmann (1951).

Macrocheles terreus (Canestrini & Fanzago)
(Fig. 15A–B, Pl. 6C)

Gamasus terreus Canestrini & Fanzago 1877. *Atti R. Ist. veneto Sci.* (V) **4**: 48.
Holostaspis echinatus Berlese, 1904. *Redia* **2**: 20.
Holostaspis terreus (Canestrini & Fanzago), Halbert, 1915. *Proc. R. Ir. Acad.* **31**: 66.
Macrocheles (M.) opacus Krauss, 1970. *Acarologie* **14**: 22.
Macrocheles terreus (Canestrini & Fanzago); Krantz, 1972. *Ent. Mitt. zool. Mus. Hamburg* **4**: 270.

FEMALE. The dorsal shield has twenty-nine pairs of setae (Fig. 15A) including pairs in both the *J2* and *J3* positions. The setae are generally shorter and blunter than in other members of the species group and pilose or plumose almost to the base; setae *j1* are strongly flattened, almost fan-shaped. The dorsal shield ornamentation consists of faint reticulations and a dense microsculpture of fine pores. The lateral margins are bluntly dentate.

All the ventral shields are finely punctured, many of the punctures are arranged in lines. The setae on the ventral shields are basically simple, except the genital setae, which may appear finely pilose, and the pilose post anal seta. The sternal shield has a symmetrical pattern of punctate areas and lines of fine punctures. The metasternal platelets are elongate oval. The genital shield is semicircular behind and the associated pores are free on the membrane. The subcircular ventrianal shield is well separated from the genital with three pairs of apodomes between. The median structures of the spermathecal complex are indistinct.

The gnathosoma is typical of the species group with free spike-like lateral processes on the gnathotectum and the chelae with offset subterminal and central teeth on the fixed chela and two central teeth on the movable chela (Fig. 15B). The hypognathal groove has six rows of denticles.

The legs are normal for the species group except that many setae are somewhat flattened or blade-like instead of pilose.

TYPE MATERIAL. *H. echinatus*: **Lectotype** ♀ (here designated), Italy, Firenze, Boboli, Foglia marce palme, 'tipico *M. echinatus* Berl.' slide 22/38 [ISZA]. *G. terreus*: **Neotype** ♀ (here designated), the lectotype of *H. echinatus*, from Firenze, Italy, slide 22/38 [ISZA].

Although Berlese indicated a type designation on slide 22/38 and in his notebooks, this designation was not published.

MATERIAL EXAMINED. 6 collections—6 ♀♀.
ENGLAND: Hampshire, Kent, Suffolk, North Yorkshire, Humberside.
IRELAND: Mayo (Halbert, 1915).

HABITAT. From arable and grassland soils and beech forest litter, also recorded from moss and leaf litter by Krauss (1970) and from moss and under bark by Halbert (1915).

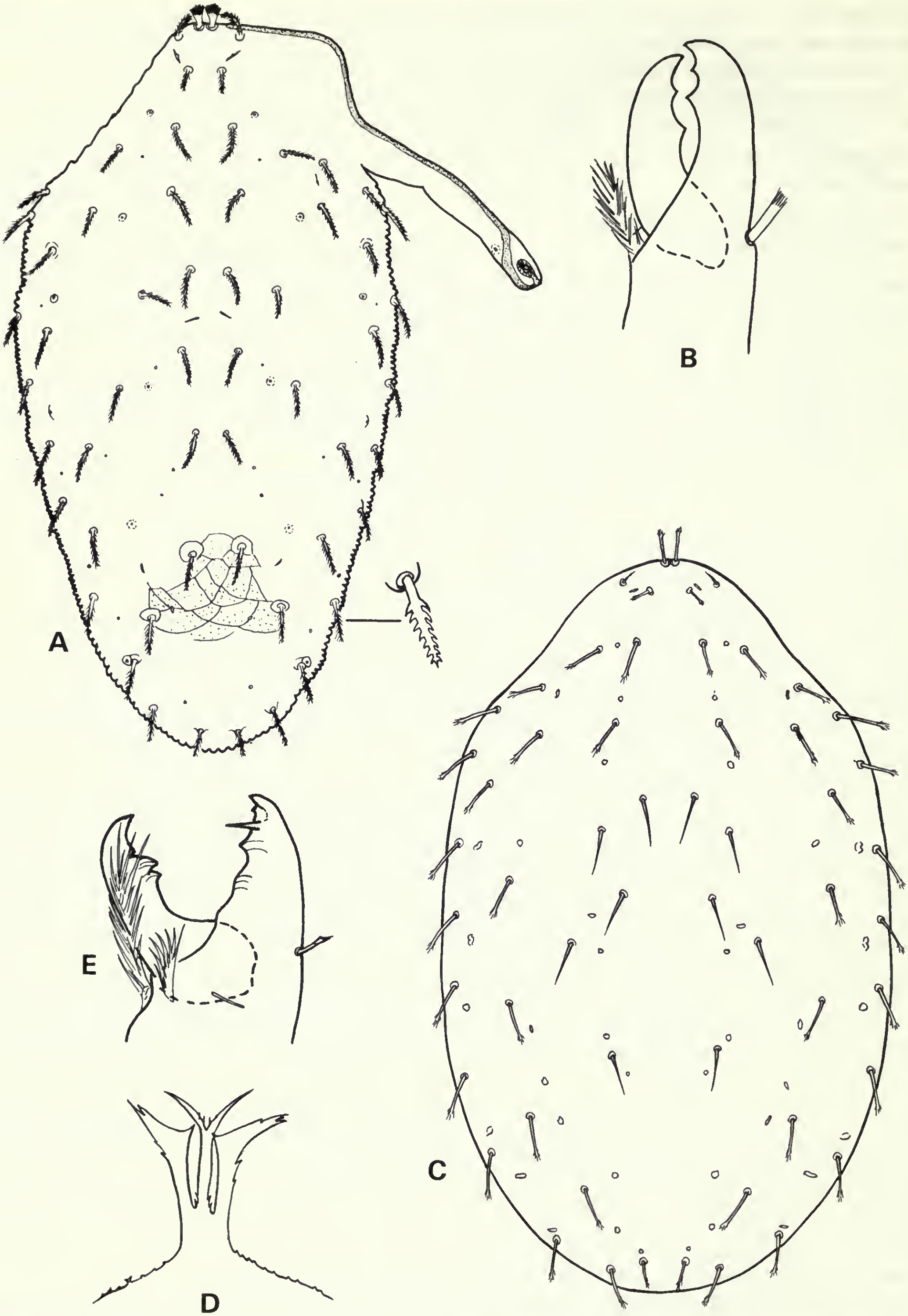

Fig. 15 *Macrocheles terreus* (Canestrini & Fanzago): **female**—A dorsal shield with right seta *S4* enlarged; B chelicera. *Macrocheles muscaedomesticae* (Scopoli): **female**—C dorsal shield; D gnathotectum; E chelicera. After Evans & Browning (1956).

DISTRIBUTION. According to Krauss (1970) it is known from Germany and Spain (as *opacus*). Since Krauss's concept of *M. opacus* varies from that of most other authors, the literature records he cites are probably for several species.

REMARKS. The original material of *Gamasus terreus* was stated (Canestrini & Fanzago, 1877) to have come from Padova. The type material is not present in the Canestrini Collection in Padova (see remarks under *M. tardus*) and must be presumed lost.

Valle (1955) records two vials listed under *terreus* in the catalogue of the Canestrini Collection. The first vial (jar no. XX, vial no. 703) apparently contained specimens of *terreus* from Rome, when seen by Valle, but now only contains two feather-mites. The other vial (jar no. XIII, vial no. 504) contained *Geholaspis longispinosus* when seen by Valle, but is now empty. It is labelled 'Messina'. Neither of these vials could have contained the types as these came from Padova.

In the absence of Canestrini and Fanzago's type material of *G. terreus* a neotype has been selected, this is necessary in view of the likelihood of there being a complex of closely similar species centred on *M. terreus*.

The lectotype specimen of *echinatus* has been chosen as neotype of *terreus*. This will have the effect of making *echinatus* an objective synonym of *terreus* and confirming a synonymy indicated by Berlese on the slide of *echinatus* and in his notebooks.

Berlese's (1904) original drawing of *echinatus* (Plate II, Fig. 33) differs from his later drawing in his notebook and from the designated type of *echinatus* in having a truncate posterior margin to the genital shield and in having a larger, more triangular ventrianal shield.

Macrocheles terreus evidently belongs to a complex of very closely related species within the *opacus* species group of which *M. beieri* Johnston from Austria may be a member. It is possible that the species described above may also represent a different taxon based on the simple setae of the ventral shields, the six rather than five rows of hypognathal denticles and fine differences in the sculpture of the shields. However, a decision on this must await the discovery of more British material and direct comparison of the various forms involved.

The present authors have followed Krantz (1972) in the synonymy of *M. opacus*, Krauss, with *M. terreus* (Canestrini & Fanzago).

Macrocheles muscaedomesticae (Scopoli)
(Fig. 15C–E, Pl. 1A)

The description and synonymy of this species as given by Evans & Browning (1956) remain correct.

MATERIAL EXAMINED. 27 collections—76 ♀♀, see below.

ENGLAND: Cornwall, Devon, Wiltshire, Hampshire, Sussex, Surrey, Kent, London, Essex, Middlesex, Hertfordshire, Cambridgeshire, Lancashire, Cheshire.

A sample from a deep-litter house in which partridges *Perdix perdix* were being reared in Cambridgeshire in 1978 contained thousands of females of this species.

HABITATS. Mostly associated with synanthropic flies, i.e. *Musca domestica, Fannia* spp., *Stomoxys calcitrans*, also with fly breeding places, compost heaps, rotting seaweed and artificial nests of rats.

DISTRIBUTION. Apparently cosmopolitan wherever suitable phoretic hosts exist, although surprisingly, the only British material examined is from England.

Macrocheles pisentii (Berlese)

This species almost certainly does not occur in the British Isles. Its inclusion by Evans & Browning (1956) was based on three records of Hull (1918), but they were unable to examine his specimens. The present authors have examined material labelled as *M. pisentii* in the Hull Collection, but without locality data, and found it to be *M. glaber*.

Costa (1967) has shown *M. pisentii* to be very closely associated with *Scarabaeus semipunctatus* F., even to the exclusion of other species of *Scarabaeus*. Since *S. semipunctatus* is not present in the British fauna it seems that *M. pisentii* is also unlikely to be present.

Costa (1967) redescribed *M. pisentii* and distinguished it from other closely related species.

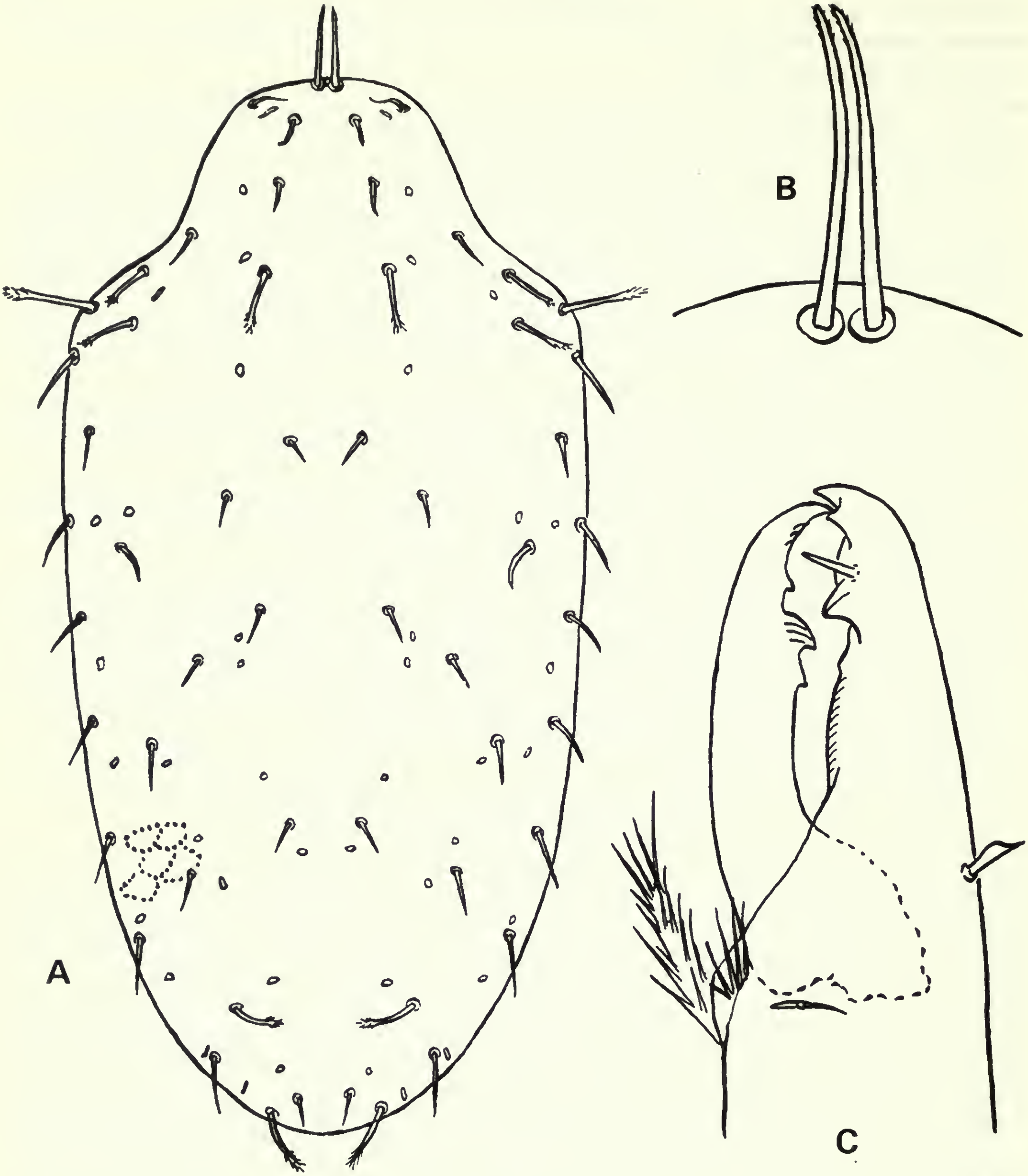

Fig. 16 *Macrocheles robustulus* (Berlese): **female**—A dorsal shield; B seta *j1*; C chelicera. After Evans & Browning (1956).

Macrocheles robustulus (Berlese)

(Fig. 16A–C, Pl. 1B)

Holostaspis subbadius var. *robustulus* Berlese, 1904. *Redia* **1**: 264.
Holostaspis humeratus Berlese 1908. *Redia* **5**: 13.
Nothrholaspis punctillatus Willmann, 1939. *Abh. naturw. Ver. Bremen* **31**: 176.
Macrocheles coprophila Womersley, 1942. *Trans. Roy. Soc. S. Aust.* **66**: 167.
Macrocheles rothamstedensis Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 15.
Macrocheles robustulus: Axtell, 1961. *Ann. ent. Soc. Am.* **54**: 748.

The first British record of this species was that of Evans & Browning (1956) who described it under the name *M. rothamstedensis*. This was synonymised with *M. punctillatus* (Willmann) by Bregetova & Koroleva (1960) and with *M. robustulus* (Berlese) by Axtell (1961). For the complete synonymy see Krantz & Filipponi (1964).

Evans & Browning's (1956) description needs no amendment.

MATERIAL EXAMINED. 3 collections—3 ♂♂, 64 ♀♀.
ENGLAND: Essex, Hertfordshire, Bedfordshire.

HABITATS. Cattle dung, 'colony on cucumber leaves'. Elsewhere this species is most often collected from cattle manure (Axtell, 1961), and phoretic on scarabaeine beetles (Costa, 1966*a*).

DISTRIBUTION. Widespread in temperate regions of the world; Italy (Filipponi & Pegazzano, 1962), Germany (Krantz, 1972), U.S.S.R. (Bregetova & Koroleva, 1956), Israel (Costa, 1966*a*), U.S.A. (Axtell, 1961), Australia (Krantz & Filipponi, 1964), New Zealand (Emberson, unpublished).

glaber group

This species group was defined by Filipponi & Pegazzano (1962) and is here slightly modified to include another obviously related species. The species are medium sized with the 28 pairs of setae on the dorsal shield being mainly simple, but there are from four to ten pairs that are pilose. These usually include *j1, j4, z3* which are pilose distally and *J5* pilose over their entire length. Males usually have additional pilose setae. The dorsal shield is lightly ornamented with transverse reticulations and, in the females, is divided by a procurved line passing close to the bases of setae *z6* and extending laterally towards setae *r4* (Fig. 17A). The lateral margins are smooth. The male dorsal shield is strongly tapered posteriorly with crenulate lateral and posterior margins. The type of sternal shield pattern is characteristic, with lines often edged with punctures. The *linea media transversa* is well developed and straight, the *linea angulata* is similar in all species and there are one or two *lineae arcuatae* of varying form. Behind the *linea media transversa* the *lineae obliquae posteriores* are bifurcate distally and the *areae punctatae posteriores* are well developed. The ventrianal shield is usually more or less pentagonal and ornamented with concentric lines and reticulations, at least anteriorly. The males have separate sternogenital and ventrianal shields. All the ventral setae are simple, except the postanal which is finely serrated. The gnathotectum has free lateral processes and a bifurcate median process which is minutely spiculate medially. The fixed chela is bidentate, with a proximal major tooth and a distal minor one, it is bidentate or tridentate in the male. The movable chela is basically tridentate with two adjoining proximal teeth, lacking in the male, and a minor distal tooth. The spermatodactyl extends dorsally then posteriorly and is about the length of the movable chela. The cheliceral dorsal seta is simple to slightly lanceolate. The legs have mainly simple setae with some pilose setae on trochanters, femora, genua and tibiae. The male leg armature consists of complex spurs on trochanter and femur IV, a strong spur on femur II and a series of other small spurs and tubercles on the genua, tibiae and tarsi of legs II and IV. The spermathecal sacculus is of the normal two-lobed variety with the lobes close together and broadly joined, the corniculum is wide, almost cup-shaped.

INCLUDED SPECIES. *M. glaber* (Müller), *M. nataliae* Bregetova & Koroleva, *M. scutatus* (Berlese).

M. nataliae, here included in the *glaber* group, is obviously closely related to the other species although it differs slightly from them in having setae *j4* and *z3* simple, and the *lineae obliquae posteriores* are not obviously bifurcate as they are in other species. Krantz (1981), in describing *M. eurygaster*, assigned it to the *glaber* group in spite of setae *j4* and *z4* being simple in the female. They are pilose distally in the immatures and males.

Macrocheles glaber (Müller)
(Fig. 17A–D, Pl. 1C)

The description and synonymy given by Evans & Browning (1956) remain adequate although Filipponi & Pegazzano (1962) have redescribed this species and give an extended synonymy, including *M. alecto* Berlese and its varieties.

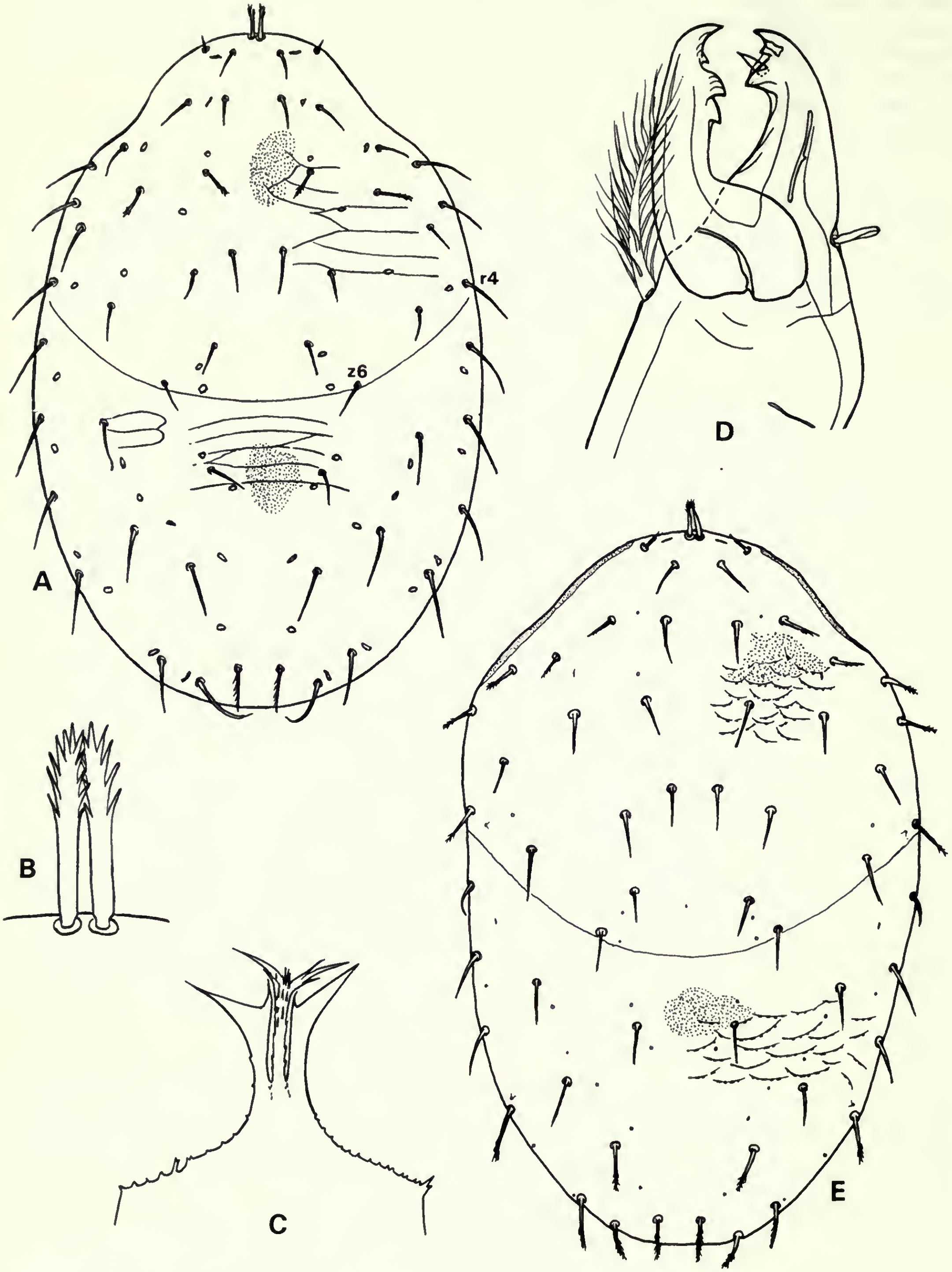

Fig. 17 *Macrocheles glaber* (Müller): **female**—A dorsal shield; B seta *j1*; C gnathotectum; D chelicera. After Evans & Browning (1956). *Macrocheles nataliae* Bregetova & Koroleva: **female**—E dorsal shield.

TYPE MATERIAL. *M. alecto*: **Syntype** ♀ only, Italy, Firenze, Giarbino R. Stazione, humus. Slide 186/15 [ISZA]. *Holostaspis marginatus* var. *littoralis* Halbert, 1915: **Lectotype** ♀ here designated, Westport, Co. Mayo, Ireland, on seashore, July 1910. Slide 55—1923 [National Museum of Ireland, Dublin]. **Paralectotypes** 2 ♀♀ on same slide, same data, 1 ♂ (dissected) on two separate slides, both 55—1923, also same data.

MATERIAL EXAMINED. 170 collections—9 DNN, 42 ♂♂, *c*. 3, 100 ♀♀.

ENGLAND: Isles of Scilly, Cornwall, Devon, Dorset, Gloucestershire, Somerset, Isle of Wight, Hampshire, Sussex, Surrey, Kent, London, Essex, Middlesex, Hertfordshire, Buckinghamshire, Suffolk, Norfolk, Cambridgeshire, Warwickshire, Derbyshire, Yorkshire, Lancashire, Cheshire, Cumbria (Cumberland, Westmorland), Northumberland.

SCOTLAND: Dumfries & Galloway (Kirkcudbrightshire), Strathclyde (Argyllshire), Inner Hebrides (Mull), Outer Hebrides (Shillay), Shetland.

WALES: Dyfed (Cardiganshire), Gwynedd (Anglesey, Caernarvonshire, Merionethshire), Clywd (Denbighshire).

IRELAND: Cork, Clare, Galway, Mayo.

HABITATS. Most often collected associated with coprophagous beetles (79 collections), records include: *Geotrupes mutator* Marsham, *G. pyrenaeus* Charpentier, *G. spiniger* Marsham, *G. stercorosus* (Scriba), *G. vernalis* (L.), *Typhaeus typhoeus* (L.), *Aphodius rufipes* (L.) and *A. scybalarius* (F.). *M. glaber* has also been collected from burying beetles *Nicrophorus humator* F., (2 collections), from bumble bees *Bombus agrorum* F., from a fox corpse (Smith, 1975), from small mammals and their nests, and from a variety of manure and rotting vegetation habitats, including occasionally seaweed.

DISTRIBUTION. Found everywhere in the British Isles where suitable habitats occur and probably in most temperate regions of the world. Filipponi & Pegazzano (1962) report it as widespread in Europe and the Meditteranean area. Outside these areas it has been recorded throughout the U.S.S.R. (Bregetova & Koroleva, 1960), U.S.A. (Axtell, 1963) and New Zealand (Emberson, 1973*a*).

Macrocheles nataliae Bregetova & Koroleva
(Fig. 17E, Pl. 6D)

Macrocheles nataliae Bregetova & Koroleva, 1960. *Parazit. Sb.* **19**: 140.
Macrocheles (Macrocheles) melisii Krauss, 1970. *Acarologie* **14**: 24. **Syn. nov.**

FEMALE. The dorsal shield (Fig. 17E) is ornamented with mainly transverse reticulations and a microsculpture of very fine regular punctations. There are twenty-eight pairs of setae on the dorsal shield of which *j1, z2, s2, r2, r3, r4, J5, Z4, Z5, S4* and *S5* are pilose distally, other dorsal setae are simple.

The sternal shield (Pl. 6D) has a characteristic pattern of lines and fine punctures, there are no coarse punctures. The *linea media transversa* is well defined, there is one *linea arcuata* which tends to be concave anteriorly and meet with polygonal reticulations laterally. There is an area of fine punctures just posterior to the *linea angulata*. The *lineae obliquae posteriores* are poorly defined and not noticeably bifurcate. The *areae punctatae posteriores* are represented mainly by a series of fine edging punctures. The metasternal plates are small elongate-ovate. The genital shield is weakly ornamented, with fine lines and punctures. The ventrianal shield is noticeably longer than broad and ornamented with more or less concentric reticulations anteriorly which tend to become polygonal posteriorly.

The gnathosoma is typical of the species group, the gnathotectum having free lateral processes and a bifurcate median process which is minutely spiculate in the fork. The fixed chela has one major tooth and one minor distal tooth, the movable chela is tridentate, the two proximal teeth arising from a common base; the cheliceral dorsal seta is slightly flattened and leaf-shaped.

The legs are normal for the group with a mixture of simple setae and stubby, faintly pilose setae on all segments except the coxae, trochanters, and on leg I, the tibia and tarsus.

MALE. The male is unknown in the British Isles. Krauss (1970) described a male which is probably this species (as *melisii*), it differs from other males of the species group mainly in the distribution of pilose dorsal setae.

TYPE MATERIAL. *M. nataliae*: 1 ♀ **syntype**, Lithuanian S.S.R., Plunge, on the corpses of *Microtus arvalis*, 11.vii.1954, coll. Likyavichene [ZINL]. 1 ♀ **syntype**, Tatar A.S.S.R., Kuibyshev region, in soil at experiment station, under grass 11.vi.1957, coll. Aleinikova [ZINL].
The type material of *M. melisii* was not available for study, but there can be little doubt of the synonymy based on the description and drawing of Krauss (1970).

MATERIAL EXAMINED. 6 collections—20 ♀♀.
ENGLAND: Cornwall, Hampshire, London, Lincolnshire.

HABITATS. The first record for the British Isles. On burying beetles *Nicrophorus humator* F., *N. investigator* Zett. and *N. vespillo* L. Bregetova & Koroleva (1960) report it from a variety of small mammals and also from soil samples, whilst Bregetova *et al.* (1977) record it from *Geotrupes.*

DISTRIBUTION. Widespread in U.S.S.R., from Lithuanian SSR, to the Maritime region of Siberia (Bregetova & Koroleva, 1960); also reported from Germany (Karg, 1970; Krauss, 1970).

REMARKS. There are several small inconsistencies in the details of the description and drawings of Bregetova & Koroleva (1960) both when compared with their syntypes and with British material. They do not describe setae *z2, s2, Z4* and *S3* as pilose and seta *r4* is described as pilose but drawn simple, these setae are only very faintly pilose in British material. They mention that there is some variation in the presence of pilose setae and certainly in two syntypes examined *z2* was simple, although it is pilose in British material. Krauss (1970) also records it as simple. The other setae mentioned were pilose in both syntypes from the U.S.S.R., in British material and in that illustrated by Krauss (1970). It appears that there may be some slight variation in the distribution of pilose dorsal setae but this is perhaps not surprising in a species distributed across the whole of the Palaearctic region.

Macrocheles scutatus (Berlese)
(Fig. 18, Pl. 1E)

Holostaspis subbadius var. *scutatus* Berlese, 1904. *Redia* **1**: 264.
Macrocheles subbadius: Evans & Browning, 1956, *non* Berlese, 1904. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 19.
Macrocheles scutatus (Berlese): Filipponi & Pegazzano, 1962. *Redia* **47**: 228.

The female of this species is adequately described by Evans & Browning (1956) under the name *M. subbadius* (Berlese) which Filipponi & Pegazzano (1963) have shown to be a completely different species.

The male has been described on the basis of reared material by Filipponi & Pegazzano (1962). It differs from related species chiefly in the distribution of pilose dorsal setae, in details of the shape and ornamentation of the ventral sclerotisation and in the leg armature.

MATERIAL EXAMINED. 5 collections—17 ♂♂, 24 ♀♀.
ENGLAND: Worcestershire, Derbyshire, Yorkshire.
WALES: Glamorgan.

HABITATS. Farmyard manure. Filipponi & Pegazzano (1962) record this species from dung and compost habitats, also associated with coprophagous beetles, but not muscid flies.

DISTRIBUTION. Italy (Filipponi & Pegazzano, 1962), U.S.S.R. (Bregetova & Koroleva, 1960—as *M. subbadius*—and Bregetova *et al.*, 1977), New Zealand (Emberson, 1973*b*). The continuing confusion of closely related species, including *M. vicinus* Leitner (1946), makes assessment of the distribution of this species problematical.

subbadius **group**

This species group was reviewed by Filipponi & Pegazzano (1963) who defined it as consisting of small species, with 28 pairs of simple needle-like setae in the females, with setae *j1* short, spine-like

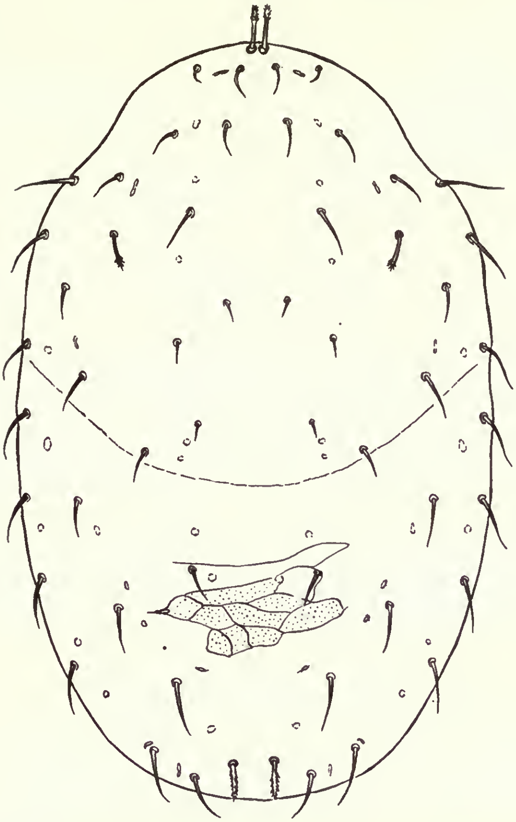

Fig. 18 *Macrocheles scutatus* (Berlese): **female**—dorsal shield. After Evans & Browning (1956).

and diverging. The dorsal shield of males is more or less strongly tuberculate posteriorly, and has at least two pairs of large blunt, slightly spatulate setae (*j4, z4*). The ventral shields are ornamented with a series of punctate lines; in the females the sternal shield has the *lineae oblique anteriores* connected transversely by 4 or 5 lines, the most posterior of which is the *linea media transversa*. All the ventral setae are simple. The males have a holoventral shield. The gnathotectum has the lateral processes free and the median process bifurcate and minutely spiculate distally. Both chelae are basically bidentate in the female, but in the male the fixed chela is tridentate and the movable chela unidentate; the dorsal seta is simple and the spermatodactyl is elongate, tapering, strongly recurved and almost twice as long as the movable digit. All the leg setae are simple, although spinose on tarsi II–IV. The males have the femora, genua, tibiae and tarsi of legs II armed with spines and tubercles, leg III is unarmed and the armature of leg IV is more variable.

INCLUDED SPECIES: *M. subbadius* (Berlese), *M. insignitus* Berlese and *M. merdarius* (Berlese).

Macrocheles subbadius (Berlese)
(Fig. 19A, Pl. 6E)

Holostaspis subbadius Berlese, 1904. *Redia* **1**: 264. *non Macrocheles subbadius*, Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 19.

The species described as *M. subbadius* by Evans & Browning (1956) is in fact *M. scutatus* (*vide* Filipponi & Pegazzano, 1962). However, *M. subbadius* does occur in the British Isles and a short description is given below. For a detailed description and synonymy see Filipponi & Pegazzano (1963).

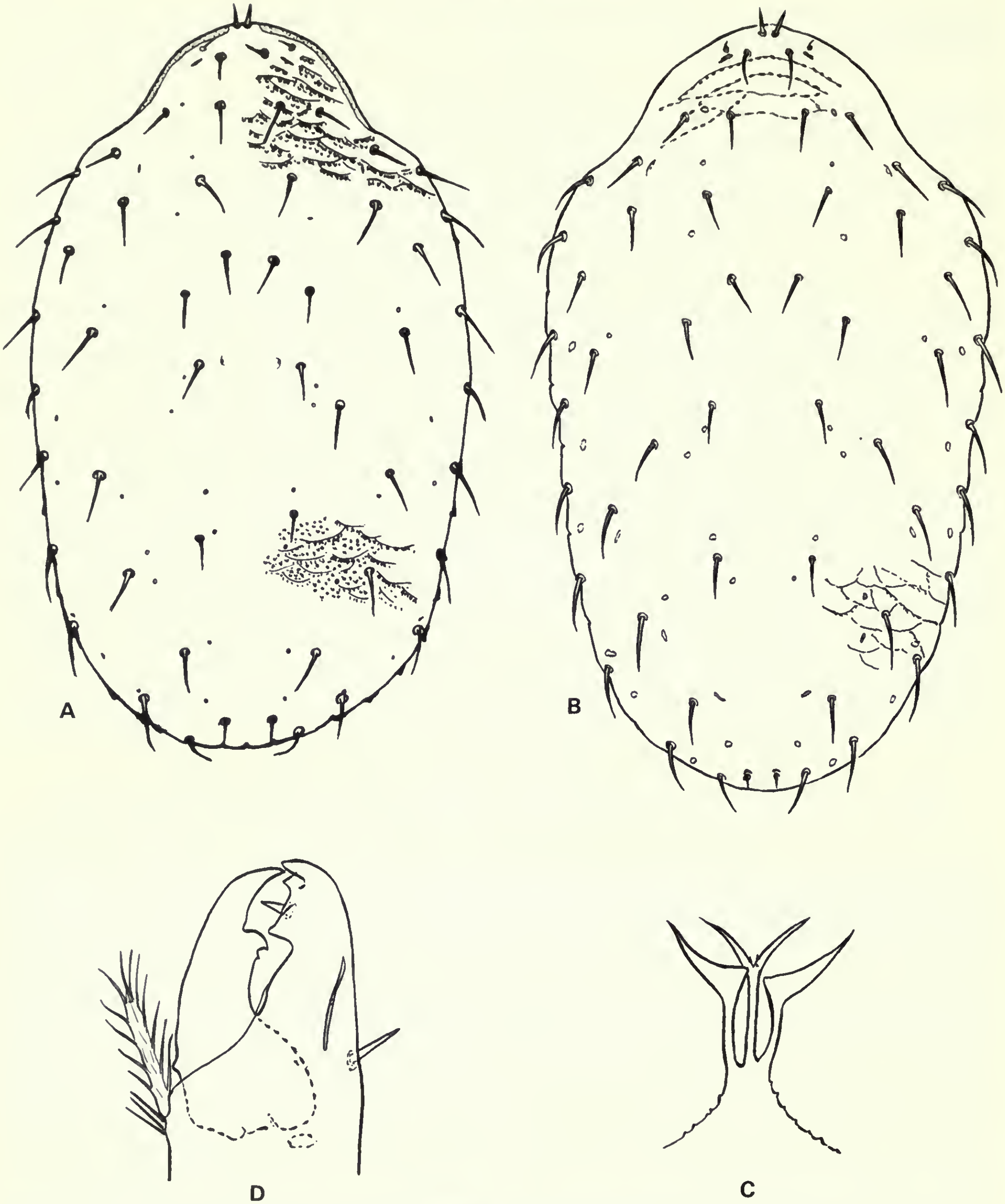

Fig. 19 *Macrocheles subbadius* (Berlese): **female**—A dorsal shield. *Macrocheles merdarius* (Berlese): **female**—B dorsal shield; C gnathotectum; D chelicera. B–D after Evans & Browning (1956).

FEMALE. The dorsal shield (700–750 µm long × 400–440 µm wide) is punctate-reticulate, the lateral margins are slightly dentate and the posterior margin has three small incisions between setae *Z5* (Fig. 19A).

The sternal shield is strongly patterned with punctate lines (Pl. 6E) and the *lineae oblique anteriores* are connected by five transverse lines, the most posterior of which, the *linea media* *transversa*, is straight. Genu IV has seven setae, seta pl_1 being present. Other characters similar to those of *M. insignitus*.

MALE. Unknown from the British Isles, but distinguished from *M. insignitus* and *M. merdarius* by having only two pairs of enlarged dorsal setae and three pairs of dorsal tubercles, also tarsus II lacks a strong medial spine and femur IV has a strong spur (Filipponi & Pegazzano, 1963).

TYPE MATERIAL. Lectotype ♀, Italy, Padova, letamai [manure], 1882, Vecchia coll. Designated by Filipponi & Pegazzano, 1963, slide 19/41 [ISZA].

MATERIAL EXAMINED. 7 collections—40 ♀♀.
ENGLAND: Surrey, Oxfordshire, Northumberland, Cheshire.
IRELAND: Clare.

HABITATS. The first record for the British Isles. Phoretic on houseflies and in garden refuse. It has also been found on other species of flies and in manure. Thirteen females were removed from 11 specimens of the dipteran *Meroplius minutus* Wiedemann (Sepsidae) from Goring-on-Thames, Oxfordshire, coll. A. C. and B. Pont, 26.8.1985. Ten of the flies were carrying one apiece and the eleventh was carrying three when examined by K.H.H., although a few of the mites had been lost during the setting of the flies. They were attached to the ventral side of either the abdomen or the thorax.

DISTRIBUTION. Widespread in temperate regions. Italy (Filipponi & Pegazzano, 1963), Germany (Karg, 1971), U.S.A. (Axtell, 1961), New Zealand (Emberson, 1973*b*).

Macrocheles insignitus Berlese
(Pl. 1F)

The description of the female of this species as given by Evans & Browning (1956) needs no amendment. The male has been described from rearing experiments by Filipponi & Pegazzano (1963).

TYPE MATERIAL. **Holotype** ♀, France, Longuy Orne, musco [moss] Cordier coll., slide 58/50 [ISZA].

MATERIAL EXAMINED. 4 collections—1 ♂, 3 ♀♀.
ENGLAND: Norfolk, Warwickshire, Lancashire.
WALES: Gwynedd (Caernarvonshire).

HABITAT. Grass cuttings, compost, nest of bumble-bees *Bombus* sp. and wet mosses.

DISTRIBUTION. France, Italy (Filipponi & Pegazzano, 1963). Apparently a European species that is only rarely collected.

Macrocheles merdarius (Berlese)
(Fig. 19B–D, Pl. 2A)

Holostaspis merdarius Berlese, 1889. *Acari, Myriapoda et Scorpiones, etc.* Fasc. 52, T.1.
Holostaspis adulescens Berlese, 1910. *Redia* **6**: 252.
Macrocheles merdarius: Sellnick, 1940. *Göteborgs K. Vetensk.-o. vitterhSamh. Handl.* B **6**, 14: 86.

The description of the female given by Evans & Browning (1956) remains unchanged. The male remains unknown in collections from the British Isles, but has been redescribed by Filipponi & Pegazzano (1963).

TYPE MATERIAL. **Neotype** ♀, Italy, Vittorio, Veneto, letamai [manure]. Designated by Filipponi & Pegazzano (1963). Not seen, but slide material from the same collection has been examined, slides 89/15, 17, 46, 48 [ISZA].

MATERIAL EXAMINED. 3 collections—*c*. 30 ♀♀.
ENGLAND: Surrey, Hertfordshire.

HABITATS. Two collections from cattle dung and stable manure and one collection from a guinea-pig breeding unit. Elsewhere this species has been collected from flies.

DISTRIBUTION. *M. merdarius* appears to be practically cosmopolitan and has been recorded from many countries in Europe, the Americas, Africa and Australia (*vide* Filipponi & Pegazzano, 1963). In addition to these records it has been reported from Israel (Costa, 1966*b*) and New Zealand (Emberson, 1973*a*).

Genus *GLYPTHOLASPIS* Filipponi & Pegazzano

Glyptholaspis Filipponi & Pegazzano, 1960. *Redia* **45**: 136. Type species: *Nothrholaspis fimicola* Sellnick, 1931 = *Gamasus tardus* Berlese, 1882. *non* C. L. Koch, 1841.

All the shields are strongly reticulate. The posterior and lateral margins of the dorsal shield are dentate, with 28 pairs of setae, supernumerary setae are sometimes present between setae *j6* and *J2*. The sternal shield has a characteristic raised polygonal pattern (Pl. 3C) and extends posteriorly to the level of the posterior margins of coxae III, where it abuts rounded metasternal platelets. The genital and ventrianal shields also have a raised polygonal pattern; the ventrianal shield is truncate and angled anteriorly and rounded posteriorly. The median process of the gnathotectum is strongly bifid and spiculate, the lateral processes are sometimes partially fused basally. The fixed chela has four or five teeth in the female and three in the male, the movable chela usually has three teeth in the female and one in the male, the dorsal seta is dentate distally and the male spermatodactyl is simple, dorsally directed, tapering and recurved distally. The male has a holoventral shield and spurs on legs II, III and IV.

Filipponi & Pegazzano (1960) erected the genus for a clearly defined group of species formerly included in the genus *Macrocheles* under a variety of names. There is however some doubt as to the rank that should be assigned to this group (Krantz, 1962).

The recent synonymy of the three species of *Glyptholaspis* found in the British Isles with *Macrocheles tardus* (C. L. Koch) by Krauss (1970) cannot be supported, whether the genus *Glyptholaspis* is accepted or not. Filipponi & Pegazzano (1960) have shown the three species to be consistently different morphologically, in samples from various parts of the world, and Filipponi & Ilardi (1958) showed them to be reproductively isolated. The present authors also follow Sellnick (1931) and most other recent European authors in regarding *Gamasus tardus* C. L. Koch, 1841, as being a common European *Macrocheles* species in moss and leaf litter, whereas the *Glyptholaspis* species, including Berlese's 1882 concept of *Gamasus tardus*, are usually found in compost heaps, dung and associated with flies. Three species are known from the British Isles, two of which were previously confused under the name *Macrocheles plumiventris* Hull. All species are described in detail with full synonymies by Filipponi & Pegazzano (1960).

Key to the species of *Glyptholaspis* known to occur in the British Isles

1 Posterior margin of the dorsal shield between setae *Z5* with five large teeth, and, in the females, numerous minute teeth, setae *j6* and *z6* more or less in a straight line, seta *J5* no longer than setae *Z5*; trochanter II of male with a spur 2

– Posterior margin of the dorsal shield between setae *Z5* with two large teeth and numerous minute teeth (Fig. 20A), setae *j6* anterior to setae *z6*, setae *J5* distinctly longer than setae *Z5*; trochanter II of male unarmed . . . . **Glyptholaspis americana** (Berlese) (p. 116)

2 Setae *j5* strongly pilose and erect, setae *J5* shorter than *Z5*; gnathotectum with lateral processes fused (Fig. 20E); female sternal shield pattern symmetrical, with a posterior median ridge (Pl. 3C); male trochanter IV with three subequal ventral spurs, femur IV unarmed . . . . **Glyptholaspis confusa** (Foà) (p. 116)

– Setae *j5* lightly pilose and adpressed, setae *J5* about equal in length to *Z5* in the female; gnathotectum with lateral processes free. Female sternal pattern asymmetrical, without a distinct posterior median ridge (Pl. 5E); male trochanter IV and femur IV each with a posteriorly directed spur . . . . **Glyptholaspis fimicola** (Sellnick) (p. 117)

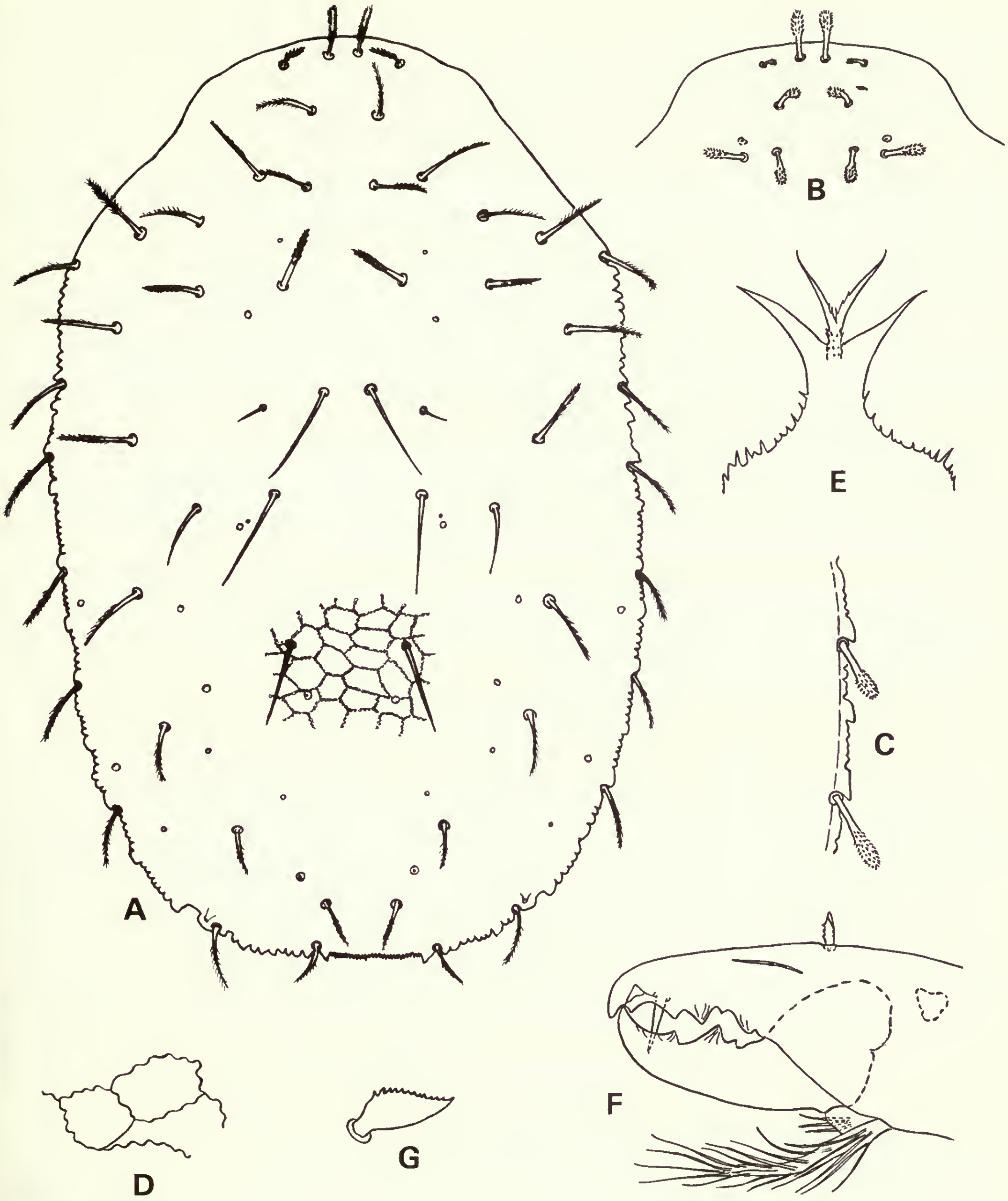

Fig. 20 *Glyptholaspis americana* (Berlese): **female**—A dorsal shield. *Glyptholaspis confusa* (Foà): **female**—B anterior region of dorsal shield; C lateral margin of dorsal shield; D ornamentation of dorsal shield; E gnathotectum; F chelicera; G dorsal seta of chelicera. B–G after Evans & Browning (1956).

Glyptholaspis americana (Berlese)
(Fig. 20A, Pl. 6F)

Holostaspis marginatus var. *americanus* Berlese, 1888. *Boll. Soc. ent. ital.* **20**: 195.
Holostaspis vagabundus Berlese, 1889. *Acari, Myriopoda et Scorpiones, etc.* Fasc. 52, T. 9.
Macrocheles tardior Hull, 1925. *Ann. Mag. nat. Hist.* (9) **15**: 126. **Syn. nov.**
Glyptholaspis americana (Berlese): Filipponi & Pegazzano, 1960. *Redia* **45**: 148.
Macrocheles (M.) tardus: Krauss, 1970. *Acarologie* **14:** 20, *partim, nec* C. L. Koch, 1841.

FEMALE. The dorsal setae *j6, J2* and *z5* are glabrous, setae *j5, z6* and *J5* are slightly pilose, other setae are strongly pilose. Setae *j5, j6, z6* and *J2* are relatively long and slender, of similar length; setae *J5* are distinctly longer than setae *Z5*. The posterior and lateral margins of the dorsal shield are strongly dentate, the posterior margin between setae *Z5* has two large teeth and an even row of minute ones (Fig. 20A).

All ventral shields are strongly reticulated with raised polygonal pattern. Sternal shield pattern (Pl. 6F) slightly asymmetric without a distinct median posterior ridge. Sternal and metasternal setae simple, genital setae moderately plumose, setae *Jv1–3* plumose, adanal setae simple, postanal seta short and plumose.

The gnathotectum has fused lateral processes and a bifurcate median process. The fixed chela has four teeth, the movable chela has three teeth.

The legs are normal for the genus with plumose setae on all segments except tarsus I.

MALE. The male is unknown from the British Isles, but has been adequately described by Filipponi & Pegazzano (1960). The main distinguishing features are the chaetotaxy of the dorsum which is similar to the female and the form of the spurs on legs II, III and IV.

TYPE MATERIAL. *Gamasus americanus*: Holotype ♀, South America, Balzan, slide 33/21 [ISZA]. *M. tardior*: Syntype ♀, Oxfordshire [? R. S. Bagnall] [BMNH].

MATERIAL EXAMINED. 4 collections—11 ♀♀.
ENGLAND: Isles of Scilly, Sussex, Oxfordshire.
IRELAND: Clare.

HABITATS. *Geotrupes spiniger*, also known elsewhere from compost heaps and associated with synanthropic flies.

DISTRIBUTION. Apparently practically cosmopolitan. Filipponi & Pegazzano (1960) report it from Brazil, Argentina, Uruguay, Australia, South Africa, Italy and France. It has also been reported from the U.S.S.R. (Bregetova & Koroleva, 1960, as *M. vagabundus*), Bulgaria (Balogh, 1958, as *M. vagabundus*), Germany (Krantz, 1972), Israel (Costa, 1963) and New Zealand (Emberson, 1973*a*).

REMARKS. In examining the Hull Collection, Professor G. O. Evans (*in litt.*) did not believe the specimen of *M. tardior* to be the type as it is larger than the dimensions stated by Hull. However, it is labelled from Oxfordshire, the type locality, and agrees fairly well with the description, which undoubtedly refers to a species of *Glyptholaspis*, so we see no good reason to doubt its status.

Glyptholaspis confusa (Foà)
(Fig. 20B–G, Pl. 3C)

Holostaspis confusa Foà, 1900. *Boll. Soc. ent. Ital.* **32**: 137.
Macrocheles plumiventris Hull, 1925. *Ann. Mag. nat. Hist.* (9) **15**: 216.
Macrocheles plumiventris: Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 32. *partim*, female only.
Glyptholaspis confusa: Filipponi & Pegazzano, 1960. *Redia* **45**: 154.

The female of this species has been adequately described by Evans & Browning (1956) under the name *Macrocheles plumiventris* Hull. The male described under that name is in fact a specimen of *G. fimicola*.

The only necessary additions to the description of the female are to note that there are usually one or two small glabrous or finely pilose supernumerary setae between *j6* and *J2*, that setae *J5* are shorter than setae *Z5* and that the posterior margin of the dorsal shield between setae *Z5* is irregularly dentate with about five major teeth and many small teeth.

MALE. The sculpturing and chaetotaxy of the dorsal shield are similar to that of the female. The reticulate pattern on the holoventral shield is interrupted in the region of coxae IV. Setae *st* 1 are plumose, *st* 2–3 simple, *st* 4–5 plumose. All the ventrianal setae except the adanals are plumose.

The gnathotectum is similar to the female. The fixed chela has three teeth and the movable chela one tooth. The spermatodactyl is simple, tapered and recurved towards the tip, about as long as the movable digit.

Leg I is similar to that of the female. Leg II has sclerotized spurs on the trochanter, femur, genu and tibia. The spur on trochanter II is towards the posterior lateral surface and bears a plumose seta distally. Femur II has a number of sclerotised protuberances, including a small ventral spur with a simple seta and another spur on the posterior lateral surface at the distal margin. Genu II has a ventral spur and three other small protuberances and tibia II has a ventral spur on the distal margin and trochanter IV has three strong ventral spurs.

TYPE MATERIAL. *Macrocheles plumiventris*: A single female without habitat data in the Hull Collection [BMNH]. Hull (1925) gave 'a manure-heap in West Allendale' [Northumberland] for his solitary example.

MATERIAL EXAMINED. 8 collections—8 ♂♂, 31 ♀♀.
ENGLAND: Sussex, Essex, Hertfordshire, Middlesex, Berkshire, Buckinghamshire, Bedfordshire.
WALES: Gwynedd (Merionethshire).

HABITATS. Manure, granary refuse, leaf litter, also known from compost and associated with synanthropic flies.

DISTRIBUTION. *G. confusa* has been reported from Italy, Argentina and Australia (Filipponi & Pegazzano, 1960), Bulgaria (Balogh, 1958 as *M. plumiventris*), U.S.S.R. (Bregetova & Koroleva, 1960 as *M. plumiventris*), Germany (Krantz, 1972) and New Zealand (Emberson, 1973*a*).

Glyptholaspis fimicola (Sellnick)
(Pl. 5E)

Gamasus tardus: Berlese [*non* C. L. Koch, 1841], 1882 *Boll. Soc. ent. Ital.* **14**: 108.
Holostaspis marginatus: Berlese [*non* Hermann, 1804], 1889, *Acari, Myriopoda et Scorpiones*, etc. Fasc. 52, T. 4–5.
Nothrholaspis fimicola Sellnick, 1931. *Sber. Akad. Wiss. Wien* **140**: 765. *Nom. nov. pro Holostaspis marginatus*: Berlese [*non* Hermann, 1804,] 1889.
Macrocheles plumiventris: Evans & Browning, 1956. *Bull. Br. Mus. nat. Hist.* (Zool.) **4**: 38, male only.
Glyptholaspis fimicola (Berlese) [*sic*]: Filipponi & Pegazzano, 1960. *Redia* **45**: 139.

As suggested by Filipponi & Pegazzano (1960) the specimen described as the male of *M. plumiventris* by Evans & Browning (1956) from the Michael Collection is not conspecific with the females ascribed to that species and is the only known specimen of *G. fimicola* from the British Isles.

FEMALE. The following brief description is taken from Filipponi & Pegazzano (1960) supplemented by examination of Italian material.

Generally most similar to *G. confusa* but differing as follows. On the dorsal shield many of the setae are longer than their counterparts in *G. confusa: j5, j6, J2* and *z6* are similar in form and length, lightly pilose; in *G. confusa j5* is more strongly pilose than the others and erect rather than adpressed; *j6* is longer than the distance between the bases of *j6* and *z6*. *J2* is about equal in length to the distance between the bases of seta *J2*, without supernumerary setae between setae *j6* and *J2*. *J5* is about equal in length to *Z5*.

Setae *st* 1 on the sternal shield are simple, not pilose, the sculpturing of the sternal shield (Pl. 5E) is very similar to that of *G. americana*, lacking the median posterior ridge found in *G. confusa*.

The gnathotectum has the two lateral processes free, not fused as in *G. confusa* and *G. americana*. The fixed chela has four teeth and the movable chela three teeth.

The legs are very similar to those of *G. confusa*.

Male. The male of this species has been described by Evans & Browning (1956) under the name *M. plumiventris* Hull.

The chaetotaxy of the dorsum is generally similar to that of the female, except that *J5* tends to be shorter than *Z5*. Between setae *Z5* there are five large teeth and no small teeth (Italian specimens). The pattern of the holoventral shield is not interrupted in the region of coxae IV.

The gnathotectum is similar to that of the female. The fixed chela has four teeth and the movable chela a single tooth, the spermatodactyl is longer than the movable digit, strongly recurved and pointed distally.

Leg II has spurs on the trochanter, femur, genu and tibia, the distal spur on the femur has a pilose seta terminally. There are posteriorly directed spurs on genu III, trochanter IV and femur IV, the spur on trochanter IV has a terminal pilose seta.

Material examined. 1 collection—1 ♂, A. D. Michael Collection (1930.8.25.2215).
england: Warwickshire: Austrey. May 1892. No habitat given.

Habitats. Known from a variety of sorts of dung and compost (Filipponi & Pegazzano, 1960).

Distribution. Apparently only previously recorded from southern Europe, Italy (Filipponi & Pegazzano, 1960) and Greece (Sellnick, 1931).

Genus *HOLOSTASPELLA* Berlese

Holostaspella Berlese, 1903. *Redia* **1**: 241. Type species: *Holostaspis (Holostaspella) sculpta* Berlese, 1903.
Prholaspina Berlese, 1918. *Redia* **13**: 174. Type species: *Holostaspella (Prholaspina) micrarrhena* Berlese, 1916.
Areolaspis Trägårdh, 1952. *Ark. Zool.* **4** (3): 60. Type species: *Areolaspis bifoliatus* Trägårdh, 1952.

Most species are heavily sclerotised with strong ornamentation of the main shields. Dorsal shield with 28 pairs of setae, *j1* short and pectinate, usually borne on a tuberculate anterior extension of the shield; lateral region of the dorsal shield often with a series of depressions. The sternal shield nearly always has a strong median ridge; the metasternal platelets are often enlarged and fused to the endopodal sclerites. The ventrianal shield may be narrow or broad with 2–4 pairs of preanal setae (four pairs in species from the British Isles). The peritrematic shield may be fused with the expodal sclerites. Males have either a holoventral shield or separate ventrianal shields. The spermathecal apparatus is of the normal bilobed *Macrocheles* type. The gnathosoma is normal for the family. The lateral processes of the gnathotectum are free and the cheliceral brushes are shorter than the movable digit of the chelicera. Legs II in the females are armed with one or more spurs on the femora. Spurs or protuberances may also be present on the coxae, trochanters and genua, seta *mv* of tarsus II is also developed into a strong spine in all British species. Male leg armature is limited to femur II. Leg chaetotaxy is normal for the family.

Following Krantz (1962) and Petrova & Taskaeva (1964) the concept of *Holostaspella* has been considerably broadened. Filipponi & Pegazzano (1967) and Krantz (1967) have both revised the genus and split it into a number of species groups. The species from the British Isles fit into the *ornata* group of Filipponi & Pegazzano and the *sculpta* group of Krantz.

Key to species of *Holostaspella* known to occur in the British Isles

1 Dorsal shield lacking distinct depressions, setae *z1* more than half as long as *j2, j3* distinctly anterior to *z2* (Fig. 22C); female sternal shield lacking cruciform pattern . . . . . . **_Holostaspella subornata_** Bregetova & Koroleva (p. 122)
– Dorsal shield with lateral depressions, setae *z1* less than half as long as *j2, j3* and *z2* more or less level (Fig. 21A); female sternal shield with cruciform pattern (Pl. 5C, D) 2
2 Seta *z1* pilose, setae *j3* and *z2* as long as or longer than the distance between the bases of *j3* and *j4* (Fig. 21A); female sternal shield as in Pls 4D, 5C . **_Holostaspella ornata_** (Berlese) (p. 120)
– Setae *z1* simple, not pilose, setae *j3* and *z2* shorter than the distance between the bases of *j3* and *j4* (Fig. 22A); female sternal shield as in Pl. 5D . . . . **_Holostaspella exornata_** Filipponi & Pegazzano (p. 120)

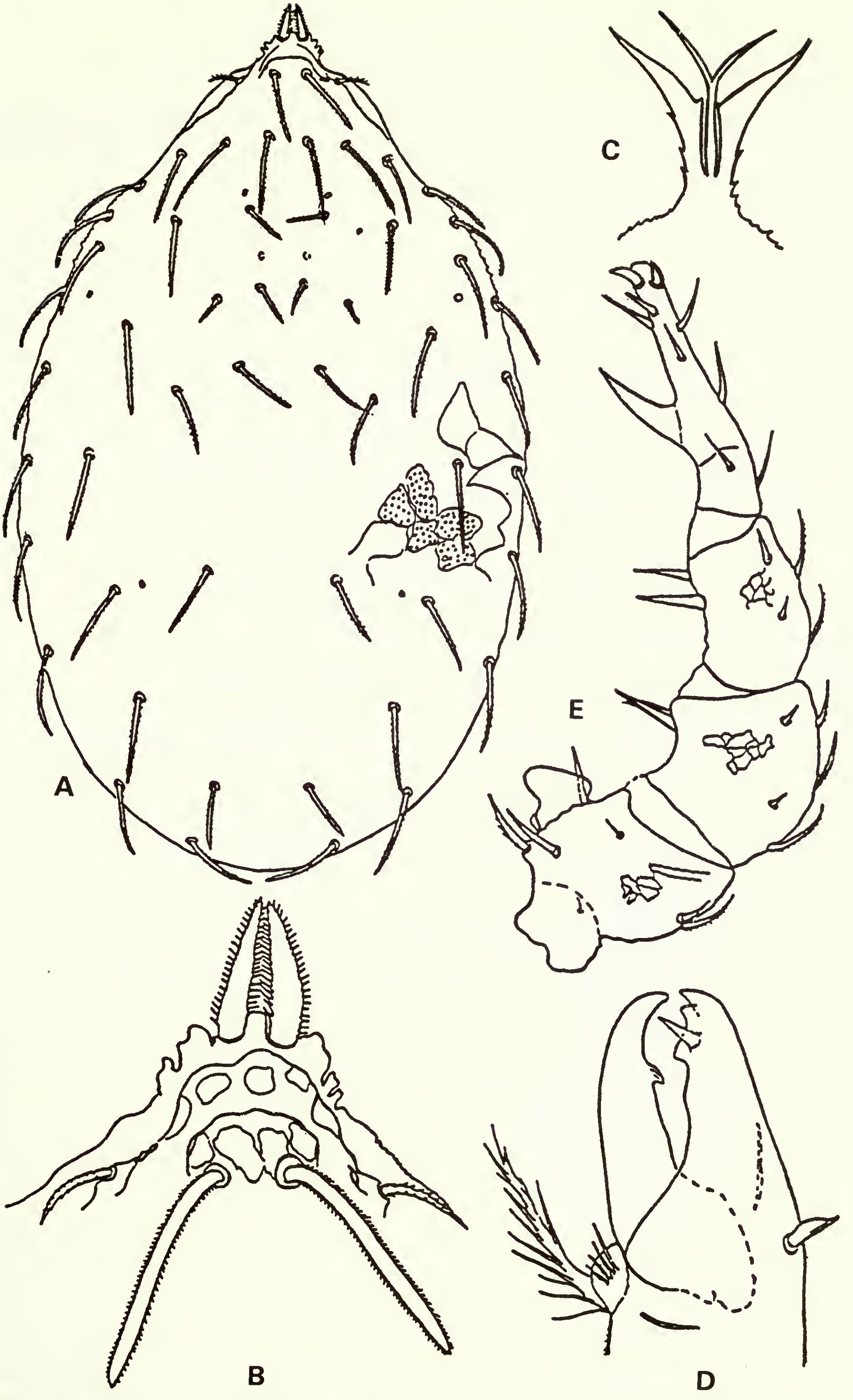

Fig. 21 *Holostaspella ornata* (Berlese): **female**—A dorsal shield; B anterior region of dorsal shield; C gnathotectum; D chelicera; E leg II, ambulacrum omitted. After Evans & Browning (1956).

Holostaspella ornata (Berlese)
(Fig. 21A–E, Pls 4D, 5C)

The description and synonymy of this species are as given by Evans & Browning (1956), the description being based on the type in the Oudemans Collection, although the British specimen they mentioned belongs in fact to the next species, *H. exornata*.

MATERIAL EXAMINED. 7 collections—12 ♀♀.
ENGLAND: Isles of Scilly, Surrey, Kent, Yorkshire, Cumbria (Cumberland).
IRELAND: Clare.

HABITATS. The first record for the British Isles. Under a board, in leaf litter, dead reeds, compost and manure.

DISTRIBUTION. A European species, Holland (Berlese, 1904), Russia (Bregetova & Koroleva, 1960), Austria (Franz, 1954), Germany (Krauss, 1970; Krantz, 1972), also recorded from Zaire (Krantz, 1967), but this could be a closely related species.

REMARKS. Filipponi & Pegazzano (1967) have suggested that some of the material assigned to this species by Bregetova & Koroleva (1960) belongs in fact to the following species. Their illustrations of the dorsal and ventral surfaces certainly appear to be of specimens of *H. exornata* and the size range overlaps those of both species as given by the former authors.

Holostaspella exornata Filipponi & Pegazzano
(Fig. 22A–B, Pl. 5D)

Holostaspella exornata Filipponi & Pegazzano, 1967. *Redia* **50**: 230.

Recorded by Evans & Browning (1956) as *Holostaspella ornata* (Berlese).

This species is morphologically extremely similar to the preceding species but differs from it consistently in a number of ways, most obviously in size, female dorsal shield length 649–800 µm as against 917–948 µm for *H. ornata* (Filipponi & Pegazzano, 1967).

FEMALE. Setae of the dorsal shield (Fig. 22A) generally shorter than in *H. ornata, j3* not reaching bases of *j4, s5* shorter than distance between *s5* and *z6, J5* shorter than the distance between its base and the posterior margin of the dorsal shield. Setae *j1* broadly pectinate, *z1* smooth, simple, all other setae finely pilose.

Sternal shield divided by cross-shaped ridges into quadrants, the point where the arms of the cross meet is not expanded and reticulated (Pl. 5D). Anterior margin of sternal shield with four tooth-like projections medially (smoothly concave in *H. ornata*), *st* 1 lightly pilose, other sternal setae simple. Metasternal platelets elongate, abutting endopodals. The ventrianal shield has four pairs of simple preanal setae and is ornamented with a series of small reticulations within large reticulations.

The gnathosoma is very similar to that of *H. ornata*. The fixed chela has two teeth and the movable chela one tooth. The lateral processes of the gnathotectum are free.

The legs are strongly rugose, with all segments finely granular. On leg II the femur and trochanter are armed with small spurs and tibia II has seta *mv* produced into a spine (Fig. 22B).

MALE. Not known from the British Isles, but described by Filipponi & Pegazzano (1967) from reared material.

The chaetotaxy is generally similar to the female. The holoventral shield has a strong median longitudinal ridge in the sternal region. The spermatodactyl is elongate, tapering, more than twice as long as the movable digit. Legs unarmed.

MATERIAL EXAMINED. 5 collections—9 ♀♀.
ENGLAND: Kent, London, Berkshire, Warwickshire.

HABITATS. Phoretic on *Sphaerocera* spp. (Diptera) in rotting vegetation. It is of interest to note that in two of the five collections the specimens were associated with *Sphaerocera* spp. Filipponi &

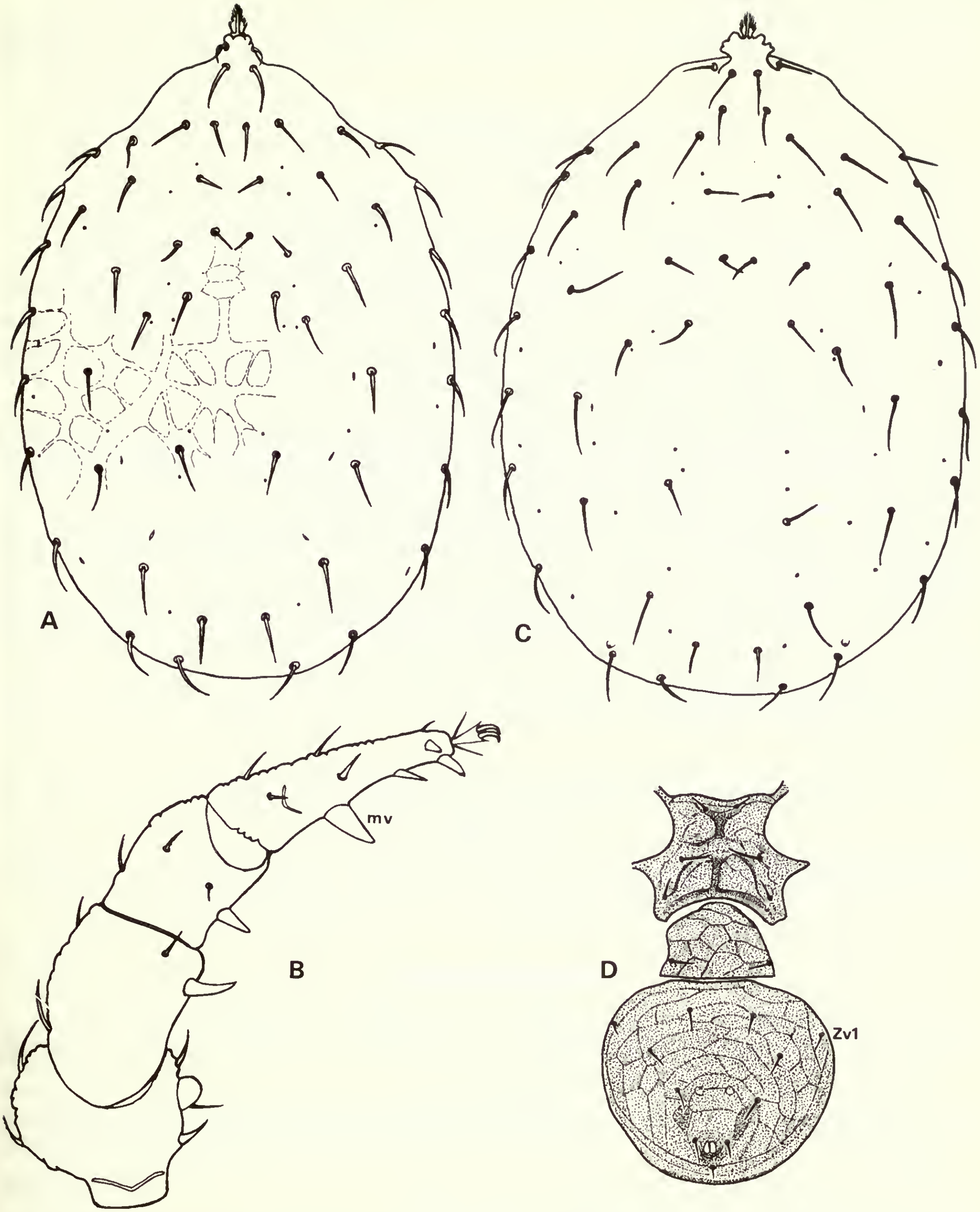

Fig. 22 *Holostaspella exornata* Filipponi & Pegazzano: **female**—A dorsal shield; B leg II. *Holostaspella subornata* Bregetova & Koroleva: **female**—C dorsal shield; D ventral sclerotisation. D after Bregetova & Koroleva (1960).

Pegazzano (1967) mention a specimen in the Berlese Collection from the nest of an ant *Acromymex lundi* in Argentina.

DISTRIBUTION. Italy, Argentina, ? U.S.S.R. Filipponi & Pegazzano (1967) suspect that some of the material reported from U.S.S.R. by Bregetova & Koroleva (1960) as *H. ornata* may be referrable to this species.

Holostaspella subornata Bregetova & Koroleva
(Fig. 22C, D)

Holostaspella subornata Bregetova & Koroleva, 1960. *Parazit. Sb.* **19**: 60

This species is generally similar to the preceding two but differs from them most noticeably in the lack of strong lateral sculpturing on the dorsal shield and in details of the dorsal chaetotaxy.

FEMALE. Dorsal shield (Fig. 22C) lacking lateral depressions, ornamented with densely packed fine punctures. Setae of the dorsal shield relatively long, as in *H. ornata*, but simple to minutely barbed rather than conspicuously pilose. Setae *j1* are broadly pectinate and in close proximity. Setae *j2* reach the bases of *j3, j3* are displaced substantially anterior to *z2*, so that they do not reach the bases of *j4, z1* are elongate, more than half as long as *j2*.

The sternal shield (Fig. 22D) is punctate reticulate, lacking the cruciform pattern of *H. ornata* and *H. exornata*, and the anterior margin is smoothly concave. All the ventral setae are simple. The metasternal platelets are barely separated from the posterior corners of the sternal shield and the endopodals. The genital and ventrianal shields are punctate reticulate.

The gnathosoma is very similar to the other species of *Holostaspella*. The fixed chela has one major and two minor teeth and the movable chela one tooth. The lateral processes of the gnathotectum are free.

The legs are rugose and all segments covered in fine granulations. Leg II has small spurs on the trochanter and femur and seta *mv* on the tibia is produced into a spine.

MALE. Unknown.

MATERIAL EXAMINED. 1 collection—1 ♀.
IRELAND: Clare.

HABITAT. The first British record. Amongst grass roots. Bregetova & Koroleva report this species from leaf litter and associated with the musk-rat *Ondatra zibethicus*.

DISTRIBUTION. Only otherwise known from the Leningrad and Omsk regions of the U.S.S.R. (Bregetova & Koroleva, 1960).

Taxonomic Summary

(*a*) *Macrocheles analis* sp. nov. is described.

(*b*) Neotypes are designated for *Macrocheles tridentinus* (G. & R. Canestrini, 1882) and *Macrocheles terreus* (Canestrini & Fanzago, 1877).

(*c*) Lectotypes are selected for *Macrocheles submotus* Falconer, 1924, *Macrocheles matrius* Hull, 1925, *Holostaspis echinatus* Berlese, 1904, and *Holostaspis marginatus* var. *littoralis* Halbert, 1915.

(*d*) The genus *Dissoloncha* Falconer, 1923, is resurrected.

(*e*) The following new synonymy is proposed:
Macrocheles melisii Krauss, 1970, is a junior synonym of *Macrocheles nataliae* Bregetova & Koroleva, 1960.
Macrocheles bombophilus Götz, 1970, is a junior synonym of *Macrocheles rotundiscutis* Bregetova & Koroleva, 1960.

Macrocheles multisetosus Götz, 1970, is a junior synonym of *Macrocheles dentatus* (Evans & Browning, 1956).

Macrocheles tardior Hull, 1925, is a junior synonym of *Glyptholaspis americana* (Berlese, 1888).

(*f*) Species new to the British Isles:
Geholaspis (Geholaspis) aeneus Krauss, 1970.
Geholaspis (Longicheles) hortorum (Berlese, 1904).
Macrocheles rotundiscutis Bregetova & Koroleva, 1960.
Macrocheles analis sp. nov.
Macrocheles punctatissimus Berlese, 1918.
Macrocheles nataliae Bregetova & Koroleva, 1960.
Macrocheles subbadius (Berlese, 1904).
Holostaspella ornata (Berlese, 1904), *nec* Evans & Browning, 1956.
Holostaspella subornata Bregetova & Koroleva, 1960.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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A revision of *Haplocaulus* Precht, 1935 (Ciliophora: Peritrichida) and its morphological relatives

Alan Warren

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Contents

Synopsis

The species of *Haplocaulus* and of five closely related genera have been revised. A diagnosis for each genus is given with a key to its constituent species. Two new genera, *Piesika* n. gen. and *Pseudohaplocaulus* n. gen. are described. All extant species are described and figured. These include *Haplocaulus*—of which 26 species are recognised; *Baikalonis*—3 species; *Cotensita*—1 species; *Parazoothamnium*—2 species; *Piesika*—1 species; *Pseudohaplocaulus*—2 species. Two other genera, *Monintranstylum* and *Tucolesca*, are also considered.

Introduction

In two previous papers (Warren, 1986, 1987) the peritrich genera *Vorticella* and *Pseudovorticella* were revised. Both are solitary forms the stalks of which coil up in a helical fashion upon contraction. The genera dealt with in this paper are also solitary and borne on unbranched contractile stalks but, upon contraction, the stalks do not coil helically.

Two of the principal generic characters used here are the mode of stalk contraction and the presence of pellicular tubercles with their underlying reticulate silverline system. Nevertheless for some species, details concerning these characters are not available. For example, with the exception of *Haplocaulus terrenus*, no species of the genera reviewed have been impregnated with silver—the possession of reticulate silverline systems has been assumed from the presence of pellicular tubercles. However, although pellicular tubercles are usually associated with reticulate silverline systems, this may not be true in every case (Foissner, pers. comm.).

The major genus included here is *Haplocaulus* Precht, 1935 which is found in marine, freshwater and terrestrial habitats attached to plant, animal and inanimate substrates. The only previous revision of *Haplocaulus* was that of Stiller (1971); seven new species have since been described and several species have been transferred from other genera. *Baikalonis*, *Cotensita* and *Parazoothamnium*, three genera closely related to *Haplocaulus*, are revised and two new genera, *Piesika* and *Pseudohaplocaulus*, are described. All extant species are described and figured and keys to their identification are provided. A brief account of the morphological structures important in the taxonomy of the Vorticellidae is given in Warren (1986).

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Key to genera

1	Zooid with pellicular tubercles	2
–	Zooid without pellicular tubercles	3
2	Stalk contracts in two stages, initially shortening in a concertina-like fashion and then bending in a zigzag manner	***PIESIKA***
–	Stalk contracts in zigzag manner only	***PSEUDOHAPLOCAULUS***
3	Stalk sheath folded below zooid	***COTENSITA***
–	Stalk sheath not folded below zooid	4
4	Upon contraction stalk shortens longitudinally and is enveloped by zooid	***BAIKALONIS***
–	Contraction does not result in zooid enveloping stalk	5
5	Stalk contracts in two stages, initially shortening in a concertina-like fashion and then bending in a zigzag manner	***PARAZOOTHAMNIUM***
–	Stalk contracts in zigzag manner only	***HAPLOCAULUS***

Genus *HAPLOCAULUS* Precht, 1935

The genus *Haplocaulus* was erected by Precht (1935) to include solitary vorticellids whose stalks are circular in cross-section and which contract in a zigzag rather than helical fashion. Impregnation by silver reveals a pattern of equally spaced horizontal lines or striations which encircle the body. These striations may or may not be visible in the living zooid.

Two species were originally described by Precht (1935), *H. nicoleae* and *H. furcellariae*, although he failed to designate either as the type. *H. nicoleae* is here transferred to the genus *Pseudohaplocaulus*. *H. furcellariae* is designated the type species. Stiller (1971) transferred ten species to *Haplocaulus* all of which had previously belonged to the genus *Vorticella*. Three more vorticellids are here assigned to *Haplocaulus* for the first time.

DIAGNOSIS. Zooid borne upon an unbranched stalk which is circular in cross-section and contracts in a zigzag manner. Zooids usually oval, cylindrical or inverted bell-shaped. Impregnation by silver reveals a transverse silverline system. Spasmoneme lies either parallel to the walls of the stalk sheath or is slightly twisted in the form of a shallow helix.

Key to the species of *Haplocaulus*

1	Diameter of peristomial lip greater than or equal to maximum body width	2
–	Diameter of peristomial lip less than maximum body width	15
2	Pellicular striations visible on live zooid	3
–	Pellicular striations not visible on live zooid	10
3	Zooid elongate and cylindrical in shape	4
–	Zooid either cone- or inverted bell-shaped	8
4	Pellicle with knob-like projections	***H. eforianus***
–	Pellicle without knob-like projections	5
5	Zooid with two contractile vacuoles	***H. dipneumon***
–	Zooid with one contractile vacuole	6
6	Zooid with distinct, broadly spaced striations	***H. fluviatilis***
–	Zooid with fine, narrow-spaced striations	7
7	Macronucleus C-shaped and situated in anterior part of zooid	***H. procerus***
–	Macronucleus irregular and situated in centre of zooid	***H. furcellariae***
8	Zooid inverted bell-shaped with constriction beneath peristome	9
–	Zooid cone-shaped, not constricted beneath peristome	***H. conosomus***
9	Macronucleus lies horizontally in anterior part of zooid	***H. epizoicus***
–	Macronucleus lies longitudinally in centre of zooid	***H. distinguendus***
10	Zooid elongate, length at least × 3 maximum body width	11
—	Zooid length less than × 3 maximum body width	12
11	Upon contraction, zooid assumes characteristic nodding position	***H. crassicaulis***
—	Upon contraction, zooid remains vertical	***H. extensa***
12	Zooid with endosymbiotic zoochlorellae	***H. sertulariarum***
—	Zooid without endosymbiotic zoochlorellae	13
13	Zooid cone-shaped, not constricted beneath peristome	***H. pelagicus***
—	Zooid inverted bell-shaped, usually with constriction beneath peristome	14

14	Pellicular granules present	***H. leanderi***	
—	Pellicular granules absent	***H. elegans***	
15	Pellicular striations visible on live zooid		16
—	Pellicular striations not visible on live zooid		21
16	Striations distinct and widely spaced		17
—	Striations fine with narrow spacing		18
17	Pellicle with concave ribbing between striations	***H. terrenus***	
—	Pellicle with convex ribbing between striations	***H. kahlii***	
18	Zooid elongate, length at least × 2 maximum body width		19
—	Zooid rotund, length less than × 2 maximum body width		20
19	Macronucleus U-shaped; spasmoneme extends full length of stalk	***H. fusiformis***	
—	Macronucleus C-shaped; spasmoneme does not extend complete stalk length	***H. claudicans***	
20	Marine; epizoic on the echinoderm *Amphiurae squamata*	***H. amphiurae***	
—	Freshwater; epizoic on the amphibian *Rana temporaria*	***H. longinucleatus***	
21	Zooid elongate, length at least × 2 maximum body width		22
—	Zooid length less than maximum body width		24
22	Macronucleus spirally twisted and lies longitudinally in zooid	***H. macronucleatus***	
—	Macronucleus C-shaped and lies horizontally in zooid		23
23	Zooid 134—155 µm long; epizoic on the amphibian *Rana temporaria*	***H. amphibiarum***	
—	Zooid 60 µm long; epizoic on the crustacean *Gammarus pulex*	***H. stilleri***	
24	Macronucleus C-, S-, or irregular in shape; infundibulum reaches at least one-third zooid length		25
—	Macronucleus J-shaped; infundibulum less than one-third zooid length	***H. walteri***	
25	Macronucleus S-shaped or irregular; stalk about equal to body length	***H. brehmi***	
—	Macronucleus C-shaped or irregular; stalk up to × 2 body length	***H. carinogammari***	

Species descriptions

Haplocaulus furcellariae Precht, 1935

DESCRIPTION (Fig. 1). The zooid of this, the type species is elongate, almost cylindrical in shape, approximately 98 µm long × 40 µm wide. Peristomial lip 50–55 µm in diameter. Disc convex. Contractile vacuole small and situated in the peristomial region. Macronucleus elongate and irregular in shape. Pellicle with distinct transverse striations. Stalk up to 400 µm long.

HABITAT. Marine, originally found as an epizoite of *Furcellaria*.

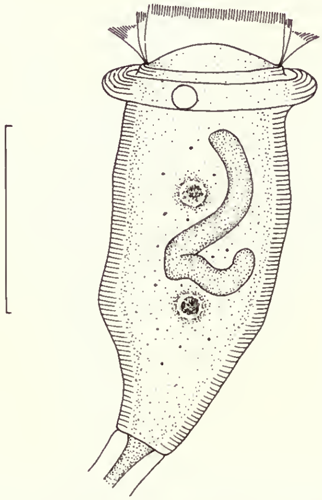

Fig. 1 *Haplocaulus furcellariae*, after Precht, 1935. Bar = 50 µm.

Haplocaulus amphibiarum Banina, 1982

Description (Fig. 2). Zooid 134–155 µm long × 52–65 µm wide, tapering at both ends and widest in the central region. Diameter of peristomial lip less than maximum body width. Disc cone-shaped and prominent. Infundibulum reaches one-third body length. Contractile vacuole situated in upper half of zooid. Macronucleus C-shaped and lies horizontally across centre of body. Food vacuoles often numerous and spindle-shaped. Stalk less than body length.

Habitat. Freshwater, originally found near Leningrad, U.S.S.R. attached to the amphibian *Rana temporaria*.

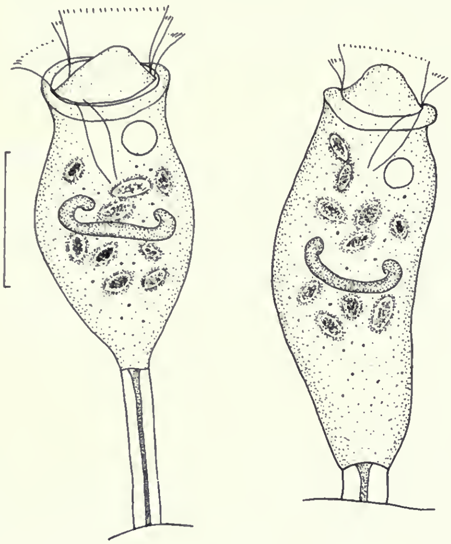

Fig. 2 *Haplocaulus amphibiarum,* after Banina, 1982. Bar = 50 µm.

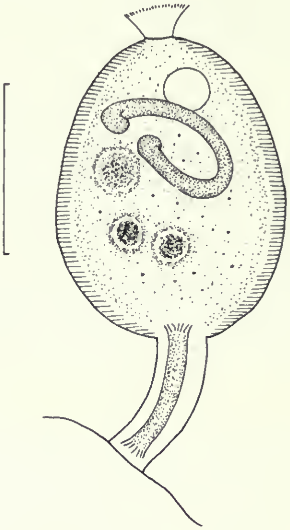

Fig. 3 *Haplocaulus amphiurae,* after Cuénot, 1891 (called *Vorticella amphiurae*). Bar = 25 µm.

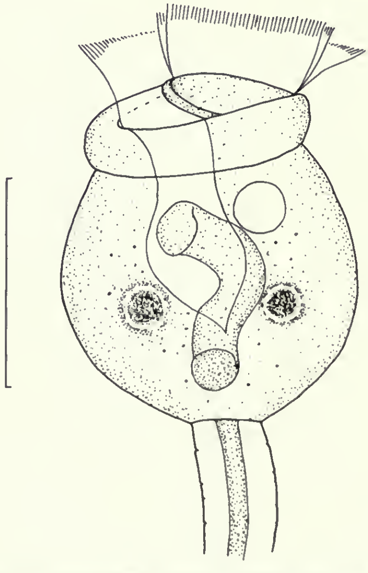

Fig. 4 *Haplocaulus brehmi,* after Lüpkes, 1975. Bar = 50 µm.

NOTE. *H. amphibiarum* bears a strong morphological similarity to *H. fusiformis* (Nenninger, 1948) Stiller, 1971 and to *Carchesium amphibiarum* Nenninger, 1948 which are also epibionts of amphibians. It is possible that these three species may be synonymous.

Haplocaulus amphiurae (Cuénot, 1891) n. comb.

Vorticella amphiurae Cuénot, 1891

DESCRIPTION (Fig. 3). Zooid 40 μm long × 25–30 μm wide, oval in shape, rounded posteriorly and with a narrow peristome. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped or occasionally irregular. Pellicle with fine transverse striations. Stalk less than body length.

HABITAT. Marine, originally isolated from the Bay of Naples as an epizoite of the echinoderm *Amphiurae squamata*.

NOTE. *H. amphiurae* is morphologically similar to *Baikalonis*. The original description of *H. amphiurae*, however, was made from partially contracted specimens. In order to determine the correct taxonomic position of this species, a redescription based on observations of healthy living specimens is required.

Haplocaulus brehmi Lüpkes, 1975

DESCRIPTION (Fig. 4). Zooid oval in shape, 80 μm long × 70 μm wide. Peristomial lip well developed, 50 μm in diameter. Disc slightly convex. Infundibulum broad and reaches two-thirds body length. Contractile vacuole situated just below the peristome. Macronucleus S-shaped or irregular, and lies longitudinally with respect to the major body axis. Pellicular striations not observed. Stalk about equal to body length.

HABITAT. Freshwater, originally found attached to the gills of larvae of the caddis-fly *Agapatus*.

Haplocaulus carinogammari Stiller (1963), 1971

Vorticella carinogammari Stiller, 1963

DESCRIPTION (Fig. 5). Zooid inverted bell-shaped, rounded, 45–75 μm long. Peristomial lip well developed, diameter about equal to maximum body width. Disc convex. Infundibulum narrow and reaches centre of zooid. Contractile vacuole situated just beneath peristome. Macronucleus elongate and irregular in shape. Pellicular striations visible on fixed specimens. Stalk up to × 2 body length.

HABITAT. Freshwater, originally found attached to the crustaceans *Carinogammarus roeselii* var *triacanthus* and *Gammarus fossarum*; also occurs on *Rivulogammarus* (Piesik, 1975) and *Asellus aquaticus* (Szczepanowski, 1978).

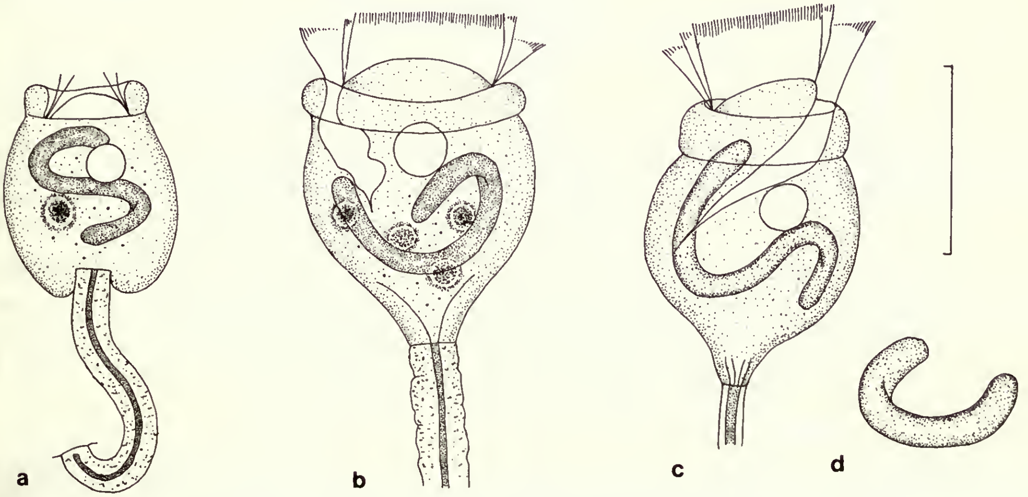

Fig. 5 *Haplocaulus carinogammari* (a) contracted; (b) relaxed, after Stiller, 1963 (called *Vorticella carinogammari*); (c) & (d) showing variation of macronucleus, after Szczepanowski, 1978. Bar = 50 μm.

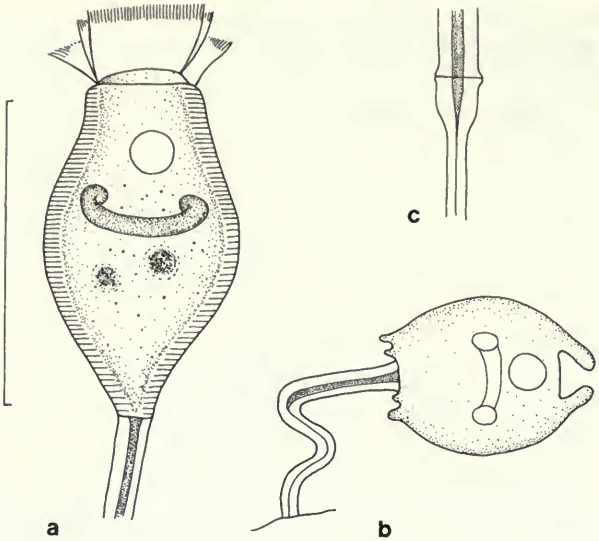

Fig. 6 *Haplocaulus claudicans*, (a) relaxed zooid; (b) contracted zooid; (c) detail of stalk, after Penard, 1922 (called *Vorticella claudicans)*. Bar = 25 µm.

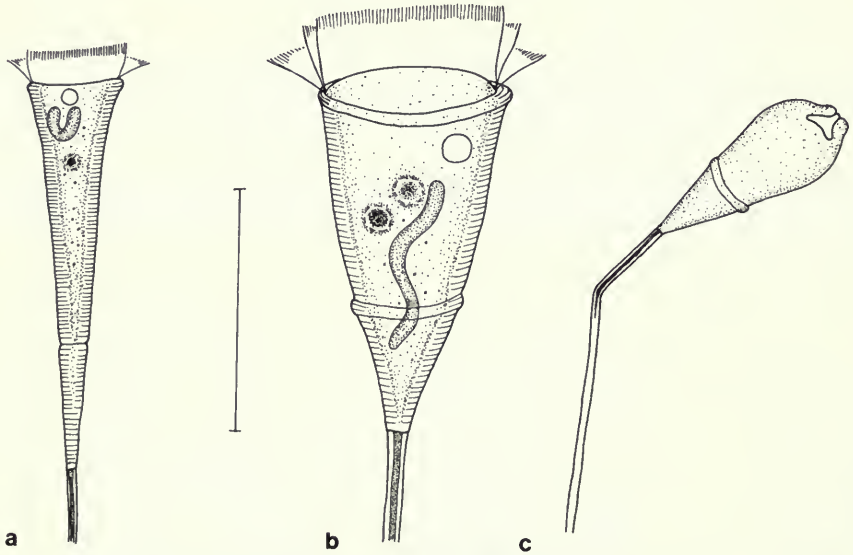

Fig. 7 *Haplocaulus conosomus*, (a) after Stokes, 1889 (called *Vorticella conosoma)*; (b) relaxed zooid; (c) contracted zooid, after Gajewskaja, 1933 (called *Vorticella conesoma)*. Bar = 50 µm.

Haplocaulus claudicans (Penard, 1922) Stiller, 1971

Vorticella claudicans Penard, 1922

Description (Fig. 6). Zooid elongate, almost cylindrical in shape, 40–55 µm long × 30 µm wide. Diameter of peristomial lip less than or occasionally equal to maximum body width. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped and lies horizontally across centre of zooid. Pellicle with fine transverse striations. Stalk about equal to body length. Spasmoneme terminates about half-way down the stalk and is connected to the base of the stalk by a fibre.

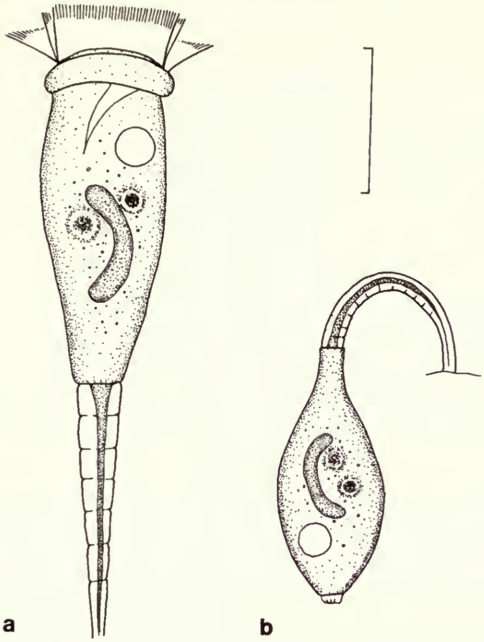

Fig. 8 *Haplocaulus crassicaulis,* (a) relaxed zooid; (b) contracted zooid, composite after Kent, 1881 (called *Vorticella crassicaulis*) and Nenninger, 1948. Bar = 25 µm.

HABITAT. Freshwater, originally found attached to mosses.

NOTE. It is unclear whether the 'fibre' in the lower part of the stalk is an extension of the spasmoneme, or a separate structure. In the case of the latter, it may be necessary to transfer this species to the genus *Monintranstylum.*

Haplocaulus conosomus (Stokes, 1889) n. comb.

Vorticella conosoma Stokes, 1889
Vorticella conesoma Gajewskaja, 1933

DESCRIPTION (Fig. 7). Zooid conical and elongate, 75 µm long × 30 µm wide, and with a distinct ridge in the region of the telotroch band. Peristomial lip 35 µm in diameter. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped or irregular, and situated either centrally or in the anterior part of the body. Pellicular striations visible on zooid. Stalk 150–200 µm long.

HABITAT. Freshwater.

NOTE. In his original description, Stokes (1889) did not describe the spasmoneme. According to Gajewskaja (1933), however, the spasmoneme terminates in the upper part of the stalk. If spasmoneme length is accepted as a generic character, it may be necessary to transfer this species to the genus *Monintranstylum.*

Haplocaulus crassicaulis (Kent, 1881) Stiller, 1971

Vorticella crassicaulis Kent, 1881

DESCRIPTION (Fig. 8). Zooid elongate, 45–50 µm long × 25 µm wide. Peristomial lip 20 µm in diameter. Contractile vacuole situated in upper one-third of body. Macronucleus C-shaped and situated in centre of zooid. Stalk × 1— × 2 body length. Stalk sheath has several transverse folds.

HABITAT. Freshwater, originally isolated as an epizoite of the crustacean *Asellus aquaticus.*

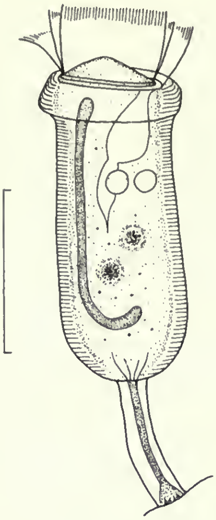

Fig. 9 *Haplocaulus dipneumon*, after Penard, 1922 (called *Vorticella dipneumon*). Bar = 25 µm.

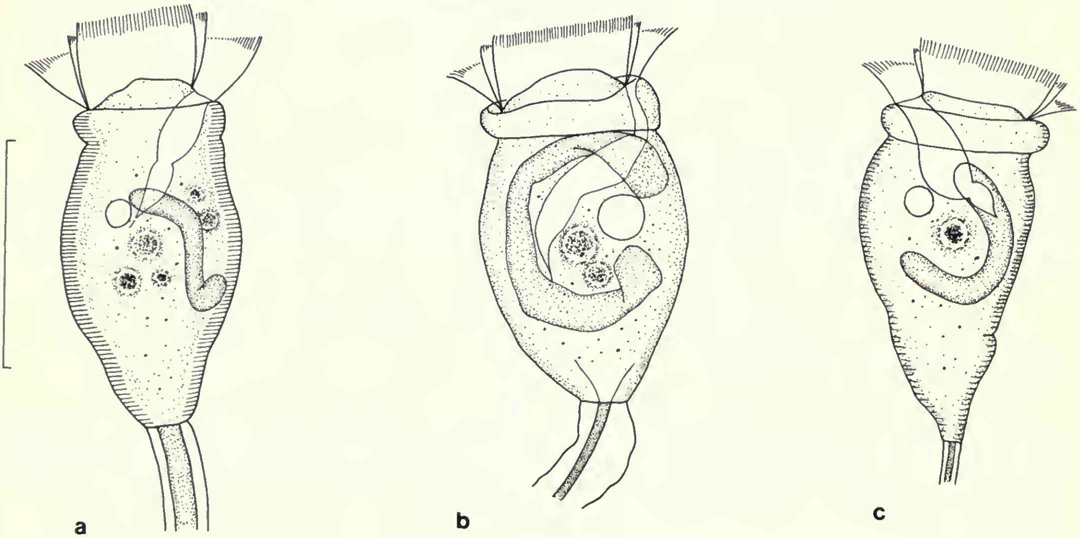

Fig. 10 *Haplocaulus distinguendus*, (a) after Sommer, 1951; (b) after Bierhof & Roos, 1976 (called *Haplocaulus distinguendis)*; (c) after Lüpkes, 1976 (called *Haplocaulus hengsti)*. Bar = 50 µm.

Haplocaulus dipneumon (Penard, 1922) Stiller, 1971

Vorticella dipneumon Penard, 1922

Description (Fig. 9). Zooid almost cylindrical in shape, 50–56 µm long × 25 µm wide. Peristomial lip well developed, 25–30 µm in diameter. Disc convex and raised centrally to a point. Infundibulum almost reaches centre of zooid. Two contractile vacuoles situated in upper one-third of body. Macronucleus elongate and lies longitudinally with respect to the major body axis. Transverse striations visible on pellicle. Stalk less than body length. Spasmoneme flared at either end.

HABITAT. Freshwater, originally found as an epizoite of the crustacean *Gammarus pulex*.

NOTE. This species bears a strong morphological resemblance to *Baikalonis*. Until its mode of contraction has been described, however, *H. dipneumon* should remain in the genus *Haplocaulus*.

Haplocaulus distinguendus Sommer, 1951

Haplocaulus distinguendis (Sommer, 1951) Bierhof & Roos, 1976
H. hengsti Lüpkes, 1976

DESCRIPTION (Fig. 10). Zooid ovoid, 60–79 µm long × 34–49 µm wide, and constricted beneath peristome. Peristomial lip well developed, 27–40 µm in diameter. Disc convex. Infundibulum broad and reaches almost to centre of body. Contractile vacuole situated in upper half of zooid. Macronucleus irregular or C-shaped. Transverse pellicular striations visible on zooid. Stalk up to 190 µm long × 7·0–9·0 µm wide.

HABITAT. Freshwater, attached to the river weed *Enteromorpha intestinalis* (Sommer 1951), to inanimate substrates (Lüpkes, 1976), and to the crustaceans *Asellus aquaticus* (Sommer, 1951) and *Gammarus* spp. (Bierhof & Roos, 1976).

NOTE. *H. hengsti* is synonymysed with *H. distinguendus* because of their morphological similarity. The main differences between the two are the size of the zooid, *H. hengsti* (79 µm) being slightly longer than *H. distinguendus* (60–75 µm), and stalk length (*H. distinguendus* up to 190 µm long: *H. hengsti*—less than body length). Neither of these characters are particularly reliable for separating species, and there are insufficient differences here to recognise the two as separate taxa.

Haplocaulus eforianus (Tucolesco, 1962) n. comb

Vorticella eforiana Tucolesco, 1962

DESCRIPTION (Fig. 11). Zooid 55–60 µm long × 20 µm wide. Upper part of body cylindrical in shape, lower part conical. Peristomial lip 20–25 µm in diameter. Pellicle with transverse striations, and convex ribbing between the striations. Pellicle also ornamented with numerous knob-like projections. Stalk × 1– × 2 body length.

HABITAT. Marine

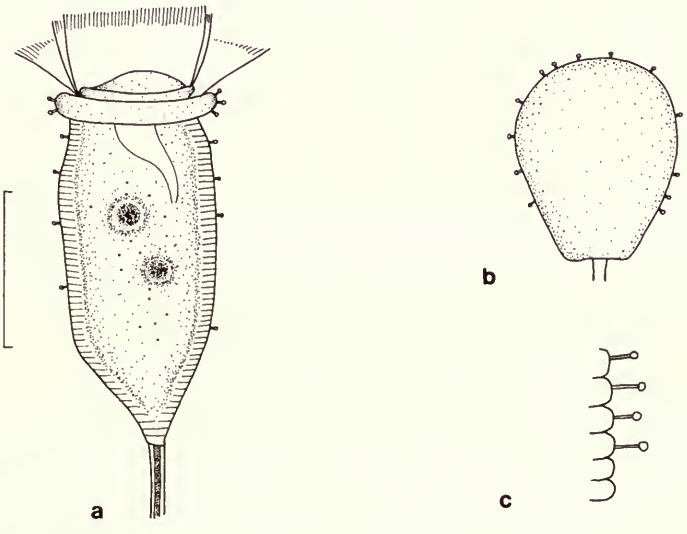

Fig. 11 *Haplocaulus eforianus*, (a) relaxed zooid; (b) contracted zooid; (c) pellicle, showing convex ribbing and knob-like projections, after Tucolesca, 1962 (called *Vorticella eforiana*). Bar = 25 µm.

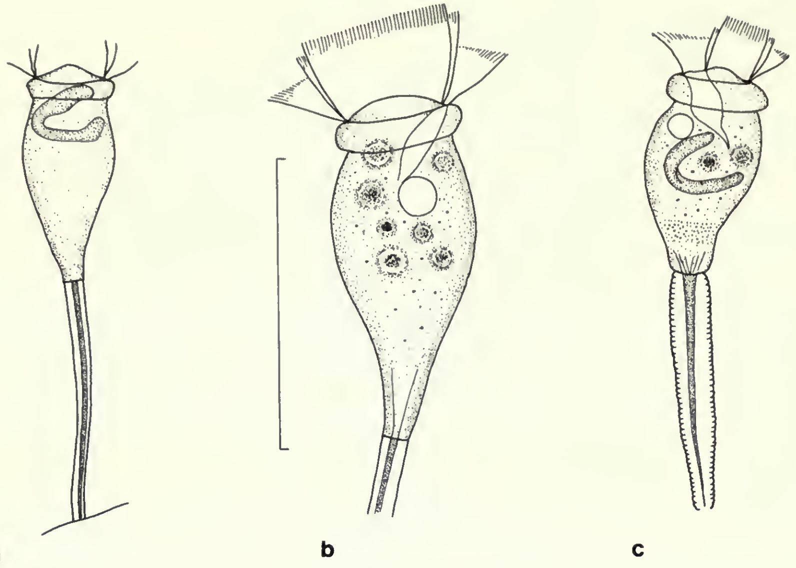

Fig. 12 *Haplocaulus elegans* (a) showing macronucleus; (b) relaxed zooid, after Nenninger, 1948 (called *Vorticella elegans*); (c) after Szczepanowski, 1978. Bar = 50 µm.

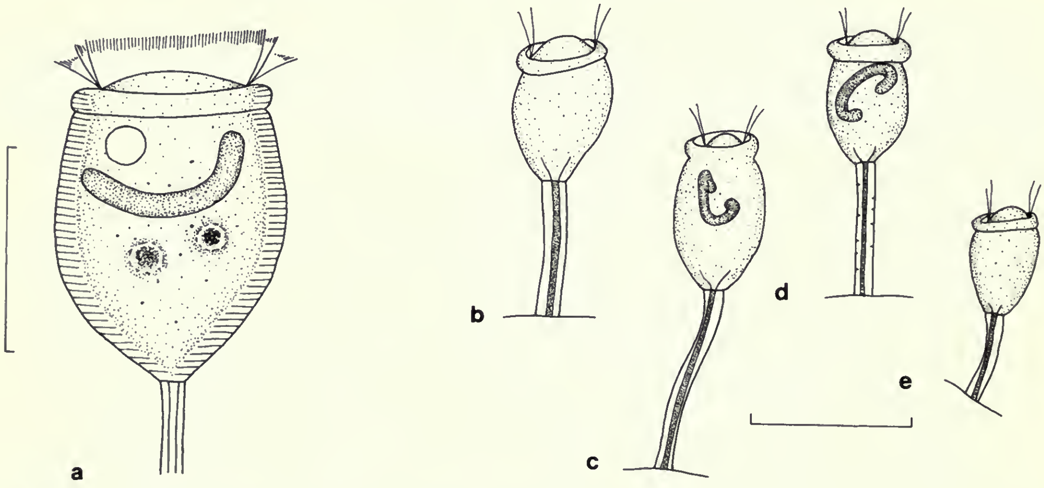

Fig. 13 *Haplocaulus epizoicus* (a) after Sramek-Husek, 1948 (called *Vorticella epizoica*), bar = 25 µm; (b)–(e) after Piesik, 1975, bar = 25 µm.

Haplocaulus elegans (Nenninger, 1948) Stiller, 1971

Intranstylum elegans Nenninger, 1948
Haplocaulus elegans f. gammari Piesik, 1975

DESCRIPTION (Fig. 12). Zooid 42–84 µm long, constricted beneath the peristome and tapering posteriorly towards the stalk. Diameter of peristomial lip less than maximum body width. Disc convex. Contractile vacuole situated in upper one-third of zooid. Macronucleus C-shaped and lies horizontally in the anterior part of the body. Pellicular striations not observed. Stalk × 1– × 2 body length.

HABITAT. Freshwater, originally found attached to the crustaceans *Asellus aquaticus* and *Cyclops* sp.

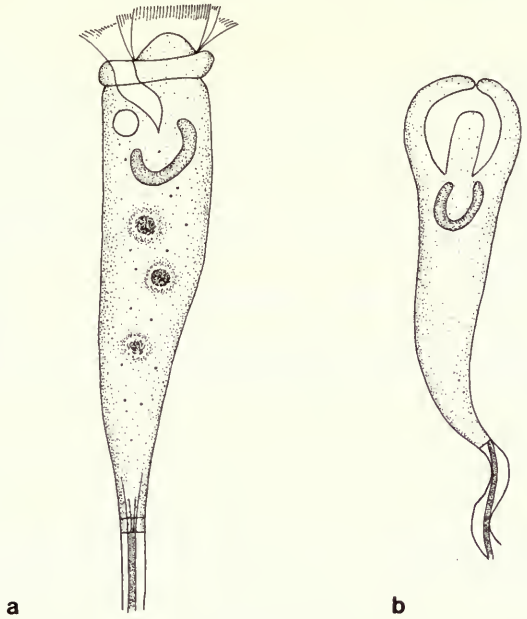

Fig. 14 *Haplocaulus extensus* (a) relaxed zooid; (b) contracted zooid, after Kahl, 1935 (called *Vorticella extensa)*. Bar = 50 µm.

Haplocaulus epizoicus (Sramek-Husek, 1948) Stiller, 1971

Vorticella epizoica Sramek-Husek, 1948

Description (Fig. 13). Zooid 25–46 µm long × 18–37 µm wide, inverted bell-shaped and rounded posteriorly. Diameter of peristomial lip about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies either horizontally or obliquely in the anterior part of the zooid. Pellicle with fine transverse striations. Stalk × 1– × 2 body length.

Habitat. Freshwater, found as an epizoite of the crustaceans *Megacyclopsis viridis* (Sramek-Husek, 1948) and *Gammarus pulex fossarum* (Piesik, 1975).

Haplocaulus extensus (Kahl, 1935) Sommer, 1951

Vorticella extensa Kahl, 1935

Description (Fig. 14). Zooid elongate, 50–100 µm long × 15–27 µm wide (Kahl (1935) described two morphological forms of this species, one 90–100 µm the other 50–70 µm long). Peristomial lip 35 µm in diameter. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies transversely in anterior part of zooid. Pellicle with fine transverse striations. Stalk up to 200 µm long.

Habitat. Freshwater, found by Sommer (1951) attached to the river weed *Enteromorpha intestinalis.*

Haplocaulus fluviatilis Shubernetskij & Chorik, 1977

Description (Fig. 15). Zooid barrel-shaped with broadened scopular region, 28–48 µm (mean 38 µm) long × 14–30 µm (mean 22 µm) wide. Peristomial lip 17–25 µm (mean 21 µm) in diameter. Disc elevated at angle to peristome and raised centrally to a point. Infundibulum reaches one-third body length. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across upper part of zooid. Pellicle with distinct transverse striations, and convex ribbing between the striations. Stalk up to 50 µm long.

Habitat. Freshwater, originally found attached to the ostracod *Heterocypris.*

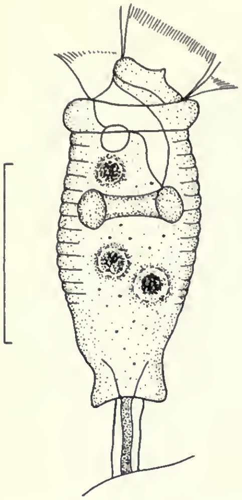

Fig. 15 *Haplocaulus fluviatilis*, after Shubernetskij & Chorik, 1977. Bar = 25 µm.

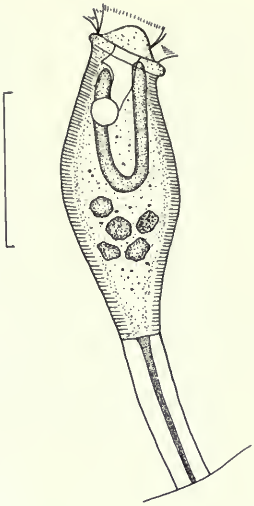

Fig. 16 *Haplocaulus fusiformis*, after Nenninger, 1948 (called *Vorticella fusiforma*). Bar = 75 µm.

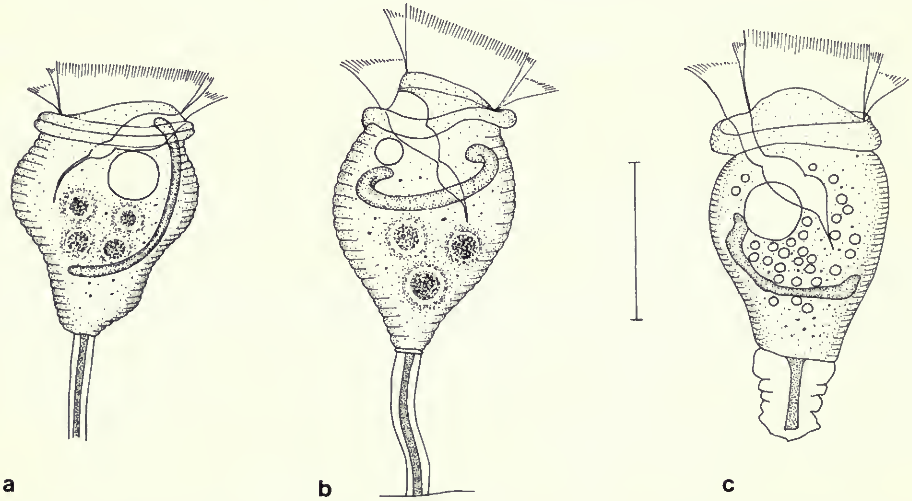

Fig. 17 *Haplocaulus kahlii* (a) & (b) after Stiller, 1931 (called *Vorticella kahlii*); (c) after Bierhof & Roos, 1976. Bar = 25 µm.

Haplocaulus fusiformis (Nenninger, 1948) Stiller, 1971

Vorticella fusiforma Nenninger, 1948

DESCRIPTION (Fig. 16). Zooid 140–162 µm long × 60 µm wide, spindle-shaped with prominent central bulge. Peristomial lip 45 µm in diameter. Disc prominent and conical in shape. Infundibulum reaches one-quarter body length. Contractile vacuole situated in upper one-third of zooid. Macronucleus U-shaped and lies in anterior half of body. Food vacuoles large, dark and hexagonal in shape. Fine transverse striations visible on pellicle. Stalk less than body length.

HABITAT. Freshwater, originally found attached to the tails of tadpoles.

NOTE. Food vacuoles are not accepted as a taxonomic character among the Vorticellidae (Noland & Finley, 1931; Warren, 1986) or, indeed, the rest of the phylum Ciliophora.

Haplocaulus kahlii (Stiller, 1931) Sommer, 1951

Vorticella kahlii Stiller, 1931

Description (Fig. 17). Zooid pyriform with prominent bulge in anterior region, 32–44 µm long × 24–36 µm wide. Peristomial lip well developed, occasionally with central furrow giving the appearance of a double lip. Diameter of lip less than maximum body width. Macronucleus elongate, variable in shape. Pellicle distinctly striated with convex ribbing between striations. Stalk equal to or less than body length.

Habitat. Freshwater, found as an epizoite of the crustaceans *Leptodora kindlii*, *Daphnia longispina* var *hyalina* and *Salpinia* sp. (Stiller, 1931), *Megacyclopsis viridis* (Sramek-Husek, 1948), and *Gammarus tigrinus* (Bierhof & Roos, 1976).

Haplocaulus leanderi Stiller, 1968

Description (Fig. 18). Zooid inverted bell-shaped, 30–32 µm long × 22–24 µm wide. Peristomial lip well developed, 26–28 µm in diameter. Infundibulum reaches one-third body length. Macronucleus C-shaped and lies horizontally in anterior half of body. Pellicle furnished with numerous small granules. Stalk × 1– × 2 body length.

Habitat. Marine, originally isolated as an epizoite of the crustacean *Leander* sp.

Haplocaulus longinuclei Banina, 1982

Description (Fig. 19). Zooid 43–61 µm long × 41–49 µm wide, somewhat variable in shape but usually oval or spherical and tapering sharply towards the stalk. Diameter of peristomial lip less than maximum body width. Infundibulum reaches centre of zooid. Macronucleus elongate and irregular in shape. Fine transverse striations visible on pellicle. Stalk less than body length.

Habitat. Freshwater, originally isolated as epizoites of tadpoles of the amphibian *Rana temporaria*.

Haplocaulus macronucleatus (Nenninger, 1948) Stiller, 1971

Vorticella extensa var *macronucleata* Nenninger, 1948

Description (Fig. 20). Zooid elongate almost cylindrical in shape, 91·5 µm long × 35 µm wide. Diameter of peristomial lip about equal to maximum body width. Disc convex and raised centrally to a point. Contractile vacuole small and situated in upper one-third of body. Macronucleus broad, S-shaped and lies longitudinally with respect to major body axis. Pellicular striations not visible. Stalk about equal to body length.

Habitat. Freshwater, originally isolated as an epizoite of the hexapod *Ephemera vulgata*.

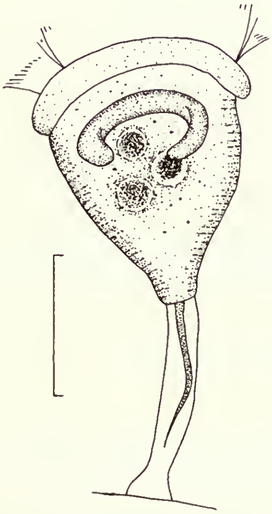

Fig. 18 *Haplocaulus leanderi*, after Stiller, 1968. Bar = 25 µm.

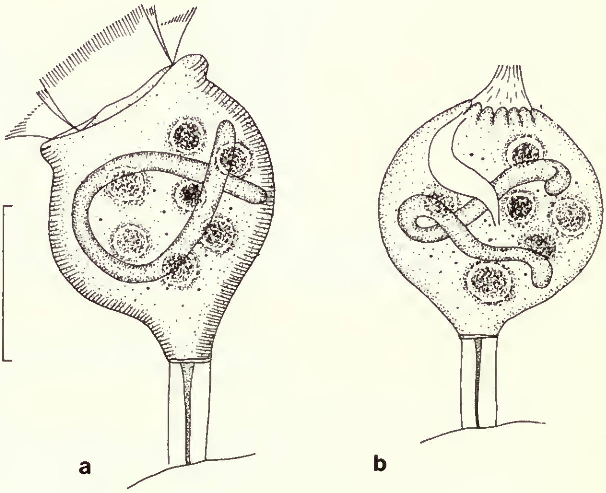

Fig. 19 *Haplocaulus longinuclei* (a) relaxed zooid; (b) contracted zooid, after Banina, 1982. Bar = 25 µm.

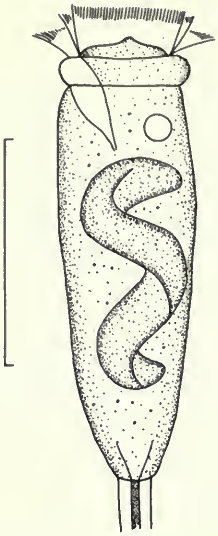

Fig. 20 *Haplocaulus macronucleatus,* after Nenninger, 1948 (called *Vorticella extensa* var. *macronucleata).* Bar = 50 µm.

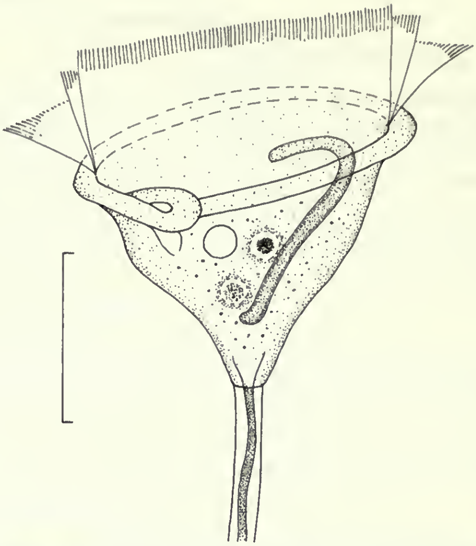

Fig. 21 *Haplocaulus pelagicus,* after Gajewskaja, 1933 (called *Vorticella pelagica).* Bar = 25 µm.

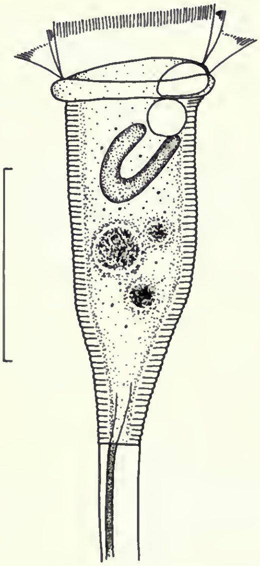

Fig. 22 *Haplocaulus procerus,* after Nenninger, 1948 (called *Vorticella procera).* Bar = 50 µm.

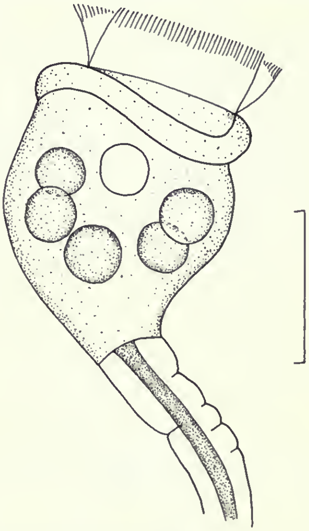

Fig. 23 *Haplocaulus sertulariarum,* after Entz, 1884 (called *Spastostyla sertulariarum).* Bar = 50 µm.

Haplocaulus pelagicus (Gajewskaja, 1933) Stiller, 1971

Vorticella pelagica Gajewskaja, 1933

Description (Fig. 21). Zooid conical or inverted bell-shaped, 30–40 µm long × 50 µm wide. Peristomial lip 70 µm in diameter. Contractile vacuole situated just below peristome. Macronucleus elongate, irregular in shape and lies longitudinally with respect to major body axis. Pellicular striations not visible. Stalk usually less than body length.

Habitat. Marine

Haplocaulus procerus (Nenninger, 1948) Stiller, 1971

Vorticella procera Nenninger, 1948

Description (Fig. 22). Zooid elongate, almost cylindrical in shape, 103 µm long × 40 µm wide. Peristomial lip 50 µm in diameter. Disc flat. Contractile vacuole situated just beneath peristomial lip. Macronucleus C-shaped and lies either horizontally or obliquely in the anterior part of the zooid. Food vacuoles typically large. Fine transverse striations visible on pellicle. Stalk × 2– × 3 body length.

Habitat. Freshwater, originally found attached to the tails of tadpoles. Typically forms pseudocolonies.

Haplocaulus sertulariarum (Entz, 1884) Banina, 1982

Spastostyla sertulariarum Entz, 1884
Vorticella sertulariarum (Entz, 1884) Kahl, 1935

Description (Fig. 23). Zooid inverted bell-shaped, 60–109 µm long × 34–48 µm wide. Diameter of peristomial lip greater than maximum body width. Disc flat. Infundibulum reaches centre of zooid. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across centre of anterior part of zooid. Zoochlorellae may be present in cytoplasm. Stalk broad, and equal to or less than body length. Stalk sheath frequently with distinct transverse folds.

Habitat. Freshwater or marine, originally isolated from the Bay of Naples attached to polyps and sea urchins (Entz, 1884); also found as epizoites of tadpoles of *Rana temporaria*.

Note. Entz (1884) considered this organism to be identicle to *Rhabdostyla sertularium* Kent, 1881. *Rhabdostyla sertularium*, however, does not possess a spasmoneme and the stalk is non-contractile whereas Entz's organism clearly has a spasmoneme. *S. sertulariarum* Entz, 1884 was transferred to *Vorticella* by Kahl (1935) and, more recently, to *Haplocaulus* by Banina (1982).

Haplocaulus stilleri Piesik, 1975

Description (Fig. 24). Zooid spindle-shaped, 60 µm long × 27 µm wide, with prominent central bulge. Peristomial lip 20 µm in diameter. Disc convex. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped and lies horizontally across centre of zooid. Pellicular striations not observed. Stalk up to 60 µm long and 12 µm wide.

Habitat. Freshwater, originally described as an epibiont attached to the crustaceans *Gammarus pulex pulex* (L) and *Gammarus pulex fossarum* (Koch).

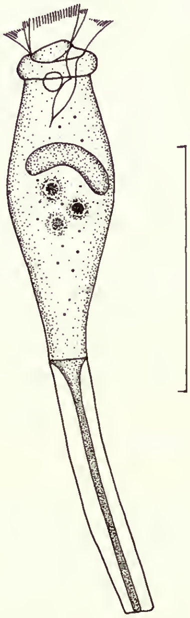

Fig. 24 *Haplocaulus stilleri*, after Piesik, 1975. Bar = 50 µm.

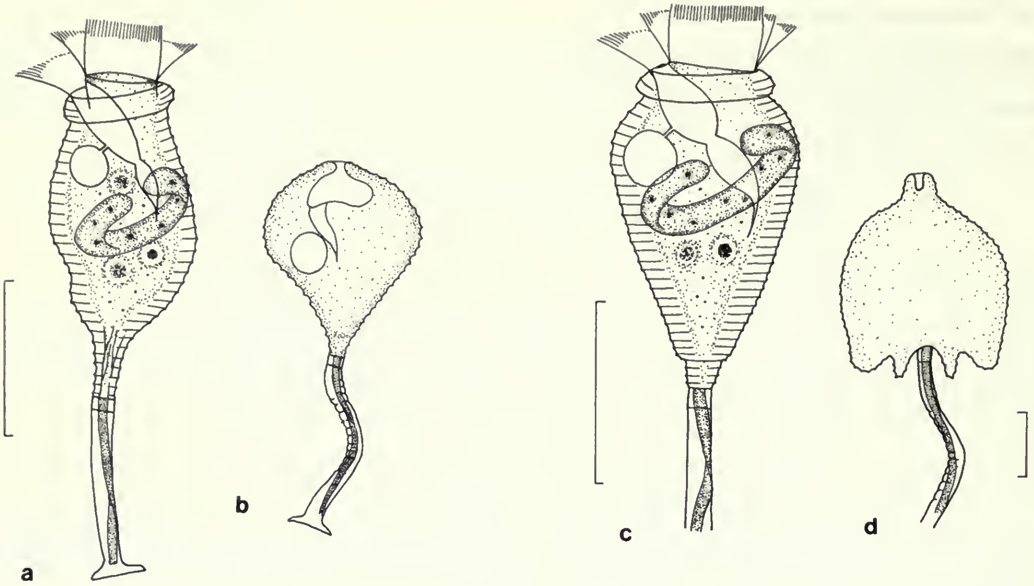

Fig. 25 *Haplocaulus terrenus,* showing variability in relaxed and contracted zooids, (a) relaxed; (b) contracted, bar = 25 µm; (c) relaxed, bar = 25 µm; (d) contracted, bar = 15 µm, after Foissner, 1981.

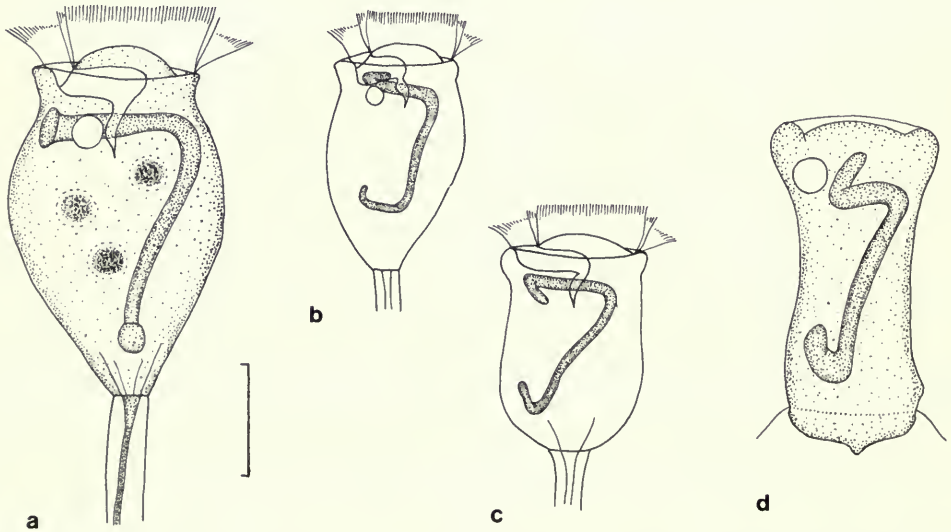

Fig. 26 *Haplocaulus walteri,* (a) typical zooid; (b & c) variations in zooid shape under poor conditions; (d) telotroch, after Guhl, 1985. Bar = 25 µm.

Haplocaulus terrenus Foissner, 1981

Description (Fig. 25). Zooid somewhat variable in shape, 40–60 µm long × 20–26 µm wide. Peristomial lip 20 µm in diameter. Infundibulum reaches centre of zooid. Contractile vacuole large, situated in anterior part of zooid and empties into infundibulum via a short channel. Macronucleus C-shaped and lies either horizontally or obliquely across centre of body. Zooid has 30 transverse striations with concave ribbing between striations. Stalk 2·5–3·5 µm wide, and one-half— × 3 body length. Upon contraction posterior end of zooid may become folded, overlapping the stalk.

Habitat. Terrestrial, originally isolated from Alpine soils.

Haplocaulus walteri Guhl, 1985

Description (Fig. 26). Zooid 55–75 µm long × 40–60 µm wide, cylindrical to inverted bell-shaped. Diameter of peristomial lip usually less than maximum body width. Infundibulum short. Contractile vacuole situated just below peristome. Macronucleus J- or 7-shaped. Pellicular striations not observed. Stalk up to 158 µm long, and with rod-shaped bacteria attached to the stalk sheath.

Habitat. Freshwater, originally found in activated sludge.

Genus *BAIKALONIS* Jankowski, 1982

The main distinguishing feature of this genus is the mode of contraction during which the stalk shortens longitudinally and is enveloped by the zooid. When *Baikalonis* was first described (Jankowski, 1982) just one species, *B. foissneri*, was known. *B. foissneri* thus became the type species by monotypy. Two more species, *Vorticella undulata* (Dons, 1918) Noland & Finley, 1931 and *Haplocaulus* sp. Bierhof & Roos, 1976 are here transferred to *Baikalonis*. Three other species of *Haplocaulus*, *H. amphiurae*, *H. dipneumon* and *H. fusca*, also bear a strong morphological resemblance to *Baikalonis* although their modes of contraction have yet to be described.

Diagnosis. Solitary, borne upon an unbranched stalk which is typically much shorter than the body. Spasmoneme straight and extends the entire length of the stalk. Upon contraction, the zooid envelopes the stalk which shortens longitudinally.

Key to the species of *Baikalonis*

1	Freshwater; zooid with a contractile vacuole	2
–	Marine; zooid without a contractile vacuole	***B. undulata***
2	Infundibulum broad and reaches centre of zooid. Contractile vacuole centrally located. Peristomial lip with central furrow	***B. foissneri***
–	Infundibulum lies diagonally and reaches one-third body length. Contractile vacuole situated just below peristome. Peristomial lip without a furrow	***B. gammari***

Species descriptions

Baikalonis foissneri Jankowski, 1982

Description (Fig. 27). This the type species is cylindrical in shape, 56–60 µm long × 20 µm wide. Peristomial lip well developed with central furrow giving the appearance of a double lip. Disc prominently arched above peristome. Infundibulum broad and reaches centre of zooid. Contractile vacuole situated centrally in body. Macronucleus cylindrical in shape and slightly curved. Stalk 12–14 µm long. Spasmoneme broad.

Habitat. Freshwater, originally found as an epizoite of the larvae of the caddis-fly *Baicalina bellicosa* in Lake Baikal, U.S.S.R.

Baikalonis gammari n. sp.

Haplocaulus sp. Bierhof & Roos, 1976

Description (Fig. 28). Zooid cylindrical in shape, narrowing slightly towards the stalk, 75 µm long × 45 µm wide. Peristomial lip well developed, diameter about equal to maximum body width. Infundibulum reaches one-third body length. Contractile vacuole situated just below peristome. Macronucleus C-shaped and lies longitudinally in centre of zooid. Fine transverse striations visible on pellicle. Stalk 10 µm long × 8 µm wide.

Habitat. Freshwater, originally isolated as an epizoite of the crustacean *Gammarus pulex*.

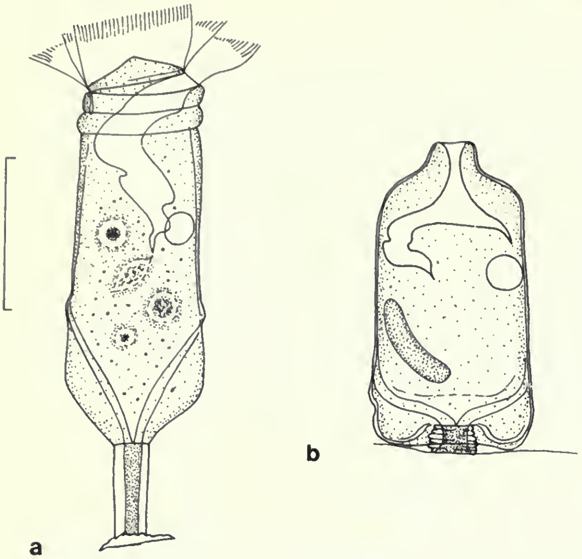

Fig. 27 *Baikalonis foissneri*, (a) relaxed; (b) contracted, after Jankowski, 1982. Bar = 25 μm.

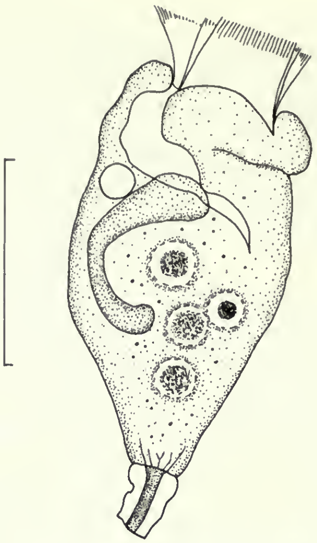

Fig. 28 *Baikalonis gammari*, after Bierhof & Roos, 1976 (called *Haplocaulus* sp.). Bar = 50 μm.

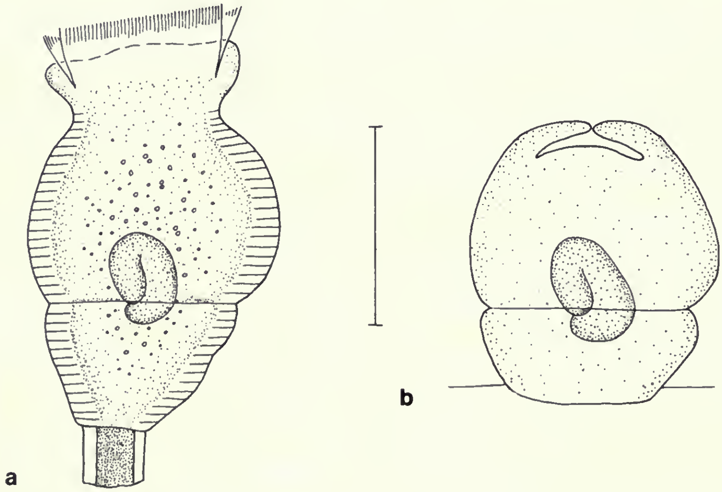

Fig. 29 *Baikalonis undulata*, (a) relaxed; (b) contracted, after Dons, 1918 (called *Vorticellopsis undulata*). Bar = 50 μm.

Baikalonis undulata (Dons, 1918) n. comb.

Vorticellopsis undulata Dons, 1918
Vorticella undulata (Dons, 1918) Noland & Finley, 1931

Description (Fig. 29). Zooid pyriform, 110 μm long × 72 μm wide. Peristomial lip 57 μm in diameter. Two distinct constrictions present on body, one beneath the peristomial lip and the other in the region of the telotroch band. Contractile vacuole not observed. Macronucleus C-shaped, 30 μm long × 20 μm wide and lies longitudinally with respect to major body axis. Transverse striations clearly visible on pellicle. Stalk 115 μm long × 19 μm wide. Spasmoneme 12 μm in diameter.

Habitat. Marine, originally found attached to the alga *Desmaresita viridis*.

Note. Both Noland & Finley (1931) and Kahl (1935) considered that *Vorticellopsis undulata* Dons, 1918 should belong to the genus *Vorticella*. In a recent revision of *Vorticella*, Warren (1986) noted that the stalk of *V. undulata* does not contract spirally and should not, therefore, be included in the genus *Vorticella*. The mode of contraction and the morphology of the stalk both indicate that this species should belong to the genus *Baikalonis*.

Genus ***COTENSITA*** Jankowski, 1982

The main distinguishing feature of the genus *Cotensita* is the stalk sheath which is folded in a characteristic fashion just beneath the zooid. Although some colonial peritrichs such as *Craspedomyoschiston* have ornamentation of the stalk sheath, this feature has not previously been recorded among solitary vorticellids. The spasmoneme of *Cotensita* is straight and extends to about two-thirds of the stalk length. *C. commensalis* Jankowski, 1982 is the type species by monotypy.

Diagnosis. Spasmoneme straight, not extending the full length of the stalk. Stalk sheath twisted in the region just below the stalk. Upon contraction the zooid bends over to one side and assumes a characteristic 'nodding' position.

Species description

Cotensita commensalis Jankowski, 1982

Description (Fig. 30). This the type species is inverted bell-shaped, 46 µm long × 36 µm wide. Diameter of peristomial lip about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus C-shaped. Stalk 85–90 µm long. Stalk sheath twisted to form 1–2 helical coils just below zooid. Spasmoneme reaches two-thirds stalk length with the posterior end tapering to a point.

Habitat. Freshwater, originally isolated as an epizoite of the larvae of the caddis-fly *Baicalina bellicosa* from Lake Baikal, U.S.S.R.

Genus ***PARAZOOTHAMNIUM*** Piesik, 1975

The main distinguishing feature of this genus is the mode of stalk contraction which takes place in two stages: initially the stalk shortens longitudinally in a concertina-like fashion but, if the stimulus is sufficiently strong, it loops and bends in the more usual manner.

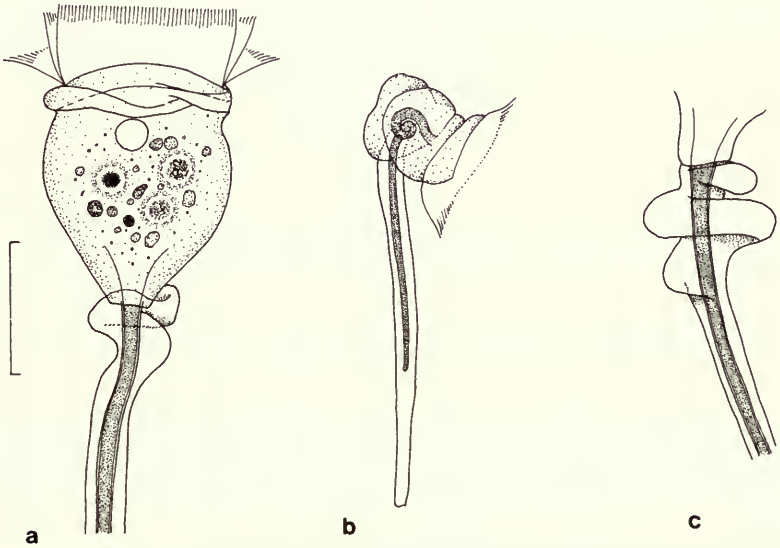

Fig. 30 *Cotensita commensalis*, (a) relaxed zooid, bar = 25 µm. (b) partially contracted; (c) detail of stalk, after Jankowski, 1982.

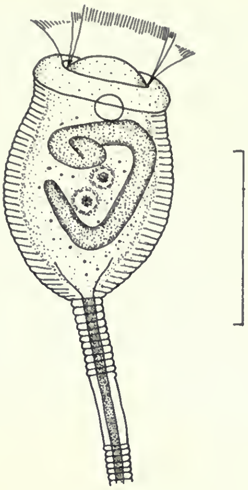

Fig. 31 *Parazoothamnium stenotica,* after Piesik, 1975. Bar = 50 µm.

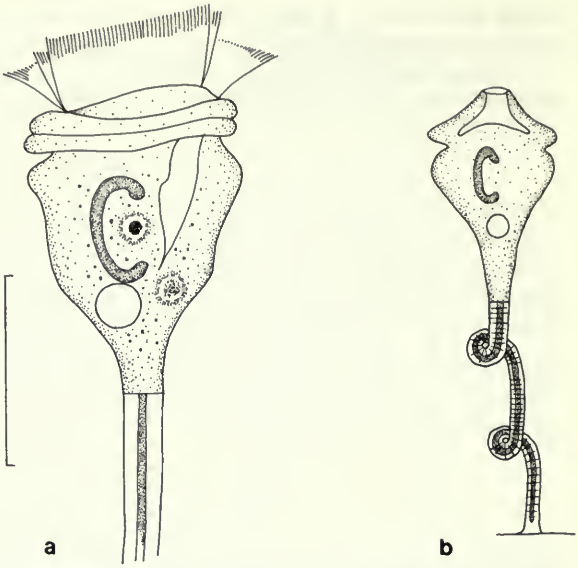

Fig. 32 *Parazoothamnium claparedei,* (a) relaxed zooid; (b) contracted, after Andrussowa, 1886 (called *Vorticella claparedei).* Bar = 50 µm.

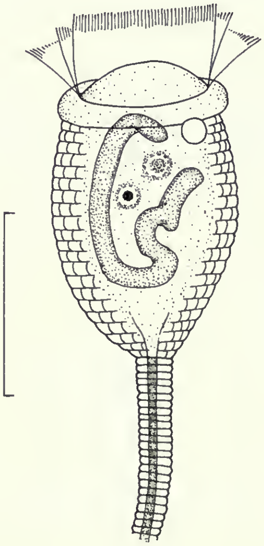

Fig. 33 *Piesika gammari,* after Piesik, 1975 (called *Parazoothamnium gammari).* Bar = 50 µm.

Piesik (1975) originally described two species of *Parazoothamnium, P. stenotica* and *P. gammari.* The latter species, however, has rows of regularly arranged tubercles and, since this is recognised as a generic character among the Vorticellidae, *P. gammari* is transferred to the new genus *Piesika. P. claparedei* is included in the genus *Parazoothamnium* for the first time. *P. stenotica* is designated the type species.

DIAGNOSIS. Solitary, borne upon an unbranched stalk. Spasmoneme extends the complete length of the stalk. Stalk contraction takes place in two stages; initially it shortens longitudinally in a concertina-like fashion but, if the stimulus is sufficiently strong, it loops and folds. Zooid has a transverse silverline system.

Key to the species of *Parazoothamnium*

1	Macronucleus J-shaped; contractile vacuole situated in anterior half of body .	***P. stenotica***
–	Macronucleus C-shaped; contractile vacuole situated in posterior half of body .	***P. claparedei***

Species descriptions

Parazoothamnium stenotica Piesik, 1975

DESCRIPTION (Fig. 31). This the type species is inverted bell-shaped, somewhat rotund, 70 μm long × 50 μm wide. Peristomial lip well developed, diameter about equal to maximum body width. Contractile vacuole situated just beneath peristome. Macronucleus J-shaped. Pellicle with fine transverse striations. Stalk up to 9·0 μm wide.

HABITAT. Freshwater, originally isolated as an epizoite of the crustacean *Gammarus pulex*.

Parazoothamnium claparedei (Andrussowa, 1886) n. comb.

Vorticella claparedei Andrussowa, 1886

DESCRIPTION (Fig. 32). Zooid campanulate, 85 μm long × 60 μm wide and with a distinct swelling just below the peristome. Peristomial lip 60 μm in diameter and with a central furrow to give the appearance of a double lip. Disc raised obliquely above peristome. Infundibulum reaches centre of zooid. Single contractile vacuole situated in posterior half of zooid. Macronucleus C-shaped and lies longitudinally with respect to major body axis. Pellicular striations not observed. Upon contraction stalk sheath assumes a wrinkled appearance and stalk coils into two or three unevenly spaced loops.

HABITAT. Marine, attached to filamentous algae.

Genus ***PIESIKA*** n. gen.

The possession of regularly arranged pellicular tubercles along with an underlying reticulate silverline system is regarded as a generic character among peritrichs (Foissner & Schiffmann, 1974; Warren, 1986). The genus *Piesika* is erected to include solitary vorticellids which both possess pellicular tubercles, and exhibit the two stage stalk contraction process seen in *Parazoothamnium*. *P. gammari* is the type species by monotypy.

DIAGNOSIS. Solitary zooids borne upon an unbranched stalk. Spasmoneme extends the complete length of the stalk. Contraction of the stalk takes place in two stages; initially the stalk shortens longitudinally in a concertina-like fashion but, if the stimulus is sufficiently strong, it loops and folds. Zooid with rows of regularly aligned pellicular tubercles.

Species description

Piesika gammari (Piesik, 1975) n. comb.

Parazoothamnium gammari Piesik, 1975

DESCRIPTION (Fig. 33). This the type species is inverted bell-shaped, 70 μm long × 50 μm wide. Diameter of peristomial lip about equal to maximum body width. Disc convex. Contractile vacuole situated just below peristome. Macronucleus elongate and irregular in shape. Stalk up to 240 μm long × 10 μm wide. Cysts nearly spherical in shape, 49 μm × 43 μm.

HABITAT. Freshwater, originally found as an epizoite of the crustacean *Gammarus pulex pulex*.

Genus ***PSEUDOHAPLOCAULUS*** n. gen.

Foissner & Schiffmann (1974) reported that two types of silverline system are found among vorticellids; (i) transverse, in which the lines encircle the body in one direction only, and (ii) reticulate, which consists of a network of vertical and horizontal lines. Furthermore, it has been established that vorticellids with regularly arranged rows of pellicular tubercles also possess reticulate silverline systems (Foissner, 1979, 1981; Carey & Warren, 1983; Warren, 1987). The genus *Pseudohaplocaulus* is erected to include *Haplocaulus*-like peritrichs which possess rows of regularly aligned pellicular tubercles and, therefore, reticulate silverline systems. There are two species of

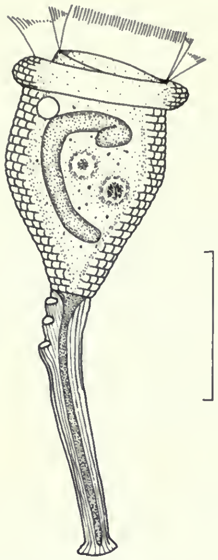

Fig. 34 *Pseudohaplocaulus nicoleae,* after Precht, 1935 (called *Haplocaulus nicoleae).* Bar = 25 µm.

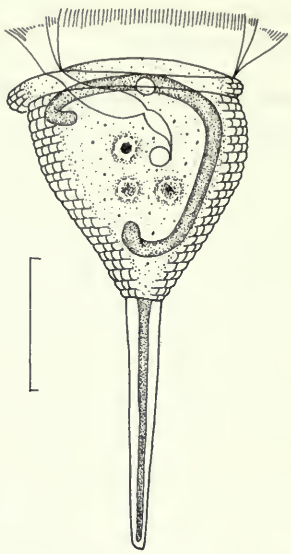

Fig. 35 *Pseudohaplocaulus anabaenae,* after Stiller, 1940 (called *Vorticella anabaenae).* Bar = 25 µm.

Pseudohaplocaulus, both formerly belonging to the genus *Haplocaulus*. *Pseudohaplocaulus nicoleae* (Precht, 1935) n. comb. is the type species.

Diagnosis. Solitary, borne upon an unbranched stalk that is circular in cross-section and contracts in a zigzag manner. Zooid with rows of regularly aligned pellicular tubercles and a reticulate silverline system.

Key to species of *Pseudohaplocaulus*

1 Marine. Zooid with one contractile vacuole . . . . ***P. nicoleae***
– Freshwater. Zooid with two contractile vacuoles . . . . ***P. anabaenae***

Species descriptions

Pseudohaplocaulus nicoleae (Precht, 1935) n. comb.

Haplocaulus nicoleae Precht, 1935

Description (Fig. 34). This the type species is inverted bell-shaped, 35–40 µm long × 25 µm wide. Peristomial lip 30 µm in diameter. Contractile vacuole situated just below the peristome. Macronucleus J-shaped. Stalk × 1– × 2 body length. Sites of previous zooid division may be visible as short lateral extensions of the stalk sheath (see Fig. 34).

Habitat. Marine, originally found as an epizoite of the polychaete, *Nicolea zostericola.*

Pseudohaplocaulus anabaenae (Stiller, 1940) n. comb.

Vorticella anabaenae Stiller, 1940
Haplocaulus anabaenae Stiller, (1940) 1971

Description (Fig. 35). Zooid inverted bell-shaped, 40–45 µm long × 40 µm wide. Peristomial lip 45 µm in diameter. Disc flat. Infundibulum reaches one-third body length. Two contractile vacuoles, one situated near the base of the infundibulum, the other just below the peristome. Macronucleus J-shaped. Stalk × 1– × 2 body length.

Habitat. Freshwater, originally isolated as an epibiont attached to the Cyanobacterium *Anabaena.*

Incertae Sedis

Genus *MONINTRANSTYLUM* Banina, 1977

Monintranstylum is a solitary peritrich the stalk of which contracts in a zigzag rather than helical fashion. The main distinguishing feature of *Monintranstylum* is the spasmoneme which is short and terminates above the base of the stalk, unlike that of *Haplocaulus* and other related genera where the spasmoneme is usually about the same length as the stalk.

Spasmoneme length has long been recognised as a generic character among colonial peritrichs. *Intranstylum* Fauré-Fremiet, 1904, for example, differs from *Carchesium* Ehrenberg, 1830 by the absence of the spasmoneme in the central trunk of the stalk. *Myoschiston* Precht, 1935 may similarly be recognised from *Zoothamnium* Bory, 1826. Among the solitary peritrichs, however, the situation is less clear and several species belonging to genera in which the whole stalk is normally contractile, have short or otherwise incomplete spasmonemes. The spasmoneme of *Vorticella intermissa* Nenninger, 1948, for example, begins a short distance below the scopula and is therefore absent in the uppermost part of the stalk; and in *Haplocaulus claudicans* a small 'fibre' connects the short spasmoneme to the stalk base (see p. 132). Furthermore, the author has frequently observed both solitary and colonial peritrichs in which the spasmoneme appears to have partially degenerated and lost its contractility (unpublished data). Clearly, further research is necessary before spasmoneme length can be accepted as a generic character among solitary peritrichs.

Note. The name *Monintranstylum* was first mentioned in an abstract (Banina, 1976). A full description of *Monintranstylum*, however, did not appear until the following year (Banina, 1977*a*), the date from which the genus should properly be recognised. The first named species of *Monintranstylum* were described in a second article later in the same journal (Banina, 1977b). No type species was designated.

Diagnosis. Zooid borne upon a stalk which contracts in a zigzag manner. Solitary, never colonial, and carried upon an unbranched stalk. Spasmoneme present only in the upper part of the stalk.

Species of *Monintranstylum*

Three species of *Monintranstylum* were described by Banina (1977*b*), *M. rotundus*, an epibiont of *Daphnia longispina; M. stammeri*, an epibiont of *Polyphemus pediculus, Daphnia pulex, Ceriodaphina quadrangulata* and *Cyclops* sp.; and *M. sommeri* on the abdomen of *Eucyclops serrulatus* and the shell of *Cypris* sp. The original descriptions of these species were not available for this revision.

Banina (1982) also transferred *Intranstylum ranae* Stiller, 1953 to the genus *Monintranstylum* on the basis that *I. ranae* is solitary rather than colonial, and that its spasmoneme terminates above the base of the stalk. However, for the reasons given above, *M. ranae* and the three other species of *Monintranstylum* may perhaps more properly belong to the genus *Haplocaulus*.

Monintranstylum ranae (Stiller, 1953) Banina, 1982

Intranstylum ranae Stiller, 1953

Description (Fig. 36). Zooid 65–90 μm long × 35–50 μm wide. Diameter of peristomial lip usually less than the maximum body width. Contractile vacuole situated just below the peristome. Macronucleus variable, usually S-shaped. Pellicle with fine transverse striations. Stalk up to × 3 body length. Stalk base flattened to form a large attachment area, the diameter of which often exceeds that of the body.

Habitat. Freshwater, attached to the tail fins of frog tadpoles.

Genus *TUCOLESCA* (Tucolesco, 1962) Lom in Corliss, 1979

Leptodiscus Tucolesco, 1962.

The main distinguishing features of this genus are (i) the reported absence of a peristomial lip, and (ii) upon contraction, the peristome remains open with the cilia extended while the stalk folds into several (usually three) loose coils. *T. mirabilis* is the type species by monotypy.

The name originally assigned to this genus was *Leptodiscus*, a homonym of the dinoflagellate

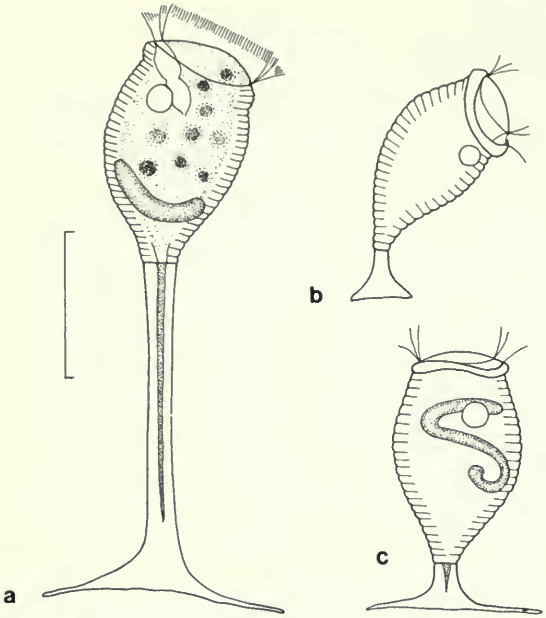

Fig. 36 *Monintranstylum ranae,* (a) typical form; showing variability of (b) zooid, and (c) macronucleus, after Stiller, 1953 (called *Intranstylum ranae)*. Bar = 50 µm.

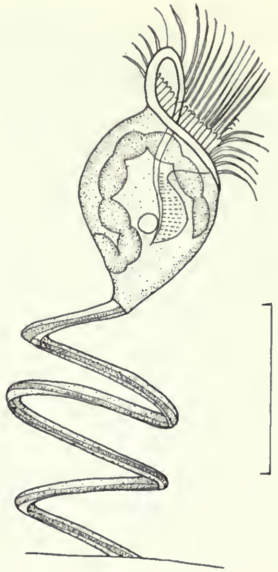

Fig. 37 *Tucolesca mirabilis,* after Tucolesco, 1962 (called *Leptodiscus mirabilis)*. Bar = 25 µm.

Leptodiscus Hartwig, 1877 (Corliss, 1979). The genus was renamed *Tucolesca* by Lom (unpublished—see Corliss, 1979). The taxonomic status of the genus and validity of the name are both considered doubtful.

DIAGNOSIS. Zooid with long, prominent cilia and without a peristomial disc. Upon contraction, peristome remains open with the cilia extended while the stalk is folded into several loose coils.

Species description

Tucolesca mirabilis (Tucolesco, 1962) Lom

Leptodiscus mirabilis Tucolesco, 1962

DESCRIPTION (Fig. 37). Zoöid 27–30 µm long × 19 µm wide. Peristomial lip 20 µm in diameter and obliquely orientated with respect to major body axis. Cilia 16–19 µm long. Infundibulum reaches two-thirds of the body length. Contractile vacuole located near base of infundibulum. Macronucleus S-shaped and moniliform. Stalk up to 80 µm long.

HABITAT. Originally isolated from Lake Tekirghiol, a saline lake in Romania.

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Manuscript accepted for publication 14 July 1987

Index to species

(Names given in roman refer to synonyms)

British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

1986, 129pp. Hardback. 0 565 00982 6 £17.50.

Titles to be published in Volume 54

The cranial muscles and ligaments of macrouroid fishes (Teleostei: Gadiformes); functional, ecological and phylogenetic inferences. By Gordon J. Howes

A review of the Macrochelidae (Acari: Mesostigmata) of the British Isles. By Keith H. Hyatt & Rowan M. Emberson

A revision of *Haplocaulus* Precht, 1935 (Ciliophora: Peritrichida) and its morphological relatives. By Alan Warren

Echinoderms of the Rockall Trough and adjacent areas. 3. Additional records. By R. Harvey, J. D. Gage, D. S. M. Billet, A. M. Clark & G. L. J. Paterson

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Echinoderms of the Rockall Trough and adjacent areas
3. Additional records

R. Harvey, J. D. Gage, D. S. M. Billett, Ailsa M. Clark & G. L. J. Paterson

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Echinoderms of the Rockall Trough and adjacent areas
3. Additional records

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Introduction

This paper is the third part of a study primarily on the distribution of the echinoderm fauna of the Rockall Trough. Part 1 dealt with the crinoids, asteroids and ophiuroids, while Part 2 covered the echinoids and holothurians (Gage *et al.* 1983, 1985*a*). Taxonomic descriptions and discussion of new or problematic species in these collections are given separately in papers cited in the text.

The present paper results from sampling undertaken from RRS *Challenger* by the Scottish Marine Biological Association (SMBA) since the publication of Parts 1 and 2. This has resulted in the recovery of four additional species of crinoids, ten asteroids, seven ophiuroids, one echinoid and eight holothurians. Of these, one asteroid, the goniasterid *Mediaster bairdi*, is a new record for the NE. Atlantic while another, a pterasterid, appears to be undescribed. Seven of the species mentioned in Parts 1 and 2 (one crinoid, one ophiuroid, one asteroid, one echinoid and three holothurians) are identified or re-identified as a result of further research. Additional records of species included in Parts 1 and 2 are given, together with a summary of the zoogeographic and bathymetric distribution with details of any range extension within the Trough provided by the new records. These data have mainly resulted from a greater intensity of sampling effort in the depth range 500–2000 m than in the period 1973 to 1982 covered by the previous papers. The majority of new records are from the Feni Ridge and Hebridean Slope, the latter having been obtained largely from fishing cruises by Dr J. D. M. Gordon of SMBA using a semi-balloon otter trawl (Gordon, 1986).

In addition to records from new stations, an updated total is given for the number of specimens recovered from old stations where sorting of additional subsamples have provided more material. The depth range at the end of the list of stations for each species is the new range within the Rockall Trough area as indicated by our samples.

The format of Part 3 broadly follows that of the two previous papers. Details of the gears employed in the sampling programme may be found in Part 1, while lists of sampling stations worked are distributed among all three parts.

List of Species

Only species additional to those included in Parts 1 and 2 are listed below. An asterisk denotes species included in Parts 1 and 2 under another name.

Class Crinoidea
  Order Millericrinida
    Family Bathycrinidae
      Bathycrinus gracilis Wyville Thomson
      **Democrinus parfaiti* Perrier

Bull. Br. Mus. nat. Hist. (Zool.) **54**(4): 153–198
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- Order Comatulida
  - Family Antedonidae
    - _Trichometra cubensis_ (Pourtales)
    - _Poliometra prolixa_ (Sladen)
  - Family Atelecrinidae
    - _Atelecrinus balanoides_ (P. H. Carpenter)

Class Asteroidea
- Order Paxillosida
  - Family Astropectinidae
    - *_Persephonaster patagiatus_ (Sladen)
- Order Notomyotida
  - Family Benthopectinidae
    - _Cheiraster sepitus_ (Verrill)
- Order Valvatida
  - Family Asterinidae
    - _Anseropoda placenta_ (Pennant)
  - Family Goniasteridae
    - _Ceramaster granularis_ (Retzius)
    - _Mediaster bairdi_ (Verrill)
  - Family Poraniidae
    - _Chondraster grandis_ (Verrill)
    - _Poraniomorpha hispida rosea_ Danielssen & Koren
- Order Spinulosida
  - Family Pterasteridae
    - _Pteraster (Apterodon)_ sp.
    - _Diplopteraster multipes_ (M. Sars)
    - _Hymenaster regalis_ Verrill
- Order Brisingida
  - Family Brisingidae
    - _Novodinia pandina_ Sladen
- Order Forcipulatida
  - Family Asteriidae
    - _Neomorphaster talismani_ E. Perrier

Class Ophiuroidea
- Order Phrynophiurida
  - Family Ophiomyxidae
    - _Ophiomyxa serpentaria_ Lyman
    - _Ophioscolex glacialis_ Müller & Troschel
    - _Ophiophrixus spinosus_ (Storm)
- Order Myophiurida
  - Family Ophiacanthidae
    - Subfamily Ophiacanthinae
      - _Ophiolebes bacata_ Koehler
    - Subfamily Ophiotominae
      - _Ophiotoma coriacea_ Lyman
    - Subfamily Ophioplinthacinae
      - _Ophiomitrella clavigera_ (Ljungman)
  - Family Amphiuridae
    - _Amphiura tritonis_ Hoyle
  - Family Ophiuridae
    - Subfamily Ophiurinae
      - *_Ophiura scomba_ Paterson

Class Echinoidea
- Order Spatangoida
  - Family Spatangidae
    - *_Brissopsis ?lyrifera_ (Forbes)
    - _Brisaster fragilis_ (Düben & Koren)

Class Holothurioidea
Order Dendrochirotida
Family Paracucumidae
Paracucumaria hyndmani (Thompson)
Family Sclerodactylidae
Pseudothyone raphanus (Düben & Koren)
Family Cucumariidae
Thyone fusus (O. F. Müller)
Order Aspidochirotida
Family Synallactidae
Mesothuria intestinalis (Ascanius & Rathke)
Mesothuria verrilli (Théel)
Order Elasipodida
Family Elpidiidae
Ellipinion delagei (Hérouard)
Order Apodida
Family Synaptidae
Leptosynapta decaria (Östergren)
Family Myriotrochidae
*_Myriotrochus clarki_ Gage & Billett
*_Prototrochus zenkevitchi rockallensis_ Gage & Billett
*_Parvotrochus belyaevi_ Gage & Billett
Order Molpadiida
Family Caudinidae
Hedingia albicans (Théel)

Systematic Account

A chart showing the localities of all records covered by the three papers is given in Fig. 1. Classification of the Ophiuroidea follows Fell (1982). Treatment of the other four classes follows Parts 1 & 2 with the following exceptions: Asteriidae Blake (1987), Brisingidae Downey (1986), and Dendrochirotida Panning (1949) as amended by Pawson & Fell (1965). References to works describing species have only been given for those species which are listed here for the first time or where a new work has appeared since the publication of Parts 1 & 2, as in the case of the monograph of the deep North Atlantic Ophiuroidea (Paterson, 1985).

Taxonomic responsibility is shared as follows: Crinoids, A.M.C.; Asteroids, A.M.C. & R.H.; Ophiuroids, G.L.J.P.; Echinoids, J.D.G.; Holothurians, D.S.M.B. & J.D.G.

Class **CRINOIDEA**
Order **MILLERICRINIDA**
Family **BATHYCRINIDAE**

Bathycrinus gracilis Wyville Thomson, 1872

See: A. M. Clark, 1977: 164–167, fig. 1; A. M. Clark, 1980: 206–207, fig. 5.

SAMPLE. ES 27 (1). [*c.* 2900 m]

DISTRIBUTION. Previously known from the West European and Iberian Basins in 4430–5275 m; the northernmost and also the least deep record was from the Porcupine Abyssal Plain, *c.* 50°N, 15°55′W (A. M. Clark, 1977). There is also an unpublished intermediate record in the collections of the Institute of Oceanographic Sciences (IOS), Wormley, from the Porcupine Seabight (Sta. 51109 #2) in *c.* 3985 m depth. The new record, from the southern Rockall Trough, is somewhat shallower and farther north.

REMARKS. The specimen consists of a crown including proximal parts of some arms to the sixth brachial. The total height is *c.* 6 mm. The appearance is similar to that of the specimen shown in Fig. 5 in A. M. Clark (1980), except that the knob-like fused basals and short uppermost columnals

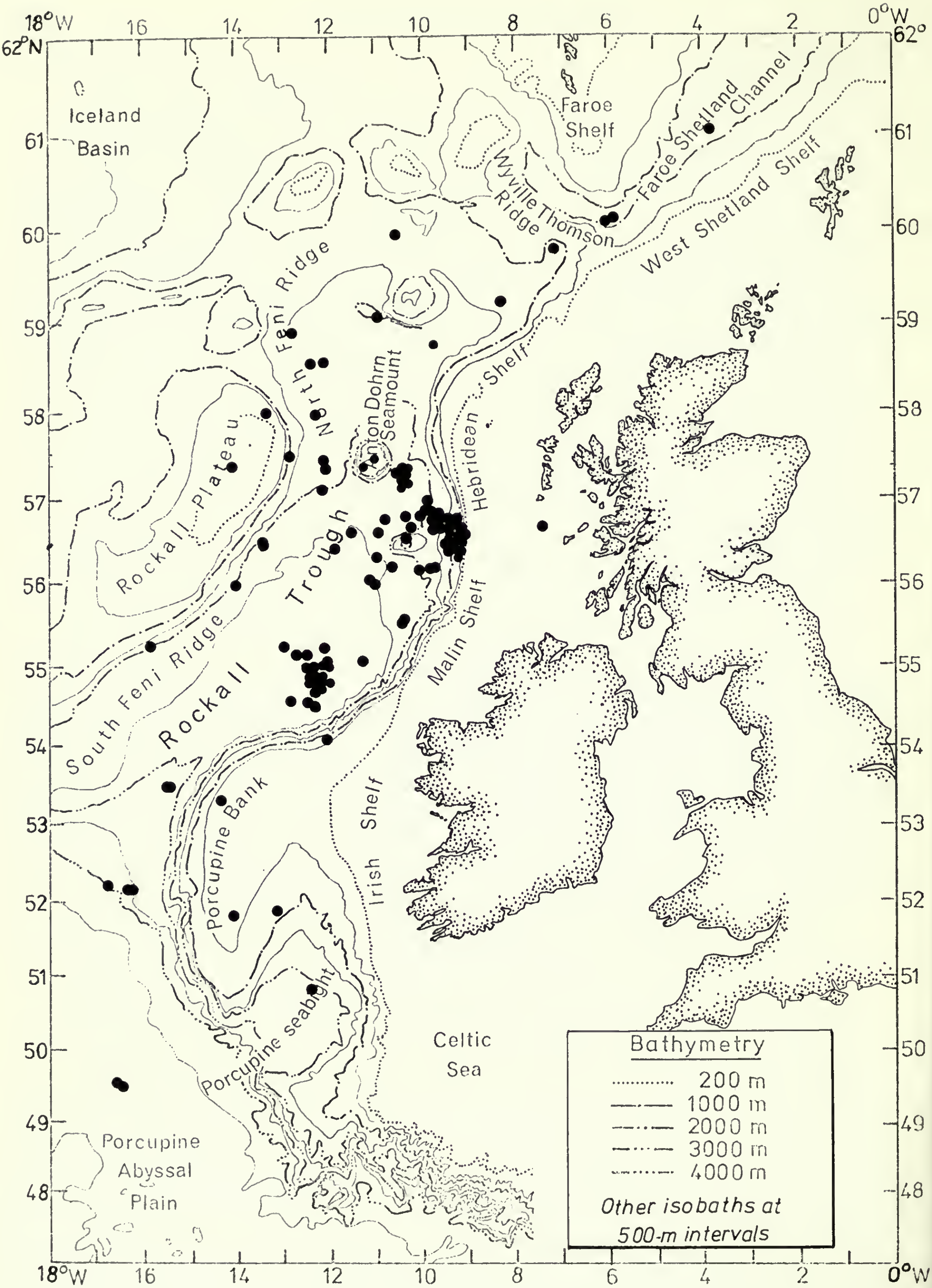

Fig. 1 Bathymetric chart of the area sampled showing location of all stations yielding echinoderms.

are missing. The division series have sharp lateral flanges and a median keel, unlike the medially rounded ossicles of *B. carpenteri* (Danielssen & Koren), known from the deep basin of the Norwegian Sea in 1360–2815 m.

In addition the collections include a very young specimen of *Bathycrinus* from SBC 211 on the Hebridean Slope in the anomalous depth of 402 m. This is at the same stage of development as the small *B. gracilis* figured by A. M. Clark (1977, fig. 1e) from the Porcupine Abyssal Plain, with rudimentary arms and an inverted conical calyx with all the sutures distinct and the basal ring 'integrated' with the radial ring, so that the suture between the two rings forms a zigzag. In larger specimens of *Bathycrinus* the articulation becomes almost a straight line. Only two division series remain attached to the calyx and these are too poorly developed to exhibit the specific characters. It is just possible that the specimen may be a juvenile *Bathycrinus carpenteri* that has been carried over the Wyville Thomson Ridge.

Democrinus parfaiti Perrier, 1883

See: Roux, 1977: 39–40, figs 4, 9, 10, 11, 16, pl. 2, figs 6–8, pl. 5, figs 1–6; A. M. Clark, 1977: 172–177, fig. 3a. Also Gage *et al.*, 1983: 270 (as *Rhizocrinus lofotensis*).

SAMPLES. SBC 66 (? frag.), SBC 67(2), SBC 216(1), AT 230(15), SBC 280 (1) [also ES 18(3), ES 20(8) in Part 1 as *Rhizocrinus lofotensis*]. [*c.* 1000–2200 m]

DISTRIBUTION. The most northerly record hitherto is from SW. Ireland at *c.* 50°N. The discovery of these specimens since the completion of Part 1 suggests that the species represented in the Rockall Trough is not *Rhizocrinus lofotensis*, as thought by A.M.C. in 1983, but *Democrinus parfaiti*. The depths of more than 1000 m are also indicative of this species which ranges from 870–2500 m (and possibly 2959 m) off Western Europe and NW. Africa to the Azores. The specimen from Sta. 10 of the *Ingolf*, off SW. Iceland, that was figured by A.M.C. (1970, fig. 4e) as *Rhizocrinus lofotensis*, is likely to be referable to *Democrinus parfaiti* on the basis of the Rockall Trough records, thus extending the range even further. Records from *Knight Errant, Lightning* and *Porcupine* are also likely to be *D. parfaiti*. However the fragment described by Doderlein (1912) from the Wyville Thomson Ridge in 547 m under the name of *R. rawsoni* may well have been *R. lofotensis*, the latter species occupying relatively shallow depths of 140–700 m in the southern part of the Norwegian Basin. It has however been recorded from down to 3475 m off Greenland. An unpublished recent IOS record of *D. parfaiti* in the Porcupine Seabight (Sta. 10111 ♯8) in *c.* 1630 m helps to confirm the *Helga* record of A. H. Clark (1913), that specimen now being in a badly decalcified condition. The distinction between *D. parfaiti* and *Rhinzocrinus lofotensis* is discussed in Clark (1970: 21).

REMARKS. The calyx of the largest of the present specimens, from SBC 67, is only 2.5 mm high, the same size as the smallest one given in the table of measurements of *D. parfaiti* in A. M. Clark (1977). Study of the material indicates that the supposition made in 1977 that the calyx is consistently narrow, even in young specimens of this species, was incorrect. Judging from the smaller specimens from the Rockall Trough, the initial shape is inverted conical as in the other species of the genus for which ontogenic series have been observed.

Order **COMATULIDA**
Family **ANTEDONIDAE**

Trichometra cubensis (Pourtales, 1869)

See: A.M. Clark, 1970: 46–48; 1980: 195–197.

SAMPLES. AT 219(1), AT248(41), AT249(1), ES 250(3). [1150–1991 m]

DISTRIBUTION. North Atlantic from the Gulf of Mexico to the Davis Strait and from Morocco to Portugal and NW. Spain; 210–2380 m (?2432 m). Also recorded from SW. of Iceland in 311 m. The present records from W. of the Anton Dohrn Seamount and from the North Feni Ridge represent an extension of range in the deeper NE. Atlantic. It is possible that the smaller specimens recorded from *Helga* stations in the Bay of Biscay and W. of Ireland under the name *T. delicata* A. H. Clark, 1911, will also prove to be conspecific with *T. cubensis*.

REMARKS. The colour in life (AT 248) was brownish except for the very flared arm joints which were white.

Poliometra prolixa (Sladen, 1881)

See: A. M. Clark, 1970: 42–45, figs 15, 16.

SAMPLES. ES 87(1), AT 226(11). [*c*. 1050–1118 m]

DISTRIBUTION. Known only from the Arctic and Norwegian Sea, from Greenland to the seas off western Siberia. The present records from the Faeroe Bank Channel and Faeroe-Shetland Channel represent the southernmost limit of the range. The bathymetric range is 20–1960 m, but all of the more southern records exceed 500 m.

Family **ATELECRINIDAE**

Atelecrinus balanoides P. H. Carpenter, 1881

See: A. H. Clark, 1913: 45 (as *A. helgae*; A. M. Clark, 1970: 49–51, fig. 19 (as *A. balanoides*).

SAMPLES. AT 223(1), AT 230(2), AT 248(3), AT 249(1), ES 250(1). 13/83/6 OTSB(1), 3/85/20 OTSB(2). [980–1005 m to 1270 m]

DISTRIBUTION. Known in the western tropical Atlantic from Florida to NW. Brazil, and in the NE. Atlantic from the southern Rockall Trough (*Helga*) *c*. 54°N, 12°30′W and south west of the Faeroes (*Thor*). The present records are intermediate in position between these last two. The recorded bathymetric range is 532–1256 m.

REMARKS. The very long straight delicate and easily lost cirri of this species contrast with the relatively short, curly ones of *Trichometra cubensis* which was often collected in the same haul, both in the Rockall Trough and in the western tropical Atlantic where both species extend. They are also distinguished by their habitats, *T. cubensis* being epizoic on other organisms such as the gorgonian *Acanella*, while *A. balanoides* is self-supporting on muddy substrates with its widely spread cirri. The colour in life (AT 249) was a yellowish-buff.

Class **ASTEROIDEA**
Order **PAXILLOSIDA**
Family **LUIDIIDAE**

Luidia ciliaris (Philippi, 1837)

SAMPLES. AT 291(2), AT 292(4). 13/83/3 GT(11), 13/83/4 GT(7), 13/83/7 OTSB(6), 13/83/8 OTSB(23), 3/85/14 OTSB(10), 3/85/38 OTSB(1), 3/85/43 OTSB(9), 3/85/44 OTSB(1). [220–270 m to 650–805 m]

DISTRIBUTION. The new shallower records from the Hebridean Slope are more typical of the distribution of this common bathyal species than the single record from 650–805 m given in Part 1.

Family **ASTROPECTINIDAE**

Astropecten irregularis (Pennant, 1777)

SAMPLES. RD 258(1), 13/83/7 OTSB(5). [135 m to 650–805 m]

DISTRIBUTION. The new shallow records from Rockall Bank and the Hebridean Slope are not unexpected given the sublittoral and bathyal distribution of this species.

Bathybiaster vexillifer (Thomson, 1873)

SAMPLES. ES 34(?[juveniles] 4), ES 197(2), ES 200(3,?[juvenile] 1, AT 201(17), AT 218(1), AT 219(15), AT 228(1), ES 232(2), AT 233(14), ES 244(1), AT 245(8), AT 247(juveniles 2), AT 248(1), AT 267(juveniles 2), AT 271(10), AT 273(2), AT 288(22), 13/83/5 OTSB(1), 3/85/7 OTSB(3), 3/85/17 OTSB(16). [992–2600 m]

DISTRIBUTION. The record from AT 267 provides a slight increase in the lower bathymetric range within the Rockall Trough.

Plutonaster bifrons (Thomson, 1873)

SAMPLES. ES 184(2, ?[juvenile] 1), ES 190(?[juveniles] 2), AT 201(11), ES 202(5), ES 218(1;?[juvenile] 1), AT 219(18), AT 221(1), AT 223(15), AT 228 (?[juveniles] 3), AT 229(1, juvenile 1), AT 230(103, ?[juvenile] 1), ES 232(2), AT 233(1), AT 239(5), ES 244(2), AT 245(4), AT 247(5), AT 249(4), ES 250(6), AT 251(7), ES 252(juvenile 1), AT 254(2), ES 255(juvenile 1), AT 256(23), ES 264(juveniles 6), AT 267(7), AT 271(3), AT 273(1), ES 285(?[juvenile] 1), AT 286(juvenile 1), AT 287(?[juvenile] 1), AT 288(8), ES 289(1), 13/83/1 OTSB(?[juvenile] 1), 13/83/2 OTSB(38), 13/83/5 OTSB(71), 13/83/6 OTSB(13), 13/83/7 OTSB(1), 9/84/9 OTSB(22), 9/84/10 OTSB(1), 9/84/13 OTSB(12), 3/85/9 OTSB(1), 3/85/17 OTSB(77), 3/85/18 MBA(11), 3/85/19 MBA(1), 3/85/20 OTSB(10), 3/85/25 OTSB(2), 3/85/29 OTSB(10), 3/85/30 OTSB(55). [580–630 m to 2965 m]

DISTRIBUTION. The new records from the Hebridean Slope give an upward extension of bathymetric range by *c.* 400 m.

Psilaster andromeda (Müller & Troschel, 1842)

SAMPLES. ES 23(3), AT 223(12), AT 230(juvenile 1), AT 239(8), AT 291(20), GT 2(1), GT 7(1), GT 11(5), GT 14(2), GT 15(1), GT 16(4), AT 1(3), 13/83/6 OTSB(15), 13/83/7 OTSB(16), 9/84/1 OTSB(2), 9/84/13 OTSB(4), 3/85/9 OTSB(8), 3/85/10 OTSB(2), 3/85/13 OTSB(111), 3/85/14 OTSB(5), 3/85/18 MBA(27), 3/85/19 MBA(2), 3/85/25 OTSB(2), 3/85/28 OTSB(1). [640–780 m to 990–1075 m]

DISTRIBUTION. Further studies on this and the related *Persephonaster patagiatus* (formerly *Psilaster*) (see remarks below and under that species) have shown that in the Rockall Trough on the Hebridean Slope *Psilaster andromeda* has a more restricted distribution than hitherto recorded, being common in the 700–1000 m zone.

REMARKS. Following additional studies of the Astropectinidae by A.M.C., the distinction of *Psilaster andromeda* and *Persephonaster patagiatus* by the relative breadth of the superomarginal plates in dorsal view as shown by Mortensen (1927) was found to be fallacious. This character is variable in both species. A better distinction is the more convex contours of individual marginals in dorsal view in *Persephonaster patagiatus* compared with the flat surface but sharply-cut intermarginal fascioles visible in *Psilaster andromeda*, when specimens are denuded with bleach. In section, the marginals of *Psilaster andromeda* tend to form continuously rounded arcs. In *Persephonaster patagiatus* however, the superomarginals in particular are more abruptly bent, making the sides of the arms flatter. Other differences are the more attenuated arms of *P. patagiatus* with somewhat longer and fewer marginal plates, usually 25–30 at R 60–90 mm as opposed to 35+ in *P. andromeda* at this size. The armament of the marginals is also different, the inferomarginal spines being more needle-like in *P. patagiatus*, and the armament at the apex of the jaw projecting horizontally below the mouth is very different. In *Persephonaster patagiatus* there is a pair of inset fascicles of blunt spines partly concealed above the apical spines, which are rounded in section, whereas in *P. andromeda* there is only a line of 3 or 4, very flat spade-like apical spines. Indeed this last character coupled with the absence of well-defined intermarginal fascioles in *P. patagiatus* justifies generic isolation of the species in the genus *Persephonaster*, which has previously been confused to some extent with *Psilaster* but can now be distinguished by these characters. The nomenclature is therefore restored to the combinations used by Mortensen (1927).

Use of the above characters has resulted in the re-identification of some of the samples recorded in Part 1.

Persephonaster patagiatus (Sladen, 1889)

SAMPLES. ES 15(2), ES 18(3), AT 68A(1), AT 107A(5), AT 186(3), AT 192(30,?[juveniles] 5), AT 221(4,?[juvenile] 1), AT 229(63), AT 254(1), AT 256(37), AT 287(27,?[juvenile] 1), SWT 18(8), SWT 27(4?), 13/83/1 OTSB(274), 13/83/2 OTSB(10), 13/83/5 OTSB(15), 9/84/9 OTSB(3), 3/85/20 OTSB(?[juvenile] 1), 3/85/29 OTSB(13), 3/85/30 OTSB(66). [1265–1130 m to 1809 m (?2965 m)]

DISTRIBUTION. This species is widely distributed in the N. Atlantic (but see notes in Part 1. for possible complications). On the Hebridean Slope it occurs slightly deeper than *Psilaster andromeda*.

Curiously there are no samples in which both species occurred. Following the reassignment of this species to the genus *Persephonaster*, as explained above, further clarification of the depth limits of the two species was sought by recourse to the collections from the Porcupine Seabight held at IOS, Wormley. These were found to include 21 samples of *Psilaster andromeda* identified by D.S.M.B. with positive depths ranging from 700 to 1490 m, compared with 11 samples of *Persephonaster patagiatus* from 1360–2000 m. The deepest sample of *P. andromeda* also included seven specimens of *P. patagiatus*. The SMBA record from SWT 27 (a fishing station) in 2965 m therefore seems doubtful, and may be a contaminant from an earlier haul.

Family **PORCELLANASTERIDAE**

Porcellanaster ceruleus Wyville Thomson, 1877

Samples. ES 4(5, juveniles 2), ES 10(101, juveniles 7), ES 27(99), ES 57(1, juveniles 7), ES 111(75), ES 118(43), ES 129(75), ES 152(61 juvenile 1), SBC 174(juveniles 2), ES 184(5), ES 185(330), ES 190(165), ES 197(2, juveniles 3), ES 204(90), ES 207(344), ES 218(3), ES 231(201), ES 266(7), AT 267(37), AT 282(4), ES 283(317), AT 284(6), ES 285(21), AT 286(3). [1993 m to 3425–3500 m]

Distribution. No change.

Order **NOTOMYOTIDA**

Family **BENTHOPECTINIDAE**

Benthopecten simplex Perrier, 1881

Samples. ES 105(?[juvenile] 1), ES 184(17, ?[juvenile] 1), ES 197(37), ES 200(11, ?[juveniles] 8), AT 201(61), ES 202(3,?[juveniles] 8), AT 218(44), AT 219(103), AT 228(132), ES 232(12), AT 233(95), ES 244(12), AT 245(70), AT 247(4), ES 255(juvenile 1), AT 256(41), ES 257(1), ES 264(9), AT 271(82), AT 273(60), AT 288(102), ES 289(32), 13/83/5 OTSB(75), 13/83/6 OTSB(4), 9/84/9 OTSB(3), 3/85/7 OTSB(2), 3/85/17 OTSB(239), 3/85/29 OTSB(13). [1595 m to 3425–3500 m]

Distribution. The new records raise the upper bathymetric limit in the Rockall Trough from 1785–1845 m to 1595 m.

Pectinaster filholi Perrier, 1885

Samples. ES 34(8), ES 197(juveniles 20), AT 201(1), AT 219(4), AT 233(3), AT 267(3), AT 288(4), 3/85/7 OTSB(34). [1752–2909 m]

Distribution. No change.

Cheiraster sepitus (Verrill, 1885)

See: Sladen, 1889: 52–55, pl. 8, figs 5 & 6, pl. 12, figs 5 & 6 (as *Pontaster venustus*); A. M. Clark, 1981: 117–118, figs 4i–r & 5c.

Samples. AT 229(7), AT287(9), 13/83/1 OTSB(45), 3/85/29 OTSB(4), 3/85/30 OTSB(23), 3/85/45 OTSB(2). [1383 m to 1690–1740 m]

Distribution. Nova Scotia south to the Caribbean, Azores and Bay of Biscay south to Cape Verde; 485–3703 m, but mainly 1000–2000 m. The present records from the Hebridean Slope extend the known distribution in the NE. Atlantic to *c*. 56° 30′N. confirming the prediction of Mortensen (1927) that *Pontaster venustus* Sladen, a synonym of *Cheiraster sepitus* according to A. M. Clark (1981), would probably be found in British waters.

Remarks. The 45 specimens measured from Sta. 13/83/1 OTSB range from R 45 mm to R 22 mm, R/r 4.8/1 to 3.0/1 (mean 3.7/1). Arm length varied within individuals and several specimens had regenerating arm tips. There was little tendency for the arm tips to curl dorsally in preserved specimens unlike those of *Pontaster tenuispinus*. The specimens are of a robust appearance due to the encroachment of the superomarginal plates on to the abactinal surface of the arms, and the tumidity of the inferomarginals. Sladen (1889) states that no pedicellariae of any kind are to be found in *Cheiraster*, whereas A. M. Clark (1981) found some to be present but only rarely. At least 8 of the Rockall specimens have small pectinate pedicellariae on the actinal interradii formed by the opposition of short spines on the plates. Their occurrence varies between interradii but where present they are distinctive.

Pontaster tenuispinus (Düben & Koren, 1846)

Samples. AT 226(1), AT 239(2), AT 271(2), AT 273(2), AT 291(22), 13/83/2 OTSB(1), 13/83/7 OTSB(159), 13/83/8 OTSB(6), 9/84/1 OTSB(9), 9/84/2 OTSB(1), 9/84/10 OTSB(1), 3/85/10 OTSB(174), 3/85/11 OTSB(2), 3/85/14 OTSB(1), 3/85/43 OTSB(1), 3/85/44 OTSB(2). [500–560 m to 2255 m]

Distribution. The record from AT 271 extends the lower bathymetric limit to 2255 m.

Order **VALVATIDA**

Family **ODONTASTERIDAE**

Hoplaster spinosus Perrier, 1882

Samples. ES 266(1), AT 267(1). [2300–2910 m]

Distribution. The new records from the Feni Ridge are intermediate in depth between those of the two specimens recorded in Part 1. R was 12 mm in the specimen from ES 266.

Family **RADIASTERIDAE**

Radiaster tizardi (Sladen, 1882)

Samples. AT 223(22), 13/83/2 OTSB(2), 3/85/20 OTSB(1). [1075 m to 1130–1265 m]

Distribution. The new records confirm the occurrence of this species in the Rockall Trough, the record in Part 1 being from a single juvenile. They are all within the previously known bathymetric range.

Remarks. The specimens from AT 223 and 3/85/20 OTSB have R 60–110 mm.

Family **ASTERINIDAE**

Anseropoda placenta (Pennant, 1777)

See: Mortensen, 1927: 99–101, fig. 57.

Samples. 13/83/3 GT(14), 13/83/4 GT(4), 13/83/8 OTSB(4). [220–270 m to 500–560 m]

Distribution. Known from the Shetlands to the Mediterranean around both the west and east coasts of Britain in 10–200 m, but previously down to 600 m only in the eastern Mediterranean. The present records from the Hebridean Shelf and Slope provide an extension of bathymetric range in northern waters.

Remarks. This species is thought to prefer sandy ground, which may explain its failure to penetrate far beyond the shelf edge.

Family **GONIASTERIDAE**

Ceramaster granularis (Retzius, 1783)

See: Mortensen, 1927: 81–82, fig. 44.

Samples. AT 229(1), AT 248(1), AT 259(1), AT 273(1), AT 287(1). [1150–2185 m]

Distribution. Widely distributed on both sides of the North Atlantic. Previously recorded from British waters from the Faeroe Channel, Lousy Bank, and on the Irish slope; 20–1400 m. The present records from the Feni Ridge and Hebridean Slope extend the lower bathymetric limit by nearly 800 m. Some of the specimens appear to intergrade morphologically with the more southern species *C. grenadensis* (recorded as *C. balteatus* by Mortensen, 1927).

Pseudarchaster parelii (Düben & Koren, 1846)

Samples. AT 201(1), ES 202(juvenile 1), AT 223(1), AT 229(1), AT 230(2), AT 248(3), AT 251(juvenile 1;?3), AT 259(1), AT 267(?4), AT 287(?4), AT 288(4), AT 291(1), 13/83/8 OTSB(3), 3/85/10 OTSB(?1), 3/85/14 OTSB(7), 3/85/20 OTSB(2), 3/85/29 OTSB(1), 3/85/30 OTSB(4), 3/85/43 OTSB(2), 3/85/44 OTSB(2). [225–2965 m]

Distribution. No change.

Remarks. The distinction between *P. parelii* and *P. gracilis* is not clear in the Rockall samples. Halpern (1972) has separated the species on the basis of the armament of the actinal and inferomarginal plates, those of *P. gracilis* bearing cylindrical spines 3 to 5 times longer than wide, while in *P. parelii* the spines, if any, are short and flattened. Some of the specimens identified as *P. parelii* from the Rockall area have a few longer cylindrical spines. Mortensen (1927) states that *P. parelii* grows to nearly 200 mm R, and Farran (1913) recovered specimens from the west of Ireland reaching R 192 mm, the majority of the Irish specimens measured being >80 mm R. None of the Rockall specimens with $R > 60$ mm appear to be *P. parelii*, having very thorny actinal plates and a conspicuous pectinate pedicellaria-like arrangement of subambulacral spines said to be characteristic of *P. gracilis* (Halpern, 1972). It is possible therefore that the '*P. parelii*' specimens from the Rockall area are merely the young of '*P. gracilis*'. Until more work can be done on the distinction of these two nominal species, the Rockall records of *P. parelii* refer to the small specimens with few spines on the actinal plates and less obvious 'pectinate pedicellariae'.

Pseudarchaster gracilis (Sladen, 1889)

Samples. AT 219(1), AT 223(3), AT 229(2), AT 233(1,?[juvenile] 1), AT 254(?1), AT 287(1, ?1), AT 288(2), ES 289(1), 13/83/1 OTSB(6), 13/83/2 OTSB(1), 13/83/5 OTSB(21), 13/83/6 OTSB(5), 13/83/7 OTSB(7), 13/83/8 OTSB(1), 9/84/9 OTSB(1), 9/84/13 OTSB(1), 3/85/7 OTSB(5), 3/85/8 OTSB(1), 3/85/17 OTSB(14), 3/85/29 OTSB(1), 3/85/30 OTSB(2), 3/85/36 OTSB(1). [?500–560 m to 2190 m]

Distribution. The new records extend the known distribution northwards to just south of the Wyville Thomson Ridge and the North Feni Ridge *c.* 59° 40′N (but see remarks under *P. parelii* and below).

Remarks. The above records relate to the larger specimens of *Pseudarchaster* with more thorny actinal plates and prominent 'pectinate pedicellariae' along the subambulacrals. The colour in life was a bright brick red. The largest specimen measured R 165 mm.

Paragonaster subtilis (Perrier, 1881)

Samples. ES 204(2), AT 267(18), AT 282(1), ES 283(1), AT 284(3), ES 285(juvenile 1), AT 286(18), 51301 OTSB(6), 3/85/5 OTSB(4), 3/85/7 OTSB(2). [1785–1845 m to 2970–2980 m]

Distribution. The new records slightly extend the maximum recorded depth for this species in the Rockall Trough.

Plinthaster dentatus (Perrier, 1884)

Samples. ES 129(?[juvenile] 1), AT 223(1), AT 287(17), 13/83/1 OTSB(37), 13/83/5 OTSB(1), 3/85/17 OTSB(8), 3/85/29 OTSB(1), 3/85/30 OTSB(30), 3/85/37 OTSB(1), 3/85/45 OTSB(4). [945–985 m to 2910 m]

Distribution. The new records raised the upper bathymetric limit on the Hebridean Slope by almost 400 m.

Mediaster bairdi (Verrill, 1882)

See: Gray, Downey & Cerame-Vivas, 1968: 150–151, fig. 24.

Samples. AT 229(14), ES 252(5), AT 287(49), 13/83/1 OTSB(22), 3/85/30 OTSB(72), 3/85/45 OTSB(2). [1383–1587 m]

Distribution. Previously known only in the W. Atlantic from Newfoundland to New Jersey, in the lesser Antilles and off Guyana; 642–1446 m. The Rockall records from the Hebridean Slope and North Feni Ridge are the first from the NE. Atlantic. Downey (pers. comm.) has found very little difference between N. American *M. bairdi* and *M. capensis* from S. Africa, and believes that any taxonomic distinction between them is infraspecific.

Remarks. The specimens from AT 287 ranged from R 53 mm to R 21 mm, R/r = 2.4–3.1/1. Gray *et al.* (1968) state that the specimen in their figure 24 has R/r 3.3/1, but measurements from this figure suggest a ratio nearer 2.5/1. The specimens from AT 287 were a pale orange-ochre when collected fading to off-white in spirit.

Family **PORANIIDAE**

Porania pulvillus (O. F. Müller, 1766)

Samples. ES 113(1, juveniles 2), AT 292(8), 13/83/3 GT(69), 13/83/4 GT(43), 13/83/8 OTSB(52), 3/85/38 OTSB(4), 3/85/43 OTSB(3). [148 m to 565–700 m]

Distribution. The new records are all from the Hebridean Slope and suggest that this species is more common below 300 m than was thought previously, four of the above samples having come from >400 m.

Poraniomorpha hispida rosea Danielssen & Koren, 1881

See: Mortensen, 1927: 92–93, fig. 53; A. M. Clark, 1984: 34, fig. 11 B, C.

Samples. ES 112(?[juvenile] 1), AT 230(1), AT 287(1). [1210–1383(?1900)m]

Distribution. This subspecies was previously recorded from just south of the Wyville Thomson Ridge under the name *Lasiaster villosus* Sladen, 1889 (*Porcupine* Sta. 47A, 990 m). The synonymy of *Poraniomorpha hispida* and *P. rosea* is complicated but *rosea* has usually been treated as a stellate variety of the more nearly pentagonal *P. hispida*. However, in 1984 A.M.C. distinguished it subspecifically on account of the isolation of *rosea* for much of its range, both geographically and bathymetrically. Whereas *P. hispida hispida* is found all round the coast of Norway extending north to the southern Barents Sea, with positive depths of 100–350 m, *P. hispida rosea* seems to be essentially an upper bathyal taxon extending south from the Norwegian Basin along the Norwegian Trench to the Skaggerak in the east and down the Rockall Trough to the Bay of Biscay further west in 290 m to *c.* 1400 m. If the small specimen (R only 3·2 mm) from ES 112 is a young *P. hispida rosea*, as its already stellate form suggests, than the depth range extends further to 1900 m.

Chondraster grandis (Verrill, 1878)

See: A. M. Clark, 1984: 27, figs 4A, B, 5A, 6, 7d.

Samples. AT 229 (1), AT 247(2), 3/85/9 OTSB(1). [945–1010 m to 2084 m]

Distribution. This species was recorded from the NE. Atlantic for the first time by A. M. Clark (1984) on the basis not only of the two deeper SMBA samples but also of six others ranging from the Lousy Bank south to the southern Bay of Biscay (BIOGAS), including *Helga* and more recent IOS material from the Porcupine Seabight. The small holotype of *Marginaster fimbriatus* Sladen, 1889 from *Porcupine* Sta. 31 (*c.* 56°N 11′W) in 2487 m is almost certainly conspecific with *C. grandis*, though this depth exceeds by *c.* 300 m the positive maximum from AT 247. The type locality of *C. grandis* is in the vicinity of Cape Cod in *c.* 400 m but other records from N. America extend down to 1640 m, while E. Atlantic records range from 840 to 2070 (?2487)m.

Remarks. The colour in life of the specimens from AT 247 was light red midradially on the dorsal surface paling laterally to cream below. The specimen collected from 3/85/9 OTSB retained vermilion red colour in formalin on the upper side and around the ventral margin, the rest of the lower side being off-white. Distinct areas of white papulae were present along each arm of the latter specimen, with a central narrow naked zone and naked interradii. The madreporite was off-white in colour.

Order **SPINULOSIDA**

Family **PTERASTERIDAE**

Pteraster militaris (O. F. Müller, 1776)

Samples. 13/83/6 OTSB(1), 3/85/13 OTSB(1), 3/85/28 OTSB(1). [934–1054 m to 990–1075 m]

Distribution. The new records bring the total number of specimens recorded from the Rockall Trough to only 6, all from the Hebridean Slope at around 1000 m.

Pteraster pulvillus M. Sars, 1861

Samples. AT 230(1), 13/83/3 GT(1), 3/85/14 OTSB(1). [168–1210 m]

Distribution. The new records, all from the Hebridean Slope, supplement the two previous records to provide a more continuous bathymetric distribution.

Pteraster reductus Koehler, 1907

Sample. AT 251(1). [1530–1900 m]

Distribution. Only two other specimens of this species have been recorded from the NE. Atlantic, both from the Feni Ridge. The new record is almost 400 m shallower than the record in Part 1.

Pteraster (Apterodon) sp. aff. ***P. acicula*** (Downey, 1970)

See: Downey, 1973: 79, pl. 34 C, D (for *P. acicula*). Also Gage *et al.*, 1983: 282 (For *P.* sp. aff. *P. acicula*).

Sample. 3/85/13 OTSB(2). [958–995 m]

Distribution. The new specimens were recovered from almost the identical position and depth on the Hebridean Slope from which a specimen subsequently confirmed as *P. acicula* (M. Downey, pers. comm.) was recorded (see Part 1). These are the only records for the NE Atlantic, the type locality being in the Gulf of Mexico.

Remarks. The specimens are plump and pentagonal, both with R 16 mm, r10 mm and in good condition with blunt arms curling dorsally at the tips. There is no webbing at all between the oral spines, an absence characteristic of the subgenus *Apterodon*. There are six spines on each oral plate, the apical spine being the largest and at least twice as long and thick as the distalmost spine. The single stout suboral spine is longer and slightly broader than the apical oral spine, glassy throughout its length and distincitively tricarinate, ending in an acute point. The grooves on the sides of these spines which give rise to their tricarinate form commence at about one third of the length from the spine base. The paxillae of the dorsal surface consist of a peripheral ring of *c.* 10 spinelets each around 0·06 mm thick with an imperforate portion immediately above the base which becomes regularly trabeculate distally without becoming broader, as in many echinoid spines. This structure continues to the spine tip. Within this ring are > 15 spinelets with more slender rod-like bases only 0·02 mm thick which become spatulate and trabeculate in their distal half and 0·14 mm in width. The tips of both types of spinelet protrude through the dorsal membrane, those of the spatulate type having trifid tips. This feature, combined with the large number of spinelets, gives the dorsal surface a dense prickly appearance with only small inter-paxillar spaces. As this description is slightly at variance with that for *P. acicula* (Downey, 1973), some doubt remains as to the specific identity of these new specimens.

Pteraster (Apterodon) sp.

See: Downey, 1973: 77, pl. 33, figs A, B (for *P. caribbaeus*).

Samples. AT 247(2), ES 264(10). [2084–2144 m]

DISTRIBUTION. North Feni Ridge at the foot of Rosemary Bank and at the foot of Rockall Bank.

REMARKS. This species is distinguished from *P. acicula* by having more attenuated arms and a distinctly hispid appearance as collected due to the protrusion through the dorsal membrane of the paxillar spinelets which end in a single point. There are *c.* 18–24 spinelets on each paxilla, all of uniform thickness for most of their length. The interpaxillar spaces are relatively large and the membrane is almost transparent. The unwebbed oral spines decrease evenly in size from the apical to the most distal sixth or occasionally seventh spine. Each oral plate bears one or sometimes two suboral spines which are larger than the apical oral spine and have a hyaline tip where the outer opaque sheath has worn away. They are trabeculate for most of their length with the exception of the slightly tricarinate distal portion. This species is superficially similar to *P. caribbaeus* Perrier, 1881, but the paxillae have almost twice as many spinelets and there are other small differences between the spines on the jaw plates and the musculature of the dorsal membrane. Seven of the specimens are in good condition.

The records of this species and *P.* sp. aff. *P. acicula* suggest that there may be some separation on the basis of habitat, given the differences in depth and geographic distribution within the Trough.

Diplopteraster multipes (M. Sars, 1865)

See: Fisher, 1911: 371, pl. 107, figs 1, 2.

SAMPLES. 3/85/20 OTSB(1), 3/85/34 OTSB(1), 3/85/36 OTSB(1). [980–990 m to 1225–1245 m]

DISTRIBUTION. This species is circumarctic extending south in the NE. Atlantic along the Norwegian coast to the Skagerrak, in the NW. Atlantic to the latitude of Chesapeake Bay, and in the Pacific to California in the east and Japan in the west. These are the first records from the Rockall Trough and they also provide an extension of the previous known bathymetric range of 91–1170 m. A further sample has been taken by IOS in the Porcupine Seabight (Sta. 50602 ♯4) in 1080–1120 m. The specimen from 3/85/34 OTSB has six arms.

REMARKS. This is the largest pterasterid occurring in British waters, R max can reach *c.* 110 mm. In life the colour is pale mauve dotted with white dorsally continuing to the ventral interradii. The wide ambulacra are emphasised by red colouration along the subambulacral plates.

Hymenaster membranaceus Wyville Thomson, 1887

SAMPLES. ES 184(82), ES 185(?[juveniles] 5), ES 197(37, ?[juveniles] 4), AT 201(324), ES 202(12), ES 218(9), AT 219(277), ES 232(15), AT 233(324), ES 244(15), AT 245(421), AT 271(104), AT 273(? 1), AT 287(1), AT 288(367), ES 289(25), 3/85/5 OTSB(juvenile 1). [1383–2909 m]

DISTRIBUTION. The record from AT 287 on the Hebridean Slope raises the upper bathymetric limit within the Trough by some 600 m, although this is still within the known distribution of this species (1000–3000 m).

Hymenaster regalis Verrill, 1895

See: Verrill, 1895: 203–204; H. L. Clark, 1941: 64.

SAMPLE. AT 195(1) [in Part 1 as *H. ?gennaeus*], AT 288(1). [2190 m]

DISTRIBUTION. *Hymenaster regalis* is a rare species known only from the holotype taken in the NW. Atlantic off N. Carolina at 36°34′N, 73°48′W; 2521 m, and from another single specimen taken off Cuba in 1847 m.

REMARKS. The specimen from AT 195 measures 75 mm R, 40 mm r, while that from AT 288 measures *c.* 75 mm R, *c.* 55 mm r, the measurements being approximate due to the arched dorsal surface and recurved arm tips. Both of the previously known specimens were of a similar size. The dorsal surface is firm and opaque with distinct muscle fibres between the paxillae which consist of only a single stout spine raising the dorsal membrane into firm peaks. The membrane is perforated by small spiraculae numbering > 50 in the space within a ring of paxillae. In the life the specimen from AT 288 was a pale red dorsally.

These are the first records of this species from the eastern Atlantic, and also represent a considerable extension of range northwards.

Hymenaster gennaeus H. L. Clark, 1923

SAMPLE. AT 233(1). [2180–2910 m]

Family **SOLASTERIDAE**

Crossaster squamatus (Döderlein, 1900)

SAMPLE. AT 287(3). [1050–1383 m)

DISTRIBUTION. Previously unknown south of the Faeroe Channel, this new record extends the range south to the Hebridean Slope at *c.* 56°N.

Family **ECHINASTERIDAE**

Henricia Gray

Madsen is currently revising this genus (pers. comm.). The synonymy is complex and rather than confuse the literature further by publishing new records at this stage, it is felt that this should await the revision. Two species with slightly different depth distributions appear to be represented (see Gage *et al.*, 1983: 284), that from the deeper stations being conspecific with *Henricia abyssicola* sensu Mortensen, 1927 (non *Cribrella sanguinolenta* var. *abyssicola* Norman, 1869) and distinguished by more attenuated arms and abactinal spinelets with a prolonged glassy point. The shallower species has less attenuated arms and abactinal spinelets ending in three points all at the same level. This taxon is conspecific with Norman's variety *abyssicola.*

Order **BRISINGIDA**

Family **BRISINGIDAE**

Brisinga endecacnemos Asbjornsen, 1856

SAMPLES. AT 201(5), AT 219(2), AT 233(1), AT 245(1), AT 254(1), ES 264(?[juvenile] 1), 13/83/5 OTSB(24), 9/84/9 OTSB(19), 3/85/17 OTSB(43), 3/85/29 OTSB(10). [1690–1740 m to 2220 m]

DISTRIBUTION. The new records raise the upper bathymetric limit on the Hebridean Slope although this is still much deeper than the shallowest known record of 286 m from Trondheim Fjord.

REPRODUCTION. Tyler *et al.* (1984) have described the reproductive biology of this species. Up to 60 000 eggs may be produced by each individual and there was no clear evidence of any seasonality in breeding in the limited number of samples available. The oocytes reach a maximum diameter of *c.* 1250 μm suggesting a direct form of demersal development.

Brisingella coronata (G. O. Sars, 1871)

SAMPLE. ES 289(1). [992–2450 m]

REMARKS. This specimen is unusual in having only eight arms instead of the usual 9–13.

DISTRIBUTION. No change.

REPRODUCTION. This appears to follow a similar pattern to that in *Brisinga endecacnemos* (Tyler *et al.*, 1984).

Novodinia pandina (Sladen, 1889)

See: Sladen, 1889: 597–601, pl. 109, figs 1–5; Mortensen, 1927: 123–125, fig. 72 (as *Odinia pandina*); Downey, 1986: 27–29, fig. 13.

SAMPLE. 3/85/28 OTSB(1). [990–1075 m]

DISTRIBUTION. Known from the 'cold' area of the NE. Atlantic from the Faeroe Channel *c.* 790–900 m (*Lightning* and *Porcupine*), to Iceland in 225 m (Einarsson, 1948). A single specimen was recently recovered from the western Atlantic off N. Carolina (Downey, 1986). The occurrence of this rarely found species at *c.* 56°N on the Hebridean Slope represents a southerly extension of range in the eastern Atlantic into the 'warm' area. Mortensen (1927) speculated however that *O. pandina* may be synonymous with *O. semicoronata* E. Perrier, 1885 recorded from the Denmark Strait and south of the Canaries in 1000–1435 m, and also *O. robusta* E. Perrier, 1885 known from the Bay of Biscay and south of the Canaries *c.* 880–1445 m. Following the discovery that the name *Odinia* is preoccupied, all these nominal species were referred to *Novodinia* by Dartnall *et al.*, (1969). In her revision of the Atlantic brisingids, Downey (1986) synonymises *N. semicoronata* with *N. robusta*, while retaining *N. pandina* as a separate entity. She suggests that *Novodinia* is a genus of only moderately deep water *c.* 250–1500 m.

REMARKS. The specimen, in common with most brisingids recovered, is incomplete, consisting of a disc of radius 18 mm with one partly detached arm and an arm fragment. There are sixteen ambulacral furrows. The attached arm measures 60 mm from the disc edge and 23 mm in height at the point of maximum gonadal swelling. The specific characters agree with Sladen's precise description and the presence of papulae on the disc and arms in particular distinguishes this specimen from all brisingids hitherto recorded from the Rockall Trough. This specimen is a male so no information can be given on the possible mode of development.

Order **FORCIPULATIDA**

Family **ASTERIIDAE**

Stichastrella rosea (O. F. Müller, 1776)

SAMPLES. RD 258(1). [135 m]

DISTRIBUTION. Further study of the bathymetric limits of *Stichastrella* suggests that in the Rockall Trough area, *S. rosea* is confined to the shelf in depths of less than 200 m. The record from GT 14 in 713–788 m listed in Part 1 is therefore reassigned to the variety *ambigua*.

Stichastrella rosea var. ***ambigua*** (Farran, 1913)

SAMPLES. AT 259(2), AT 291(7), AT 292(21), GT 14(3) [listed as *S. rosea* in Part 1], 13/83/3 GT(44), 13/83/4 GT(45), 13/83/7 OTSB(10), 13/83/8 OTSB(165), 3/85/38 OTSB(15), 3/85/43 OTSB(21), 3/85/44 OTSB(5). [220–270 m to 1632 m]

DISTRIBUTION. No change.

Neomorphaster talismani Perrier, 1894

See: Mortensen, 1927: 134–135, fig. 76.

SAMPLES. AT 259(1), 3/85/30 OTSB(1). [1041 m to 1420–1480 m]

DISTRIBUTION. Known from SW. Ireland in 1350 m and south to Morocco mainly *c.* 400–2000 m but exceptionally found at 5413 m. The above records from the Rockall Bank and Hebridean Slope extend the known geographic range of this species to the Rockall Trough.

Family **ZOROASTERIDAE**

Zoroaster fulgens Wyville Thomson, 1873

SAMPLES. AT 198(3), AT 201(1), AT 219(1), AT 223(8), AT 229(5), AT 230(2), ES 232(3), AT 233(3), AT 239(6; ?[juvenile] 1), AT 245(1), AT 256(13), AT 257(1), AT 259(14), ES 261(1), ES 264(juvenile, 1), AT 267(3), AT 273(3), AT 287(190), AT 288(4), 13/83/1 OTSB(4), 13/83/2 OTSB(1), 13/83/5 OTSB(33), 13/83/6 OTSB(21), 9/84/9 OTSB(14), 9/84/10 OTSB(3), 9/84/13 OTSB(30), 3/85/7 OTSB(182), 3/85/8 OTSB(3), 3/85/9 OTSB(1), 3/85/17 OTSB(4), 3/85/18 MBA(10), 3/85/20 OTSB(11), 3/85/25 OTSB(43), 3/85/29 OTSB(49), 3/85/30 OTSB(101). [940–975(?580–630) m to 4810 m]

DISTRIBUTION. The records from 9/84/10 OTSB approach the minimum depth known for this species, but it is possible that these specimens were contaminants from the previous samples in 1750–1770 m. This is supported by their small size, similar to the specimen figured as *Z. fulgens* var. *ackleyi* by Farran (1913 pl. 1, fig. 3). On the Hebridean Slope it is noticeable that individuals of *Z. fulgens* from depths greater than *c.* 1500 m are nearly always of this smaller slender-armed form, whereas those from around 1000 m are larger and more robust.

Class **OPHIUROIDEA**
Order **PHRYNOPHIURIDA**
Family **ASTERONYCHIDAE**

Asteronyx loveni Müller & Troschel, 1842

See: Paterson, 1985: 13–15, fig. 9.

SAMPLE. 3/85/32 OTSB(1). [1055 m to 1995–2020 m]

DISTRIBUTION. All three specimens recovered in our samples have been from the Hebridean Slope.

Family **ASTEROSCHEMATIDAE**

Asteroschema inornatum Koehler, 1906

See: Paterson, 1985: 16, fig. 10.

SAMPLE. ES 264(1). [1900–2144 m]

DISTRIBUTION. This and the previous specimen are from the west side of the Trough and both were entwined in the branches of gorgonians.

Family **GORGONOCEPHALIDAE**

Gorgonocephalus caputmedusae (Linnaeus, 1758)

See: Paterson, 1985: 11–13, fig. 8.

SAMPLES. AT 239(1), ES 250(?[juvenile] 1), GT 2(1), 13/83/2 OTSB(1), 13/83/6 OTSB(1), 9/84/13 OTSB(1), 3/85/13 OTSB(1), 3/85/19 MBA(4), 3/85/23 OTSB(1), 3/85/24 OTSB(2), 3/85/25 OTSB(4), 3/85/26 OTSB(6), 3/85/27 OTSB(4), 3/85/28 OTSB(2), 3/85/31 OTSB(3), 3/85/33 OTSB(1), 3/85/34 OTSB(2), 3/85/36 OTSB(6), 3/85/46 OTSB(1). [940–985 m to 1130–1265(?1270)]

DISTRIBUTION. All specimens, with the exception of the queried one from the Feni Ridge are from the Hebridean Slope where this species is apparently common. The new records extend the bathymetric range in this area.

Family **OPHIOMYXIDAE**

Ophiomyxa serpentaria Lyman, 1883

See: Paterson, 1985: 18–20, fig. 11.

SAMPLE. AT 259(15). [1041 m]

DISTRIBUTION. Previously recorded in the eastern Atlantic from the Faeroe Channel and SW. Ireland to the Azores; 450–2440 m. Its occurrence on the Feni Ridge is therefore not unexpected.

Ophioscolex glacialis Müller & Troschel, 1842

See: Paterson, 1985: 20–21, fig. 11.

SAMPLES. AT 248(1), AT 249(1), AT 251(1), AT 259(2), 9/84/2 OTSB(1), 3/85/28 OTSB(1). [910–960 m to 1530 m]

DISTRIBUTION. Previously recorded from both sides of the N. Atlantic and from Arctic seas; 50–2727 m. These specimens, mainly from the N. Feni Ridge but also from the Hebridean Slope, provide a link between a specimen recovered by IOS at the extreme SW. end of the Trough and the Arctic populations.

Ophiophrixus spinosus (Storm, 1881)

See: Paterson, 1985: 21–22, fig. 12.

SAMPLES. AT 287(1), 3/85/9 OTSB(1), 3/85/10 OTSB(1), 3/85/14 OTSB(1), 3/85/28 OTSB(1), 3/85/46 OTSB(1). [720–775 m to 1383 m]

DISTRIBUTION. Known from the Denmark Strait and SE. Iceland to the Azores; 40–1310 m. These specimens are all from the Hebridean Slope and provide a slight increase in bathymetric range.

Order **MYOPHIURIDA**
Family **OPHIACANTHIDAE**
Subfamily **OPHIACANTHINAE**

Ophiacantha abyssicola G. O. Sars, 1871

See: Paterson, 1985: 47–48, fig. 20.

SAMPLES. AT 239(? 1), AT 259(2), AT 290(1), GT 1(?1), 13/83/5 OTSB(2), 13/83/13 OTSB(1), 3/85/17 OTSB(9), 3/85/28 OTSB(5). [?650–805 m to 1955–1995 m]

DISTRIBUTION. The new records from the Rockall Bank and Hebridean Slope provide a considerable extension of bathymetric range in the Trough from the maximum of *c.* 1000 m given in Part 1, although still well within the range known for this species.

Ophiacantha bidentata (Retzius, 1805)

See: Paterson, 1985: 34–36, fig. 15.

SAMPLES. ES 129(2, ?[juvenile] 1), ES 184(61), ES 185(?[juvenile] 1), ES 197(160), ES 200(56), AT 201(265), ES 202(11), ES 207(?[juvenile] 1), AT 218(20), AT 219(308), AT 221(17), SBC 222(?[juvenile] 1), AT 228(6), AT 229(1), ES 232(23; ?[juvenile] 1), AT 233(95), ES 244(1, ?[juveniles] 3), AT 245(110), AT 247(32), AT 248(1), AT 251(4), ES 252(1), ES 255(3), AT 256(8), ES 257(1), ES 264(27), ES 266(2), AT 267(6), AT 271(93), AT 273(144), ES 283(juvenile 1), AT 288(1), ES 289(7), 13/83/6 OTSB(1), 3/85/7 OTSB(1), 3/85/17 OTSB(8). [980–1005 m to 2946 m]

DISTRIBUTION. The new records extend the upper bathymetric limit in the Trough from 1330 m to *c.* 1000 m.

Ophiacantha crassidens Verrill, 1885

See: Paterson, 1985: 40–41, fig. 17.

SAMPLES. AT 223(4), AT 230(1). [1075–1862 m]

DISTRIBUTION. The new records are from just south of the Wyville Thomson Ridge and Hebridean Slope and indicate a wider distribution within the Trough than the few previous samples suggested.

Ophiolebes bacata Koehler, 1921

See: Paterson, 1985: 51, fig. 22.

SAMPLE. AT 259(4). [1041 m]

DISTRIBUTION. Eastern Atlantic from the Bay of Biscay and off Madeira; 1300–2034 m. This record from the North Feni Ridge is a considerable extension of range north to *c.* 57°N and to slightly shallower depths.

Subfamily **OPHIOTOMINAE**

Ophiotoma coriacea Lyman, 1883

See: Paterson, 1985: 57, fig. 23.

SAMPLES. AT 221(1), AT 256(1). [1605–1705 m]

Distribution. Recorded from both the western and eastern Atlantic; Cape Cod 1242 m and the Azores to Iceland 1765–4106 m including a *Helga* record from SW. of Ireland. The present specimens from east of Rosemary Bank and the North Feni Ridge provide a small upward extension of bathymetric range in the eastern Atlantic and the first records from the Rockall Trough.

Ophiolimna bairdi (Lyman, 1883)

See: Paterson, 1985: 60, fig. 24.

Sample. ES 264(3). [2144–2910 m]

Distribution. This second record from the the foot of the Rockall Bank is shallower than the previous record by 750 m. The flow of cold water along the Feni Ridge and east side of the Rockall Bank may allow this circumpolar arctic species to extend into shallower depths on this side of the Trough.

Subfamily **OPHIOPLINTHACINAE**

Ophiomitrella clavigera (Ljungman, 1864)

See: Paterson, 1985: 71, fig. 28.

Sample. AT 259(1). [1041 m]

Distribution. Known from both sides of the N. Atlantic: Davis Strait and W. Greenland; the Azores to the Faeroes; 166–1348 m. The single specimen was taken from the east side of Rockall Bank.

Family **OPHIACTIDAE**

Ophiactis abyssicola (M. Sars, 1861)

See: Paterson, 1985: 76–78, fig. 32.

Samples. ES 99(juvenile 1), ES 112(783; ?[juveniles 22), AT 153(2), ES 197(22), AT 201(2), ES 202(5), ES 218(1), AT 219(2), AT 223(18), AT 226(juvenile 1), AT 228(9), AT 229(33), AT 230(39), AT 233(1), AT 239(3), AT 247(19), AT 248(47), AT 249(1), ES 250(16), AT 251(6), ES 255(6), AT 256(2), AT 259(62), ES 261(1), ES 264(237), AT 271(32), AT 273(10), AT 287(21), AT 290(1), 13/83/1 OTSB(54), 3/85/28 OTSB(32), 3/85/29 OTSB(1), 3/85/30 OTSB(59). [168–3000 m]

Distribution. No change.

Family **AMPHIURIDAE**

Amphiura tritonis Hoyle, 1884

See: Mortensen, 1927: 213; Paterson, 1985: 85–86, fig. 33.

Sample. SBC 222(juvenile 1). [1101 m]

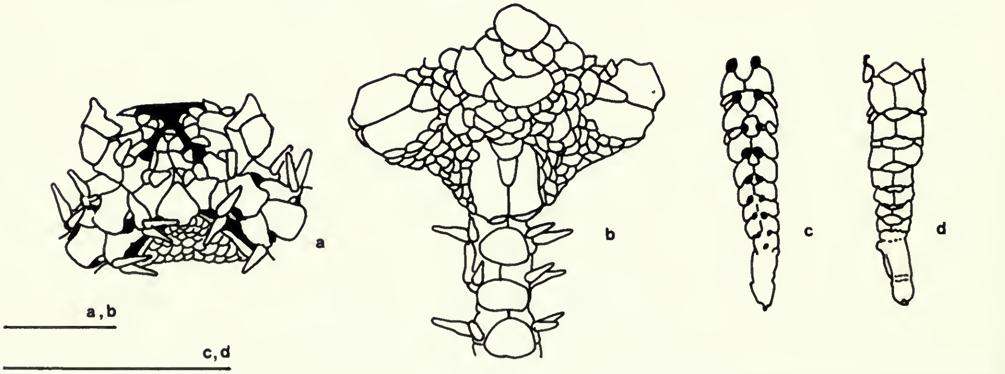

Fig. 2 *Amphiura tritonis* (a) ventral (b) dorsal view of disk; (c) ventral (d) dorsal view of the ends of the arms. Scale bars = 1 mm.

DISTRIBUTION. A rare species having been recorded once from a position very near the current record just south of the Wyville Thomson Ridge and twice from the Bay of Biscay; 627–1290 m

REMARKS. The undamaged specimen, which was recovered from a 0·25 m^2 box core, is considerably smaller than the holotype from the same locality (disc diameters 2·5 and 12 mm respectively). The arm tips bear numerous newly added arm segments (Fig. 2c, d) which lack spines. This small specimen is characterised by the ventral interradial area being scaled; by large, broadly triangular oral papillae and by three arm spines, of which the middle one tends to be the largest (Fig. 2a). Of the three N. Atlantic species with similar characteristics, *A. tritonis, A. richardi* Koehler and *A. abyssorum* Norman, it appears to be closest to *A. tritonis*. The oral shield lacks the pronounced distal lobe seen in *A. tritonis*, but this might be due to the small size of the specimen. Both *A. richardi* and *A. abyssorum* lack scaling on the ventral interradial area and the oral papillae of *A. abyssorum* are spine-like. These features readily distinguish them from the Rockall specimens.

Amphiura otteri Ljungman, 1871

See: Paterson, 1985: 86–87, fig. 33.

SAMPLES. ES 112(1), SBC 205(1), ES 207(1), ES 231(3), ES 285(1). [1000–2906 m)

DISTRIBUTION. The new records, while mainly from the SMBA Permanent Station in *c.* 2900 m, include a record from 1900 m on the South Feni Ridge. This, together with a 1000 m record listed in Part 1 from the Hebridean Slope and its wide distribution in the N. Atlantic suggests that this species is tolerant of a variety of bottom conditions. The bathymetric range is 198–3200 m.

Amphipholis squamata (Delle Chiaje, 1829)

See: Paterson, 1985: 91, fig. 36.

SAMPLES. ES 112(17), SBC 211(juvenile 1), ES 250(1). [402–1900 m]

DISTRIBUTION. The record from ES 112 gives a further surprising extension of nearly 600 m to the known bathymetric range of this species; 0–1900 m.

Amphilepis ingolfiana (Mortensen, 1933)

See: Paterson, 1985: 93–94, fig. 37.

SAMPLES. ES 27(2, ?[juveniles] 2), ES 118(2, juveniles 2), ES 129(1), ES 135(1, ?1), SBC 160(juvenile 1), ES 184(15, ?[juvenile] 1), ES 185(21), ES 197(76), ES 200(16), AT 201(1), ES 202(3), ES 204(5), ES 207(9), ES 218(juveniles 5), AT 219(5), SBC 220(juveniles 2), AT 221(1), ES 231(7), ES 232(6), AT 239(1), ES 244(juveniles 17), ES 255(1), AT 267(7), AT 271(1), SBC 272(3), AT 273(1), SBC 275(?[juvenile] 1), SBC 276(juvenile 1), AT 282(20), ES 283(9), ES 285(1), AT 286(4), ES 289(juveniles 31). [1047–2946 m]

DISTRIBUTION. The record from AT 239 raises the upper limit of this species in the Rockall Trough to near the minimum of 957 m quoted by Mortensen (1933).

Family **OPHIOCHITONIDAE**

Ophiochiton ternispinus Lyman, 1883

See: Paterson, 1985: 96–97, fig. 39.

SAMPLES. AT 221(5), AT 223(3), AT 228(4), AT 229(1), AT 230(1), AT 239(1), AT 251(1), ES 255(1), AT 256(2), AT 287(1), 13/83/1 OTSB(2), 13/83/2 OTSB(2), 13/83/5 OTSB(1), 9/84/9 OTSB(1), 3/85/17 OTSB(1), 3/85/29 OTSB(7), 3/85/30 OTSB(6). [1047–2200 m]

DISTRIBUTION. The new records from the Hebridean Slope raise the known upper bathymetric limit within the Trough by 700 m.

Family **OPHIURIDAE**
Subfamily **OPHIURINAE**

Ophiopleura inermis (Lyman, 1878)

See: Paterson, 1985: 128, fig. 48.

SAMPLES. AT 223(6), AT 230(5), AT 239(3), AT 248(4), AT 249(1), ES 250(4), AT 259(6), AT 290(10), 13/83/2 OTSB(3), 13/83/6 OTSB(182), 9/84/13 OTSB(3), 3/85/8 OTSB(3), 3/85/9 OTSB(28), 3/85/13 OTSB(35), 3/85/20 OTSB(18), 3/85/23 OTSB(2), 3/85/24 OTSB(52), 3/85/25 OTSB(8), 3/85/26 OTSB(11), 3/85/27 OTSB(3), 3/85/28 OTSB(119), 3/85/31 OTSB(1), 3/85/32 OTSB(2), 3/85/33 OTSB(21), 3/85/36 OTSB(6), 3/85/46 OTSB(3). [650–805 m to 1271 m]

DISTRIBUTION. No change.

Homophiura tesselata (Verrill, 1894)

See: Paterson, 1985: 135–138.

SAMPLES. AT 181(4), AT 228(1). [1785–1845 m to 2264 m]

DISTRIBUTION. No change.

Amphiophiura saurura (Verrill, 1894)

See: Paterson, 1985: 134, fig. 50.

SAMPLE. 3/85/20 OTSB(4). [1225–1245 m to 1900 m]

DISTRIBUTION. This record extends the known distribution within the Trough to the Hebridean Slope and into shallower water.

Ophiocten gracilis (G. O. Sars, 1871)

See: Paterson, 1985: 130, fig. 50.

SAMPLES. ES 6(juveniles 1583), ES 14(juveniles 88), ES 15(juveniles 2908), ES 27(juveniles 5), ES 57(juveniles 76), ES 105(juveniles 3362), ES 129(juveniles 5, ?[juvenile] 1), SBC 150(juveniles 39), SBC 160(juveniles 3), SBC 163(juveniles 5), SBC 174(juvenile 1), ES 178(juveniles 789), ES 184(juveniles 654), SBC 188(juvenile 1), ES 197(juveniles 2700), ES 200(juveniles 9), ES 202(juvenile 1), ES 204(juvenile 1), ES 207(juveniles 38), SBC 215(juveniles 2), SBC 216(?[juvenile] 1), ES 218(juveniles 1768), SBC 220(juvenile 1), AT 226(3), AT 239(162), ES 244(juveniles 285), ES 264(9), SBC 276(juveniles 4), SBC 278(juveniles 3), ES 283(juveniles 10), AT 290(11), 13/83/6 OTSB(118), 13/83/7 OTSB(95), 9/84/2 OTSB(27), 9/84/13 OTSB(54), 3/85/10 OTSB(68), 3/85/24 OTSB(10), 3/85/26 OTSB(3), 3/85/28 OTSB(25), 3/85/36 OTSB(1). [704–2946 m]

DISTRIBUTION. No change.

Ophiocten hastatum Lyman, 1878

See: Paterson, 1985: 129, fig. 49.

SAMPLES. SBC 64(1), ES 111(2), ES 129(2), ES 185(8), ES 204(1), ES 207(1, ?1), ES 266(1), AT 267(1), ES 283(2), 3/85/5 OTSB(9). [2000 m to 2970–2980 m]

DISTRIBUTION. The new records slightly extend the bathymetric range within the Trough of this esentially abyssal species.

Ophiura carnea Lütken, 1858

See: Paterson, 1985: 117, fig. 42.

SAMPLE. 3/85/9 OTSB(1). [630–2857 m]

DISTRIBUTION. The new record extends the known distribution within the Trough to the Hebridean Slope.

Ophiura scomba Paterson, 1985

See: Paterson, 1985: 125–127, figs 46 & 56; Gage *et al.*, 1983: 297–298 (as *O. irrorata*).

SAMPLES. AT 201(1), ES 218(1), AT 219(1), AT 245(1), AT 247(28), ES 252(5), AT 254(3), ES 255(11), AT 256(24), ES 257(7; ?[juvenile] 1), ES 261(17), ES 264(13), 3/85/17 OTSB(1). [1510–2220 m]

DISTRIBUTION. *O. scomba* is known from Rockall south to Morocco; 1595–4406 m. The new records are from the North Feni Ridge and also in the vicinity of a 2200 m repeat station (Sta. 'M') in the northern Rockall Trough and provide a new slightly shallower upper bathymetric limit.

REMARKS. This species was recorded as *O. irrorata* in Part 1. Subsequent studies have shown that the Rockall specimens should be referred to *O. scomba*. The swollen oral shields, rounded ventral arm plates and pointed oral papillae distinguish this species from its congener *O. ljungmani*, which has an overlapping bathymetric distribution in the Trough.

Ophiura ljungmani (Lyman, 1878)

See: Paterson, 1985: 118–120, fig. 44.

SAMPLES. ES 27(172), ES 57(927), SBC 58(2), ES 105(juveniles 13), ES 111(623), ES 118(401), ES 129(951), SBC 159(juveniles 3), SBC 160(juvenile 1), SBC 163(juveniles 2), ES 180(305), ES 184(359), ES 185(634), ES 197(807), ES 200(juveniles 70), AT 201(8), ES 202(69), ES 204(106), SBC 205(juvenile 1), ES 207(232), ES 218(194), AT 219(8), SBC 220(2), AT 228(41), ES 231(286), ES 232(26), AT 233(16), ES 244(170), AT 245(17), AT 247(3), ES 264(67), ES 266(21), AT 267(22), AT 271(6), AT 273(14), SBC 278(juvenile 1), ES 283(414), ES 285(39), AT 288(4), ES 289(juveniles 111), 13/83/5 OTSB(2). [1050 m to 3425–3500 m]

DISTRIBUTION. No change.

Ophiura ophiura (Linnaeus, 1758)

See: Süssbach & Breckner, 1911: 234–241 (as *O. ciliaris*); Mortensen, 1927: 236–238, fig. 128 (as *O. texturata*).

SAMPLES. SBC 210(?1), AT 292(2), 13/83/3 GT(8), 3/85/43 OTSB(2). [220–270 m to 704 m]

DISTRIBUTION. These new records confirm the presence of this sublittoral to bathyal species at depths >500 m on the Hebridean Slope as reported from a single record in Part 1.

Subfamily **OPHIOLEPIDINAE**

Ophiomusium lymani Wyville Thomson, 1873

See: Paterson, 1985: 147–148, fig. 58.

SAMPLES. ES 105(juveniles 2), ES 184(1196), ES 185(juvenile 1), AT 186(1015), ES 197(451), ES 200(240), AT 201(948), ES 202(31), ES 218(juveniles 12), AT 219(1458), SBC 220(juvenile 1), AT 221(44), AT 228(1224), ES 232(121), AT 233(1039), AT 239(3), ES 244(48), AT 245(392), AT 247(391), ES 250(2), AT 251(17), ES 252(6), AT 254(12), AT 256(86), ES 257(12), ES 261(3), ES 264(10), AT 271(860), AT 273(572), ES 285(20), AT 287(3), AT 288(1787), ES 289(171), 13/83/5 OTSB(417), 3/85/7 OTSB(44), 3/85/17 OTSB(1800), 3/85/29 OTSB(1614), 3/85/30 OTSB(29). [810–2921 m]

DISTRIBUTION. No change.

Class **ECHINOIDEA**
Order **CIDAROIDA**
Family **CIDARIDAE**

Cidaris cidaris (Linnaeus, 1758)

SAMPLES. AT 223(1), AT 292(3), 13/83/8 OTSB(1), 9/84/10 OTSB(1), 3/85/28 OTSB(4), 3/85/31 OTSB(1), 3/85/43 OTSB(155), 3/85/44 OTSB(52). [500–560 m to 1075 m]

DISTRIBUTION. No change.

Poriocidaris purpurata (Wyville Thomson, 1872)

Samples. AT 223(31), AT 230(4), AT 239(1), AT 248(3), AT 259(1), 13/83/2 OTSB(3). [1041–1296 m]

Distribution. The record from AT 223 is near the type locality of this species. The new records raise the known upper bathymetric limit for the Rockall Trough by *c*. 150 m.

Order **ECHINOTHURIOIDA**
Family **ECHINOTHURIIDAE**

Araeosoma fenestratum (Wyville Thomson, 1869)

Samples. 13/83/2 OTSB(1), 13/83/7 OTSB(1). [631 m to 1265–1130 m]

Distribution. These new records from the Hebridean Slope provide an extension of the lower bathymetric range of this species in the NE. Atlantic.

Calveriosoma hystrix (Wyville Thomson, 1869)

Samples. AT 223(19), AT 239(1), AT 248(2), AT 259(2), AT 291(11), AT 3(1), 13/83/2 OTSB(6), 13/83/6 OTSB(180), 13/83/7 OTSB(5), 9/84/1 OTSB(2), 9/84/2 OTSB(3), 9/84/10 OTSB(1), 9/84/13 OTSB(45), 3/85/8 OTSB(1), 3/85/9 OTSB(3), 3/85/10 OTSB(8), 3/85/13 OTSB(183), 3/85/14 OTSB(126), 3/85/18 MBA(109), 3/85/19 MBA(16), 3/85/25 OTSB(103), 3/85/28 OTSB(1). [580–630 m to 1265–1130 m]

Distribution. The new records extend both the upper and lower bathymetric limits of this species within the Trough. The numbers taken in fish trawls suggest that it is abundant on the Hebridean Slope at around 1000 m.

Remarks. The specimen from AT 239 was in excellent condition when recovered, with most of its long red spines intact and the body wall still supported by coelomic fluid. Trawled specimens are generally almost completely devoid of spines and give little impression of the magnificence of this species in life.

The size-frequencies (Table 1) from semi-balloon trawls (OTSB) suggest that the largest individuals occur at the upper end of the depth range on the Hebridean Slope, whereas recruitment occurs towards the lower end of the depth range. The occurrence of juveniles at a greater depth than adults has been noted in a number of echinoderm taxa in the Rockall Trough (Gage *et al.*, 1983, 1985*a*). The smallest individual recovered measured 55 mm, considerably larger than the smallest echinoids taken with this trawl, suggesting that recruitment may be sporadic in this non-seasonally reproducing species (Tyler & Gage, 1984*a*).

Hygrosoma petersii (A. Agassiz, 1880)

Samples. AT 230(2), AT 233(2), AT 239(1), AT 282(1), ES 283(2), AT 286(3), AT 287(2), SWT 27(2), 13/83/1 OTSB(1), 13/83/5 OTSB(1), 3/85/5 OTSB(10), 3/85/21 OTSB(1), 3/85/30 OTSB(9), 3/85/45 OTSB(3). [1160 m to 2970–2980 m]

Distribution. The new records provide a small extension of the known lower bathymetric limit, the total range now being 730–2980 m.

Sperosoma grimaldii Koehler, 1897

Samples. AT 239(9), AT 248(2), AT 249(?2), 13/83/2 OTSB(167), 13/83/5 OTSB(1), 13/83/6 OTSB(40), 9/84/13 OTSB(6), 3/85/8 OTSB(2), 3/85/9 OTSB(1), 3/85/11 OTSB(4), 3/85/13 OTSB(3), 3/85/18 MBA(88), 3/85/19 MBA(37), 3/85/20 OTSB(62), 3/85/23 OTSB(1), 3/85/24 OTSB(19), 3/85/25 OTSB(58), 3/85/28 OTSB(7), 3/85/33 OTSB(17), 3/85/43 OTSB(2). [565–700 m to 2910 m]

Distribution. Intensive trawlings on the Hebridean Slope suggest that this species is common at around 1000 m where it is frequently recovered with *Calveriosoma hystrix*. The upper bathymetric limit within the Trough is raised by around 500 m.

Remarks. Size-frequency data (Table 1) suggest that this species attains a smaller size on the Hebridean Slope than *Calveriosoma hystrix*. It appears also that as in *C. hystrix* the smallest

Table 1 Size-frequencies of echinothuriid urchins from the Hebridean Slope

Date	Station	Depth	Lower bound of size class of flattened test diameter (mm)														
Calveriosoma hystrix			50	60	70	80	90	100	110	120	130	140	150	160	170	180	190
22.9.83	13/83/6 OTSB	980–1005	1	2	4	35	66	33	6	2	0	0	0	0	0	0
5.11.84	9/84/13 OTSB	940–975	0	0	0	0	8	11	15	6	3	0	0	0	0	0
18.4.85	3/85/13 OTSB	960–995	0	0	0	3	48	67	56	8	2	0	1	0	0	0
18.4.86	3/85/14 OTSB	720–775	0	0	0	0	0	3	10	16	23	23	18	12	2	1
23.4.85	3/85/25 OTSB	1000–1005	0	0	3	4	23	41	15	5	1	0	0	0	0	0
Sperosoma grimaldi			20	30	40	50	60	70	80	90	100	110	120	130	140	150	160
21.9.83	13/83/2 OTSB	1130–1265	1	1	2	3	1	23	54	59	15	2	2	2	0	0
22.9.83	13/83/6 OTSB	980–1005	0	0	0	0	0	1	1	14	16	6	2	0	0	0
22.4.85	3/85/20 OTSB	1225–1245	2	10	7	4	0	1	6	15	10	1	1	1	0	1
23.4.85	3/85/25 OTSB	1000–1005	0	0	0	0	0	1	2	11	22	16	3	2	0	0
Phormosoma placenta			10	20	30	40	50	60	70	80	90	100					
21.9.83	13/83/2 OTSB	1130–1265	1	0	1	5	56	122	40	5	1						
21.9.83	13/83/5 OTSB	1775–1835	0	0	0	0	14	39	13	0	0						
22.9.83	13/83/6 OTSB	980–1005	0	0	1	3	47	21	3	0	0						
22.9.83	13/83/7 OTSB	750–800	0	0	0	0	0	23	45	7	0						
4.11.84	9/84/9 OTSB	1750–1770	0	0	0	0	1	39	30	0	0						
5.11.84	9/84/13 OTSB	940–975	0	0	0	0	2	44	46	11	0						
18.4.85	3/85/13 OTSB	960–995	0	0	0	0	4	20	17	4	0						
21.4.85	3/85/17 OTSB	1955–1995	1	1	10	31	90	103	24	1	0						
22.4.85	3/85/20 OTSB	1225–1245	0	4	18	20	23	2	0	0	0						
23.4.85	3/85/25 OTSB	1000–1005	0	0	0	6	57	138	109	41	1						

individuals are found in depths greater than 1000 m, with no juveniles recovered from the shallower stations sampled at or about the same time. *Sperosoma grimaldii* appears to have a non-seasonal reproductive cycle (Tyler & Gage, 1984*a*).

Family **PHORMOSOMATIDAE**

Phormosoma placenta Wyville Thomson, 1872

Samples. AT 223(88), AT 228(55), AT 230(4), ES 231(1), AT 239(34), AT 248(47), AT 249(8), ES 250(3), AT 251(2), AT 254(40), ES 255(64), AT 256(7), AT 257(1), AT 259(1), ES 261(1), AT 287(1), AT 288(2), AT 291(2), AT 292(1), GT 7(2), GT 8(1), 13/83/2 OTSB(232), 13/83/5 OTSB(753), 13/83/6 OTSB(76), 13/83/7 OTSB(91), 9/84/9 OTSB(71), 9/84/13 OTSB(104), 3/85/9 OTSB(11), 3/85/10 OTSB(2), 3/85/13 OTSB(46), 3/85/14 OTSB(3), 3/85/17 OTSB(262), 3/85/18 MBA(17), 3/85/19 MBA(8), 3/85/20 OTSB(69), 3/85/25 OTSB(353), 3/85/29 OTSB(14), 3/85/34 OTSB(1), 3/85/46 OTSB(1). [525–2898 m]

Distribution. The new records extend both the upper bathymetric limit within the Trough, and the known lower bathymetric limit of this species. The total range is now 260–2898 m.

Remarks. The size-frequency data (Table 1) indicate that as in *Calveriosoma hystrix* and *Sperosoma grimaldi* juveniles tend to occur at a greater depth than adults.

Order **ECHINOIDA**
Family **ECHINIDAE**

Echinus acutus var. *norvegicus* Düben & Koren, 1844

Samples. ES 115(?[juveniles] 4), ES 178(?2), SBC 210(juveniles 2), AT 223(65), AT 230(juveniles 7), AT 239(48, ?[juveniles] 3), AT 248(?[juveniles] 2), AT 291(214), 13/83/2 OTSB(juveniles 16), 13/83/4 GT(?1), 13/83/7 OTSB(6), 13/83/8 OTSB(134), 9/84/1 OTSB(49), 3/85/10 OTSB(26), 3/85/13 OTSB(1), 3/85/14 OTSB(1000), 3/85/18 MBA(1), 3/85/20 OTSB(4, ?1), 3/85/24 OTSB(2), 3/85/36 OTSB(2). [401 m to 1225–1245 m]

Distribution. The new records raise the upper bathymetric limit by over 300 m in the Trough and provide a small extension of the lower bathymetric limit. Intensive trawlings on the Hebridean Slope suggest that this species is most common in the 500–800 m depth interval.

Remarks. The maximum size in these samples was found to be 77 mm test diameter, which is in approximate agreement with Mortensen (1943) who thought that it does not reach a size larger than *c.* 70 mm. Morphometric data from these large samples is given by Gage *et al.*, (1986), these data showing good agreement with measurements given by Mortensen (1943) from material collected from various locations. These authors found size frequency distributions for this sea urchin to be quite variable in the hauls from the Hebridean Slope, this variability apparently being unrelated to bathymetry or time of year. This species occurs at depths similar to those yielding large numbers of its congener *E. elegans* yet analysis of these records shows that in most trawlings either one or the other species is overwhelmingly dominant, and in many only one of the two species occurs (see under Remarks for *E. elegans*).

Life History. Gage *et al.* (1986) describe the seasonal cycle in oogenesis in this species on the Hebridean Slope; spawning occurring in about March. These authors, in interpreting growth banding in the plates of the test as reflecting a seasonal pattern of growth, infer that specimens >50 mm in test diameter are 6–11 yr old. The estimated age of specimens of around 30 mm is 6 yr and agrees fairly well with results of Sime & Cranmer (1985) from a study of populations at depths of 108–149 m in the northern North Sea.

Echinus affinis Mortensen, 1903

Samples. ES 112(juveniles 94 [not 1073 as stated in Part 2]), AT 154(116), ES 176(7, ?[juveniles] 73), AT 177(548), ES 184(58), AT 192(?17), ES 197(110, ?[juveniles] 8), ES 200(62, ?[juvenile] 1), ES 218(6, juveniles 2), ES 232(11), ES 244(10, ?[juveniles] 5), AT 245(92), AT 247(291), ES 264(130, ?[juveniles] 4), AT 267(7), AT 271(154), AT 273(708), AT 288(122), ES 289(14), 13/83/5 OTSB(191), 9/84/9 OTSB(78), 3/85/7 OTSB(juvenile 1), 3/85/17 OTSB(204), 3/85/29 OTSB(22), SWT 13(none [listed as 3 in Part 2]). [1605–2605 m]

Distribution. The new records extend the known lower bathymetric limit of this species slightly.

Life History. In the northern Rockall Trough at Sta 'M' in 2200 m where this species is abundant, *E. affinis* has a seasonal reproductive cycle and probably produces a planktotrophic larva. This seasonal reproduction is thought by Tyler & Gage (1984*b*) possibly to be tuned to a pulsed annual fallout of phyto-detrital food to the sea floor in this area. Additional studies at this station have revealed skeletal banding which is thought to result from a seasonal growth pattern controlled by the same factor (Gage & Tyler, 1985). Adults were inferred to be up to *c.* 28 years old. These latter authors also indicate that postlarval survivorship is probably very low; a markedly uneven representation of ages in a large sample aged by means of growth rings was interpreted by them as probably reflecting multi-year cycles in recruitment success.

Echinus alexandri Danielssen & Koren, 1883

Samples. ES 112(12, ?[juveniles] 108), AT 248(7), AT 251(juvenile 1), AT 256(3), AT 259(4), AT 288(1), 13/83/1 OTSB(3), 3/85/30 OTSB(?[juvenile] 1). [1041–2300 m]

Distribution. The new records raise the upper bathymetric limit in the Trough by *c.* 230 m.

Echinus elegans Düben & Koren, 1844

Samples. AT 287(?18), AT 291(63), 13/83/3 GT(3), 13/83/6 OTSB(7), 13/83/7 OTSB(1), 13/83/8 OTSB(1), 9/84/2 OTSB(15), 9/84/13 OTSB(3), 3/85/9 OTSB(241), 3/85/13 OTSB(77), 3/85/14 OTSB(5), 3/85/18 MBA(9), 3/85/20 OTSB(?10), 3/85/23 OTSB(1), 3/85/24 OTSB(21), 3/85/25 OTSB(1), 3/85/28 OTSB(205), 3/85/31 OTSB(2), 3/85/36 OTSB(1). [220–270 m to 1210(?1383) m]

Distribution. The new records extend the known distribution within the Trough onto the shelf to considerably shallower depths than reported in Part 2, although still within the overall recorded range for this species.

Remarks. The maximum size of the specimens was 93 mm in test diameter, which is close to the maximum of 80 mm given by Mortensen (1927). Morphometric data from these large samples is given by Gage *et al.* (1986), these measurements showing good agreement with more limited data given by Mortensen (1943) from material collected from various other locations. The size frequencies of the Rockall samples are variable from haul to haul, with from one to three modes present; these appeared to show no relationship to either time of year or bathymetry. This species occurs at depths similar to those of trawlings yielding large numbers of its congener *E. acutus* var. *norvegicus*; yet, as pointed out above for the latter species, analysis of these hauls shows that in all of them either one or the other species is overwhelmingly dominant, while in many only one species occurs. Gage *et al.* (1986) suggest that this may result from differing habitat requirements. The muddy gut contents of *E. acutus* var. *norvegicus* indicate deposit feeding, while the varied particulate remains found in *E. elegans*, that include both sediment and small prey, suggest a more omnivorous diet (Mortensen, 1943; Gage *et al.*, 1986).

Life History. The sexes are separate and equal in number. Females show a seasonal cycle in oogenesis, spawnout probably occurring in March. An egg size up to 60 μm diameter is indicative of planktotrophic development as in other species of this genus (Gage *et al.*, 1986). These authors interpret growth banding visible in the skeletal plates as reflecting a seasonal growth pattern. Counts of these growth zones and a fitted growth curve indicate that a size of 70 mm test diameter is reached at an age of 12–20 yr.

Order **SPATANGOIDA**
Family **HEMIASTERIDAE**

Hemiaster expergitus Loven, 1874

Samples. ES 15(juveniles 2), ES 18(juveniles 3), SBC 61(juveniles 3), SBC 156(juveniles 3), SBC 160(juveniles 2), SBC 168(1), ES 172(juveniles 2), ES 176(juveniles 3), AT 177(?[juvenile] 1), ES 197(5), ES 204(juvenile 1), ES 207(1, juvenile 1), ES 218(juveniles 52), SBC 220(juveniles 2), SBC 222(juvenile 1), ES 232(2, juveniles 3), AT 239(juveniles 15), ES 244(juveniles 19), AT 245(9), ES 250(juvenile 1), AT 251(2), ES 252(40), ES 255(juveniles 4), ES 261(1), AT 271(1), AT 282(1), ES 289(juvenile 1). [1047–2910 m]

DISTRIBUTION. These records raise the upper bathymetric limit slightly within the Trough.

LIFE HISTORY. Counts of growth bands present in the test plates indicate a test length of 30 mm might be reached by *c.* 16 yr (Gage, 1987).

Family **SPATANGIDAE**

Spatangus raschi Loven, 1869

SAMPLES. SBC 210(?[juveniles] 4), AT 239(juvenile 1), AT 291(36), 13/83/7 OTSB(54), 13/83/8 OTSB(2), 9/84/1 OTSB(1), 3/85/10 OTSB(13), 3/85/13 OTSB(1), 3/85/14 OTSB(40), 3/85/18 OTSB(3), 3/85/26 OTSB(1), 3/85/43 OTSB(37). [225 m to 990–1020 m]

DISTRIBUTION. The new records are all from the Hebridean Slope and extend the lower bathymetric limit within the Trough by some 200 m. This species appears to be most common in the 500–800 m depth zone in this area.

Brissopsis ?lyrifera (Forbes, 1841)

See: Mortensen, 1907: 152–160, pl. 3, figs 2, 3, 7, 11, 12, 18, 20–23, pl. 4, figs 2, 3, 9, 14–17, pl. 18, figs 1, 6, 12, 18, 25–26, pl. 19, figs 3, 6, 10, 15, 18–21, 29, 34; 1927: 338–340, figs 200, 201; 1951: 380–390, pl. 30, figs 1–4, 7–13, pl. 32, figs 15, 20, 22, pl. 57, fig. 15; Gage *et al.*, 1985*a*: 187, fig. 3 (as *Brissopsis* sp.).

SAMPLES. ES 99(1), AT 239(31 + fragments). [1047–1160 m]

DISTRIBUTION. NE. Atlantic from Lofoten, S. and W. Iceland along the European coasts and the Mediterranean to S. of the Canaries; *c.* 5–1400 m; in soft mud.

REMARKS. Except for the specimen from ES 99, the present material is all from a large haul (AT 239) of small, very fragile specimens, most of which were broken when examined. In this haul the cod-end of the trawl was full of a muddy deposit containing *Brissopsis*, specimens of *Hemiaster expergitus* (see above), and a single specimen of *Brisaster fragilis* (see below). The largest intact specimen measures 22·9 mm and the smallest 9 mm in test length. It is likely that smaller specimens had been lost through the 10 mm-wide meshes of the trawl.

B. lyrifera is typically an inshore species, with only a few, somewhat doubtful records from deep water (Mortensen, 1927). For example, it seems very unlikely that it is this species that Thomson (1874) records from depths to 2090 fathoms (3873 m) from the *Porcupine* in 1869. However, the absence of any confluence in the posterior petals of the present material from deep water immediately distinguishes it from the species *Brissopsis atlantica* and *B. mediterranea* which are known to occur to bathyal depths in the western Atlantic (Chesher, 1968). Furthermore, *B. mediterranea*, although known from the eastern Atlantic and Mediterranean, is thought there to be restricted to relatively shallow water.

The present specimens are similar in size and appearance to two lots, each consisting of two partly broken specimens about 15 mm in length, labelled as *Brissopsis lyrifera*, in the collections of the British Museum (Natural History) (BMNH). These were dredged by the *Triton* (presumably on her voyage in 1882, see Deacon, 1977) from 942 m and 1170 m depth, respectively, from the Wyville Thomson Ridge and Faroe Bank Channel. A larger specimen at BMNH measuring 27·5 mm length was collected by the *Helga* in 1909 from the Porcupine Seabight at 956–1088 m depth (see Farran, 1913). The fragmented specimen recorded under '*Brissopsis* sp.' in Part 2 that was taken from the same area and depth on the upper Hebridean Slope as the specimens from AT 239 is now identified as *Brissopsis ?lyrifera*. On the basis of the lengths and widths of the anterior and posterior petals it is estimated that this specimen was about 30 mm in test length. The pedicellaria in Fig. 3a, b of Part 2 from this specimen is a rostrate pedicellaria and not globiferous as labelled. Similar rostrate pedicellariae were found on inshore *B. lyrifera*. Examples of the double-pronged globiferous pedicellariae typical of *B. lyrifera* were not found on any of the deep-water specimens from BMNH. The tridentate pedicellaria in figure 3c of Part 2 that was also obtained from the large fragmented specimen from ES 99 agrees somewhat with Mortensen's

Table 2 Critical morphometric characters of deep-water *Brissopsis ? lyrifera* compared to inshore specimens of *B. lyrifera* from the W. of Scotland. Measurements standardised as percentages of test length

Character (see Chesher, 1968)	LOCALITY Arran Deep 40·9–70 mm length, n = 23		The Minch 32·0–53 mm length, n = 5		Hebridean Slope 14·4–22·9 mm length, n = 4		Faroe Bank Channel, *Triton* 15·3 mm length, n = 1	Porcupine Seabight, *Helga* 27·5 mm length, n = 1
	Mean	S.D.	Mean	S.D.	Mean	S.D.		
Test height	51·43	6·41	60·5	3·9	*66·63	1·43	*73·2	*65·5
Length anterior petal	29·02	3·51	26·4	2·3	23·40	2·30	*20·9	*22·2
Length posterior petal	23·49	3·15	22·0	1·2	*15·86	1·22	*16·3	*14·5
Length from apical system to peripetalous fasciole:								
at interambulacrum 5	18·10	2·37	14·9	1·0	*12·95	0·63	*12·2	14·5
at interambulacrum 4	21·55	2·31	20·9	1·2	18·09	0·95	20·3	*16·4
Span of distal ends of anterior petals	49·63	4·68	43·6	3·0	*37·56	0·39	*33·3	*36·5
Span of distal ends of posterior petals	31·80	3·65	24·8	1·9	*19·65	1·35	*17·0	*18·2
Width of subanal fasciole	43·76	4·04	39·3	2·6	*30·81	4·85	*33·3	*31·3
Height of subanal fasciole	19·32	1·73	21·3	1·6	20·58	2·04	*25·5	15·5

*Outside ± 2 S.D. of mean of urchins from Arran Deep

(1907) third form of tridentate of *B. lyrifera*, examples of the other two kinds, although described by Mortensen as richly developed, not being found on the present specimens. However, a typical form of the largest, narrow-bladed variety of tridentate pedicellaria, with the valves rather widely separated along their lower length, was found on one of the *B. lyrifera* from the *Triton*. Not surprisingly, no pedicellariae were found on the somewhat denuded specimens from AT 239.

Measurements of 21 of the morphometric characters of the test, established by Chesher (1968), were made on the *Triton* and *Helga* specimens (although the accuracy of many of these is reduced as a result of not removing their spines) and on the present material from AT 239. In Table 2 these data are compared to similar measurements on inshore specimens dredged in 1968 from *c.* 165 m depth in the Arran Deep, Firth of Clyde, in the possession of J. D. G. The relatively small number and limited size range of the sample of inshore specimens is insufficient to adequately define the natural variation in this species, in which monstrosities in test form are known to occur (Brattstrom, 1946, Mortensen, 1951). However, measurements on specimens in BMNH trawled from stations in the Minch (*c.* 58°N, 06′W) by the Scottish Fisheries Board in 1927, nearly all lie within 2 S.D. of the mean of the measurements on those from the Arran Deep, only measurements of the span of the posterior petals on two specimens in one of the hauls falling slightly below this range. In contrast, values of 9 out of 21 characters measured on the small deep-water urchins fall outside 2 S.D. of the mean for the Arran Deep sample for some specimens while for 5 of these characters measurements on all specimens fall outside this range (Table 2).

The present, and our previous, finds of this urchin in the SMBA samples concur with Thomson (1874) who noted that at great depths specimens of *B. lyrifera* decrease in size, having '. . . all the appearance of being very young . . .'. However, on the present material genital pores were present on specimens as small as 15 mm test length, which also possessed small gonads, indicating that sexual maturity is reached at a small size.

Such differences might suggest that the deep water urchins constitute a distinct taxonomic entity. However, *Brissopsis lyrifera* is known to have a planktotrophic echinopluteus that may be dispersed over wide areas. Since such larvae are likely to stay in the plankton for some time, it seems likely that the deep-water populations off the W. of Scotland are in genetic continuity with inshore stocks. The small size of the deep-water individuals possibly then results from dwarfing as a result of resource limitation in the deep sea. The differences in test characters may possibly reflect other differences in bottom conditions as well as their smaller size. Until the range of variation amongst larger inshore samples, covering both a wider range in size and bottom environment, becomes better understood the possible separate identity of the deep-water urchins must remain uncertain.

Brisaster fragilis (Düben & Koren, 1844)

See: Mortensen, 1907: 108–123, pl. 1, figs 6–7, pl. 13, pl. 14, fig. 3, 7, 11, 13, 16, 18, 20, 24–25, 31, 37, 39, 43, 46, 50–51; 1927: 325–326, figs 187, 2–3, fig. 188, 2, fig. 189, 1–2.

SAMPLES. SBC 224(1), AT 239(juvenile 1). [903–1047 m]

DISTRIBUTION. NE. Atlantic from Finmark to Bergen, to north and west of the Shetlands, the Faroe–Shetland Channel, and from south and west of Iceland. In the western Atlantic from the Davis Strait to Florida; *c.* 65–1300 m on soft mud.

REMARKS. The single specimen recovered in perfect condition from a box-core sample (SBC 224) measures 38 mm in overall test length. It was collected from 903 m depth in the Faroe Shetland Channel, where this species was previously taken by the *Porcupine* at about the same depth. The juvenile specimen from AT 239 measures 10·5 mm test length and was recovered from 1047 m on the upper continental slope west of Barra in a haul containing a mixed sample of small *Brissopsis ?lyrifera* and juvenile *Hemiaster expergitus*. As shown in the growth series figured and described by Mortensen (1907, pl. 13) the posterior petals at this size are relatively undeveloped. Genital pores, indicating sexual maturity, were not found, although Mortensen (1907) remarks that they appear at a size of 9–11 mm.

The present records extend the recorded range of this species in the NE. Atlantic from the Faroe Shetland Channel to a latitude of 57°N in the Rockall Trough.

Reproduction. The large yolky eggs of *Brisaster fragilis* are thought to indicate direct development (Mortensen, 1907, 1927).

Order **POURTALESIOIDA**
Family **POURTALESIIDAE**

Pourtalesia miranda A. Agassiz, 1869

Samples. ES 59(8), ES 118(2), ES 120(2), ES 122(4), ES 143(3), ES 147(2), ES 152(3), ES 164(3), ES 204(9 [not 54 as stated in Part 2], ?[juvenile] 1), ES 207(6), ES 266(2), AT 282(1), ES 283(1). [2245–2946 m]

Distribution. The additional records extend the lower bathymetric limit slightly within the Trough.

Echinosigra phiale (Wyville Thomson, 1874)

Samples. ES 27(24), ES 59(2), ES 111(2), ES 118(7), AT 121(14), ES 122(10), ES 129(9), AT 153(2), ES 172(23), ES 180(3), ES 184(1), ES 185(37), ES 197(5), ES 204(19), ES 207(15), ES 218(4), ES 231(6), AT 245(2), ES 257(1), AT 267(5), AT 282(6), ES 283(14), ES 285(3), AT 286(2), ES 289(2). [1993–2946 m]

Distribution. The lower bathymetric limit within the Trough is extended slightly and predictably, given the abyssal distribution of this species.

Life History. Counts of growth zones present in the plates of the test indicate a size of 50 mm length may be reached by an age of 5–8 yr (Gage, 1987).

Class **HOLOTHURIOIDEA**
Order **DENDROCHIROTIDA**
Family **PSOLIDAE**

Psolus pourtalesi Théel, 1886

Sample. AT 247(233). [2084–2190 m]

Distribution. This sample, like the first described in Part 2 (Gage *et al.*, 1985*a*) was taken from the west side of the Trough. The specimens were recovered from the base of Rosemary Bank close to areas where this species was found during the *Ingolf* Expedition (Heding, 1942). Gage *et al.* (1985*a*) followed Mortensen (1927) in reporting *P. pourtalesi* from the West Indies. Mortensen (1927) cited specimens from the *Blake* Expedition (Theel, 1886*b*), but these came from the eastern seaboard of North America, not the West Indies. *P. pourtalesi* has not been recorded south of 39°N in the western Atlantic. The lower bathymetric limit reported in Part 2 as 2271 m should be increased slightly to 2341 m to include the records of Deichmann (1940). The total range is therefore 1096–2341 m.

Remarks. Heding (1942) and Gage *et al.* (1985*a*) refer to this species as *P. pourtalesii* but it should be referred to as *P. pourtalesi* as in the original description (Théel, 1886*b*).

The present specimens were found attached to a collection of small, probably ice-rafted, cobbles. The specimens range from 12–33 mm in length. There is some suggestion of bimodality in the size distribution, with a small mode around 16 mm and a much larger mode around 25 mm (Table 3).

Table 3 *Psolus pourtalesi* length frequencies from station AT 247

	Lower bound of size class (mm)																						
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
Frequency	1	3	2	2	5	4	3	8	13	12	13	32	28	33	24	16	13	5	7	3	2	1	(n = 230)

Family **PARACUCUMIDAE**

Paracucumaria hyndmani (Thompson, 1840)

See: Mortensen, 1927: 400-401, figs 237, 3; 239, 1 (as *Cucumaria hyndmani*); Madsen, 1942: 395–406, figs 1–6 (as *Cucumaria hyndmani*).

SAMPLE. 13/83/8 OTSB(1). [500–560 m]

DISTRIBUTION. The coasts of Europe from the Mediterranean north to the Shetland Isles and the coast of Norway including Rockall Bank. Mortensen (1927) notes that it is usually found in deep water, *c.* 20–1150 m. The present specimen was taken at the top of the Hebridean Slope.

REMARKS. Madsen (1942) recognised two forms of the species which he considered 'would prove to be of two geographical races of the same species': a more northern *P. (Cucumaria) hyndmani* f. *typica* and a more southern *P. (Cucumaria) hyndmani* f. *robusta*. Our single specimen agrees with the northern form and is close to the locality of a deep-water specimen examined by Madsen (1942, p. 405).

Family **SCLERODACTYLIDAE**

Pseudothyone raphanus (Düben & Koren, 1844)

See: Mortensen, 1927: 407–408, fig. 242: 2, 245: 1 (as *Thyone raphanus*); Panning, 1949: 456–457, fig. 52.

SAMPLE. SBC 222(4, ?[juveniles] 2), AT 248(11). [1101–1150 m]

DISTRIBUTION. *P. raphanus* occurs around the coasts of the British Isles and Norway as far north as *c.* 65°N. It is also known to occur in the Mediterranean. Bathymetric range *c.* 10–1050 m, the present records extending this slightly to 1150 m.

REMARKS. The two juvenile specimens from SBC 222, both 1 mm long, have only primary cross deposits which differ from the plate deposits normally found in adult *P. raphanus*. However, primary cross deposits are the precursors to plates, and in specimens intermediate in size, 3 to 4 mm long, both types of deposits occur.

Family **CUCUMARIIDAE**

Thyone fusus (O. F. Müller, 1776)

See: Madsen, 1941: 17–26, Figs 3b, 4g–h, 7b, 12–16.

SAMPLES. SBC 211(juvenile, 1). [402 m]

DISTRIBUTION. Northeast Atlantic from Trondheim Fjord to the Mediterranean, including the North Sea and adjacent Scandinavian Seas. There is some uncertainty in the bathymetric range of this species since *T. fusus* has been confused in the past with other species, such as *T. gadeana* Perrier and *T. wahrbergi* Madsen. From his analysis of Scandinavian holothurians, Hansen considers that *T. fusus* generally occurs between 10 and 200 m (Hansen, pers. comm.). The present specimen from 402 m increases the lower bathymetric limit. However, since the specimen is a juvenile it is possible that as with several asteroids, ophiuroids and echinoids (Gage *et al.* 1983, 1985*a*) the lower bathymetric limit is greater for juveniles than for adults.

REMARKS. The specimen is only 2·5 mm long. The deposits of the body wall are irregular polyporous plates similar to those described for *T. fusus* f. *subvillosa* (Hérouard, 1890; Madsen, 1941) with a spire made of two slender columns as in *T. fusus* and unlike those of *T. wahrbergi* and *T. gadeana*. The tubefeet are large in comparison to the size of the body and have terminal plates 100 to 125 μm in diameter. These are smaller than the plates found in adult specimens but possess the concentric circles of large holes typical of *T. fusus*. The size of the specimen precluded an examination of the tentacle deposits.

Order **DACTYLOCHIROTIDA**
Family **YPSILOTHURIIDAE**

Ypsilothuria talismani talismani E. Perrier, 1886

Samples. SBC 168(3), SBC 222(10, juvenile 1), AT 226(1), AT 230(2), AT 239(37), AT 248(8), ES 250(38). [*c.* 1000–1271 m]

Distribution. These additional records extend the distribution of this species to the North Feni Ridge and provide a geographical link between our previous records from the Rockall Trough and those of the *Ingolf* from Iceland. Furthermore they confirm the essentially bathyal distribution of this species.

Ypsilothuria bitentaculata attenuata R. Perrier, 1902

Samples. ES 27(79, juvenile 1), ES 56(15), ES 111(23), ES 118(37), ES 129(30), ES 184(31, juvenile 15), ES 185(221), ES 190(48), ES 200(113), ES 204(33 [not 78 as stated in Part 2]), ES 218(92), ES 231(97), ES 232(18), AT 233(2), ES 244(20), AT 245(268), ES 261(1), ES 266(4), AT 267(80), AT 271(4), AT 273(10), AT 282(5), ES 283(67), ES 285(5), AT 286(7), AT 288(6), ES 289(41). [1862–2951 m]

Distribution. No change.

Echinocucumis hispida (Barrett, 1857)

Samples. SBC 222(juveniles, 3), AT 248(8), ES 250(13), 3/85/9 OTSB(1). [945–1270 m]

Distribution. These records from the Feni Ridge and Hebridean Slope broaden the known geographic and bathymetric range of this species within the Trough.

Order **ASPIDOCHIROTIDA**
Family **SYNALLACTIDAE**

Bathyplotes natans (M. Sars, 1868)

Samples. AT 239(37), AT 248(3), AT 249(1), AT 259(1), 13/83/2 OTSB(25), 3/85/36 OTSB(2). [1000–1025 m to 1130–1265 m]

Distribution. No change.

Remarks. These specimens were in better condition than those described in Part 2, and had spicules present in both the skin and papillae. A mid ventral groove was a distinctive feature of the better preserved specimens. The colour in spirit was off-white with the orange body organs showing faintly through the skin.

Benthothuria funebris R. Perrier, 1902

Samples. ES 204(2), AT 284(1), ES 285(1), AT 286(9), 3/85/5 OTSB(9). [2890–2996 m]

Distribution. No change.

Paelopatides grisea R. Perrier, 1902

Samples. AT 219(1), AT 273(7), AT 288(1), 13/83/5 OTSB(35), 9/84/9 OTSB(18), 3/85/29 OTSB(3). [1690–1740 m to 2190 m]

Distribution. These are the first records from the Rockall Trough, the single sample recorded in Part 2 having been taken in the Porcupine Seabight. They are all from the area between the lower Hebridean Slope and the Anton Dohrn Seamount and fall within the known bathymetric range.

Mesothuria lactea (Théel, 1886)

Samples. AT 254(2), ES 255(7), 13/83/5 OTSB(1), 9/84/9 OTSB(13), 3/85/29 OTSB(86). [1595 m to 1775–1835 m]

DISTRIBUTION. These records from the North Feni Ridge and Hebridean Slope confirm the bathymetric distribution reported by Hérouard (1923) for the NE. Atlantic. The Rockall records suggest a ribbon-like distribution along the margins of the Trough.

Mesothuria intestinalis (Ascanius & Rathke, 1767)

See: Mortensen, 1927: 381, figs 225, 228: 3; Heding, 1942: 7, text-fig. 6.

SAMPLES. AT 292(1), 3/85/38 OTSB(1). [410–490 m to 525 m]

DISTRIBUTION. Widely distributed in the NE. Atlantic from off NW. Africa (Hérouard, 1923) to the coasts of Norway, although nowhere in the deep sea does it appear to be particularly common. A few specimens are known from the Mediterranean (see Perrier, 1902; Koehler, 1927; Sibuet, 1974) and the western Atlantic (Deichmann, 1930). The species has a wide bathymetric range *c.* 18–1445 m, but reports of this species occurring as deep as 2000 m , appear to be the result of confusion with *Mesothuria verrilli.* The shallowest records come only from cold waters off Norway. The present records are from the upper Hebridean Slope.

Mesothuria verrilli (Théel, 1886)

See: Mortensen, 1927: 381, 382, fig. 224: 4–5; Deichmann, 1930: 93–94, pl. 6, figs 1–8.

SAMPLES. AT 287(2), 3/85/30 OTSB(1). [1383 m to 1420–1480 m]

DISTRIBUTION. Widely distributed in the north Atlantic with some records from the Mediterranean. In the western Atlantic it is known from the Caribbean Sea, eastern Gulf of Mexico (Deichmann, 1954; Miller & Pawson, 1984) and off the Bahamas (Pawson, 1982). In the eastern Atlantic it is previously known from NW. Africa, the Canary Islands (Perrier, 1902), the Azores (Hérouard, 1902, 1923; Perrier, 1902), the Bay of Biscay (Sibuet, 1977) and as far north as the Porcupine Seabight, southwest of Ireland (Mortensen, 1927). The present records extend the distribution northwards into the Rockall Trough on the Hebridean Slope.

The bathymetric range is not known with certainty partly as a result of confusion with *M. intestinalis.* Hansen (1975) gives a wide bathymetric range of 618–4165 m for *M. verrilli* in the Atlantic and 280 to 1103 m in the Mediterranean. With the aid of detailed bathymetric charts available today it is possible to see that all reliable records of this species deeper than 2000 m come from areas where the seabed is particularly steep e.g. on the continental slope off NW. Africa or in the area of the King's Trough (see Perrier (1902) for details of some stations). The accuracy of the depths from which some samples were taken must therefore be called into question. This also applies to a shallow sample of *M. verrilli* on the Magazan escarpment in 550 m (Perrier, 1902). Mortensen (1927) gives a reduced range of *c.* 990–1765 m for *M. verrilli* sampled to the southwest of Ireland. Recent intensive sampling in the same area, the Porcupine Seabight, confirms this total range but indicates that *M. verrilli* is only common in a reduced range between 1250 and 1500 m (Billett, in preparation). The present samples from the Hebridean Slope fall within this narrower range, as do most of those taken off the Azores (Marenzeller, 1893; Hérouard, 1902, 1923; Perrier, 1902).

The samples from the eastern Atlantic fall within the total range proposed for *M. verrilli* in the western Atlantic of 699–3720 m (Deichmann, 1954; Miller & Pawson, 1984; Pawson, 1982; Suchanek *et al.*, 1985). The study of Suchanek *et al.* (1985) increased the lower bathymetric limit from 2141 to 3720 m. The shallowest record, from 618 m, quoted by Hansen (1975) for material from the Atlantic should be referred to specimens collected within the Mediterranean.

REMARKS. In the western Atlantic *M. verrilli* is known to cover itself with detrital seagrass and shell material such as the seagrass *Thalassia* and brachiopod shells (Suchanek *et at.*, 1985).

Family **STICHOPODIDAE**

Stichopus tremulus (Gunnerus, 1767)

SAMPLES. AT 292(4), 13/83/3 GT(14), 13/83/4 GT(29), 13/83/7 OTSB(1), 13/83/8 OTSB(91), 3/85/9 OTSB (juvenile 1), 3/85/14 OTSB(6), 3/85/18 OTSB(1), 3/85/38 OTSB(2), 3/85/43 OTSB(18), 3/85/44 OTSB(4). [168 m to 990–1020 m]

Distribution. The new records from the Hebridean Slope extend the lower bathymetric limit within the Trough by some 300 m.

Order **ELASIPODIDA**

Family **LAETMOGONIDAE**

Laetmogone violacea Théel, 1879

Samples. AT 239(11), AT 248(9), AT 249(5), ES 250(1), AT 259(37), GT 8(6), 13/83/2 OTSB(5), 13/83/6 OTSB(157), 13/83/7 OTSB(9), 9/84/13 OTSB(54), 3/85/18 MBA(4), 3/85/19 MBA(7), 3/85/20 OTSB(112), 3/85/22 MBA(7), 3/85/23 OTSB(18), 3/85/24 OTSB(35), 3/85/25 OTSB(99), 3/85/28 OTSB(3), 3/85/33 OTSB(126). [940–975 m to 1400(3000) m]

Distribution. The new records from the North Feni Ridge and Hebridean Slope indicate the presence of large populations of this species in suitable localities.

Reproduction. A non-seasonal cycle with abbreviated development is indicated (Tyler *et al.*, 1985*b*).

Benthogone rosea Koehler, 1896

Samples. AT 271(10), 13/83/5 OTSB(3). [1745–2255 m]

Distribution. No change.

Reproduction. Direct development is indicated by the large oocyte size and there is no evidence of seasonality in oogenesis (Tyler *et al.*, 1985*b*).

Family **PSYCHROPOTIDAE**

Psychropotes longicauda Théel, 1882

Sample. SWT 15(3) (incorrectly listed in Part 2 as SWT 5(3)). [2910–4810 m]

Remarks. *P. longicauda* has the largest known egg size for a holothurian at 4·4 mm diameter (Hansen, 1975). This size of egg probably leads to a prolonged form of early development within the deep-sea plankton, and juveniles of this species 13–23 mm in length have been recovered in pelagic nets fished at between 17 and 1500 m above the seabed at abyssal depths (Billett *et al.*, 1985).

Family **ELPIDIIDAE**

Peniagone azorica von Marenzeller, 1893

Samples. AT 121(79), AT 271(23). [1991–3463 m]

Distribution. No change.

Reproduction. Additional information to that given for this species in Part 2 is provided by Tyler *et al.* (1985*a*).

Kolga hyalina Danielssen & Koren, 1879

Samples. ES 266(61). [2591–2910 m]

Distribution. These records extend the geographic range within the Rockall Trough of this patchily distributed species to the north central part of the Trough and Feni Ridge.

Ellipinion delagei (Hérouard, 1896)

See: Hérouard, 1902: 39–40, pl. 6 figs 1–3, pl. 8 figs 8–9; Hansen, 1975: 163, fig. 122.

Sample. AT 247(18). [2084 m]

Distribution. An extremely rare species found previously only around the Azores and Cape Verde Islands close to steep slopes (Hérouard, 1902, 1923). The presence of specimens on the Rosemary Bank indicates a preference for steep topography by this species, particularly around seamounts and oceanic islands in the N. Atlantic. The total bathymetric range is 1165–2478 m.

Remarks. Only one specimen is in good condition. It widens towards the posterior end and has 12 pairs of tubefeet bordering the entire ventral surface. Those tubefeet at the anterior end are spaced more widely than those at the posterior end. The posterior few pairs of tubefeet are slightly smaller than the rest. The deposits include large rods (up to 550 μm long), regular c-shaped deposits (about 130 μm long) and small irregularly curved rods (40–50 μm in size) which are usually c-shaped and are often developed into tripartite deposits (Hérouard, 1902).

Order **APODIDA**

Family **SYNAPTIDAE**

Labidoplax southwardorum Gage, 1985

Samples. ES 10(1), ES 34(?2), ES 53(1), SBC 66(?3), ES 129(8, ?3), ES 137(3), ES 172(6), ES 176(10 [not 22 as stated in Part 2]), ES 185(21), ES 190(7), ES 197(?20), ES 200(1), ES 204(1), ES 218(16), SBC 220(2), ES 244(10), ES 283(37), ES 285(1), ES 289(6). [1000–2946 m]

Distribution. The new records provide a slight extension of the lower bathymetric limit.

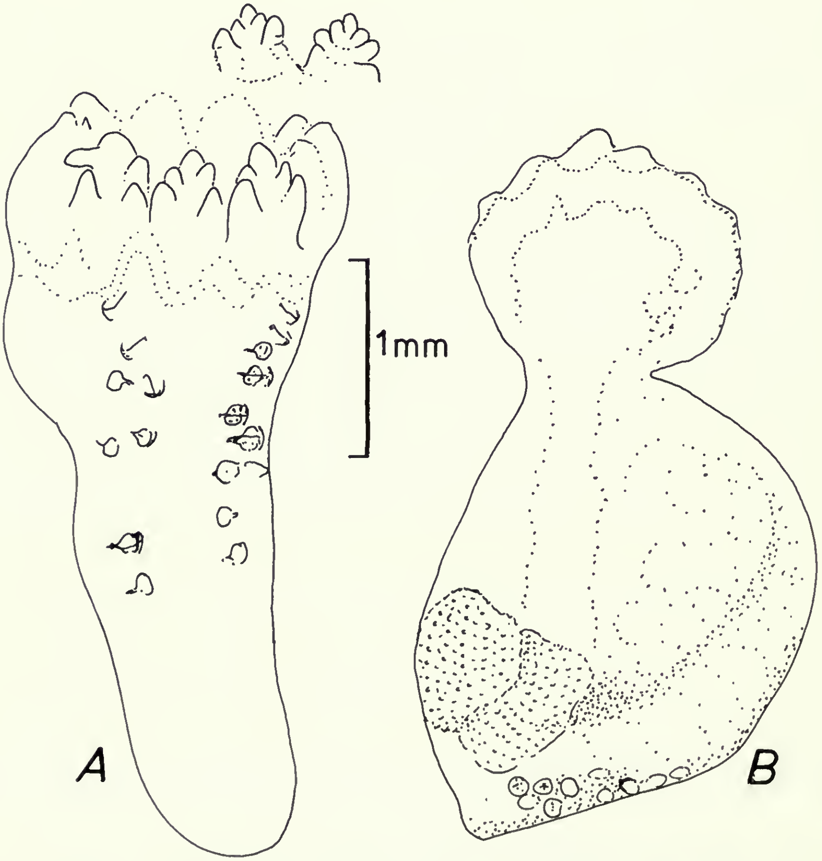

Fig. 3 (A) *Labidoplax similimedia* from SBC 222: entire, uncontracted specimen showing pinnate tentacles and position of plates and anchors in body wall; (B) *Prototrochus zenkevitchi rockallensis* from SBC 220: entire specimen showing sac-like body distended with sediment. Scale bar = 1 mm.

Labidoplax similimedia Gage, 1985

Samples. ES 118(1), ES 129(2), ES 137(4), ES 143(?1), ES 164(87), ES 169(4), ES 185(4), ES 218(?2), SBC 222(8), ES 244(1), ES 283(6), ES 285(1), ES 289(2). [1101–2946 m]

Distribution. The new records provide an upward extension of the bathymetric range by *c.* 1100 m, and also an extension of the lower bathymetric limit.

Remarks. Several of the specimens from SBC 222 are complete (Fig. 3A), with the skin deposits scattered in the body wall rather than crowded together and overlapping as described by Gage (1985), and as found in the other material from epibenthic sled hauls. This is no doubt because the specimen is not severely contracted as material usually is when collected by the epibenthic sledge. The plates and anchors have a lateral orientation in the body wall (Fig. 3A) similar to that of other synaptids. The tentacles are clearly pinnate with two pairs of rounded lateral, and a single terminal, digit (Fig. 3A).

Leptosynapta decaria (Östergren, 1905)

See: Östergren, 1905: 146–148, fig. 1B; Clark, 1907: 93; Mortensen, 1927: 431, fig. 262, 3.

Sample. SBC 210(1 + frag.). [401 m]

Distribution. Hitherto known only from the Trondheim Fjord to the Kattegat, 40–70 m depth.

Remarks. The material consists of an anterior end with the oral ring measuring 1.41 mm in diameter along with a posterior end, quite possibly from the same specimen, around 0.6 mm wide. Both fragments were whitish in colour with no trace of pigmentation when examined from spirit. There are 10 tentacles, each with a short terminal digit and three pairs of short rounded digits, increasing in size distally. Deposits consist of plates and anchors, which are found in the skin of both fragments, and rods present only in the tentacles. The rods, which are slightly curved and possess enlarged, branched ends (Fig. 4), are numerous and present throughout the tentacles, increasing in size distally. Skin deposits (Fig. 4) consist of plates typical in form of *Leptosynapta,* with nine toothed holes, the outermost and central holes being the largest. In the anterior fragment the plates have a mean length of 124·8 µm, range 116–138 ($n = 28$) and mean width of 99·1 µm, range 90–113 ($n = 14$). This agrees well with the values of 126·5 and 97·5 µm, respectively, given by Östergren (1905) for the deposits from the anterior of the animal. The anchors agree well with Östergren's description; resembling those of *Leptosynapta inhaerens* but being smaller and possessing up to 5 (usually 3) teeth on each fluke. Anchors are slightly longer but narrower than the plates, mean length 144 µm, range 127–160 µm ($n = 23$), mean width 73·1 µm, range 70–75 ($n = 8$). These values are also reasonably close to the values given by Östergren (149 × 97 µm). Besides the fully developed plates and anchors there are a number of developmental stages of both deposits present (Fig. 4).

The deposits in the posterior end are similar to those in the anterior fragment, but slightly larger (plates, mean length 130 µm, mean width 98 µm; anchors, mean length 143, mean width 72 µm $n = 4$). Assuming that the two fragments belong to the same animal, it is pertinent to note that in *Leptosynapta*, it is usual for the deposits to increase in size posteriorly (Östergren, 1905; Cherbonnier, 1953, 1963). Both the whitish colour and diameter of the head-end fragment (1·4 mm) is similar to that (1·5–3 mm) described by Östergren for *L. decaria*, and the three pairs of tentacle digits present is within the range of 2–4 pairs on each tentacle described by Östergren (1905).

Only two European species of *Leptosynapta* are known to possess 10 rather than the 12 tentacles typical of other species of the genus; *L. minuta* (Becher), a tiny viviparous species known from shallow water off NW Europe, and *L. decaria*. Both species are small and appear to lack pigmentation. The present specimen differs from *L. minuta* in possessing tentacle digits, in having anchors clearly longer than the plates (Fig. 4), and in having at the basal (articular) end of the plate small irregularly arranged holes, typical of most *Leptosynapta* species, rather than the regular slit-like holes of *L. minuta*. Östergren (1905) found specimens of *L. inhaerens* with 10, 11 or 13 tentacles, this possibly influencing Clark (1907) to suggest that '. . . it is not impossible that this [*L. decaria*] is

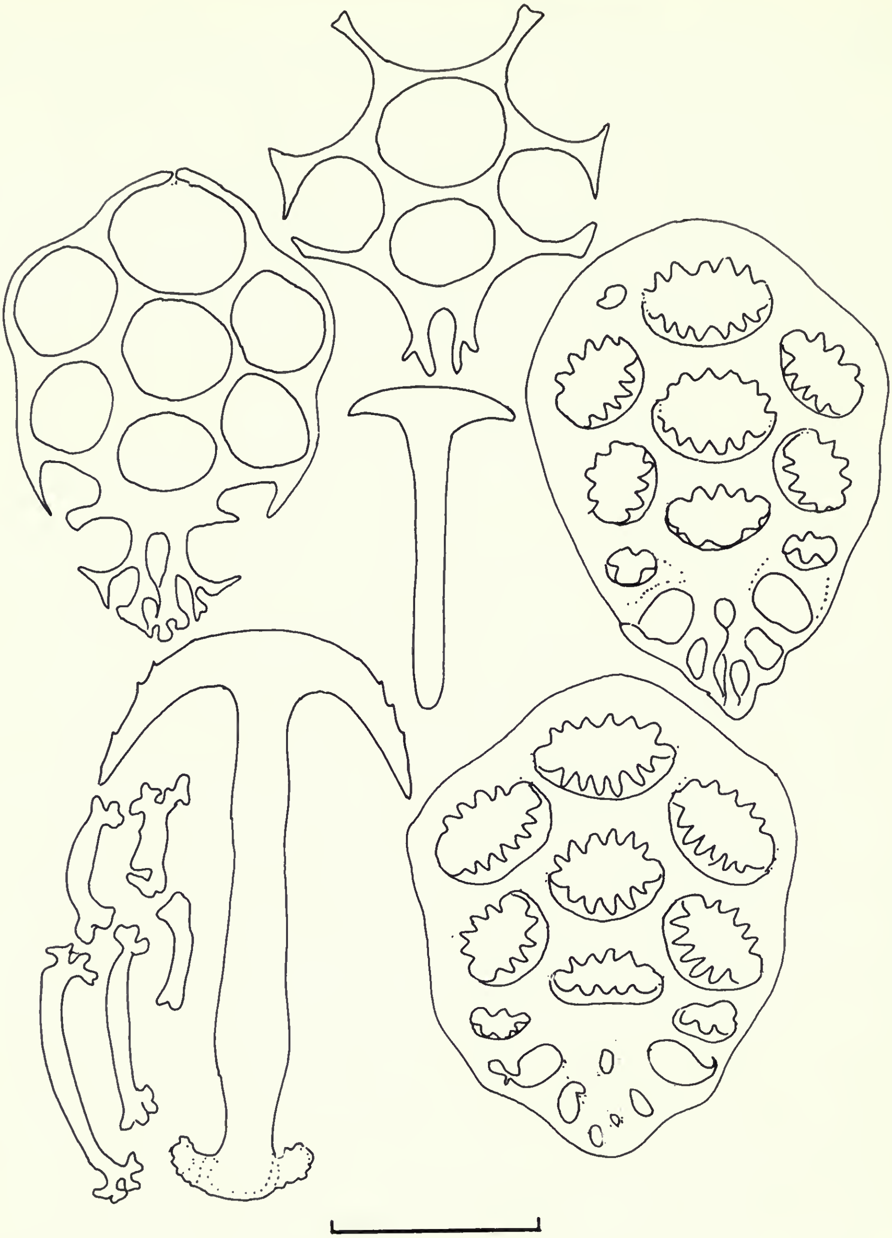

Fig. 4 Skin deposits from anterior fragment of *Leptosynapta decaria* from SBC 210. Fully developed (middle and lower right) and developing plates (upper left); fully developed (lower left) and developing (centre) anchor; rods from tentacles, lower left. Scale bar = 50 µm.

only the young of *inhaerens*. There is a striking similarity in the calcareous particles and in the tentacles, the differences in number of digits being simply a matter of age.' Dr Bent Hansen of the Zoological Museum, University of Copenhagen has confirmed (unpublished communication to J.D.G) that there appears to be no published record of *L. decaria* subsequent to Östergren's (1905) paper. Dr Hansen very kindly re-examined Norwegian material from Tromso and Oslo, including

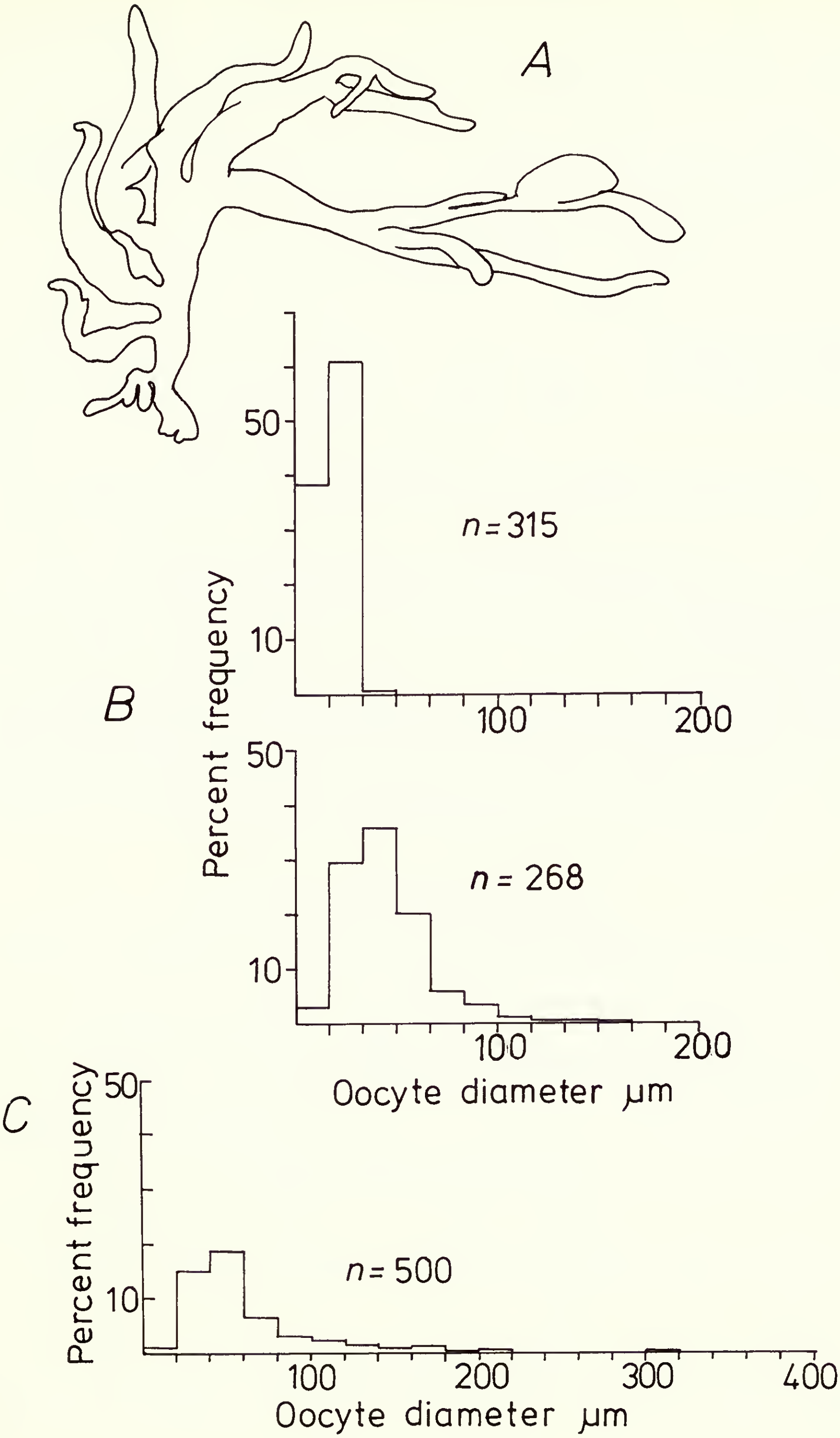

Fig. 5 (A) Ovary dissected from a female *Myriotrochus bathybius* from ES 207 with a calcareous ring diameter of 4·5 mm; (B) oocyte diameter frequencies from this specimen (lower) and from a smaller *M. bathybius* from ES 207 (upper); (C) oocyte diameter frequencies from a female of *Myriotrochus giganteus* from ES 207.

specimens examined by Östergren, held in the Zoological Museum and also informs us that he considers that *L. decaria* is a valid species. He has also drawn our attention to a single record of *L. decaria* from 1 fathom depth in Port Erin Harbour in the Isle of Man dated 1933 that he was also able to re-examine and confirm as conforming to Östergren's description of *L.* decaria. With the present record from 401 m depth we conclude that *Leptosynapta decaria* exists as a distinct species with a rather wide bathymetric distribution in muddy sediments of the continental shelf and adjacent upper slope of the more northerly areas of Europe. It is a small form that may well have been overlooked or lost when sieving benthic samples.

Protankyra brychia (Verrill, 1885)

Sample. ES 118(1). [2871–2925 m]

Distribution. No change.

Family **MYRIOTROCHIDAE**

Myriotrochus bathybius H. L. Clark, 1920

See: Gage & Billett, 1986: 234–239, figs 1, 3–6, 7A, B, 9A, B, 18B.

Samples. ES 152(2), ES 185(3), ES 231(6), AT 267(1), AT 282(3), ES 283(2), ES 289(1). [1800–2946 m]

Distribution. The combined bathymetric data for samples of *M. bathybius* taken in the Rockall Trough and on the Porcupine Abyssal Plain gives a total bathymetric range of 1800 to 4310 m (Gage & Billett, 1986).

Reproduction. The reference in Part 2 to Gage & Billett (in press) for details of the reproduction of this species was incorrect, and further information is therefore provided here. One of the pair of branched ovaries is shown in Fig. 5A from an incomplete female specimen with a calcareous ring diameter of 4·5 mm. It contained previtellogenic oocytes measuring up to 160 µm in longest diameter (Fig. 5B). In a smaller specimen from the same sample (ES 207) the maximum oocyte size did not exceed 60 µm (Fig. 5B).

Myriotrochus giganteus H. L. Clark, 1920

See: Gage & Billett, 1986: 239–247, figs 1, 7C, 8, 9C, 10–12, 24B.

Samples. ES 169(1), ES 231(1), ES 283(1). [2898–2946 m]

Distribution. The new records provide a slight extension of the lower bathymetric limit within the Trough. The total known bathymetric range is 2898 to 3800 m.

Reproduction. The maximum dimension of the irregularly shaped, vitellogenic oocytes of the specimen from ES 207 referred to by Gage *et al.* (1985*a*) is 320 µm and not 211 × 169 µm as given. However, the overall size distribution of the oocytes was, like those for *M. bathybius*, markedly skewed to the left, with the size frequencies peaking in the intervals between 20–60 µm (Fig. 5C).

Myriotrochus clarki Gage & Billett, 1986

See: Gage & Billett, 1986: 247–252, figs 1, 7D, 9D, 13–17, 18A; also Gage *et al.* 1985*a*: 203 (as *Myriotrochus* sp.)

Samples. ES 90(1), ES 185(1), ES 218(1), SBC 222(?1), ES 231(2, ?1), ES 232(1), ES 255(1). [*c.* 1040–2907 m]

Distribution. These new records increase the previously known bathymetric range of 1605–2515 m given in part 2.

Prototrochus zenkevitchi rockallensis Gage & Billett, 1986

See: Gage & Billett, 1986: 252–259, figs 1, 7E, F, 18C–E, 19–23, 24A; Gage *et al.*, 1985*a*: 204 (as *P. zenkevitchi* subsp.)

Samples. ES 56(1), ES 118(3), ES 129(7), ES 135(15), ES 147(2), SBC 156(2), SBC 159(1), SBC 160(1), SBC 163(1), SBC 168(3), ES 176(23), ES 184(1), ES 185(3), ES 197(36), ES 204(3), SBC 215(?1), SBC 216(2), ES 218(8), SBC 220(3), SBC 222(2), ES 231(1), ES 232(3), SBC 275(1), SBC 276(1), ES 283(15), ES 285(2), ES 289(5). [*c.* 1000–2946 m]

Distribution. The new records provide a slight increase in the lower bathymetric limit. Other subspecies of *P. zenkevitchi*, however, occur much deeper at between 7400 and 9735 m. A bathymetric range of 1000–9735 m is unprecedented in deep-sea holothurians. Gage & Billett (1986) suggest that the wide geographic and bathymetric separation of such records of myriotrochid species results from the problems of sampling infauna in the deep sea. Possibly, characterisation of separate species will be possible given more material.

Remarks. Developing wheels, still lacking the rim, and with developing, spike-like spokes, have been found amongst the fully developed wheels on a specimen from SBC 220. The largest of the specimens from SBC 220 is complete, the sac-like body, length 2·36 mm, being distended with sediment (Fig. 3B); some of these being calcareous particles that are quite large compared to the size of the animal.

Reproduction. Gonads have not been found in any of the specimens examined by us, perhaps indicating that they are immature.

Parvotrochus belyaevi Gage & Billett, 1986

See: Gage & Billett, 1986: 262–266, figs 1, 24C–F, 26, 27; Gage *et al.*, 1985*a*: 204 (as Myriotrochidae gen. et sp.)

Samples. ES 99(2), ES 147(2), ES 152(3), ES 172(3), ES 204(2), SBC 220(1), ES 285(4). [1160–2921 m]

Distribution. These new records are mainly from the type locality at *c.* 2900 m depth in the southern Rockall Trough. The record from ES 99 in 1160 m extends the known bathymetric range upwards by more than 500 m.

Order **MOLPADIIDA**

Family **MOLPADIIDAE**

Cherbonniera utriculus Sibuet, 1974

Samples. ES 27(242), ES 56(218), ES 111(183), ES 118(74), ES 129(151), SBC 174(1), ES 185(544), ES 190(161), ES 204(144), ES 231(667), ES 283(1180), ES 285(116). [2515–2946 m]

Distribution. The records from ES 283 provide a slight extension of the lower bathymetric range within the Trough. The total bathymetric range is 2039–4251 m.

Reproduction. The oocytes grow to a maximum diameter of 200 μm, and Tyler *et al.* (1987) suggest that development may be planktotrophic. Too few specimens were examined to determine any possible periodicity in reproduction.

Molpadia blakei (Théel, 1886)

Samples. ES 283(1), AT 288(2), 3/85/5 OTSB(1). [1991 m to 2970—2980 m]

Distribution. These records extend the lower bathymetric limit slightly within the Trough and also provide a slight extension northwards.

Molpadia borealis M. Sars, 1858

Sample. AT 107A(1 [No. of specimens omitted in Part 2]). [*c.* 2000 m]

Family **CAUDINIDAE**

Hedingia albicans (Théel, 1886)

See: Heding, 1935: 65–67, figs 18, 19, pl. 4, fig. 9, pl. 5, fig. 17, pl. 8, fig. 10 (as *Haplodactyla albicans*).

Samples. ES 252(1), ES 255(2), AT 256(1). [1510–1706 m]

DISTRIBUTION. Eastern and western Atlantic from off NW. Africa (3200 m), southwest of Iceland (1590–1628 m) and the eastern seaboard of N. America (1600–2423 m). Also known in the Mediterranean, off southern India and in the Bay of Bengal (484–814 m). A variety, var. *glabra* Théel, 1886*a* is known from off New Zealand (1280 m). The present material increases the upper bathymetric limit in the Atlantic to 1510 m, with the total worldwide range 494–3200 m.

REMARKS. Only a few specimens are known from each of these widely separated localities. This may be the result of inefficient sampling of large infaunal animals by trawls and epibenthic sledges. The specimen from AT 256 measures *c*. 27 mm in length. Specimens measuring up to 45 mm in length were found by Heding (1935) to have undeveloped gonads and were hence probably juveniles. The deposits in the body wall of our 27 mm specimen lacked both the trilobed appearance and the thorny spines on the column of some of those figured by Heding (1935, fig. XVIII), possibly because of the relatively small size of the present specimen. It is possible however, that distinct sub-species may be recognisable when more material becomes available.

Discussion

Gage *et al.* (1983, 1985*a*) found a higher species richness amongst the relatively small number of samples taken on the western side of the Trough, despite the much higher sampling effort on the eastern side. This was thought to be related to stronger currents in the west (Jones *et al.*, 1970; Ellett & Roberts, 1973; Roberts, 1975; Lonsdale & Hollister, 1979) favouring microphagous suspension feeders. Many of the species found only in the west, particularly ophiuroids and asteroids, were inferred to feed on current-borne particles. In general these distributions have been confirmed by subsequent sampling but the following species have now been found to have a wider distribution: *Hoplaster spinosus, Psilaster andromeda, Ophiacantha crassidens* and *Amphiophiura saurura.*

Bathymetric zonation for the most abundant echinoderm species in the samples covered by Parts 1 & 2 is summarised by Gage *et al.* 1985*b*. These authors also employed the coincidence-of-range statistic of Backus *et al.* (1965) to describe the rate of change in the joint bathymetric ranges of these species at 100-m depth intervals along a notional transect encompassing most of the sampling effort in the east of the Trough. Peaks in the value of this statistic occur at around 800–1200 and 1800 m depth and were thought to be related to discontinuities in hydrodynamic and water-mass properties.

Despite the frequent sampling in the Rockall Trough since 1973, the echinoderm fauna is still imperfectly known, particularly on the southern Feni Ridge on the west side of the Trough from which only one sample has been taken. Interestingly, seven of the taxa recorded in this series of papers were only found at this station. From a total of 164 echinoderm taxa listed in Parts 1–3, 66 are recorded from less than 10 specimens and 22 of these are from single specimens. Some of these 'rarities' can be explained by the wide depth and geographic distribution of our samples, coupled with a low sampling effort at most stations. It is clear, however, from the more heavily sampled stations where the bottom is thought to be relatively homogeneous, that there are a number of relatively rare species which are widely distributed in the Atlantic e.g.*Hymenaster gennaeus.* The additional species recovered on the Hebridean Slope in 1985 with the semi-balloon otter trawl may reflect the greater catching power of this gear, with an estimated swept path width of 8·5 m compared with either the Agassiz Trawl (3 m) or the epibenthic sledge (1 m).

Given the high diversity in the echinoderm fauna from the Feni Ridge revealed by the relatively low sampling effort so far, it is clear that further sampling is necessary. The clearer picture of echinoderm distribution resulting from this would help in evaluating the relative importance of sedimentary and hydrographic features in bringing about the contrasts in the echinoderm faunas of the eastern and western margins of the Trough. Until this can be accomplished, the echinoderm fauna, and its zonation on the relatively well sampled and comparatively gently sloping Hebridean Slope, should not be viewed as being typical of the margins of the Trough as a whole.

Summary

Five species of crinoids, eleven asteroids, eight ophiuroids, two echinoids and eight species of

holothurian are identified, mainly from sampling carried out between 1983 and 1985 in the deep water areas to the west of the British Isles. The following echinoderm species have not been recorded previously from this area of the NE. Atlantic.

Cheiraster sepitus
Mediaster bairdi
Pteraster (Apterodon) sp.
Hymenaster regalis
Ellipinion delagei
Leptosynapta decaria

Of these, *Mediaster bairdi* and *Hymenaster regalis* are new records for the eastern Atlantic, while the *Pteraster (Apterodon)* sp. is probably new to science.

This study confirms the generally higher species richness along the western margin of the Trough noted in earlier papers in this series and the tendency for juveniles of many species to be distributed at the lower end of the bathymetric range of those species. Extensions to the bathymetric and geographic ranges of several species are provided by these records.

Acknowledgements

We again express our gratitude to the officers and crew of RRS *Challenger*, and to colleagues too numerous to name individually who participated in cruises and helped with the processing of samples. We are particularly indebted to Miss B. Rae of Dervaig, Isle of Mull, for her help in sorting sled and box-core samples; to Mr G. Davies and Mr A MacArthur for the sorting of other samples as summer students in the years 1983–85, and to Mrs Margaret Pearson for her valuable help in sorting and careful curation of the collections up to 1983. Dr J. D. M. Gordon of SMBA kindly provided additional material from fishing cruises in which the authors did not participate. We also thank Dr J. M. Graham of SMBA for constructing a digitising caliper used to measure echinoids. The Scottish Marine Biological Association is grant-aided by the Natural Environment Research Council who have been generous in allocating cruise time on which the present records were made.

Station List

Only details of stations yielding records of echinoderms not listed by Gage *et al.* (1983, 1985*a*) are given below.

Station No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
Benthic stations			
SBC 156	5 Aug. 1979	48°27′N, 10°21′W	1310
SBC 159	8 Aug. 1979	50°55′N, 12°21′W	2036
SBC 160	8 Aug. 1979	50°55′N, 12°20′W	2030
SBC 168	13 Aug. 1979	56°44′N, 09°13′W	1206
ES 231	17 May 1983	54°42′N, 12°12′W	2898
ES 232	19 May 1983	57°17′N, 10°16′W	2195
AT 233	19 May 1983	57°17′N, 10°12′W	2180
RMT 234	20 May 1983	57°12′N, 09°54′W	c. 2000
AT 239	24 July 1983	57°07′N, 09°23′W	1047
ES 244	25 July 1983	57°23′N, 10°20′W	2150
AT 245	26 July 1983	57°21′N, 10°21′W	2165
AT 247	27 July 1983	59°02′N, 10°55′W	2084
AT 248	27 July 1983	59°59′N, 10°33′W	1150
AT 249	28 July 1983	59°44′N, 12°36′W	1265
ES 250	28 July 1983	59°43′N, 12°33′W	1270

Station No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
AT 251	30 July 1983	58°52′N, 12°56′W	1530
ES 252	30 July 1983	58°52′N, 12°53′W	1510
AT 254	31 July 1983	58°26′N, 12°35′W	1595
ES 255	31 July 1983	58°26′N, 12°42′W	1595
AT 256	31 July 1983	57°56′N, 12°21′W	1705
ES 257	31 July 1983	57°55′N, 12°18′W	1700
RD 258	1 Aug. 1983	57°56′N, 13°24′W	135
AT 259	1 Aug. 1983	57°27′N, 12°52′W	1041
ES 261	1 Aug. 1983	57°24′N, 12°05′W	1824
ES 264	2 Aug. 1983	56°26′N, 13°31′W	2144
ES 266	3 Aug. 1983	56°24′N, 11°59′W	2591
AT 267	3 Aug. 1983	56°24′N, 11°58′W	2605
AT 271	4 Aug. 1983	56°39′N, 10°35′W	2255
SBC 272	5 Aug. 1983	56°40′N, 10°30′W	2250
AT 273	5 Aug. 1983	56°05′N, 10°28′W	2185
SBC 275	6 Aug. 1983	56°13′N, 10°06′W	1961
SBC 276	6 Aug. 1983	56°14′N, 09°51′W	1792
SBC 278	6 Aug. 1983	56°15′N, 09°46′W	1631
AT 282	14 April 1985	55°06′N, 11°22′W	c. 2760
ES 283	15 April 1985	54°39′N, 12°15′W	2946
AT 284	15 April 1985	54°40′N, 12°12′W	2906
ES 285	15 April 1985	54°39′N, 12°14′W	2906
AT 286	16 April 1985	54°44′N, 12°17′W	2896
AT 287	18 April 1985	56°43′N, 09°21′W	1383
AT 288	20 April 1985	57°18′N, 10°22′W	2190
ES 289	21 April 1985	57°19′N, 10°25′W	2190
AT 290	26 April 1985	56°28′N, 09°16′W	970
AT 291	27 April 1985	56°22′N, 09°12′W	775
AT 292	27 April 1985	56°23′N, 09°08′W	525

Fishing stations		Starting position	Depth range
13/83/1 OTSB	20 Sept. 1983	56°33′N, 09°40′W	1540–1550
13/83/2 OTSB	21 Sept. 1983	56°46′N, 09°15′W	1130–1265
13/83/3 GT	21 Sept. 1983	56°36′N, 09°02′W	220–270
13/83/4 GT	21 Sept. 1983	56°32′N, 09°05′W	230–380
13/83/5 OTSB	21 Sept. 1983	56°41′N, 09°47′W	1775–1835
13/83/6 OTSB	22 Sept. 1983	56°36′N, 09°17′W	980–1005
13/83/7 OTSB	22 Sept. 1983	56°27′N, 09°10′W	750–800
13/83/8 OTSB	22 Sept. 1983	56°20′N, 09°08′W	500–560
9/84/1 OTSB	2 Nov. 1984	56°32′N, 09°13′W	760–815
9/84/2 OTSB	2 Nov. 1984	56°34′N, 09°16′W	910–960
9/84/9 OTSB	4 Nov. 1984	56°47′N, 09°36′W	1750–1770
9/84/10 OTSB	4 Nov. 1984	56°16′N, 09°13′W	580–630
9/84/13 OTSB	5 Nov. 1984	56°25′N, 09°16′W	940–975
3/85/5 OTSB	15 April 1985	54°27′N, 12°25′W	2970–2980
3/85/7 OTSB	16 April 1985	55°47′N, 10°52′W	2500–2455
3/85/8 OTSB	17 April 1985	56°27′N, 09°17′W	970–1010
3/85/9 OTSB	17 April 1985	56°43′N, 09°11′W	945–1010
3/85/10 OTSB	17 April 1985	56°31′N, 09°13′W	795–805
3/85/11 OTSB	18 April 1985	56°33′N, 09°26′W	1250–1270
3/85/13 OTSB	18 April 1985	56°28′N, 09°17′W	960–995

Station No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
3/85/14 OTSB	18 April 1985	56°30′N, 09°12′W	720–775
3/85/17 OTSB	21 April 1985	56°54′N, 10°00′W	1955–1995
3/85/18 MBA	21 April 1985	56°27′N, 09°17′W	990–1020
3/85/19 MBA	22 April 1985	56°34′N, 09°18′W	1030–1035
3/85/20 OTSB	22 April 1985	56°34′N, 09°26′W	1225–1245
3/85/21 OTSB	22 April 1985	56°31′N, 09°39′W	1480–1500
3/85/22 MBA	22 April 1985	56°25′N, 09°17′W	995–1020
3/85/23 OTSB	23 April 1985	56°25′N, 09°18′W	995–1000
3/85/24 OTSB	23 April 1985	56°26′N, 09°17′W	980–990
3/85/25 OTSB	23 April 1985	56°25′N, 09°18′W	1000–1005
3/85/26 OTSB	23 April 1985	56°25′N, 09°16′W	940–985
3/85/27 OTSB	24 April 1985	56°24′N, 09°18′W	990–1000
3/85/28 OTSB	24 April 1985	56°35′N, 09°18′W	990–1075
3/85/29 OTSB	24 April 1985	56°50′N, 09°31′W	1690–1740
3/85/30 OTSB	24 April 1985	56°29′N, 09°38′W	1420–1480
3/85/31 OTSB	25 April 1985	56°24′N, 09°17′W	995–1020
3/85/32 OTSB	25 April 1985	56°25′N, 09°19′W	1055–1060
3/85/33 OTSB	25 April 1985	56°26′N, 09°18′W	985–1000
3/85/34 OTSB	25 April 1985	56°24′N, 09°18′W	980–990
3/85/36 OTSB	26 April 1985	56°24′N, 09°19′W	1000–1025
3/85/37 OTSB	26 April 1985	56°25′N, 09°18′W	945–985
3/85/38 OTSB	26 April 1985	56°23′N, 09°08′W	410–490
3/85/43 OTSB	27 April 1985	56°17′N, 09°12′W	565–700
3/85/44 OTSB	27 April 1985	56°18′N, 09°11′W	545–600
3/85/45 OTSB	28 April 1985	56°30′N, 09°38′W	1470–1500
3/85/46 OTSB	28 April 1985	56°25′N, 09°17′W	960–985

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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A morphological atlas of the avian Uropygial gland. By David W. Johnston

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A morphological atlas of the avian uropygial gland

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Dedicated to PIERCE BRODKORB, whose encouragement, friendship, and scholarship influenced the preparation of this monograph

Contents

Introduction

The uropygial gland (also known as the uropygium, preen-, oil-, rump-, tail-, and coccygeal gland; glandula uropygii; the 'eloeodochon' of Coues 1890) is the only compact gland in the avian integument. Lying medially and dorsal to the levator muscles of the tail, this gland is usually bilobed and partly covered by skin and body feathers. It secretes a chemically complex oil through ducts in a papilla which often bears a feather tuft (*circulus uropygialis* of Baumel *et al.* 1979). Most reports and investigations on the gland for at least 150 years have concentrated on specific topics such as histology, morphology, function, chemical nature of secretions, and development.

The earliest published references to the uropygial gland focused almost entirely on function. Emperor Frederick II of Hohenstaufen about 1260 (Wood & Fyfe 1943) in his treatise on falconry gave the view that birds of prey transfer oil from the gland to their talons via the mandibles, the oil presumably being noxious and capable of killing the prey more quickly. Willughby (1678) noted that the 'oyly pap . . . recomposes and places them [feathers] in due order.' The French anatomist Cuvier (1799–1805) provided the first description of the gland's internal anatomy. Burton (1822) considered size as well as function of the gland in *Fregata aquila*. Audubon (1829) discussed the use of the glandular secretion in lubricating the plumage of 'The Bird of Washington' (the Bald Eagle, *Haliaeetus leucocephalus*). From 1832–1836, F.O. Morris and Charles Waterton exchanged acrimonious and unscientific letters in which they debated the functions ('office') of the gland

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mostly in domestic birds, and they even questioned the ability of birds to preen with oil. Macgillivray's (1837) interest in the gland was also largely functional, although he reported an increase in gland size at the time of moulting. Crisp (1860) questioned this report, and found no experimental evidence for such seasonal size change. Hussey (1860), Waterton (1860), and Matthews (1861) continued to be concerned with preening and the use of oil in 'barn-door' fowls.

Although these earlier authors were pre-occupied with the gland's functional attributes, some of their reports contained passing references to gland morphology in various birds (e.g., duck, fowl, dipper, robin). Nitzsch (1840) published the first account to include morphological information for glands in many taxa. He discussed for many groups of birds the gland's presence or absence, tufted vs. naked condition, relative sizes, and shapes. This hallmark publication by Nitzsch was followed by subsequent authors who either copied Nitzsch or provided information on gland morphology in additional species: Crisp (1860, 1862), Owen (1866), Kossmann (1871), Garrod (1874*a, b*), Coues (1890), and Newton (1893–1896). Beddard (1898) then published his renowned classification of birds in which he included some morphological notes on glands in many major taxa. Papers and books by Pycraft (1900, 1910), Lunghetti (e.g., 1906), Granvik (1913), and Paris (e.g., 1913) reported much new information about gland morphology in selected species. Thus, information about gland morphology in different groups and species was scattered among these and other publications through the first part of the 20th century. More recently, Elder (1954), Lucas & Stettenheim (1972), and Jacob & Ziswiler (1982) have provided information on gland morphology in additional taxa. These three publications and Stettenheim (1972) contain a wealth of references to various biological attributes of uropygial glands (histology, functions, and chemistry).

The degree to which any gland attribute can be used in avian taxonomy remains controversial. Early classifications of birds (Nitzsch 1840, Beddard 1898, Paris 1913, Verheyen 1955–1960) often employed gland morphology as diagnostic properties of given taxa, but many more modern schemes (e.g., Hancock & Kushlan 1984) have not. Jacob (e.g., 1978), Jacob & Ziswiler (e.g., 1982), and von Jacob & Hoerschelmann (1985) provide a chemotaxonomic approach in which they relate the qualitative chemical composition of gland secretions to the systematic positions of avian taxa. Their results seem to show qualitative differences at some ordinal, family, and subfamily levels. Perhaps it is too soon to evaluate this approach, i.e. whether it is any more fundamental in avian taxonomy than a scheme employing only gland morphology, as a taxonomic characteristic.

Despite a plethora of publications, to date no one has compiled a single, complete, comprehensive monograph on the gland's morphological variations in all major avian taxa. The present monograph covers, both generally and specifically, the morphology of the gland in all families and subfamilies, a review of the pertinent morphological literature, and corrections of erroneous and incomplete information about glands, much of this perpetuated from author to author over the years without questioning and adequate documentation. This comprehensive survey is deemed necessary prior to an accurate assessment of the function(s) of the gland's secretion and to the possible use of gland morphology as a character in avian systematics.

Materials and methods

Most birds examined in this study were preserved in alcohol or other fluids in museum collections. For a few species, where such specimens were unavailable, I examined museum study skins but only for rare species that were believed to have tufted glands. Supplementing the museum studies were (1) birds caught in mist-nets, or collected with a shotgun in Florida, (2) road kills in Virginia, England, Ireland, Belize, and Malawi and (3) some freshly-dead birds from zoos (e.g., parrots, toucans, and hornbills). I dissected a gland from one or more species in each family intact from the alcoholic specimen, and freed it from connective and other non-glandular tissues. That gland was then used for the artist's illustrations and studies of feathers. These gland examples currently remain in my collection.

Anatomical nomenclature for the gland's major parts follows that of Baumel *et al.* (1979) as illustrated in Figure 1.

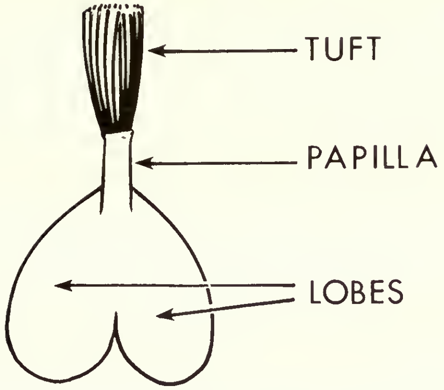


Fig. 1 External morphological nomenclature of the uropygial gland.

Body and gland weights were taken, for the most part, from freshly killed birds, but some frozen birds (e.g., penguins, ducks, hawks) were thawed, weighed, and their glands dissected free for weighing. Linear dimensions of glands were usually not made. In only a few cases were zoo birds used for weights because I did not know whether the bird might have been emaciated at the time of its death. Glands from fresh birds were never compressed before weighing in order to preserve the gland's oil content at the time of death. The gland tuft, if present, was included in the gland weight, as was any oil in the tuft.

For the microscopic study of gland feathers, two or three feathers were dissected from a gland, cleared in xylene, and mounted in Canada balsam on a microscope slide. Each feather preparation could then be studied under the microscope at magnifications up to 50X. I did not consider gland histology or development (see reviews in Lucas & Stettenheim 1972 and Jacob & Ziswiler 1982) or the number of orifices in the papilla's tip (see Jacob & Ziswiler 1982).

This study resulted in the examination of representative glands from every family and all subfamilies (except one) as identified in Peters (1931–1986). In all, I examined 3011 individuals from 1433 species and 883 genera. The objectives of this examination were to determine for each individual the presence or absence of the gland, its shape, relative size, weight, presence or absence of the papilla and feather tuft. Any individual variations in these characteristics are noted in the systematic accounts to follow.

Systematic accounts of gland morphology

Classification here follows that of Peters (1931–1986). The terminology for gland morphology (see Fig. 1) has been adapted from Baumel *et al.* (1979). At the end of the Morphology section for each family is the gland feather type (see section on Feathers on glands for definitions). Unless otherwise indicated, all specimens were considered to be adults. Format for the Material examined: for each species, the number of individuals examined; in parentheses, when available, sex, body weight in grams followed by gland weight as a percent of body weight. Z = zoo bird; SK = study skin. Accompanying gland illustrations contain a linear scale that equals 1 cm.

Order Struthioniformes

General characteristics. Absent in adult Ostrich, Rhea, Cassowary, and Emu, but present (naked) in Rhea and Emu chicks. Present (naked or with minute feathers) in Apterygidae.

Family Struthionidae (Ostriches)

Morphology. Absent in all age groups. Pycraft (1900) also found no glands in any age group of this species.
Material examined. *Struthio camelus* 11 (9 chicks of various ages, 2 ad.).

Family Rheidae (Rheas)

Morphology. Present (naked) and very small in all chicks examined; absent in adult. Pycraft (1900) found the gland in the 'embryo and nestling' but absent in the adult of *Rhea americana*.
Material examined. *Rhea americana* 14 (11 chicks up to 4 months, 3 ad.). *Pterocnemia pennata*, 1 ad.

Family Casuariidae (Cassowaries)

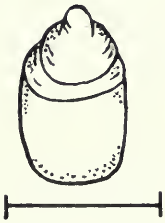
Morphology. Absent in all age groups (absent in adult *fide* Pycraft 1900).
Material examined. *Casuarius casuarius* 4 (1 chick, 1 immature, 2 ad.).

Family Dromaiidae (Emus)

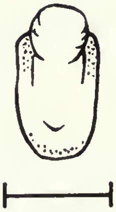
Morphology. Present (naked) in all chicks examined; probably absent in adults (first reported by Pycraft 1900).
Material examined. *Dromaius novaehollandiae* 13 (chicks up to 2 weeks).

Family Apterygidae (Kiwis)

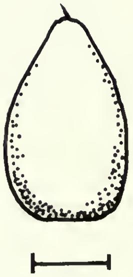
Morphology. More terminally located than in any other family, apparently single-lobed, papilla conical, naked (or 1–2 minute 'bristle-like feathers' in *A. australis mantelli fide* Beddard 1898, 1899).
Note. Beddard (1898, 1899) was apparently the first to report a gland not only in *Apteryx* but also in any ratite bird. The kiwi gland is clearly different from every nonratite gland examined because of its single-lobed appearance and terminal location. Its presence only in adults distinguishes kiwis from other ratites. The presence of the gland in kiwis supports a suggested affinity between Apterygidae and Tinamidae (see Cracraft 1981).
Material examined. *Apteryx australis* 5 (1 chick, 4 ad.); *A. owenii* 1.



Rhea americana
(chick)



Dromaius novaehollandiae
(chick)



Apteryx australis

Order Tinamiformes

General characteristics. Tufted with long feathers.

Family Tinamidae (Tinamous)

Morphology. Indistinctly bilobed, papilla small or lacking, tufted. Verheyen (1960*a*) regarded the gland as always present in the family although 'sometimes vestigial.' In *Crypturellus* spp. the four

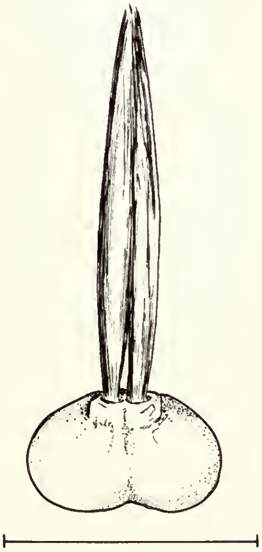
feathers, 2 long and 2 short, are 4–5, 3–4 mm in length; in *Eudromia* spp. the four feathers are 13, 12 mm; shorter (1·5 mm) in *Rhynchotus rufescens* (Jacob & Ziswiler 1982). Type II.
MATERIAL EXAMINED. *Crypturellus soui* 1; *C. undulatus* 1; *C. cinnamomeus* 2; *C. tataupa* 1; *Rhynchotus rufescens* 1; *Nothoprocta perdicaria* 1; *N. pentlandii* 1; *Eudromia elegans* 3; *E. formosa* 1; *Tinamotis pentlandii* 1.

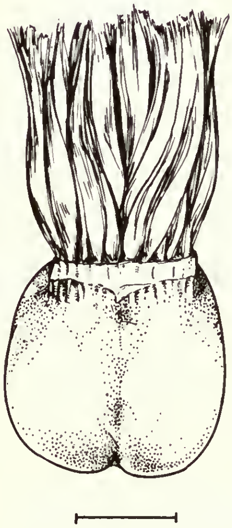
Order Procellariiformes

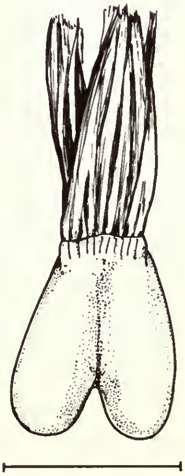
General characteristics. Densely tufted in all families.

Family Diomedeidae (Albatrosses)
MORPHOLOGY. Distinctly bilobed, papilla rounded and slightly raised, tufted (32 feathers in *Diomedea exulans,* Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Diomedea exulans* 1; *D. nigripes* 2; *D. immutabilis* 1; *D. melanophrys* 1; *Phoebetria palpebrata* 1.

Family Procellariidae (Fulmars, Petrels, Shearwaters)
MORPHOLOGY. Distinctly bilobed, papilla small or lacking, tufted (24–36 feathers, Paris 1913; 36–42 feathers in 2 species, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Macronectes giganteus* 1; *Fulmarus glacialoides* 1; *F. glacialis* 2 (F im.: 642·4, 0·67); *Thalassoica antarctica* 2; *Daption capense* 1; *Pagodroma nivea* 1 (M: 245·0, 0·25); *Pterodroma hasitata* 5 (M: 481·3, 0·36; 364.9, 0·34. F: 459·0, 0·35); *P. hypoleuca* 1; *Halobaena caerulea* 1; *Pachyptila desolata* 1; *Bulweria bulwerii* 1; *Calonectris diomedea* 1 (F:410·0, 0·40); *Puffinus gravis* 7(M: 636·6, 0·44. F: 654·5, 0·39); *P. griseus* 3; *P. puffinus* 1(unsexed: 450·0, 0·53); *P. lherminieri* 2.


Eudromia elegans


Diomedea immutabilis


Puffinus lherminieri

Family Hydrobatidae (Storm Petrels)
MORPHOLOGY. Indistinctly (*Oceanites*) or distinctly (*Oceanodroma*) bilobed, papilla small, tufted (20 feathers in *O. melania*). Type I.

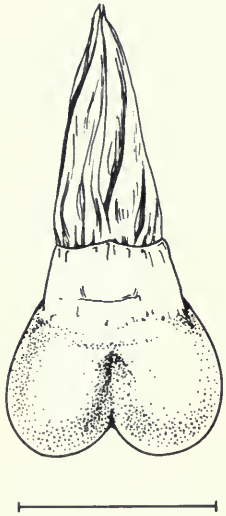
Material examined. *Oceanites oceanicus* 5 (M: 35·6, 0·40; 31·1, 0·46. F: 35·0, 0·40; 33·6, 0·38); *Oceanodroma leucorha* 1 (M: 29·5, 0·23); *O. melania* 1 (unsexed: 53·8, 0·69); *O. homochroa* 1 (M: 34·0, 0·31); *O. furcata* 1 (unsexed: 54·4; 0·39).

Family Pelecanoididae (Diving Petrels)
Morphology. Distinctly bilobed, papilla small, tufted (20 feathers). Type I.
Material examined. *Pelecanoides magellani* 1; *P. georgicus* 1; *P. urinator* 1.

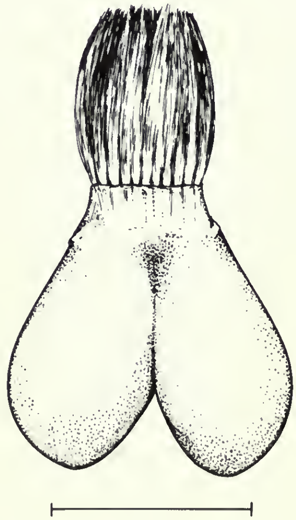
Order Sphenisciformes

General characteristics. Densely tufted.

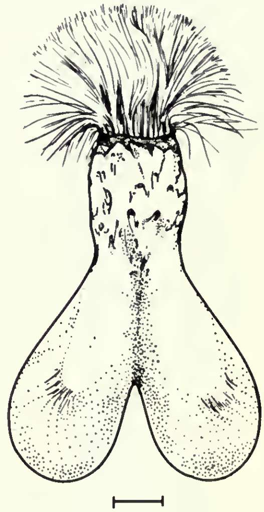
Family Spheniscidae (Penguins)
Morphology. Distinctly bilobed, flattened and raised papilla, tufted. ('about 50' feathers, Paris 1913; 44–48 feathers in 2 species, Jacob & Ziswiler 1982). Illustrations in Grassé (1950: 286) and Jacob & Ziswiler (1982, Fig. 4a, p. 216) of *Spheniscus demersus,* lacking a feather tuft, are inaccurate, copied from Paris (1913) who illustrated one gland from which the tuft had undoubtedly been removed. Type IIa.
Materials examined. *Aptenodytes patagonica* 1; *A. forsteri* 1; *Pygoscelis papua* 1; *P. adeliae* 2 (M: 4990, 0·06; 5348, 0·12); *P. antarctica* 1; *Eudyptes crestatus* 1; *E. chrysolophus* 1; *Eudyptula minor* 1; *Spheniscus humboldti* 1.



Oceanodroma melania



Pelecanoides magellani



Aptenodytes forsteri

Order Gaviiformes

General characteristics. Deeply bilobed, densely tufted.

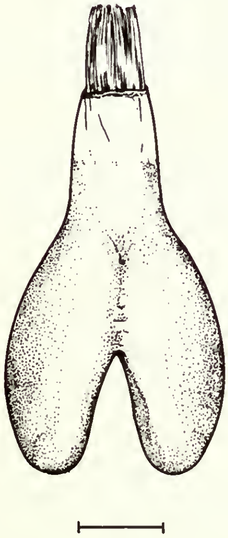
Family Gaviidae (Loons)
Morphology. Distinctly bilobed and elongated, small papilla, tufted (30–40 feathers, Paris 1913; 26–28 feathers in 2 species, Jacob & Ziswiler 1982). Type I.

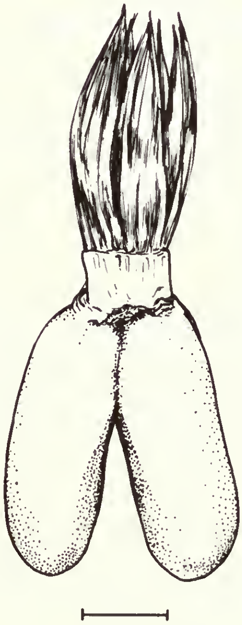
Material examined. *Gavia stellata* 5 (M: 1597, 0·19; 1638, 0·17. F: 1351, 0·21); *G. arctica* 2 (M: 1598, 0·30. 1 unsexed: 2082, 0·23); *G. immer* 15 (M: 2780, 0.09; 3180, 0·11; 3490, 0·11); *G. adamsii* 1 (unsexed: 4115, 0·19).

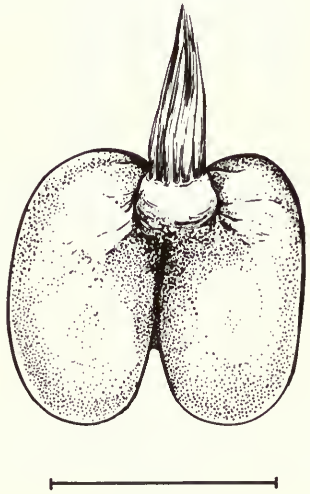
Order Podicipediformes

General characteristics. Deeply bilobed, densely tufted.

Family Podicipedidae (Grebes)
Morphology. Distinctly bilobed and somewhat flattened papilla raised nearly perpendicular to the two lobes, tufted (14–18 subterminal feathers in 2 species, Jacob & Ziswiler 1982). Verheyen (1959*d*) reported the gland as 'voluminous and crowned with long plumes.' Type I.
Material examined. *Rollandia rolland* 3; *R. microptera* 1; *Tachybaptus ruficollis* 1; *T. rufolavatus* 1; *T. dominicus* 1; *Podilymbus podiceps* 8 (M: 358·0, 0·42; 380·2, 0·19. F: 312·0, 0·22; 301·2, 0·26); *P. gigas* 1; *Podiceps major* 1; *P. auritus* 3 (M: 410·0, 0·23; 342·7, 0·22); *P. grisegena* 1; *P. nigricollis* 2; *P. occipitalis* 2; *P. taczanowskii* 1; *Aechmophorus occidentalis* 1.


Spheniscus humboldti


Gavia immer


Podiceps auritus

Order Pelecaniformes

General characteristics. Densely tufted.

Family Phaethontidae (Tropicbirds)
Morphology. Distinctly bilobed, papilla tufted (40 feathers in *P. lepturus*). Verheyen (1960*b*) stated (p. 12) that the gland 'lacks a nipple except in Phaethon.' Type I.
Material examined. *Phaethon aethereus* 1 (F: 496·0, 0·43); *P. rubricauda* 1; *P. lepturus* 3.

Family Fregatidae (Frigatebirds)

Morphology. Indistinctly bilobed, papilla broad and flattened, tufted (ca 30 feathers in *F. magnificens*). Type I.

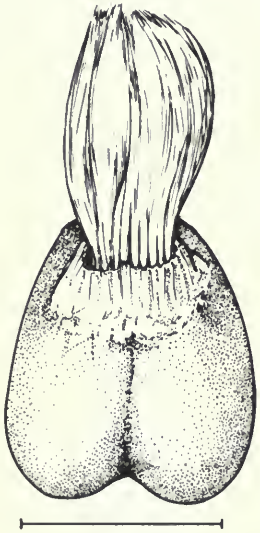
Material examined. *Fregata magnificens* 4 (M: 1365·5, 0·07; 1336, 0·07. F: 1512, 0·06); *F. aquila* 1; *F. minor* 1; *F. ariel* 1.

Family Phalacrocoracidae

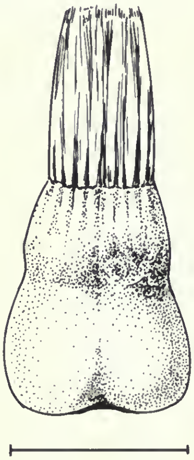
Subfamily Phalacrocoracinae (Cormorants)

Morphology. Distinctly bilobed, papilla moderately developed, tufted (36–52 feathers in 2 species, Jacob & Ziswiler 1982). Papilla and feather tuft subterminal. Type I.

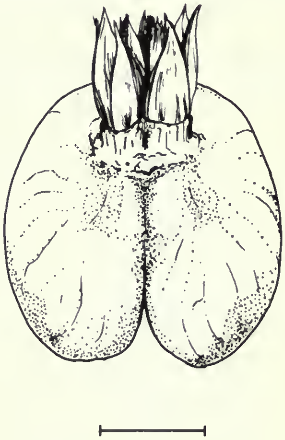
Material examined. *Phalacrocorax harrisi* 1; *P. auritus* 24 (M: 1660, 0·25; 1710, 0·25. $\bar{x}$ of 8F: 1048, 0·25); *P. aristotelis* 1; *P. magellanicus* 1; *P. bougainvillii* 1; *P. albiventer* 1.



Phaethon lepturus



Fregata ariel



Phalacrocorax auritus

Subfamily Anhinginae (Darters)

Morphology. Bilobed and somewhat flattened, papilla absent, short tuft of 14 feathers. Type I.

Material examined. *Anhinga anhinga* 11 (M: 1230, 0·16; 1352, 0·12; 1230, 0·16. F: 1307, 0·15; 1178, 0·17); *A. melanogaster* 2.

Family Sulidae (Boobies, Gannets)

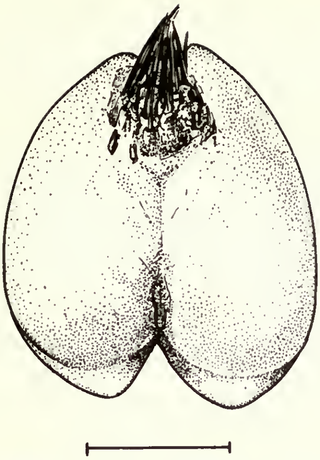
Morphology. Distinctly flattened and bilobed, papilla absent, tufted with 70 short feathers in *S. bassana* (Jacob & Ziswiler 1982). Type I.

Material examined. *Sula bassana* 3 (M subad.: 2200, 0·38; *S. dactylatra* 2; *S. sula* 1.

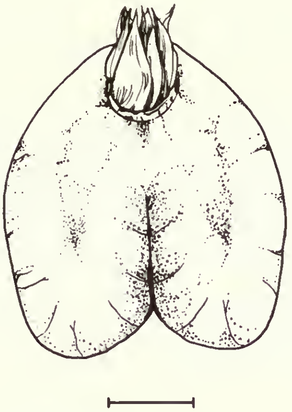
Family Pelecanidae (Pelicans)

Morphology. Large and bilobed, papilla very short and broad, tufted (70 feathers, Paris 1913; 66 feathers in *P. onocrotalus,* Jacob & Ziswiler 1982). Tuft and openings obviously subterminal, Type I.

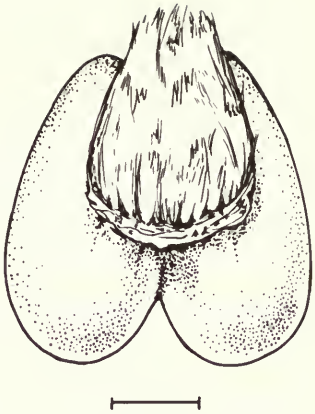
Material examined. *Pelecanus onocrotalus* 1; *P. philippensis* 1; *P. erythrorhynchos* 2 (M: 4700, 0·30; *P. occidentalis* 9 (M im.: 2730, 0·43; 3060, 0·32; unsexed ad.: 3320, 0·37).



Anhinga anhinga



Sula bassana



Pelecanus onocrotalus

Order Ciconiiformes

General characteristics. Much inter- and some intrafamilial variation: naked, sparsely or densely tufted.

NOTE. The large morphological differences among glands examined here lend support to Olson's (1979) view that the Ciconiiformes is not a natural order.

Family Ardeidae (Herons, Bitterns)

Subfamily Ardeinae (Day Herons)

MORPHOLOGY. Although considerable variation occurs in the family, the gland is generally small (see also Paris 1913: 192), bilobed, lacks a papilla (or 'very short,' Paris 1913: 192), and is tufted (4–18 feathers) or naked. Although 'small' in many species, the gland cannot be regarded as 'rudimentary' as described by Jacob (1978: 168). Verheyen (1959*b*) noted that in the Ardeae, the gland is naked or has a few vestigial feathers. Miller (1924) described variations in the tuft among 13 species, then reported the tuft as absent in *Ardea goliath, A. herodias, A. cocoi, A. occidentalis, Notophoyx novaehollandiae, N. pacifica, Egretta candidissima,* and *Hydranassa tricolor.* I found the tuft absent only in *Pilherodias pileatus, Ardea pacifica, Egretta rufescens, E. tricolor, E. novaehollandiae, E. garzetta* and *E. sacra.* In *A. herodias* (contra Miller 1924), all 10 specimens examined here had extremely small feathers, often as few as 4. Beddard (1898) and Gadow (1893) reported that all Ardeidae have feathered glands. Thus in the family, the tuft might be absent, represented by only 4–8 feathers (*Ardea herodias, Agamia agami*), or tufted with 16–18 feathers (*Ixobrychus minutus fide* Jacob & Ziswiler 1982). Type I.

MATERIAL EXAMINED. *Pilherodias pileatus* 1*; *Ardea cinerea* 1; *A. herodias* 10 (M: 2695·0, 0·21; 1281·0, 0·05; 1790, 0·14. F: 1250·0, 0.17; 1507, 0·10); *A. pacifica* 1*; *A. melanocephala* 1; *A. purpurea* 1; *A. alba* 8 (M: 478·5, 0·15; 579·0, 0·12); *Egretta rufescens* 1*; *E. tricolor* *; *E. ibis* 11 (M: 342·6, 0·03. $\bar{x}$ of 5F: 286·8, 0·04); *E. novaehollandiae* 1*; *E. caerulea* 3 (F: 372·0, 0·07); *E. garzetta* 1*; *E. sacra* 1*; *Ardeola speciosa* 1; *A. striata* 7 (M: 220·3, 0·07; 220·1, 0·07; 195·4, 0·06); *Agamia agami* 2.

NOTE. Ligon (1967: 1) believed 'that the storks and herons are dissimilar' in many features (osteology, myology, pterylography and others); the dissimilar uropygial glands of the two groups add another difference.

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*naked gland, present study.

Subfamily Nycticoracinae (Night Herons)

Morphology. Indistinctly bilobed, no papilla, tufted (*Nycticorax, Nyctanassa*) or naked (*Cochlearis*).

Material examined. *Nyctanassa violacea* 5 (M: 546·0, 0·04); *Nycticorax nycticorax* 2; *Cochlearius cochlearius* 2.

Note. Peters regarded *Cochlearis* as comprising a separate family, the Cochlearidae (Peters 1931, Vol. I, 1st ed.). Mayr & Cottrell, (1974 in their 2nd ed. of Peters' Vol. I) and Hancock & Kushlan (1984), however, included *Cochlearis* in a subfamily (Nycticoracinae) of the family Ardeidae. The gland of *Cochlearis* differs markedly from that of all other ardeids because of its relatively large size, distinctive appearance (see figure), and absence of papilla and feather tuft. Beddard (1898) and Miller (1924) both noted this distinctiveness of the gland in *Cochlearis*.

Subfamily Tigrisomatinae (Tiger Herons)

Morphology. Bilobed, short papilla, tufted. Type I.

Material examined. *Tigrisoma mexicanum* 1.

Subfamily Botaurinae (Bitterns)

Morphology. Indistinctly bilobed, no papilla, small tuft. Type I.

Material examined. *Ixobrychus exilis* 2 (M: 68·0, 0·05. F: 38·6, 0·03); *Botaurus lentiginosus* 5 (M: 564·0, 0·31; 789·0, 0·42; 720·0, 0·38. F: 599·3, 0·38).

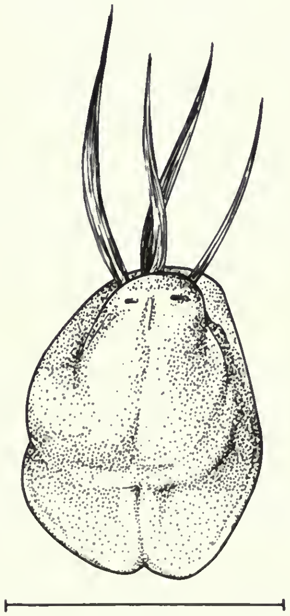
Family Scopidae (Hammerhead)

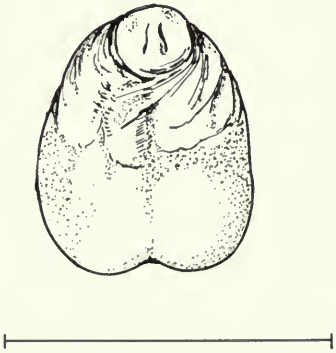
Morphology. Indistinctly bilobed, papilla short and somewhat flattened, and tufted (18 long feathers). The gland of this species is distinct from those of ardeids, more closely resembling that of *Balaeniceps* and the Ciconiidae (see figures). Type I.

Material examined. *Scopus umbretta* 2.

Family Ciconiidae (Storks)

Morphology. Distinctly bilobed and large, papilla small, tufted (36 feathers in *C. ciconia*, Jacob & Ziswiler 1982). Unlike the illustration of *Mycteria* here, in *Anastomas, Ciconia nigra*, and


Ardea herodias


Cochlearius cochlearius


Scopus umbretta

Leptoptilos the gland appears to be separated into right and left portions, each with a separate lobe, feather tufts and orifices, features implied by Nitzsch (1867: 131). Type I.

Material examined. *Mycteria americana* 3 (F: 2490·0, 0·05); *Anastomus oscitans* 1; *Ciconia nigra* 1; *C. abdimii* 1; *C. episcopus* 1; *C. ciconia* 1; *Ephippiorhynchus asiaticus* 1; *Leptoptilos crumeniferus* 1.

Family Balaenicipitidae (Shoebill)

Morphology. Indistinctly bilobed and relatively small (see figure and Bartlett 1861), papilla small, tufted. With the exception of the large tuft in *Scopus,* I agree with Miller's (1924: 322) comment that 'in *Balaeniceps* the tuft is very much larger than in any heron,' although I did not count the feathers. Type II.

Material examined. *Balaeniceps rex* 1Z.

Note. Gland morphology sheds no light on the controversy over the affinities of *Balaeniceps* (Cottam 1957, Olson 1979, Cracraft 1981).

Family Threskiornithidae (Ibises, Spoonbills)

Subfamily Threskiornithinae (Ibises)

Morphology (family). Distinctly bilobed, papilla absent, tufted (26–28 feathers, Paris 1913; 30 feathers in *E. ruber,* Jacob & Ziswiler 1982). Nitzsch (1867) implied that ibises have glands 'divided in half.' In the present study one specimen each of *Eudocimus albus* and *Platalea leucorodia* had glands with nearly separate lobes, separate orifices, and separate feather tufts. Type I.

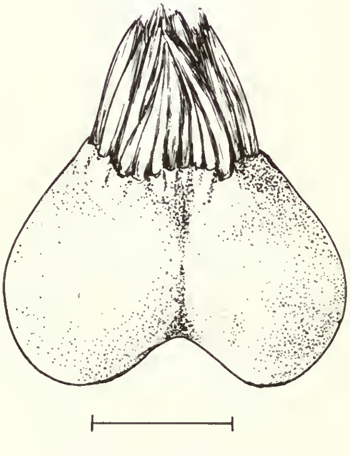
Material examined. *Eudocimus albus 2 (M, Z: 999, 0·12); E. ruber* 2; *Plegadis falcinellus* 3 (M: 530·0, 0·18; F: 420.0, 0·19); *Threskiornis aethiopicus* 2.

Subfamily Plataleinae (Spoonbills)

Material examined. *Platalea leucorodia* 1; *P. ajaja* 1 (M: 985·0, 0·11).

Mycteria americana

Balaeniceps rex



Threskiornis aethiopicus

Order Phoenicopteriformes

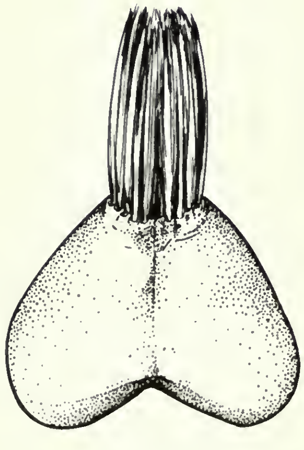
General characteristics. Densely tufted.

Family Phoenicopteridae (Flamingos)
Morphology. Bilobed, papilla absent, tufted (30 feathers, Paris 1913). Type IIa.
Note. Paris (1913: 190) believed that the gland of *Phoenicopterus roseus* closely resembles that of the Anseriformes. In contrast, I found marked differences in the gland of *Phoenicoparrus* from both the Anseriformes and Ciconiiformes (see figures), relationships suggested by Sibley (1967), and Sibley *et al.* (1969). The gland resembles that of the Recurvirostridae, suggesting a charadriiform relationship as proposed by Olson & Feduccia (1980*b*).
Material examined. *Phoenicopterus ruber* 1; *Phoeniconaias minor* 2; *Phoenicoparrus andinus* 1; *P. jamesi* 1.

Order Falconiformes

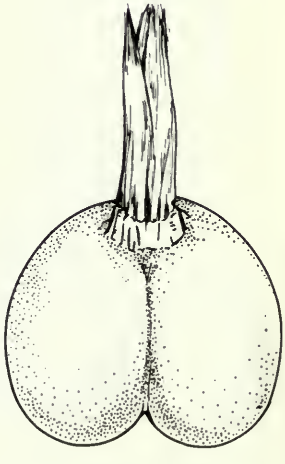
General characteristics. Inter- and some intrafamilial variation: naked or sparsely to densely tufted.

Family Cathartidae (American Vultures)
Morphology. Indistinctly bilobed, round papilla, naked; two separate, distinct orifices. Nitzsch's (1867) report that 'vultures of the New World' have a short circlet of feathers at the gland apex appears to be in error. I did not confirm Fisher's (1943) statement that down is often present on the oil gland in *Coragyps atratus*.
Note. My findings support Ligon's (1967: 1) view 'that the Cathartidae are not at all closely related to the remainder of the Falconiformes.' The naked glands of the Cathartidae, however, differ markedly from the heavily tufted glands of the Ciconiidae, to which cathartids might otherwise be related (Ligon 1967).
Material examined. *Coragyps atratus* 5 (M: 2221·0, 0·04; 2245·0, 0·04. F: 2135·0, 0·05; 2238·0, 0·04); *Cathartes aura* 7 (M: 1939·0, 0·02. $\bar{x}$ of 5F: 2019·0, 0·02); *Gymnogyps californianus* 2 (1 SK); *Vultur gryphus* 2; *Sarcoramphus papa* 2.



Phoenicoparrus jamesi

Cathartes aura



Pandion haliaetus

Family Accipitridae

Subfamily Pandioninae (Osprey)

MORPHOLOGY. Large and distinctly bilobed, indistinct papilla, tufted (18 feathers, Jacob & Ziswiler 1982). Type I.

NOTE. Sometimes included in a separate family, Pandionidae (Cracraft 1981), the Osprey's gland differs from those of the Accipitrinae by being much heavier and having a longer, usually denser feather tuft.

MATERIAL EXAMINED. *Pandion haliaetus* 5 (M: 1433·0, 0·28; 1363·0, 0·31. F: 1500·0, 0·32).

Subfamily Accipitrinae (Hawks, Eagles)

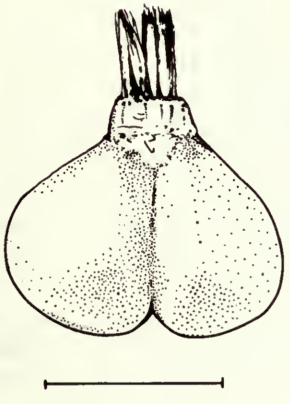
MORPHOLOGY. Bilobed, papilla moderately developed, sparsely (*Ictinia*) to densely (*Haliaeetus*) tufted (12–20 feathers in 7 species, Jacob & Ziswiler 1982). Type 1.

MATERIAL EXAMINED. *Aviceda leuphotes* 1; *Elanoides forficatus* 2 (M: 492·0, 0·13); *Harpagus bidentatus* 1; *Ictinia plumbea* 1; *I. mississippiensis* 1; *Haliaeetus leucocephalus* 3 (ad. sex?: 3625, 0·07); *Neophron percnopterus* 2; *Gyps fulvus* 1; *Circus hudsonius* 2 (F: 324·6, 0·03); *Melierax canorus* 1; *Accipiter nisus* 1; *A. striatus* 10 (subad. M: 84·2, 0·05; 98·0, 0·04; 88·9, 0·06. $\bar{x}$ of 4 ad. F: 157·3, 0·06); *A. cooperii* 4 (ad. F: 411·7, 0·07; 390·0, 0·07); *A. gentilis* 4 (subad. M: 816·0, 0·06; 775·0, 0·05; 918·0, 0·07. Ad. F: 930·0, 0·03); *Geranospiza caerulescens* 1; *Buteo lineatus* 9 (ad. M: 612·3, 0·05; 595·7, 0·06. Ad. F: 601·0, 0·05; 566·7, 0·07); *B. platypterus* 2 (subad. M: 489·4, 0·04; 309·0, 0·05); *B. swainsoni* 1 (ad. M: 874·0, 0·04); *B. jamaicensis* 14 (ad. M: 1307·3, 0·04. Subad. M: 856·3, 0·06. Subad. F: 1210·0, 0·04; 1272·0, 0·08); *B. lagopus* 3 (ad. M: 860·0, 0·04); *Pithecophaga jefferyi* 1; *Aquila chrysaetos* 1.

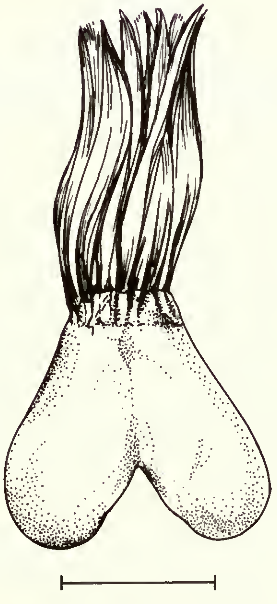
Family Sagittariidae (Secretarybird)

MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (20 feathers). In most specimens the gland appears to be nearly separated into two distinct lobes, with separate papillae and feather tufts. Although writing about 'Les Cariamiformes,' Verheyen (1957*c*) stated erroneously that the gland is absent in *Sagittarius*. Type I.

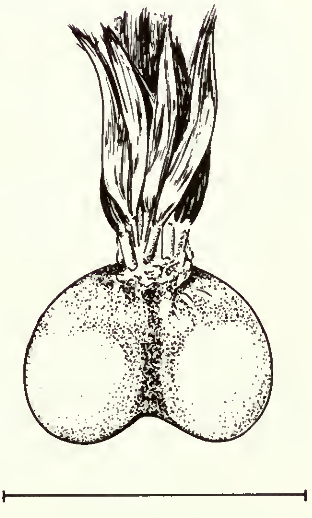
MATERIAL EXAMINED. *Sagittarius serpentarius* 6.



Buteo jamaicensis



Sagittarius serpentarius



Falco columbarius

Family Falconidae

Subfamily Polyborinae (Caracaras)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, densely tufted.
MATERIAL EXAMINED. *Daptrius ater* 1; *Polyborus plancus* 2 (unsexed im.: 900·5, 0·07).

Subfamily Falconinae (Falcons)
MORPHOLOGY. Distinctly bilobed, papilla moderately to well developed, tufted (17 feathers in *Falco tinnunculus,* Jacob & Ziswiler 1982), or rarely, naked. Both Miller (1924) and Verheyen (1959*c*) reported naked glands in *Microhierax fringillarius* and Nitzsch (1867) noted naked glands in two specimens of *M. caerulescens.* In my study all glands of 11 individuals of four species of *Microhierax* were naked, but all other genera and species in this subfamily had tufted glands. Type I.
MATERIAL EXAMINED. *Micrastur ruficollis* 1: *Spiziapteryx circumcinctus* 1; *Polihierax semitorquatus* 1; *P. insignis* 4; *Microhierax* (mostly SK) *caerulescens* 7; *M. fringillarius* 2; *M. erythrogenys* 1; *M. melanoleucus* 1; *Falco sparverius* 16 (x̄ of 6 M: 100·3, 0·05. x̄ of 6 F: 119·2, 0·08); *F. tinnunculus* 1; *F. columbarius* 2 (F: 191.0, 0·09); *F. mexicanus* 1; *F. rufigularis* 1; *F. rusticolus* 1; *F. peregrinus* 3 (M: 617·0, 0·08).

Order Anseriformes

Gland characteristics. Densely tufted.
MORPHOLOGY (order). Large and distinctly bilobed, papilla moderately developed, tufted (22–90 feathers in 15 species, Jacob & Ziswiler 1982). The Anhimidae differ from the Anatidae only by having a gland that is less distinctly bilobed. Type I.

Family Anatidae

Subfamily Anseranatinae (Pied Geese)
MATERIAL EXAMINED. *Anseranas semipalmata,* 1.

Subfamily Dendrocygninae (Whistling Ducks)
MATERIAL EXAMINED. *Dendrocygna bicolor* 1.

Subfamily Anserinae (Swans, Geese)
MATERIAL EXAMINED. *Cygnus olor* 1 (im. M: 10435, 0·16); *C. columbianus* 1; *Coscoroba coscoroba* 1; *Anser albifrons* 1 (F: 2556, 0·11); *A. caerulescens* 2 (M: 2330, 0·13; 2154, 0·12); *A. rossii* 1 (M: 1616, 0·15); *A. canagicus* 1 (M: 1855, 0·10); *Branta canadensis* 2 (M: 2435, 0·11. F: 3929, 0·15); *Cereopsis novaehollandiae* 1.

Subfamily Tadorninae (Shelducks)
MATERIAL EXAMINED. *Alopochen aegyptica* 1; *Tachyeres pteneres* 1; *T. patachonicus* 1.

Subfamily Anatinae (Typical Ducks)
MATERIAL EXAMINED. *Rhodonessa caryophyllacea* 1; *Aix sponsa* 3 (M: 642·0, 0·26; 573·1, 0·32. F: 595·2, 0·32); *A. galericulata* 1; *Anas strepera* 1 (M: 849·5, 0·20); *A. crecca* 3 (M: 251·0, 0·31; 295·5, 0·27. F: 262·0, 0·29); *A. aucklandica* 1; *A. platyrhynchos* 2 (M: 880·0, 0·23); *A. acuta* 1 (F: 708·5, 0·26); *A. discors* 8 (M: 341·5, 0·40; 368·2, 0·33. F: 365·5, 0·36; 384·0, 0·35; 430·0, 0·32); *A. clypeata* 2 (M: 672·0, 0·27); *Aythya valisineria* 3 (M: 893·3, 0·27. F: 792·0, 0·30; 884·2, 0·24); *A. americana* 2 (F: 1172·0, 0·28); *A. collaris* 11 (x̄ of 8 M: 749·6, 0·32. F: 697·5, 0·31; 745·0, 0·30); *A. marila* 2 (F: 843·0, 0·22; 991·6, 0·20); *A. affinis* 2 (M: 882·8, 0.22. F: 783·4, 0·22).

Subfamily Merginae (Sea Ducks)
MATERIAL EXAMINED. *Somateria mollissima* 1 (M: 2255, 0·18); *S. spectabilis* 1 (M: 1540, 0·26); *Melanitta perspicillata* 1 (F: 703·1, 0·20); *Bucephala clangula* 1; *B. albeola* 1; *Mergus cucullatus* 5 (M: 571·0, 0·34; 671·0, 0·37. F: 671·3, 0·30; 526·0, 0·28); *M. serrator* 1 (F: 599·5, 0·36); *M. merganser* 2 (M: 1577, 0·21. F: 1027, 0·29); *M. australis* 1.

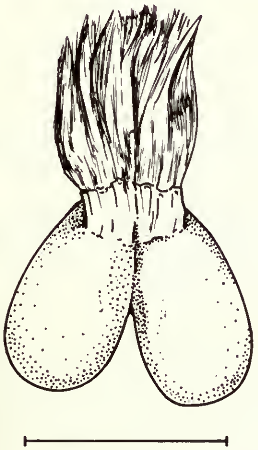
Subfamily Oxyurinae (Stifftailed Ducks)
MATERIAL EXAMINED. *Oxyura jamaicensis* 2 (M: 596·7, 0·27).

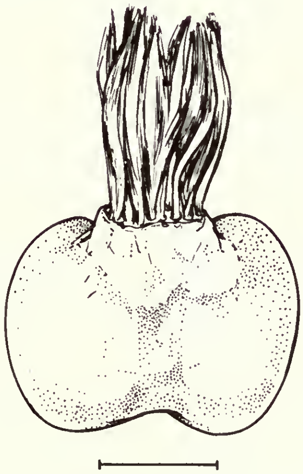
Family Anhimidae (Screamers)
MATERIAL EXAMINED. *Anhima cornuta* 1 (M, Z: 2600, 0·13); *Chauna chavaria* 1.

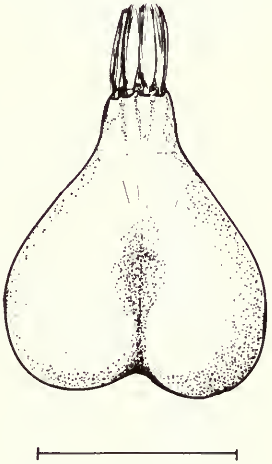
Order Galliformes

Gland characteristics. Inter- and intrafamilial variation: sparsely to densely tufted, or, rarely, naked.
NOTE. Glands of most galliform families do not resemble those of the Anseriformes. These differences do not support an anseriform-galliform relationship (see also Olson & Feduccia 1980*a*). I did not confirm Pettingill's (1985) statement that 'certain species' of Galliformes lack a gland.

Family Megapodiidae (Megapodes)
MORPHOLOGY. Bilobed, papilla large, naked or tufted (6 feathers). The present study and the reports of Miller (1924) and Clark (1964) demonstrate naked glands in *Leipoa, Alectura, Tallegalla jobiensis,* and *Aepypodius arfakianus,* whereas tufted glands are known from five species of *Megapodius* and *Macrocephalon maleo.* Beddard (1898: 302) reported that megapodes have 'oil gland nude,' and both Sharpe and Ogilvie-Grant regarded the glands of these birds as nude (*fide* Miller 1924). Type I.
MATERIAL EXAMINED. *Megapodius nicobariensis* 2; *M. freycinet* 3; *M. pritchardii* 6; *Alectura lathami* 1; *Aepypodius arfakianus* 1.


Anas discors


Anhima cornuta


Megapodius pritchardii

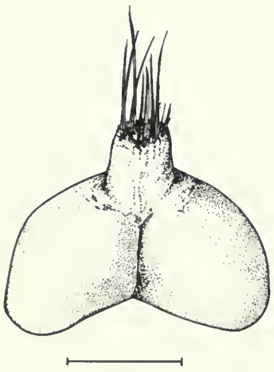
Family Cracidae (Curassows, Guans, Chachalacas)
MORPHOLOGY. Distinctly bilobed, papilla large, tuft usually short and sparsely feathered (6–12 feathers, 2–4 mm). Miller (1924: 322) reported an 'apparently bare' gland in one specimen of *Ortalis vetula,* and noted a 'virtually vestigial' tuft in all the Cracidae, this last conclusive statement confirmed in the present study. Type I.
MATERIAL EXAMINED. *Crax nigra* 1; *C. alberti* 1; *C. globulosa* 1; *Penelope jacu-caca* 1; *Ortalis guttata* 2; *O. vetula* 1; *Pipile pipile* 1.

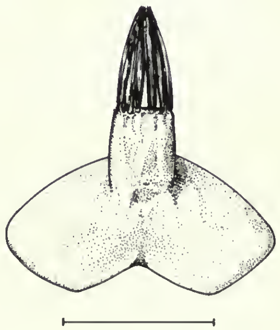
Family Tetraonidae (Grouse, Ptarmigans)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (10–12 feathers, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Tetrao urogallus* 2; *Lyrurus tetrix* 1; *Lagopus lagopus* 1 (M: 576·0, 0·18); *Canachites canadensis* 1 (M: 552·4, 0·02); *Bonasa umbellus* 3 (M: 552·2, 0·03. F: 591·5, 0·03); *Pedioecetes phasianellus* 1 (F: 664·0, 0·03); *Tympanuchus cupido* 1 (M: 863·5, 0·02); *Centrocercus urophasianus* 1 (M: 2221·7, 0·04).

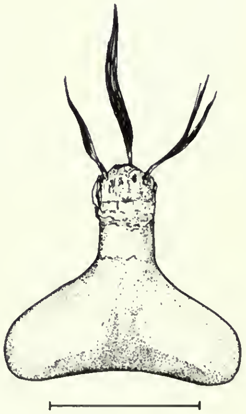
Family Phasianidae (Quails, Pheasants, Peacocks)
MORPHOLOGY (family). Usually distinctly bilobed, papilla large, tuft variable (6–12 feathers, Paris 1913; 5–10 feathers in 6 species, Jacob & Ziswiler 1982; only 2 in *Rollulus*) or, rarely, absent (one specimen of *Crossoptilon mantchuricum* was naked as were five specimens of *Argusianus*). Earlier, Nitzsch (1840), Newton (1893–1896), Beddard (1898), Grassé (1950), and Verheyen (1956*d*) had reported the absence of a gland in *Argusianus* (=*Argus*). Beddard (1898) found a tuft in one specimen of *Callipepla squamata* but a naked gland in another specimen. Type I.

Subfamily Odontophorinae (American quail)
MATERIAL EXAMINED. *Callipepla squamata* 2 (F: 209·4, 0·06); *Lophortyx californica* 3 (M: 133·2, 0·09. F: 169·4, 0·08); *Colinus virginianus* 9 ($\bar{x}$ of 4 M: 151·8, 0·15. $\bar{x}$ of 4 F: 156·5, 0·16); *Cyrtonyx montezumae* 1.

Subfamily Phasianinae (Partridges, Quails, Pheasants)
MATERIAL EXAMINED. *Francolinus adspersus* 1; *F. ahantensis* 1; *Perdix perdix* 1 (F: 360·0, 0·09); *Coturnix coturnix* 1; *Excalfactoria chinensis* 3; *Arborophila torqueola* 1; *A. brunneopectus* 1; *Rollulus roulroul* 1; *Tragopan temmincki* 1; *Lophophorus impejanus* 1; *Crossoptilon auritum* 1; *C. mantchuricum* 1; *Lobiophasis bulweri* 1; *Gallus gallus* 5 (M: 2270, 0·02); *Gallus gallus* × *Meleagris gallopavo* 1; *Catreus wallichii* 1 (M, Z: 1340, 0·05); *Phasianus colchicus* 2 (M: 1374.7, 0·03; 1292, 0·02); *Syrmaticus reevesii* 1; *Chrysolophus pictus* 1; *Argusianus argus* 5; *Pavo cristatus* 3 (M, Z: 3350, 0·02); *Afropavus congensis* 3.


Crax alberti

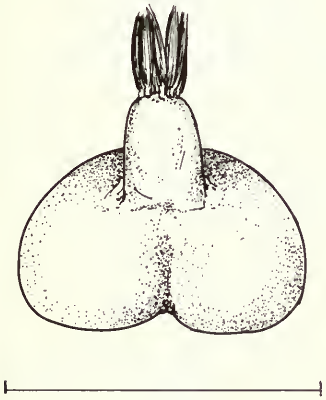

Lyrurus tetrix


Phasianus colchicus

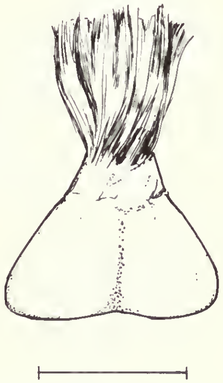
Family Numididae (Guinea fowl)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (8 feathers in *N. meleagris*, Jacob & Ziswiler 1982; only 2 in *Phasidus*). Type I.
MATERIAL EXAMINED. *Phasidus niger* 1; *Numida* sp. 1; *N. meleagris* 1; *Guttera pucherani* 1; *Acryllium vulturinum* 1.

Family Meleagrididae (Turkeys)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (7, 9 feathers, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Meleagris gallopavo* 5 (ad. M: 7400, 0.02. Subad. M: 3740, 0·02. Subad. F: 1870, 0·04).

Family Opisthocomidae (Hoatzin)
MORPHOLOGY. Bilobed, papilla small, tuft (up to 12 feathers) variable in size, or gland naked. Beddard (1898), Gadow (1893), and Verheyen (1956*c*) described the gland as feathered. I found that 9 nestlings, 'young,' or 'juveniles' had minute tufts, 2 'subadults' were naked, and 3 'adults' had tufted glands. Type I.
MATERIAL EXAMINED. *Opisthocomus hoazin* 14.


Numida sp.


Meleagris gallopavo


Opisthocomus hoazin

Order Gruiformes

Gland characteristics. Inter- and intrafamilial variation: gland absent, naked, or sparsely to densely tufted.

Family Mesoenatidae (Mesites, Monias)
MORPHOLOGY. Absent (also reported as such by Gadow 1893, Miller 1924, Verheyen 1958*a*, Van Tyne & Berger 1976). Beddard (1898: 381) erroneously reported the gland as present and nude.
MATERIAL EXAMINED. *Mesoenas variegata* 1; *M. unicolor* 1; *Monias benschi* 2.

Family Turnicidae (Bustard-Quails)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (also reported by Verheyen 1958*a*; ca 10 feathers). Type I.
MATERIAL EXAMINED. *Turnix sylvatica* 2; *T. tanki* 1; *T. suscitator* 1; *Ortyxelos meiffrenii* 1.

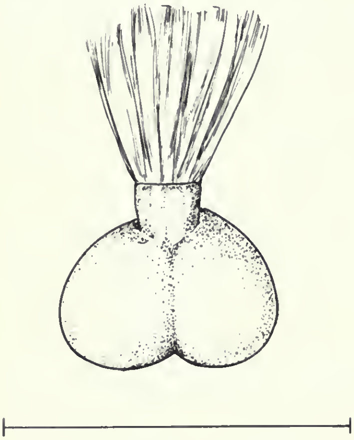
Family Pedionomidae (Collared Hemipodes)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (12 feathers). Type I.
NOTE. Gadow (1891) and Beddard (1898) reported a tufted gland in this family. Olson & Steadman (1981) believe that *Pedionomus* is a charadriiform, but the tufted gland supports no specific relationship for this family.
MATERIAL EXAMINED. *Pedionomus torquatus* 2.

Family Gruidae (Cranes)
MORPHOLOGY (family). Large and bilobed, papilla small with the end large and tufted (14–16

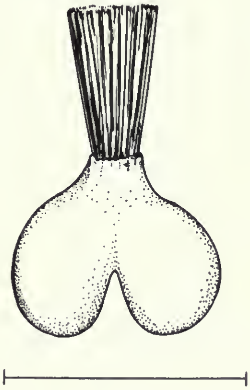
feathers, Paris 1913; 32 feathers in *G. grus*, Jacob & Ziswiler 1982; 20 feathers in *Grus*, Nitzsch 1867). Gadow (1893) described the gland of *Grus grus* as naked, but that report was probably erroneous because of the tufted glands now known from all other species examined. Type I.

Subfamily Gruinae

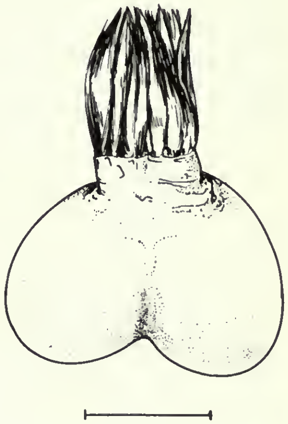
MATERIAL EXAMINED. *Grus canadensis* 9 (ad. M: 3520, 0·05. Subad. M: 2360, 0·03. Ad. F: 3880, 0·05; 3560, 0·05); *G. antigone* 1; *Anthropoides paradisea* 2.



Turnix suscitator



Pedionomus torquatus



Grus canadensis

Subfamily Balearicinae

MATERIAL EXAMINED. *Balearica pavonina* 2.

Family Aramidae (Limpkin)

MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (14 feathers). Type I.
MATERIAL EXAMINED. *Aramus scolopaceus* 9 ($\bar{x}$ of 6 M: 1128·6, 0·28. F: 1300, 0·29).

Family Psophiidae (Trumpeters)

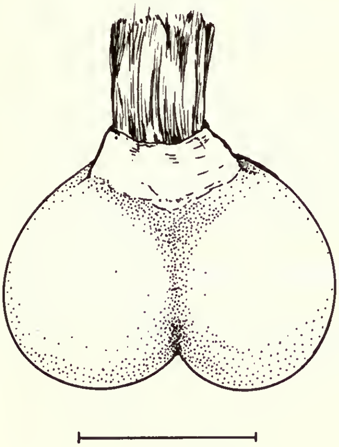
MORPHOLOGY. Indistinctly bilobed, papilla absent, sparse and short tuft (20 feathers). Nitzsch (1867) made the contradictory statement (p. 123), '... of the naked oil-gland, which is furnished with a circlet of feathers at the tip.' Type I.
MATERIAL EXAMINED. *Psophia crepitans* 1; *P. leucoptera* 3.

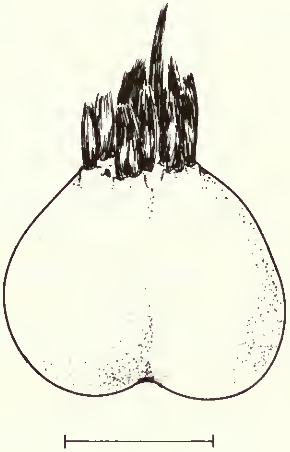
Family Rallidae (Rails, Coots, Gallinules)

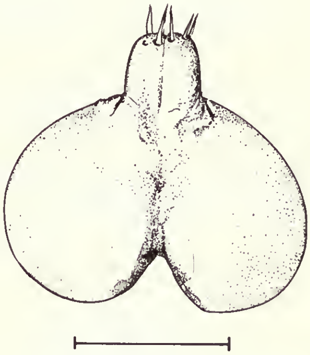
MORPHOLOGY (family). Distinctly bilobed, papilla usually large, tuft variable (Verheyen 1957*b*) (11–17 feathers in 5 species, Jacob & Ziswiler 1982; 6 in *Porphyrio*) or gland naked. Miller (1924), Verheyen (1957*b*), and Ripley (1976) stated that *Himantornis* has a naked gland, a condition that I confirmed. Beddard (1898: 321) stated that Ralli 'have as a rule a tufted oil gland but *Porzana carolina* is an exception.' Miller (1924) and I each found that 5 different specimens of this species all had tufted glands. In *Atlantisia rogersi* 2 specimens at the British Museum had naked glands, but 2 specimens at the American Museum of Natural History and Museum of Comparative Zoology each had tufted glands. Type I.

Subfamily Rallinae

MATERIAL EXAMINED. *Rallus longirostris* 3 (F: 186·3, 0·23); *R. elegans* 3 (F: 298·0, 0·16; 372·7, 0·29); *R. limicola* 6 (M: 66·3, 0·34. F: 65·3, 0·09), *R. owstoni* 1; *R. wakensis* 1; *Atlantisia rogersi* 5; *Tricholimnas sylvestris* 1; *Dryolimnas cuvieri* 1; *Rallina eurizonoides* 1; *Cyanolimnas cerverai* 1; *Gallirallus australis* 2; *Himantornis haematopus* 1; *Crecopsis egregia* 1; *Crex crex* 1; *Anurolimnas* *castaneiceps* 2; *Limnocorax flavirostra* 2; *Porzana carolina* 5 (M: 66·9, 0·15. F: 65·9, 0·22); *P. albicollis* 1; *Porzanula palmeri* 2; *Laterallus albigularis* 1; *Micropygia schomburgkii* 1; *Coturnicops noveboracensis* 1; *Sarothrura rufa* 1; *Poliolimnas cinerus* 1; *Tribonyx mortierii* 1; *Amaurornis phoenicurus* 1; *Gallicrex cinerea* 1; *Gallinula chloropus* 8 (M: 364·2, 0·11; 211·5, 0·23. $\bar{x}$ of 4 F: 274·3, 0·18; *Porphyriornis nesiotis* 1; *P. comeri* 1; *Porphyrula alleni* 1; *P. martinica* 4 (F: 203·6, 0·16); *Porphyrio porphyrio* 1, *P. poliocephalus* 1; *Notornis mantelli* 1.


Aramus scolopaceus


Psophia leucoptera


Porphyrio porphyrio

Subfamily Fulicinae
Material examined. *Fulica americana* 8 (M: 625·0, 0·11. F: 395·4, 0·16; 386·5, 0·17).

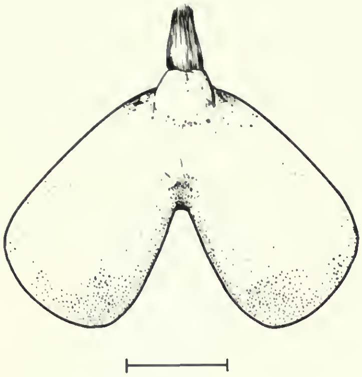
Family Heliornithidae (Sun-Grebes)
Morphology. Broad and bilobed, papilla moderately developed, tufted (16 feathers). Type I.
Material examined. *Podica senegalensis* 1; *Heliopais personata* 1; *Heliornis fulica* 1.

Family Rhynochetidae (Kagu)
Morphology. Apparently single-lobed, indistinct papilla, naked. The gland is not 'rudimentary' as stated by Jacob (1978: 168).
Material examined. *Rhynochetos jubatus* 1.

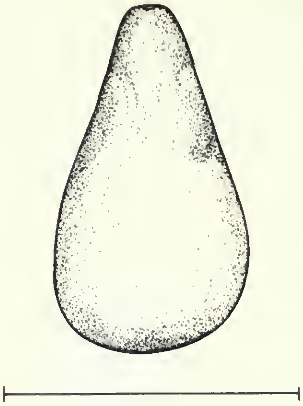
Family Eurypygidae (Sun-Bittern)
Morphology. Indistinctly bilobed, papilla moderately developed, tufted (10 1–2 mm feathers). Miller (1924: 322) concluded: 'Gadow gives the oil-gland of *Eurypyga* as bare; Beddard states that it is generally nude but occasionally tufted. In each of my two fresh examples, . . . there was a small tuft present.' Type I.
Material examined. *Eurypyga helias* 3.

Family Cariamidae (Cariamas)
Morphology. Apparently single-lobed, papilla large, naked. The unusual shape is described by Nitzsch (1867) as distinctly 'of a conical pyriform shape.'
Material examined. *Cariama cristata* 1.

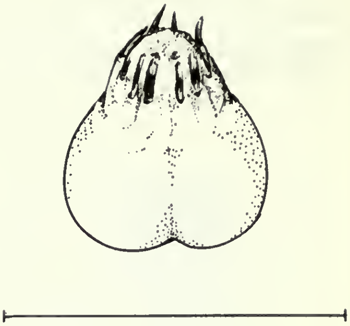
Family Otidae (Bustards)
Morphology. Gland absent in all species examined, a condition previously noted by Nitzsch (1840), Gadow (1893), Beddard (1898), Paris (1913), Grassé (1950), Verheyen (1957*b*) and Van Tyne & Berger (1976). Paris (1913) reported 'well marked outlines of the gland' in embryos.



Heliopais personata



Rhinochetos jubatus



Eurypyga helias

Material examined. *Choriotis kori* 2; *C. australis* 1; *Lophotis ruficrista* 1; *Eupodotis senegalensis* 2; *Lissotis melanogaster* 1.

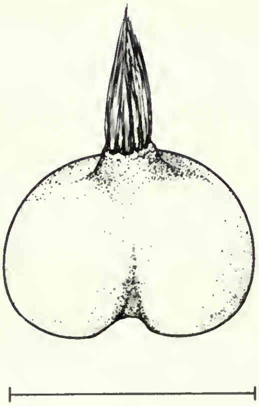
Order Charadriiformes

Gland characteristics. Heavily tufted.
Note. 10 families were described by Verheyen (1958*b*) as being tufted. All individuals of 16 families in the present study had tufted glands. Type I.

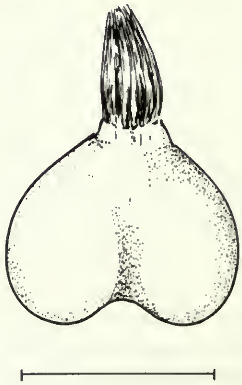
Family Jacanidae (Jacanas)
Morphology. Bilobed, papilla moderately developed (*contra* 'without a well-developed nipple' Verheyen 1957*d*), tufted (12 feathers).
Material examined. *Jacana spinosa* 2.

Family Rostratulidae (Painted Snipe)
Morphology. Bilobed, papilla indistinct, tufted (12 feathers).
Material examined. *Rostratula benghalensis* 1.

Cariama cristata



Jacana spinosa



Rostratula benghalensis

Family Haematopodidae (Oyster-catchers)

MORPHOLOGY. Bilobed, papilla small, tufted (28 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Haematopus ostralegus* 2.

Family Charadriidae (Lapwings, Plovers)

MORPHOLOGY (family). Distinctly bilobed, papilla moderately developed, tufted (12–24 feathers, Paris 1913; 12–14 feathers, Jacob & Ziswiler 1982).

Subfamily Vanellinae

MATERIAL EXAMINED. *Vanellus vanellus* 2; *Hoplopterus spinosus* 2; *Hoploxypterus cayanus* 1; *Zonifer tricolor* 1.

Subfamily Charadriinae

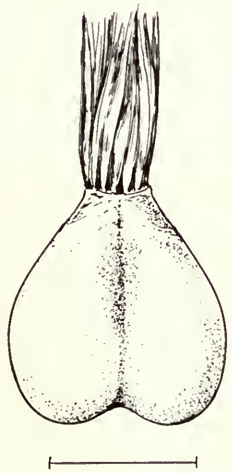
MATERIAL EXAMINED. *Squatarola squatarola* 2 (M: 205·3, 0·22. F: 216·2, 0·14); *Charadrius hiaticula* 1; *C. vociferus* 4 (F: 92·0, 0·08; 94·1, 0·07); *Eupoda montana* 1.

Family Scolopacidae (Woodcock, Sandpipers)

MORPHOLOGY (family). Distinctly bilobed, papilla small, tufted (12–24 feathers in 4 species, Jacob & Ziswiler 1982).

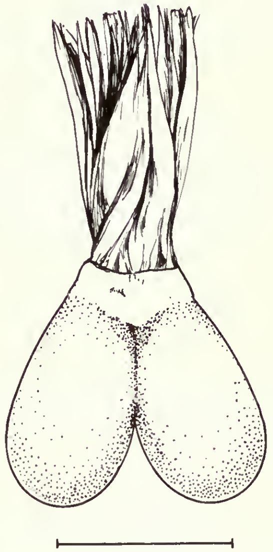
Subfamily Tringinae

MATERIAL EXAMINED. *Bartramia longicauda* 1; *Numenius minutus* 1; *Tringa totanus* 1; *Actitis macularia* 2 (F: 28·5, 0·12); *Catoptrophorus semipalmatus* 5 (M:297·8, 0·19).



Haematopus ostralegus

Charadrius vociferus



Catoptrophorus semipalmatus

Subfamily Arenariinae

MATERIAL EXAMINED. *Arenaria interpres* 5.

Subfamily Scolopacinae

MATERIAL EXAMINED. *Limnodromus scolopaceus* 8 ($\bar{x}$ of 4M: 104·2, 0·18. F: 121·1, 0·20); *L. griseus* 6 (F: 101·9, 0·12; 85·2, 0·12); *Capella gallinago* 3 (F: 101·5, 0·09); *Philohela minor* 5 (M: 106·0, 0·09. $\bar{x}$ of 4F: 179·2, 0·09).

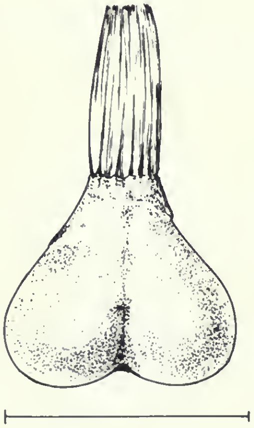
Subfamily Eroliinae

MATERIAL EXAMINED. *Calidris canutus* 2 (M: 94·5, 0·08); *Crocethia alba* 2 (F; 49·9, 0·07); *Ereunetes pusillus* 2; *Erolia minutilla* 1; *E. fuscicollis* 1; *E. alpina* 2.

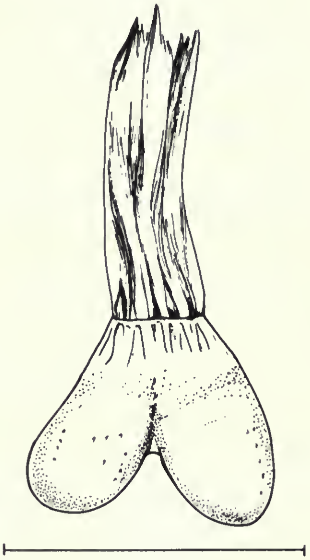
Family Recurvirostridae (Avocets, Stilts)
Morphology. Bilobed, papilla small, tufted (ca 20 feathers).
Material examined. *Himantopus himantopus* 3; *Recurvirostra americana* 1 (F: 289·4, 0·20).

Family Phalaropodidae (Phalaropes)
Morphology. Distinctly bilobed, papilla small, tufted.
Material examined. *Phalaropus fulicarius* 4 (unsexed: 40·5, 0·62; 40·4, 0·53. F: 42·0, 0·79); *Lobipes lobatus* 3 (F: 27·7, 0·42).

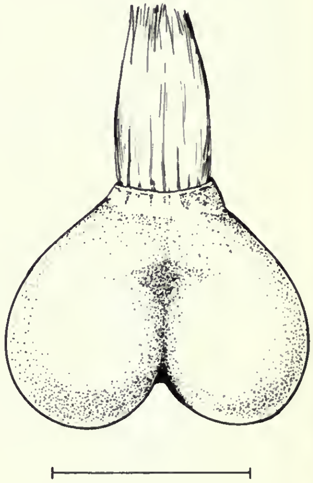
Family Dromadidae (Crab-plovers)
Morphology. Distinctly bilobed, papilla apparently absent, tufted (16 feathers).
Material examined. *Dromas ardeola* 1.



Himantopus himantopus



Phalaropus fulicarius



Dromas ardeola

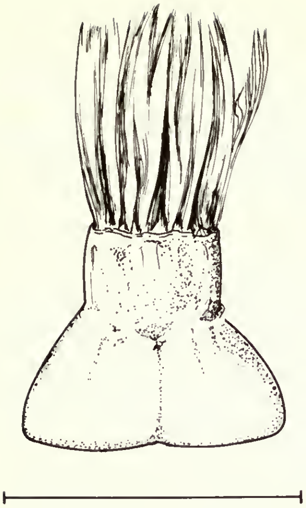
Family Burhinidae (Thick-knees)
Morphology. Indistinctly bilobed, broad papilla, tufted (14 feathers in *B. oedicnemus*, Jacob & Ziswiler 1982).
Material examined. *Burhinus oedicnemus* 1; *B. senegalensis* 1; *Esacus recurvirostris* 1.

Family Glareolidae (Pratincoles, Coursers)
Morphology (family). Indistinctly bilobed, large and round papilla, tufted (14 feathers).

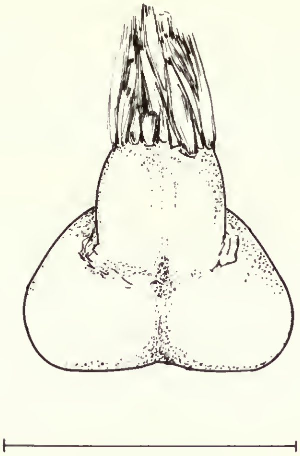
Subfamily Cursoriinae
Material examined. *Cursorius cursor* 1.

Subfamily Glareolinae
Material examined. *Stiltia isabella* 1; *Glareola pratincola* 1.

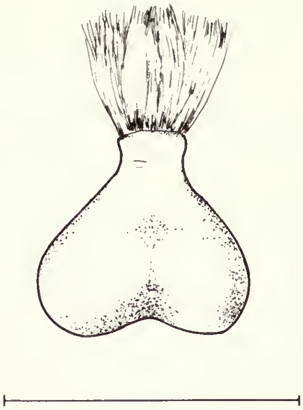
Family Thinocoridae (Seed-snipe)
Morphology. Indistinctly bilobed, papilla moderately developed, tufted (16 feathers).
Note. Based upon comparisons of gland morphologies, the present study confirms the belief of Sibley *et al.* (1968: 243) that seed-snipe 'are more like ... the Charadriiforms than any other group.'
Material examined. *Thinocorus orbignyianus* 1; *T. rumicivorus* 1.



Burhinus oedicnemus



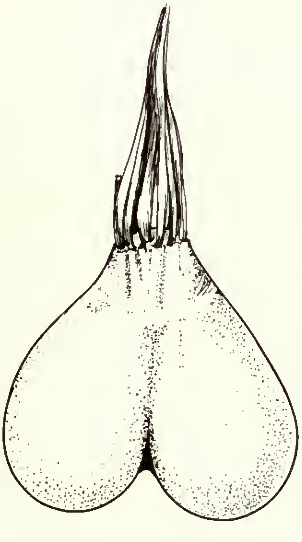
Cursorius cursor



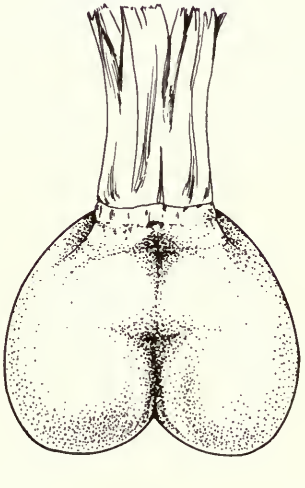
Thinocorus rumicivorus

Family Chionididae (Sheath-bills)
MORPHOLOGY. Distinctly bilobed, papilla moderately developed, tufted (16–18 feathers, Paris 1913).
MATERIAL EXAMINED. *Chionis alba* 1.

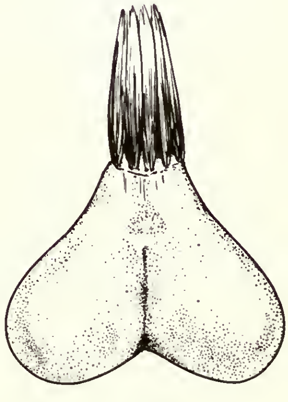
Family Stercorariidae (Skuas, Jaegers)
MORPHOLOGY. Distinctly bilobed, papilla apparently absent, tufted.
MATERIAL EXAMINED. *Stercorarius pomarinus* 2 (F: 616·0, 0·37); *S. longicaudus* 4 (ad M: 333·9, 0·23. Subad. F: 271·5, 0·28).



Chionis alba



Stercorarius pomarinus



Larus atricilla

Family Laridae

Subfamily Larinae (gulls)

Morphology. Distinctly bilobed and broad (see also Verheyen 1954*a*), papilla moderately developed, tufted (18–26 feathers in 4 species, Paris 1913; 22–29 feathers, Jacob & Ziswiler 1982).
Material examined. *Larus delawarensis* 5 (ad. M: 330·0, 0·15. Ad. F: 440·0, 0·13); *L. atricilla* 8 (ad. M: 368·5, 0·29. Ad. F: 320·0, 0·20); *L. philadelphia* 2 (ad. F: 179·8, 0·21); *Rissa tridactyla* 2.

Subfamily Sterninae (Terns)

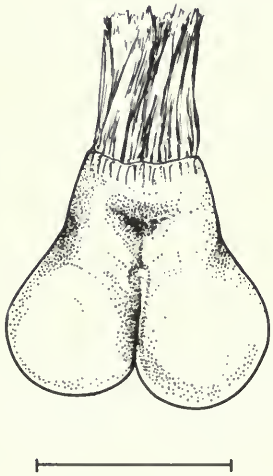
Morphology. Similar to Larinae except gland is more compact (see figures); 6–8 feathers in 4 species, Jacob & Ziswiler 1982.
Material examined. *Chlidonias nigra* 2; *Hydroprogne caspia* (*tschegrava* of Peters) 4 (F: 686·0, 0·18; 698·0, 0·18); *Sterna hirundo* 9 (M: 117·4, 0·26. F: 137·7, 0·33); *S. paradisea* 2 (M: 110·9, 0·16); *S. forsteri* 4 (F: 147·0, 0·33); *S. anaethetus* 6 (M: 130·0, 0·43; 135·0, 0·31); *S. fuscata* 8 (M: 218·0, 0·29; 218·6, 0·25. F: 141·0, 0·38; 156·0, 0·35; 174·0, 0·38); *S. albifrons* 5 (M: 46·1, 0·46; 51·3, 0·57); *Thalasseus maximus* 7 (M: 385·9, 0·35. F: 353·2, 0·26); *T. sandvicensis* 3; *Larosterna inca* 2 (M, Z: 153·3, 0·21); *Anous stolidus* 4; *Gygis alba* 2 (M: 117·9, 0·43; 113·3, 0·47).

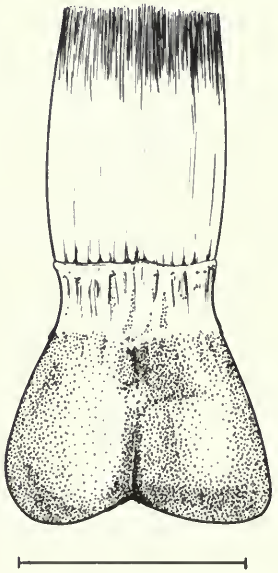
Family Rynchopidae (Skimmers)

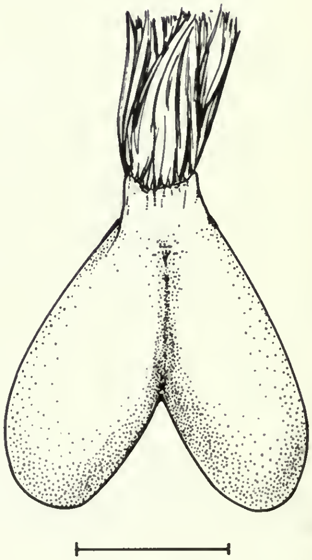
Morphology. Bilobed, papilla broad and apparently double, densely tufted (24 feathers).
Material examined. *Rynchops niger* 6 (M: 211·4, 0·20).

Family Alcidae (Auks, Murres, Puffins)

Morphology. Elongated and bilobed, papilla moderately developed, tufted (Verheyen 1958*d*; 30–50 feathers, Paris 1913; 2–8 (sic?) feathers, Jacob & Ziswiler 1982; 20–40, present study).
Material examined. *Plautus alle* 2; *Pinguinus impennis* (mounted bird) 1; *Uria lomvia* 1; *U. aalge* 1; *Cepphus grylle* 1 (F: 363·0, 0·22); *C. columba* 3 (M: 380·0, 0·18. F: 371·5, 0·19); *Synthliboramphus antiquus* 2 (M: 180·5, 0·25); *Ptychoramphus aleuticus* 2 (F: 207·9, 0·47); *Aethia cristatella* 1; *Cerorhinca monocerata* 2 (M: 631·5, 0·31); *Lunda cirrhata* 2 (F: 673·5, 0·30; 792·4, 0·20).


Sterna fuscata


Rynchops niger


Lunda cirrhata

Order Columbiformes

Gland characteristics. Naked or absent.

Family Pteroclididae (Sand-grouse)
MORPHOLOGY. Indistinctly bilobed, papilla broad and well developed, naked.
MATERIAL EXAMINED. *Syrrhaptes paradoxus* 1; *Pterocles namaqua* 1; *P. decoratus* 1; *P. lichtensteinii* 1.

Family Columbidae (Pigeons and Doves)

Subfamily Treroninae (Fruit pigeons)
MORPHOLOGY. Absent or, when present, indistinctly bilobed, papilla large, naked.
MATERIAL EXAMINED. *Sphenurus apicauda* 1*; *S. oxyura* 1*; *Treron curvirostra* 2*; *T. pompadora* 2*; *T. olax* 1*; *T. vernans* 2*; *T. bicincta* 1*; *T. s. thomae* 1*; *T. australis* 1*; *T. calva* 1*; *T. waalia* 1*; *Phapitreron leucotis* 2; *P. amethystina* 1; *Leucotreron occipitalis* 1; *Ptilinopus*** *dupetithouarsii* 1; *P. regina* 1; *P. insularis* 1*; *P. raratongensis* 1; *P. huttoni* 1; *P. porphyraceus* 1; *P. greyii* 1; *P. richardsii* 1; *P. perousii* 1; *P. superbus* 3; *P. pulchellus* 2*; *P. coronulatus* 2*; *P. monacha* 1; *P. iozonus* 1*; *P. rivoli* 3*; *P. eugeniae* 1*; *P. hypogastra* 1*; *P. jambu* 1; *P. aurantiifrons* 1; *P. ornatus* 2; *P. tannensis* 1*; *Chrysoena victor* 1*; *Alectroenas pulcherrima* 1; *A. madagascariensis* 2; *Megaloprepia magnifica* 1*; *Ducula oceanica* 1; *D. pacifica* 1; *D. aenea* 1; *D. bicolor* 1; *D. spilorrhoa* 1; *D. badia* 1*; *D. rufigaster* 1; *D. zoeae* 1*.

Subfamily Columbinae (Pigeons, Doves)
MORPHOLOGY. Except for some individuals or varieties of *Columba livia*, the gland is present in all genera and species of Columbinae thus far examined. Indistinctly bilobed, papilla large, naked. Reported by Beddard (1898) as absent in *Ptilopas puella* (= *Columba puella* of Peters), *Starnoenas* (also absent *fide* Garrod 1874*a*), and *Turacoena*, all genera and species unavailable for the present study.
MATERIAL EXAMINED. *Columba livia*† 2 (M: 268·0, 0·05. F: 312·8, 0·08); *C. palumbus* 1; *C. leucocephala* 3 (F: 205·2, 0·10; 264·0, 0·05); *C. guinea* 1; *C. fasciata* 1; *Macropygia unchall* 1; *M. amboiensis* 2; *M. ruficeps* 1; *M. phasianella* 1; *M. nigrirostris* 2; *Ectopistes migratoria* 2; *Zenaidura macroura* 8 (M: 123·0, 0·01; 134·4, 0·03; 105·7, 0·02. F: 123·4, 0·01; 117·1, 0·03); *Z. auriculata* 1; *Zenaida asiatica* 1 (M: 173·2, 0·02); *Nesopelia galapagoensis* 1; *Streptopelia orientalis* 1; *S. capicola* 1; *S. senegalensis* 3; *Geopelia humeralis* 1; *G. striata* 2; *G. cuneata* 1; *Metriopelia melanoptera* 1; *M. aymara* 1; *Scardafella inca* 1; *Columbigallina passerina* 1 (F: 41·5, 0·02); *C. talpacoti* 1; *C. minuta* 1; *Claravis pretiosa* 3; *Oena capensis* 6; *Turtur afer* 1; *T. chalcospilos* 2; *Chalcophaps indica* 3; *C. stephani* 1; *Henicophaps albifrons* 1; *Phaps chalcoptera* 1; *Ocyphaps lophotes* 3; *Lophophaps ferruginea* 1; *Geophaps smithii* 2; *Aplopelia larvata* 1; *A. simplex* 1; *Leptotila verreauxi* 1; *L. rufaxilla* 1; *L. plumbeiceps* 3; *L. cassini* 5; *Oreopelia caniceps* 1; *Geotrygon versicolor* 1; *Gallicolumba luzonica* 1; *G. beccarii* 1; *G. rubescens* 2; *Otidiphaps nobilis* 1; *Caloenas nicobarica* 2.

Subfamily Gourinae (Crowned Pigeons)
MORPHOLOGY. Absent
MATERIAL EXAMINED. *Goura cristata* 1; *G. scheepmakeri* 1; *G. victoria* 1.

Subfamily Didunculinae (Tooth-billed Pigeons)
MORPHOLOGY. Absent. Jacob & Ziswiler (1982) reported a gland in 2 specimens of *Didunculus*, an inexplicable difference from the present and all previous reports (Newton 1893–1896, Beddard 1898, Verheyen 1957*a*).
MATERIAL EXAMINED. *Didunculus strigirostris* 3.

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*gland absent, present study; absent in *Treron* (Garrod 1874*a*). Jacob & Ziswiler (1982 and V. Ziswiler in litt.) found glands in adult *Treron pompadora, T. vernans, T. waalia*.

**gland 'very small in *Ptilinopus*' *fide* Garrod 1874*a*.

†absent in some varieties such as Fantail, Oriental, Roller, Maltese, White Carneau (Darwin 1900, Johansson 1927, Levi 1941, Verheyen 1957*a*).

Order Psittaciformes*

Gland characteristics. Tufted or absent.

Family Psittacidae (Lories, Parrots, Macaws)

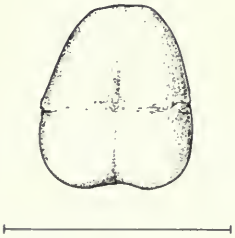
Subfamily Strigopinae (Owl Parrots)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted.
MATERIAL EXAMINED. *Strigops habroptilus* 1.

Subfamily Nestorinae (Keas)
MORPHOLOGY. Distinctly bilobed, papilla well developed, tufted (13 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Nestor notabilis* 3.

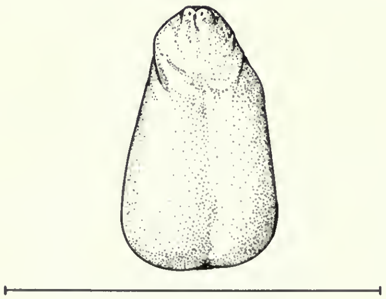
Subfamily Loriinae (Lories)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (5–8 feathers in 3 species, Jacob & Ziswiler 1982). Type I.
MATERIAL EXAMINED. *Chalcopsitta atra* 1; *Eos cyanogenia* 1; *E. squamata* 1; *E. bornea* 3; *Trichoglossus ornatus* 1; *T. haematod* 3; *T. chlorolepidotus* 1; *Psitteuteles johnstoniae* 1; *Domicella garrula* 3; *Vini stepheni* 1; *Glossopsitta porphyrocephala* 1; *Charmosyna josefinae* 1; *C. papou* 1; *Oreopsittacus arfaki* 1; *Neopsittacus musschenbroekii* 1.

Subfamily Micropsittinae (Pigmy Parrots)
MORPHOLOGY. Distinctly bilobed, papilla large, tufted (3–4 feathers, Jacob & Ziswiler 1982).
MATERIAL EXAMINED. *Micropsitta pusio* 1.

Subfamily Kakatoeinae (Cockatoos)
MORPHOLOGY. Absent or when present, distinctly bilobed, papilla large, tufted (4–8 feathers in 2 species, Jacob & Ziswiler 1982).
NOTE. Newton (1893–1896: 653) stated that the gland 'exists, though hardly in a functional condition, in ... *Cacatua cristata* (Cockatoo) ...' =*Kakatoe sulphurea citrino-cristata* of Peters. Nitzsch (1867), Garrod 1874*b*, Gadow (1893), and Grassé (1950), noted no gland in *Cacatua sulfurea* and its absence in *C. roseicapella* was reported by Paris (1913). I found that specimens of both of these species had tufted glands.



Pterocles lichtensteinii



Zenaidura macroura

Ara chloroptera

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*many zoo and captive birds.

Material examined. *Probosciger aterrimus* 4†; *Calyptorhynchus baudinii* 1; *Callocephalon fimbriatum* 2; *Kakatoe galerita* 7; *K. sulphurea* 4; *K. alba* 3; *K. moluccensis* 1; *K. haematuropygia* 1; *K. leadbeateri* 1; *K. sanguinea* 1; *K. tenuirostris* 1; *K. roseicapella* 3; *Nymphicus hollandicus* 4.

Subfamily Psittacinae (Macaws, Parrots)
Morphology. Distinctly bilobed, papilla large, tufted (12 feathers, Paris 1913; 3–11 feathers in 33 species, Jacob & Ziswiler 1982) or gland absent. Type I.
Note. Miller (1924: 324) reported no gland in *Orthopsittaca* and *Diopsittaca* (= *Ara* of Peters), but listed no species. Jacob (1978: 168) stated that the gland is absent in *Ara* but indicated on species.
Material examined. *Anodorhynchus hyacinthus* 5*; *A. leari* 1*; *Ara*** *ararauna* 2; *A. militaris* 2; *A. macao* 4 (F, Z: 996·5, 0·05); *A. chloroptera* 3; *A. auricollis* 1; *A. severa* 1; *A. manilata* 3*; *Aratinga acuticaudata* 1; *A. guarouba* 1; *A. leucophthalmus* 1; *A. holochlora* 1; *A. jandaya* 1; *A. solstitialis* 2; *A. canicularis* 1; *A. aurea* 2; *Nandayus nanday* 1; *Conuropsis carolinensis* 1; *Rhynchopsitta pachyrhyncha* 1; *Cyanoliseus patagonus* 1; *Pyrrhura rhodogaster* 1; *P. molinae* 1; *P. hoffmanni* 1; *Myiopsitta monachus* 1; *Psilopsaigon aurifrons* 1; *Forpus conspicillatus* 1; *Brotogeris tirica* 1*; *B. versicolurus* 2*; *B. pyrrhyopterus* 1*; *B. jugularis* 2*; *B. cyanoptera* 2*; *B. chrysopterus* 4*; *B. st. thoma* 1*; *Pionites melanocephala* 2; *Graydidascalus brachyurus* 2*; *Pionus**** *menstruus* 2*; *P. maximiliani* 1*; *P. senilis* 1*; *P. chalcopterus* 1*; *Amazona leucocephala* 1*; *A. ventralis* 1*; *A. xantholora* 1*; *A. albifrons* 1*; *A. agilis* 1*; *A. vittata* 1*; *A. viridigenalis* 1*; *A. autumnalis* 1*; *A. barbadensis* 1*; *A. aestiva* 1*; *A. ochrocephala* 3*; *A. amazonica* 1*; *A. farinosa* 1*; *A. vinacea* 1*; *A. guildingii* 1*; *A. imperialis* 2*; *Triclaria malachitacea* 1; *Poicephalus senegalus* 2; *P. meyeri* 1; *P. ruppellii* 2; *Psittacus erithacus* 1; *Coracopsis nigra* 1; *Psittrichas fulgidus* 1; *Lorius roratus* 1; *Prioniturus discurus* 1; *Psittacula krameri* 5; *P. alexandri* 1; *P. cyanocephala* 1; *Polytelis swainsonii* 2; *P. alexandrae* 2; *Aprosmictus erythropterus* 3; *Psittinus cyanurus* 2; *Agapornis roseicollis* 2; *A. fischeri* 1; *A. lilianae* 3; *Loriculus vernalis* 1; *Platycercus elegans* 1; *P. eximius* 3; *P. icterotis* 2; *P. zonarius* 2; *Psephotus haematonotus* 3; *P. varius* 3; *Neophema elegans* 3; *N. chrysostomus* 1; *N. petrophila* 1; *N. pulchella* 7; *N. splendida* 3; *N. bourkii* 6; *Cyanoramphus auriceps* 2; *Melopsittacus undulatus* 1.

Order Cuculiformes

Gland characteristics. Tufted or naked.

Family Musophagidae (Plantain-eaters)
Morphology. Flattened and distinctly bilobed, papilla moderately developed, tufted (8 feathers). Verheyen (1956*b*) was evidently in error when he noted (p. 2) that touracos have a naked gland. Type I.
Material examined. *Tauraco corythaix* 1; *T. leucolophus* 1; *Gallirex porphyreolophus* 1; *Musophaga violacea* 3; *Crinifer leucogaster* 1; *C. africanus* 2.

Family Cuculidae (Cuckoos, Roadrunner, Anis)
Morphology (family). Flattened and more or less distinctly bilobed, papilla large and often appearing double, naked.

Subfamily Cuculinae
Material examined. *Clamator glandarius* 1; *Cuculus canorus* 1; *Cacomantis merulinus* 1; *Chrysococcyx cupreus* 1; *C. klaas* 1; *C. caprius* 9; *Chalcites basalis* 1.

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†gland absent, this study and Beddard (1898).
*gland absent, present study; Jacob & Ziswiler (1982, V. Ziswiler in litt.) found a gland in adult *Pionus fuscus*.
**gland present in *A. ambigua* and *maracana* (*fide* Garrod 1874*b*).
***gland also absent in *P. sordidus* (*fide* Garrod 1874*b*).

Subfamily Phaenicophaeinae
MATERIAL EXAMINED. *Coccyzus americanus* 4 (unsexed: 46·7, 0·09); *Piaya cayana* 2; *Saurothera vetula* 2; *Ceuthmochares aereus* 1; *Rhopodytes diardi* 1; *R. tristis* 2; *Rhamphococcyx curvirostris* 2; *Dasylophus superciliosus* 1.

Subfamily Crotophaginae (Anis, Guiras)
MATERIAL EXAMINED. *Crotophaga ani* 3 (M: 113·9, 0·03); *C. sulcirostris* 7; *Guira guira* 1.

Subfamily Neomorphinae (Roadrunners, Ground Cuckoos).
MATERIAL EXAMINED. *Tapera naevia* 1; *Morococcyx erythropygus* 2; *Geococcyx californiana* 3.

Subfamily Couinae (Couas)
MATERIAL EXAMINED. *Coua cristata* 1.

Subfamily Centropodinae (Coucals)
MATERIAL EXAMINED. *Centropus viridis* 2; *C. toulou* 1; *C. benegalensis* 2.

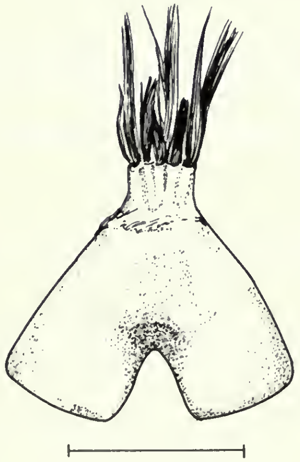
Order Strigiformes

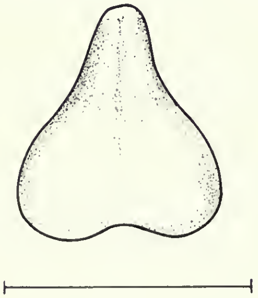
Gland characteristics. Naked or minutely tufted.
NOTE. Glands of various strigiform species have usually been described as 'naked' or 'nude' (Gadow 1893, Beddard 1898, Jacob & Ziswiler 1982). Nitszch (1840), Miller (1924), and I used magnification and identified 1 to 12 'rudimentary,' 'vestigial,' or 'minute' feathers on the papilla's tip in some individual specimens.

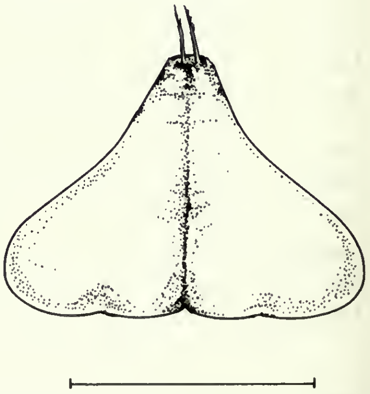
Family Tytonidae (Barn Owls)

Subfamily Tytoninae
MORPHOLOGY. Indistinctly bilobed, papilla moderately developed, tufted with minute feathers (1 or 2 5-mm feathers) or naked. Nitzsch (1867: 71) noted minute feathers on the papilla's apex in *Strix flammea, S. perlata,* and *S. furcata* (all = *Tyto alba*). Type I.
MATERIAL EXAMINED. *Tyto alba* 7* (M: 502·0, 0·07; 490·0, 0·04. F: 530·0, 0·12; 488·4, 0·11).

Subfamily Phodilinae
MORPHOLOGY. Like Tytoninae. Nitzsch (1867: 71) reported minute feathers at the gland apex in *Strix badia* (= *Phodilus badius*), but none were seen on 3 specimens in the present study.
MATERIAL EXAMINED. *Phodilus badius* 3.


Tauraco corythaix


Saurothera vetula


Tyto alba

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*minute feathers in 3 specimens.

Family Strigidae (Typical Owls)
Morphology (family). More superficial than in any other avian family, appearing to lie on top of the skin ('almost standing up,' Paris 1913: 180), bilobed, papilla large, tufted (up to 10 1-mm minute feathers) or naked. Type I.

Subfamily Buboninae
Material examined (naked unless otherwise indicated). *Otus spilocephalus* 1†; *O. scops* 1; *O. bakkamoena* 1; *O. asio* 26††, ††† (M: 103·2, 0·07; 107·7, 0·08. F: 149·3, 0·07; 108·4, 0·11); *O. trichopsis* 1†; *O. guatemalae* 1†; *O. choliba* 1†, †††; *O. watsonii* 1; *O. leucotis* 1; *Lophostrix cristata* 2; *Bubo virginianus* 8††† (M: 1207·0, 0·04; 1407·0, 0·04. F: 1887·0, 0·04; 1670·0, 0·03); *B. bubo* 1; *B. africanus* 1†††; *B. lacetus* 1†††; *Ketupa*†††*ketupu* 1; *Pulsatrix perspicillata* 1†††; *Nyctea scandiaca* 2†††; *Surnia ulula* 3 (M: 310·0, 0·07. F: 355·7, 0·04); *Glaucidium brasilianum* 2; *G. brodiei* 1; *Micrathene whitneyi* 1; *Ninox novaeseelandiae* 1†††; *N. philippensis* 1; *Athene noctua* 2; *A. brama* 1; *Speotyto cunicularia* 4; *Ciccaba virgata* 1†; *C. nigrolineata* 1; *C. woodfordii* 1.

Subfamily Striginae
Material examined (naked unless otherwise indicated): *Strix aluco* 1*; *S. varia* 20**, **** (M: 762·9, 0·09. x̄ of 9 F: 775·4, 0·07); *S. nebulosa* 1*; *Rhinoptynx clamator* 1; *Asio otus* 5***, **** (F: 306·0, 0·09); *A. madagascariensis* 1*; *A. flammeus* 3*****; *Pseudoscops grammicus* 1; *Aegolius acadicus* 5 (M: 97·1, 0·10).

Order Caprimulgiformes

Gland characteristics. Naked or rarely absent.

Family Steatornithidae (Oil-bird)
Morphology. Indistinctly bilobed, papilla large, naked (first reported by Garrod 1873). Described by Paris (1913: 177) and Newton (1893–1896: 653) as 'large.' (See section on Weights and sizes of glands.)
Material examined. *Steatornis caripensis* 1.

Family Podargidae (Frogmouths)
Morphology. *Podargus*—absent (see also Gadow 1893, Verheyen 1956*a*, Grassé 1950, Miller 1924). *Batrachostomus*—indistinctly bilobed, papilla large, naked. The implication by Van Tyne & Berger (1976) that the gland is absent in (all) Podargidae is incorrect.
Material examined. *Podargus strigoides* 2; *P. papuensis* 1; *P. ocellatus* 2; *Batrachostomus auritus* 1; *B. septimus* 2; *B. stellatus* 1; *B. javensis* 1.

Family Nyctibiidae (Potoos)
Morphology. Very small, indistinctly bilobed, papilla large, naked.
Note. Miller (1924: 324) reported 'the loss of the oil-gland' in *Nyctibius*.
Material examined. *Nyctibius griseus* 3.

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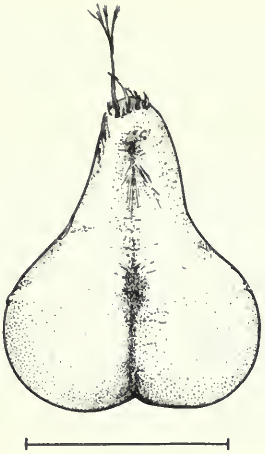
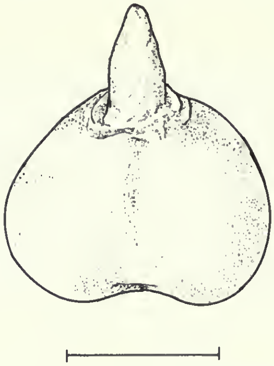
†minute tuft, present study.
††minute tuft, up to 8 1-mm feathers in 8 specimens.
†††some specimens with minute tuft *fide* Miller (1924: he also reported tufts in *Ketupa zeylonensis, Bubo bubo, Gymnoglaux lawrencii*).

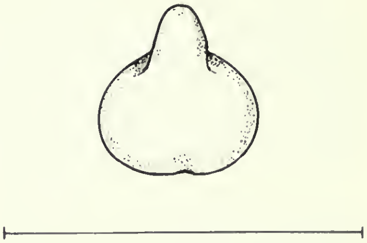
*minute tuft, present study.
**minute feathers in 6 specimens.
***minute feathers in 3 specimens.
****some specimens with minute tuft (Nitszch 1840, Beddard 1898, Miller 1924, or Verheyen 1956*a*).
*****'one or 2 very small white feathers,' Paris 1913: 182.



Asio flammeus



Steatornis caripensis



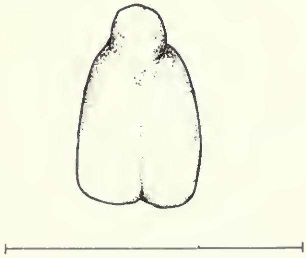
Batrachostomus septimus

Family Aegothelidae (Owlet-nightjars)
Morphology. Broad, flattened and bilobed, papilla large, naked.
Material examined. *Aegotheles insignis* 1.

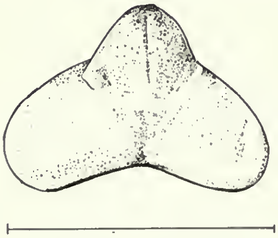
Family Caprimulgidae (Nighthawks, Goatsuckers)
Morphology (family). Very small not apparently bilobed (see also Paris 1913: 173), papilla large, naked. I did not confirm the report by Arnall & Keymer (1975) that the gland is absent 'in nightjars.'

Subfamily Chordeilinae (Nighthawks)
Material examined. *Lurocalis semitorquatus* 1; *Chordeiles minor* 6 (M: 64·8, 0·01; 67·5, 0·01. F: 75·4, 0·01; 87·5, 0·01; 79·6, 0·01); *Podager nacunda* 2.

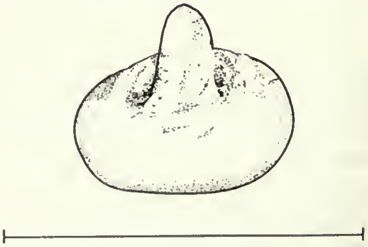
Subfamily Caprimulginae (Goatsuckers)
Material examined. *Eurostopodus macrotis* 1; *Nyctidromus albicollis* 4; *Phalaenoptilus nuttallii* 2; *Otophanes yucatanicus* 1; *Caprimulgus carolinensis* 10 (M: 113·0, 0·01; 80·7, 0·01; 124·8, 0.01. $\bar{x}$ of 4 F: 114·2, 0·01); *C. vociferus* 2 (M: 55·5, 0·02. F: 52·5, 0·02); *Scotornis climacurus* 1; *Semeiophorus vexillarius* 1; *Hydropsalis brasiliana* 1.



Nyctibius griseus



Aegotheles insignis



Podager nacunda

Order Apodiformes

Gland characteristics. Naked.
Note. The reference by Elder (1954) and Pettingill (1985) to gland absence in 'certain species' of Apodiformes was unsubstantiated by me.

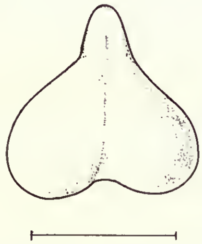
Family Apodidae (Swifts)
Morphology (family). Indistinctly bilobed, papilla moderately developed, naked.

Subfamily Chaeturinae (Spine-tailed Swifts)
Material examined. *Collocalia inexpectata* 1; *C. vanikorensis* 1; *Hirund-apus giganteus* 2; *Streptoprocne zonaris* 1; *Chaetura pelagica* 3; *C. rutilus* 1.

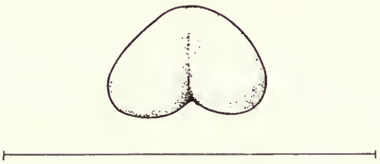
Subfamily Apodinae (Typical Swifts)
Material examined. *Apus apus* 1; *Aeronautes saxatalis* 1; *Reinarda squamata* 1; *Cypsiurus parva* 1.

Family Hemiprocnidae (Crested Swifts)
Morphology. Indistinctly bilobed, papilla absent, naked.
Material examined. *Hemiprocne mystacea* 1; *H. comata* 1.

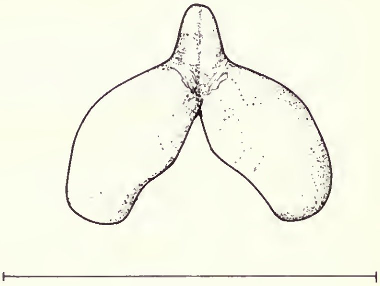
Family Trochilidae (Hummingbirds)
Morphology. Distinctly bilobed with lobes greatly separated, papilla large, naked.
Material examined. *Glaucis hirsuta* 1; *Phaethornis superciliosus* 2; *P. eurynome* 1; *P. longuemareus* 2; *Eutoxeres condamini* 2; *Phaeochroa cuvierii* 2; *Campylopterus curvipennis* 8; *C. hemileurcurus* 1; *C. ensipennis* 1; *Eupetomena macroura* 1; *Florisuga mellivora* 1; *Colibri serrirostris* 1; *Anthracothorax nigricollis* 1; *Chrysolampis mosquitus* 1; *Stephanoxis lalandi* 1; *Chlorestes notatus* 1; *Thalurania furcata* 1; *Hylocharis chrysura* 1; *Chrysuronia oenone* 1; *Leucochloris albicollis* 1; *Amazilia candida* 1; *A. versicolor* 1; *A. cyanocephala* 1; *A. rutila* 1; *A. tzacatl* 13; *Patagona gigas* 1; *Ensifera ensifera* 1; *Archilochus colubris* 3; *Selasphorus rufus* 1.



Hirund-apus (Chaetura) giganteus



Hemiprocne comata



Glaucis hirsuta

Order Coliiformes

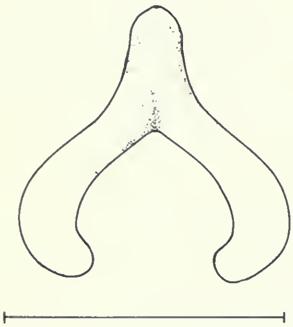
Gland characteristics. Tufted.

Family Coliidae (Colies)
Morphology. Distinctly bilobed, papilla large, tufted. Verheyen (1956*e*) makes the unsubstantiated comment that the gland of *Urocolius* (= *Colius indicus* and *C. macrourus* of Peters) is naked. Both Nitzsch (1867) and Garrod (1876) reported that the gland of *Colius* is tufted. Type I.
Material examined. *Colius striatus* 4; *C. colius* 1; *C. indicus* 2; *C. macrourus* 1.

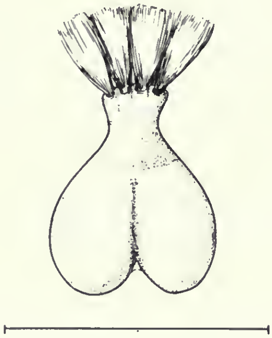
Order Trogoniformes

Gland characteristics. Naked.

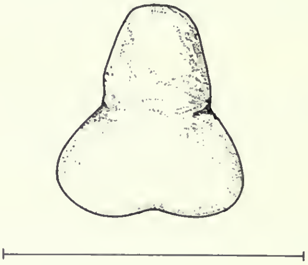
Family Trogonidae (Trogons)
Morphology. Indistinctly bilobed, papilla large, naked.
Material examined. *Pharomachrus mocino* 2; *Priotelis temnurus* 1; *Temnotrogon roseigaster* 1; *Trogon strigilatus* 1; *T. citreola* 1; *Apaloderma marina* 1; *Harpactes erythrocephalus* 1.



Patagona gigas



Colius macrourus



Pharomachrus mocino

Order Coraciiformes*

Gland characteristics. Much inter- and intrafamilial variation: naked, or sparsely to densely tufted.

Family Alcedinidae (Kingfishers)

Subfamily Cerylinae
Morphology. Indistinctly bilobed, papilla absent or small, tufted (16 feathers in *C. alcyon*).
Material examined. *Ceryle torquata* 1; *C. alcyon* 6 (M: 102·5, 0·25. F: 104·5, 0·22); *C. rudis* 7; *Chloroceryle americana* 6; *C. aena* 4.

Subfamily Alcedininae
Morphology. Like Cerylinae (12 feathers, Paris 1913, Jacob & Ziswiler 1982).
Material examined. *Alcedo atthis* 1; *A. meninting* 1; *A. euryzona* 1; *A. leucogaster* 1; *Ispidina picta* 1; *I. madagascariensis* 1; *Ceyx argentatus* 1; *C. azureus* 1; *C. erithacus* 1.

Subfamily Daceloninae
Morphology. Indistinctly or distinctly bilobed, papilla absent (*Pelargopsis*) to large (*Tanysiptera*), tufted (small in *Lacedo*, large in *Halcyon*) or gland naked (*Tanysiptera*) (12 feathers in *Dacelo*). *Tanysiptera* species apparently have no distinctive ecological or behavioral traits that might be correlated with the unusual naked gland condition (Fry 1980). Type I.
Material examined. *Pelargopsis capensis* 1; *Lacedo pulchella* 2; *Dacelo novaeguineae* 3; *D. leachii* 1; *Clytoceyx rex* 1; *Melidora macrorrhina* 1; *Halcyon coromanda* 1; *H. smyrnensis* 1; *H. pileata* 1; *H. senegalensis* 1; *H. malimbica* 1; *H. albiventris* 1; *H. macleayii* 1; *H. cinnamomina* 1; *H. chloris* 1; *Tanysiptera galatea* 2; *T. sylvia* 1.

Family Todidae (Todies)
Morphology. Indistinctly bilobed, papilla large, tufted (6 feathers in *T. subulatus*). Nitzsch (1867: 88) erroneously stated that *Todus* has a naked oil-gland, a point corrected by Forbes (1882). Type I.
Material examined. *Todus angustirostris* 1; *T. subulatus* 2.

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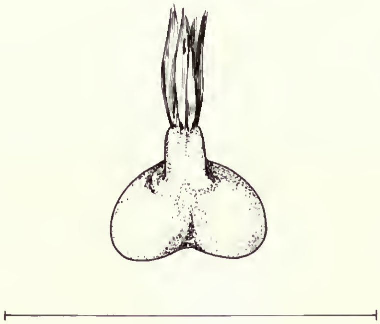
*morphology reported here is, with exceptions noted below, consistent with the descriptions in Verheyen (1955, *a, b, c*).

Family Momotidae (Motmots)

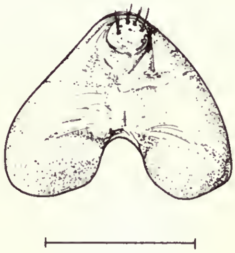
Morphology. Flattened and distinctly bilobed with lobes widely divergent, papilla moderately to well developed, minutely tufted or naked. Much difference of opinion is found in the literature concerning the feathered condition of glands in this family probably because some investigators failed to use magnification in their examinations of glands. By combining here the comments of Garrod (1878), Forbes (1882), Newton (1893–1896), Beddard (1898), Miller (1915), and Verheyen (1955*a*) plus microscopic examinations in the present study, it is apparent that any specimen of any species might have a gland that is naked or one that is tufted with 1–8 'vestigial,' 'rudimentary,' or very small feathers (ca. 1 mm). Type I.

Material examined. *Hylomanes momotula* 1; *Electron platyrhynchum* 1; *Eumomota superciliosa* 5; *Baryphthengus ruficapillus* 3; *Momotus momota* 5.

Dacelo novaeguineae



Todus subulatus



Momotus momota

Family Meropidae (Bee-eaters)

Morphology. Indistinctly bilobed, papilla large, naked (also reported by Paris 1913: 175).

Material examined. *Melittophagus pusillus* 1; *Merops apiaster* 2; *M. viridis* 1; *Nyctyornis amicta* 1.

Family Leptosomatidae (Cuckoo-rollers)

Morphology. Indistinctly bilobed, papilla large, naked. The gland, about 10 mm in length, does not conform to Nitzsch's description of 'atrophy and almost total disappearance . . .' (1867:161).

Material examined. *Leptosomus discolor* 2.

Family Coraciidae (Rollers)

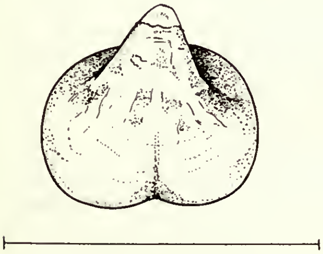
Morphology (family). Flattened and indistinctly bilobed, papilla large, naked.

Subfamily Brachypteraciinae

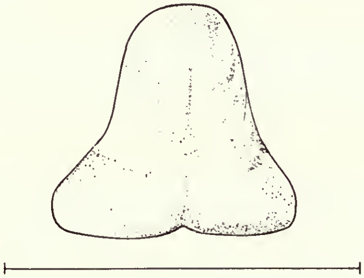
Material examined. *Brachypteracias leptosomus* 1; *Uratelornis chimaera* 1.

Subfamily Coraciinae

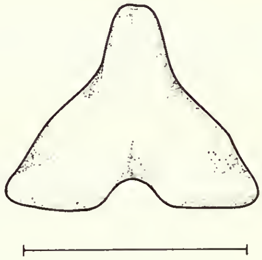
Material examined. *Coracias garrulus* 1; *Eurystomus orientalis* 1.



Merops apiaster



Leptosomus discolor

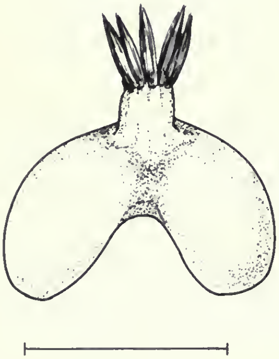


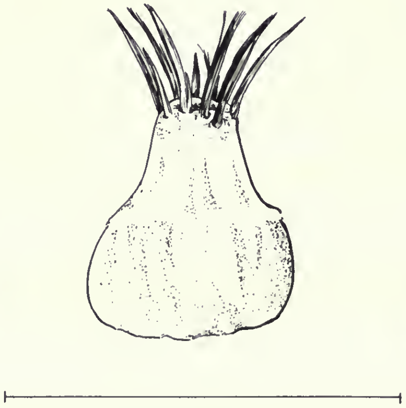
Coracias garrulus

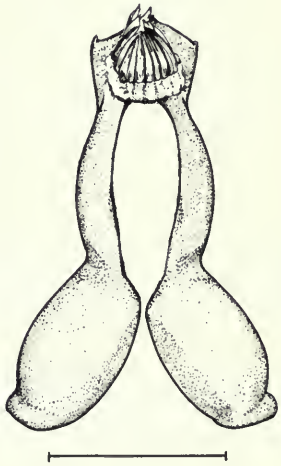
Family Upupidae (Hoopoes)
Morphology. Distinctly bilobed with widely diverging lobes, papilla large, tufted (10 feathers, Paris 1913, Grassé 1950; 14 feathers, Jacob & Ziswiler 1982). Type I.
Material examined. *Upupa epops* 2.

Family Phoeniculidae (Wood-hoopoes)
Morphology. Small and not apparently bilobed, papilla large, tufted (10 feathers). Type IIa.
Material examined. *Phoeniculus purpureus* 1; *P. bollei* 1; *Rhinopomastus minor* 1; *R. cyanomelas* 1.

Family Bucerotidae (Hornbills)
Morphology. Distinctly bilobed (lobes completely separated), papilla small, tufted (50 feathers, Paris 1913; 32–48 feathers in *T. erythrorhynchus*, Jacob & Ziswiler 1982). In *Tockus hartlaubi* the gland and its feather tuft are 'vestigial' (Verheyen 1955*a*). Type II.
Material examined. *Tockus alboterminatus* 1; *T. erythrorhynchus* 1; *T. flavirostris* 1; *T. deckeni* 1; *Aceros undulatus* 1; *A. plicatus* 1; *Anthracoceros malabaricus* 1; *A. coronatus* 1; *Ceratogymna atrata* 1; *Buceros bicornis* 1; *B. hydrocorax* 1; *Bucorvus abyssinicus* 2.


Upupa epops


Phoeniculus purpureus


Tockus erythrorhynchus

Order Piciformes

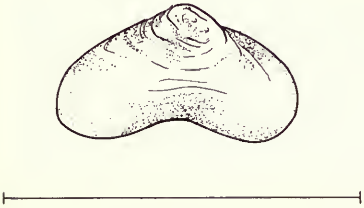
Gland characteristics. Much inter- and intrafamilial variation: absent (rarely), naked, or sparsely to densely tufted.
Note. Differences (see figures) in gland morphology among the six families lend evidence to a polyphyletic origin of the Piciformes as suggested by Olson (1983).

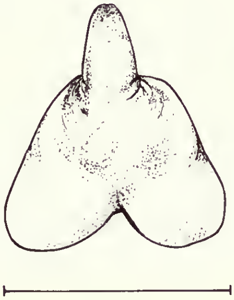
Family Galbulidae (Jacamars)
Morphology. Indistinctly bilobed, papilla moderately developed, naked.
Material examined. *Galbalcyrhynchus leucotis* 1; *Brachygalba lugubris* 1; *Galbula albirostris* 5; *G. galbula* 1; *G. ruficauda* 3; *Jacamerops aurea* 1.

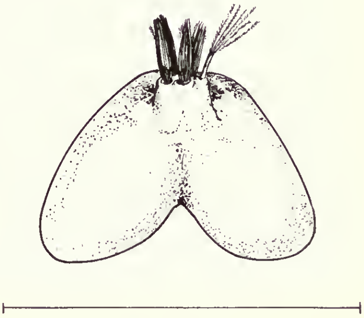
Family Bucconidae (Puff-birds)
Morphology. Distinctly bilobed, papilla large, naked. Gadow (1893), Nitzsch (1867: 94), and Beddard (1898) each refer to some bucconids (e.g., *Malacoptila fusca, Bucco, Monasa*) as having glands with 'a few fine hairs at the apex' or 'feathered.' However, Miller (1915) and I found that all species and individuals in the Bucconidae that we examined had naked glands.

Material examined. *Notharchus macrorhynchos* 3; *Nystalus maculatus* 1; *Hypnelus bicinctus* 1; *Malacoptila striata* 1; *M. fusca* 1; *M. panamensis* 6; *Monasa nigrifrons* 1; *M. atra* 1; *M. morphoeus* 1; *Chelidoptera tenebrosa* 2.

Family Capitonidae (Barbets)
Morphology. Distinctly bilobed, papilla moderately developed, naked or sparsely tufted (8–12 feathers in 2 species, Jacob & Ziswiler 1982). In addition to the species marked * below, the following species were reported by Miller (1924: 323) as having naked glands: *Stactolaema, Pogoniulus duchaillui, Trachyphonus cafer,* and *T. margaritatus*. Individual differences (naked vs. tufted) have been found in *Trachyphonus vaillantii, T. darnaudii,* and *Lybius torquatus*. A feathered gland was reported for *Pogonias* (*Lybius*) by Nitzsch (1867: 93). Beddard (1898: 168) noted that (all) capitonids have feathered glands. I did not confirm the statement by Verheyen (1955*b*) that different species in the Capitonidae lack a gland. Type I.
Material examined (tufted unless otherwise indicated). *Semnornis frantzii* 1; *S. ramphastinus* 1; *Psilopogon pyrolophus* 2; *Megalaima rafflesii* 2; *M. mystacophanos* 1; *M. flavifrons* 1; *M. asiastica* 1; *M. henricii* 1; *M. haemacephala* 1; *Gymnobucco bonapartei* 2*; *Smilorhis leucotis* 1*; *Pogoniulus simplex* 1; *P. bilineatus* 1; *P. subsulphureus* 1; *Tricholaema leucomelan* 1*; *T. diadematum* 1*; *Lybius guifsobalito* 1*; *L. leucocephalus* 1*; *L. dubius* 2*; *Trachyphonus purpuratus* 1; *T. vaillantii* 2*; *T. darnaudii* 1*.


Galbula ruficauda


Notharchus macrorhnychos


Megalaima rafflesii

Family Indicatoridae (Honey-guides)
Morphology. Indistinctly bilobed, papilla moderately developed, tufted (2 feathers). Miller (1924: 323) correctly noted that the Indicatoridae are invariably tufted 'but the tuft is vestigial in *Prodotiscus*.' I did not confirm the statement by Verheyen (1955*b*) that different species in the Indicatoridae lack a gland. Type I.
Material examined. *Prodotiscus insignis* 2; Indicator exilis 1; *I. minor* 1; *I. maculatus* 2; *Melichneutes robustus* 1.

Family Ramphastidae (Toucans)
Morphology. Distinctly bilobed, papilla poorly developed, tufted (8 feathers). Type I.
Material examined. *Aulacorhynchus prasinus* 1; *Pteroglossus torquatus* 2 (M, Z: 183·3, 0·14; 186·3, 0·12); *Andigena hypoglauca* 1; *Ramphastos vitellinus* 1; *R. discolorus* 1; *R. sulfuratos* 1; *R. swainsoni* 1; *R. tucanus* 1; *R. cuvieri* 1; *R. inca* 1; *R. toco* 2.

Family Picidae (Wryneck, Piculets, Woodpeckers)
Morphology (family). Absent or distinctly bilobed with widely separated lobes, papilla usually moderately developed, naked or tufted (8–12 feathers in 3 species, Jacob & Ziswiler 1982). In some

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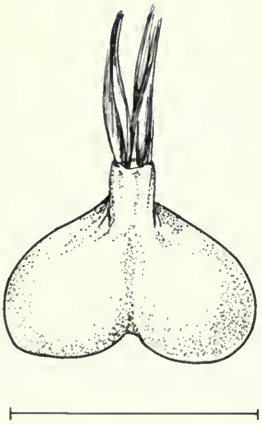
*naked, present study.

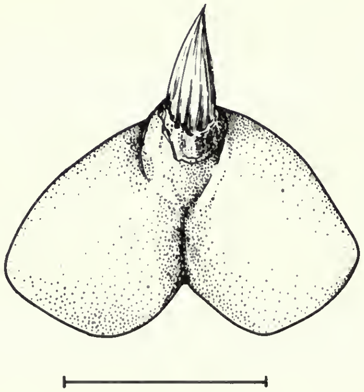
North American species (e.g., *Dryocopus, Colaptes*) each lobe narrows down to an extremely small 'band' before joining at the papilla, making dissection and removal of an intact gland difficult. Miller (1924) noted the gland's absence in *Campethera maculosa, permista, caroli,* and *nivosa,* these in addition to *C. cailliartii* in the present study. The gland is naked in *Dinopium* and *Gecinulus* and naked or tufted in specimens of *Chrysocolaptes validus fide* Miller (1924).

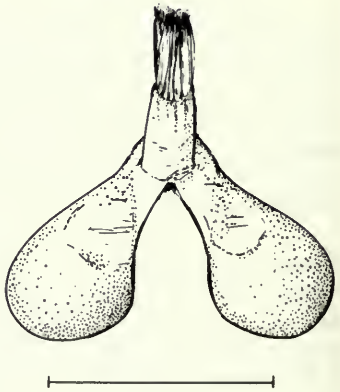
Subfamily Jynginae (Wrynecks)
MORPHOLOGY. 'Well developed and clearly bilobed' (Paris 1913: 168), tufted (8 feathers, Paris 1913). Type II.
MATERIAL EXAMINED. *Jynx torquilla* 1.

Subfamily Picumninae (Piculets)
MORPHOLOGY. Tufted.
MATERIAL EXAMINED. *Picumnus cirratus* 1; *Nesoctites micromegas* 1; *Sasia ochracea* 2; *S. abnormis* 1.

Subfamily Picinae (Woodpeckers)
MORPHOLOGY. Tufted, naked, or absent. Type I.
MATERIAL EXAMINED (tufted unless otherwise indicated). *Colaptes auratus* 7 (M: 100·9, 0·12. F: 131·9, 0·12; 137·7, 0.11; 98·5, 0·12); *Piculus simplex* 1; *Campethera punctuligera* 2; *C. nubica* 4; *C. bennettii* 1; *C. cailliautii* 2*; *C. abingoni* 2; *C. permista* 1*; *C. caroli* 2**; *C. nivosa* 7*; *Celeus flavescens* 2; *Micropternus brachyurus* 1; *Picus viridis* 1; *Dinopium beneghalense* 2***; *D. javanense* 1***; *Dryocopus pileatus* 5 (M: 240·8, 0·15. F: 220·8, 0·12); *Asyndesmus lewis* 1; *Melanerpes erythrocephalus* 2; *M. carolinus* 7 (M: 76·0, 0·09; 72·2, 0·14. F: 54·9, 0·12); *M. aurifrons* 3; *M. flavifrons* 1; *Leuconerpes candidus* 1; *Sphyrapicus varius* 4 (M: 43·4, 0·12; 50·3, 0·08. F: 45·5, 0·14); *Trichopicus cactorum* 2; *Veniliornis fumigatus* 2; *V. passerinus* 1; *V. affinis* 1; *Dendrocopos hyperythrus* 1; *D. villosus* 1 (F: 54·3, 0·11); *D. pubescens* 2; *Picoides arcticus* 1; *Xiphidiopicus percussus* 1; *Thripias pyrrhogaster* 1; *Hemicircus canete* 1; *Blythipicus pyrrhotis* 1; *B. rubiginosus* 1; *Chrysocolaptes validus* 2***; *C. lucidus* 8; *Phloeoceastes guatemalensis* 1; *P. melanoleucus* 1; *P. leucopogon* 1; *P. haematogaster* 1; *Campephilus principalis* 1; *C. magellanicus* 1.
NOTE. In his comprehensive study of woodpeckers of the world, Short (1982) presents no ecological, structural, or behavioral information that might correlate with gland presence/absence, tufted/naked condition in different species of *Campethera, Dinopium,* or *Chrysocolaptes.*


Indicator maculatus


Ramphastos toco


Colaptes auratus

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*gland absent, this study; also absent in *C. maculosa* (Miller 1924).
**gland present (tufted) or absent in some specimens, this study.
***gland naked, this study. Tuft is individually variable in specimens of *Chrysocolaptes* (Miller 1924: 324).

Order Passeriformes

Gland characteristics. Naked.
MORPHOLOGY (order). Indistinctly or distinctly bilobed, papilla moderately or well developed, naked. Although varying slightly in shape ('kidney-vs heart-shaped'), weight, and relative length of papilla (Jacob & Ziswiler 1982), glands of all passerines have been uniformly described by all authors as being present and naked. In the present comprehensive study, representatives of all passerine families (68, Peters 1931–1986) and subfamilies were examined: 1187 individuals of 349 genera and 482 species. Except for relative size (see Weights and sizes of glands section), I found no consistent, major morphological differences between or among any taxa. Paris (1913: 67) in his extensive study reported only slight variations in shape among at least 11 passerine families.

Suborder Eurylaimi

Family Eurylaimidae (Broadbills)

Subfamily Eurylaiminae
MATERIAL EXAMINED. *Smithornis capensis* 1; *Eurylaimus javanicus* 1; *Psarisomus dalhousiae* 1.

Subfamily Calyptomeninae
MATERIAL EXAMINED. *Calyptomena whiteheadi* 1.

Suborder Tyranni

Superfamily Furnarioidea

Family Dendrocolaptidae (Wood-hewers)
MATERIAL EXAMINED. *Dendrocincla anabatina* 8; *D. homochroa* 4; *Sittasomus griseicapillus* 4; *Glyphorhynchus spirurus* 10; *Drymornis bridgesii* 1; *Dendrocolaptes certhia* 7; *Xiphorhynchus ocellatus* 1; *X. guttatus* 2; *X. flavigaster* 3; *Lepidocolaptes souleyetii* 3; *Campylorhamphus trochilirostris* 1;

Family Furnariidae (Ovenbirds)
MATERIAL EXAMINED. *Geositta cunicularia* 1; *Upucerthia validirostris* 1; *Cinclodes fuscus* 1; *Furnarius leucopus* 1; *Aphrastura spinacauda* 2; *Phleocryptes melanops* 2; *Schizoeaca fuliginosa* 1; *Synallaxis albescens* 1; *S. erythrothorax* 2; *Poecilurus candei* 1; *P. scutatus* 1; *Asthenes hudsoni* 1; *Phacellodomus striaticollis* 1; *Coryphistera alaudina* 2; *Anumbius annumbi* 2; *Margarornis squamiger* 1; *Pseudoseisura lophotes* 2; *Ancistrops strigilatus* 1; *Syndactyla rufosuperciliata* 2; *Philydor erythrocercus* 1; *Automolus infuscatus* 1; *A. albigularis* 1; *A. ochrolaemus* 7; *Heliobletus contaminatus* 1; *Xenops minuta* 11; *Sclerurus guatemalensis* 4.

Family Formicariidae (Ant-thrushes)
MATERIAL EXAMINED. *Taraba major* 1; *Thamnophilus doliatus* 5; *T. aethiops* 1; *Myrmotherula surinamensis* 1; *Microrhopias quixensis* 2; *Formicivora grisea* 1; *Drymophila caudata* 1; *Cercomacra tyrannina* 5; *C. nigricans* 1; *Hypocnemis cantator* 1; *Myrmeciza longipes* 1; *Formicarius colma* 1; *F. analis* 5; *Chamaeza ruficauda* 1; *Pithys albifrons* 1; *Gymnopithys leucaspis* 1; *Hylophylax naevioides* 1; *Grallaria guatimalensis* 1.

Family Conopophagidae (Ant-pipits)
MATERIAL EXAMINED. *Conopophaga lineata* 1; *C. castaneiceps* 1; *Corythopis torquata* 1.

Family Rhinocryptidae (Tapaculos)
MATERIAL EXAMINED. *Pteroptochos tarnii* 1; *Scelorchilus rubecula* 1; *Rhinocrypta lanceolata* 1; *Teledromas fuscus* 1; *Melanopareia maximiliani* 1; *Scytalopus latebricola* 1.

Superfamily Tyrannoidea

Family Tyrannidae (Tyrant Flycatchers)

Subfamily Elaeniinae

MATERIAL EXAMINED. *Sublegatus modestus* 1; *Myiopagis viridicata* 2; *Elaenia flavogaster* 3; *E. pallatangae* 1; *Mionectes olivaceus* 1; *M. oleagineus* 28; *Leptopogon amaurocephalus* 7; *Oncostoma cinereigulare* 8; *Todirostrum sylvia* 1; *T. cinereum* 2; *Rhynchocyclus brevirostris* 1; *Tolmomyias sulphurescens* 4; *Platyrinchus cancrominus* 4; *P. mystaceus* 4.

Subfamily Fluvicolinae

MATERIAL EXAMINED. *Onychorhynchus coronatus* 3; *Terenotriccus erythrurus* 1; *Myiobius barbatus* 2; *Contopus virens* 1; *C. cinereus* 1; *Empidonax flaviventris* 3; *E. virescens* 1; *E. minimus* 5; *Sayornis phoebe* 2; *Ochthoeca fumicola* 1; *Myiotheretes striaticollis* 1; *Xolmis irupero* 1; *Muscisaxicola* sp. 1; *Knipolegus aterrimus* 1; *Fluvicola pica* 1.

Subfamily Tyranninae

MATERIAL EXAMINED. *Attila spadiceus* 7; *Rhytipterna simplex* 1; *Myiarchus tuberculifer* 2; *M. nuttingi* 2; *M. crinitus* 2 (M: 42·4, 0·08); *Pitangus sulphuratus* 3; *Megarhynchus pitangua* 2; *Myiodynastes bairdii* 1; *Tyrannus tyrannus* 2 (F: 40·0, 0·10); *T. melancholicus* 1.

Subfamily Tityrinae

MATERIAL EXAMINED. *Pachyramphus cinnamomeus* 1; *Tityra semifasciata* 2; *T. inquistor* 3.

Family Pipridae (Manakins)

MATERIAL EXAMINED. *Schiffornis turdinus* 3; *Chloropipo uniformis* 1; *Xenopipo atronitens* 1; *Manacus manacus* 10; *Chiroxiphia lanceolata* 1; *Pipra filicauda* 1; *P. mentalis* 40; *P. chloromeros* 1.

Family Cotingidae (Cotingas)

MATERIAL EXAMINED. *Ampelion rubrocristatus* 1; *Pipreola arcuata* 1; *P. chlorolepidota* 1; *Lipaugus vociferans* 1; *Gymnoderus foetidus* 1; *Querula purpurata* 1; *Pyroderus scutatus* 1; *Cephalopterus ornatus* 1; *Perissocephalus tricolor* 1; *Procnias nudicollis* 1; *Rupicola peruviana* 1.

Family Oxyrunicidae (Sharpbills)

MATERIAL EXAMINED. *Oxyruncus cristatus* 1.

Family Phytotomidae (Plantcutters)

MATERIAL EXAMINED. *Phytotoma rutila* 1.

Family Pittidae (Pittas)

MATERIAL EXAMINED. *Pitta erythrogaster* 1; *P. granatina* 1.

Family Philepittidae (Asitys)

Subfamily Philepittinae

MATERIAL EXAMINED. *Philepitta castanea* 1.

Subfamily Neodrepanidinae

MATERIAL EXAMINED. *Neodrepanis coruscans* 1.

Family Acanthisittidae (New Zealand Wrens)

MATERIAL EXAMINED. *Acanthisitta chloris* 2; *Xenicus longipes* 5; *X. gilviventris* 1.

NOTE. Most specimens available for examination were poorly preserved. I identified a gland in *Acanthisitta*, in only 1 of the 5 *Xenicus longipes*, and not in *X. gilviventris*.

Suborder Menurae

Family Menuridae (Lyrebirds)
Material examined. *Menura novaehollandiae* 2.

Family Atrichornithidae (Scrub-birds)
Material examined. *Atrichornis clamosus* 1.
Note. B. Gillies (in litt., 4 April 1985) reported that this specimen (R11353) has a naked gland; another specimen (A15926) is illustrated in Zusi (1985) as having a naked gland.

Suborder Oscines

Family Alaudidae (Larks)
Material examined. *Mirafra javanica* 1; *M. assamica* 1; *Eremopterix signata* 1; *Alaemon alaudipes* 1; *Melanocorypha yeltoniensis* 1; *Calandrella cinerea* 1; *Galerida cristata* 1; *Lullula arborea* 1; *Eremophila alpestris* 1.

Family Hirundinidae (Swallows)
Material examined. *Tachycineta bicolor* 2; *Progne subis* 7 (F: 63·1, 0·03); *Hirundo rustica* 3; *H. smithii* 1.

Family Motacillidae (Wagtails, Pipits)
Material examined. *Dendronanthus indicus* 1; *Motacilla alba* 2; *M. aguimp* 1; *Macronyx croceus* 1; *Anthus spinoletta* 1 (M: 19·2, 0·13).

Family Campephagidae (Cuckoo-shrikes)
Material examined. *Coracina novaehollandiae* 1; *C. striata* 1; *C. morio* 1; *C. panayensis* 1; *C. melaschistos* 1; *Lalage nigra* 1; *Campephaga phoenicea* 1; *Pericrocotus cinnamomeus* 1; *P. flammeus* 1; *Hemipus picatus* 1.

Family Pycnonotidae (Bulbuls)
Material examined. *Pycnonotus barbatus* 8; *P. goiavier* 1; *Chlorocichla flaviventris* 2; *Bleda eximia* 1; *Criniger phaeocephalus* 1; *Setornis criniger* 1; *Hypsipetes everetti* 1.

Family Irenidae (Leaf Birds)
Material examined. *Irena puella* 1.

Family Laniidae (Shrikes and Allies)

Subfamily Prionopinae
Material examined. *Eurocephalus ruppelli* 1; *Prionops plumata* 1.

Subfamily Malaconotinae
Material examined. *Dryoscopus cubla* 3; *D. sabini* 1; *Tchagra senegala* 1; *T. australis* 2; *Laniarius ferrugineus* 3; *L. barbarus* 1; *Telophorus sulfureopectus* 1; *T. multicolor* 1.

Subfamily Laniinae
Material examined. *Corvinella corvina* 1; *Lanius collurio* 1; *L. ludovicianus* 2.

Subfamily Pityriasinae
Material examined. *Pityriasis gymnocephala* 1.

Family Vangidae (Vangas)
Material examined. *Calicalicus madagascariensis* 1; *Vanga curvirostris* 1.

Family Bombycillidae (Waxwings)

Subfamily Bombycillinae
Material examined. *Bombycilla garrulus* 1; *B. cedrorum* 1 (F: 29·2, 0·10).

Subfamily Ptilogonatinae
Material examined. *Ptilogonys cinereus* 1.

Subfamily Hypocoliinae
Material examined. *Hypocolius ampelinus* 1.

Family Dulidae (Palm Chat)
Material examined. *Dulus dominicus* 1.

Family Cinclidae (Dippers)
Material examined. *Cinclus cinclus* 1; *C. pallasii* 1; *C. mexicanus* 4 (unsexed: 63·6, 0·48; 58·3, 0·65; 59·7, 0·71).
Note. Nitzsch (1867: 73) reported that the gland of *Cinclus* 'bears small down-feathers upon its surface,' but it is not clear that his 'surface' refers to the papilla's tip. All specimens examined in the present study had naked glands.

Family Troglodytidae (Wrens)
Material examined. *Campylorhynchus rufinucha* 1; *Cistothorus platensis* 2; *C. palustris* 2; *Thryothorus pleurostictus* 2; *T. maculiectus* 2; *T. ludovicianus* 1; *T. rufalbus* 1; *Troglodytes aedon* 2; *Uropsila leucogastra* 1; *Henicorhina leucosticta* 3.

Family Mimidae (Mockingbirds and Allies)
Material examined. *Dumetella carolinensis* 17 (F: 35·4, 0·18); *Mimus polyglottos* 5 (M: 47·6, 0·16); *Toxostoma rufum* 5 (M: 55·3, 0·07. F: 69·1, 0·14).

Family Prunellidae (Accentors)
Material examined. *Prunella collaris* 1.

Family Muscicapidae*

Subfamily Turdinae (Thrushes)
Material examined. *Zeledonia coronata* 4; *Sialia currucoides* 1; *Catharus fuscescens* 2 (F: 28·1, 0·09); *C. minimus* 2; *C. ustulatus* 3; *C. guttatus* 2; *Hylocichla mustelina* 28 (F: 47·4, 0·09; 59·7, 0·07); *Turdus merula* 1; *T. iliacus* 1; *T. philomelos* 1; *T. viscivorus* 1; *T. grayi* 4; *T. migratorius* 4 (M: 85·3, 0·09. F: 72·4, 0·09; 85·7, 0·12).

Subfamily Orthonychinae (Logrunners)
Material examined. *Cinclosoma cinnamomeum* 1.

Subfamily Timaliinae (Babblers)
Material examined. *Trichastoma bicolor* 1; *Malacopteron magnum* 1; *Pomatorhinus schisticeps* 1; *Napothera brevicaudata* 1; *Chamaea fasciata* 2; *Turdoides squamiceps* 1; *Garrulax leucolophus* 3; *Actinodura ramsayi* 1; *Alcippe castaneceps* 1.

Subfamily Panurinae (Parrotbills)
Material examined. *Paradoxornis heudei* 1.

Subfamily Picathartinae (Picathartes)
Material examined. *Picathartes oreas* 1.

Subfamily Polioptilinae (Gnatcatchers and allies)
Material examined. *Ramphocaenus melanurus* 2; *Polioptila caerulea* 1.

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*nomenclature and inclusive taxa according to Peters (Vol. X, 1964).

Family Sylviidae (Old World Warblers)
MATERIAL EXAMINED. *Locustella lanceolata* 1; *Acrocephalus scirpaceus* 1; *Cisticola erythrops* 1; *Sylvietta rufescens* 1; *Hylia prasina* 1; *Abroscopus schisticeps* 1; *Sylvia communis* 1; *S. hortensis* 1; *Regulus calendula* 6; *R. satrapa* 1.

Family Muscicapidae (Old World Flycatchers)**
MATERIAL EXAMINED. *Muscicapa dauurica* 1.

Family Platysteiridae (Puffback Flycatchers)
MATERIAL EXAMINED. *Batis molitor* 1.

Family Maluridae (Australo-Papuan Wrens)
MATERIAL EXAMINED. *Malurus lamberti* 1.

Family Acanthizidae (Australasian Warblers)

Subfamily Acanthizinae
MATERIAL EXAMINED. *Sericornis magnirostris* 1.

Subfamily Mohouinae
MATERIAL EXAMINED. Unavailable.

Family Monarchidae (Monarch Flycatchers)

Subfamily Monarchinae
MATERIAL EXAMINED. *Terpsiphone viridis* 1; *T. atrocaudata* 1; *Chasiempis sandwichensis* 1.

Subfamily Rhipidurinae
MATERIAL EXAMINED. *Ripidura albicollis* 1.

Family Eopsaltriidae (Australasian Robins)
MATERIAL EXAMINED. *Petroica phoenicea* 1; *P. vittata* 1; *Tregellasia leucops* 1.

Family Muscicapidae***

Subfamily Pachycephalinae (Whistlers)
MATERIAL EXAMINED. *Pachycephala lanioides* 1.

Family Aegithalidae (Long-tailed Tits, Bush Tits)
MATERIAL EXAMINED. *Aegithalos caudatus* 2.

Family Remizidae (Penduline Tits)
MATERIAL EXAMINED. *Auriparus flaviceps* 2.

Family Paridae (Titmice)
MATERIAL EXAMINED. *Parus atricapillus* 1; *P. carolinensis* 1; *P. bicolor* 1; *Hypositta corallirostris* 1.

Family Sittidae

Subfamily Sittinae (Nuthatches)
MATERIAL EXAMINED. *Sitta pusilla* 1; *S. canadensis* 1; *S. carolinensis* 1.

Subfamily Daphoenosittinae (Treerunners)
MATERIAL EXAMINED. *Neositta chrysoptera* 3; *Daphoenositta miranda* 2.

**nomenclature and inclusive taxa according to Peters (Vol. XI, 1986).

***nomenclature and inclusive taxa according to Peters (Vol. XII, 1967).

Subfamily Tichodromadinae (Wallcreepers)
Material examined. *Tichodroma muraria* 1.

Family Certhiidae (Creepers)

Subfamily Certhiinae (Treecreepers)
Material examined. *Certhia familiaris* 2.

Subfamily Salpornithinae (Spotted Creeper)
Material examined. *Salpornis spilonotus* 1.

Family Rhabdornithidae (Philippine Creepers)
Material examined. *Rhabdornis mysticalis* 1.

Family Climacteridae (Australian Treecreepers)
Material examined. *Climacteris melanura* 1.

Family Dicaeidae (Flowerpeckers)
Material examined. *Rhamphocharis crassirostris* 1; *Prionochilus olivaceus* 1; *Dicaeum concolor* 1; *D. cruentatum* 1; *Oreocharis arfaki* 1; *Pardalotus rubricatus* 1.

Family Nectariniidae (Sunbirds)
Material examined. *Anthreptes malacensis* 1; *Hypogramma hypogrammicum* 1; *Nectarinia olivacea* 1; *N. senegalensis* 7; *N. sericea* 1; *N. jugularis* 2; *N. asiatica* 1; *N. venusta* 1; *N. talatala* 2; *N. habessinica* 1; *Aethopyga boltoni* 1; *Arachnothera longirostra* 1.

Family Zosteropidae (White-eyes)
Material examined. *Zosterops griseotincta* 1.

Family Meliphagidae (Honeyeaters)
Material examined. *Oedistoma iliolophum* 1; *Myzomela sanguinolenta* 1; *Meliphaga fusca* 1; *M. pencillata* 1; *Melithreptus brevirostris* 1; *Philemon citreogularis* 1; *Melidectes fuscus* 1; *Acanthorhynchus tenuirostris* 1; *Anthochaera carunculata* 1.

Family Emberizidae

Subfamily Emberizinae (Buntings and American Sparrows)
Material examined. *Emberiza flaviventris* 1; *Calcarius lapponicus* 1; *Zonotrichia melodia* 4 (M: 17·6, 0·12); *Z. georgiana* 3; *Z. albicollis* 7; *Junco hyemalis* 1; *Ammodramus sandwichensis* 3; *A. savannarum* 3; *Spizella passerina* 1; *S. pusilla* 1; *Pooecetes gramineus* 1; *Aimophila aestivalis* 2; *Sicalis olivascens* 1; *Volatinia jacarina* 2; *Sporophila torqueola* 6; *S. telasco* 1; *Camarhynchus crassirostris* 1; *Pipilo erythrophthalmus* 3 (M: 43·8, 0·26. F: 36·7, 0·22); *Arremon aurantiirostris* 3; *Arremonops rufivirgatus* 3; *A. chloronotus* 1.

Subfamily Catamblyrhynchinae (Plush-capped Finch)
Material examined. *Catamblyrhynchus diadema* 1.

Subfamily Cardinalinae (Cardinal-grosbeaks)
Material examined. *Pheucticus ludovicianus* 1; *P. melanocephalus* 1 (F: 40·5, 0·09); *Cardinalis cardinalis* 5 (M: 40·3, 0·09; 33·0, 0·07. F: 40·0, 0·09); *Saltator atriceps* 1; *S. maximus* 2; *S. aurantiirostris* 1; *Passerina cyanoides* 8; *P. caerulea* 2; *P. cyanea* 6.

Subfamily Thraupinae (Tanagers)
Material examined. *Eucometis pencillata* 2; *Lanio aurantius* 3; *Tachyphonus luctuosus* 1; *Habia rubica* 3; *H. fuscicauda* 16; *Piranga rubra* 2; *P. olivacea* 3 (F: 26·5, 0·06); *Ramphocelus sanguinolentus* 4; *R. passerinii* 4; *Thraupis episcopus* 1; *T. bonariensis* 1; *Euphonia affinis* 2; *Dacnis cyana* 1; *Cyanerpes cyaneus* 4; *Diglossa carbonaria* 1.

Subfamily Tersininae (Swallow-tanager)
MATERIAL EXAMINED. *Tersina viridis* 1.

Family Parulidae (Wood Warblers)
MATERIAL EXAMINED. *Mniotilta varia* 3; *Vermivora peregrina* 2; *Parula americana* 1; *Dendroica petechia* 4; *D. magnolia* 1; *D. coronata* 3; *D. cerulea* 1; *D. fusca* 3; *D. pensylvanica* 2; *D. castanea* 2; *D. striata* 1; *D. pinus* 1; *D. palmarum* 1; *Setophaga ruticilla* 4; *Seiurus aurocapillus* 6; *S. noveboracensis* 9 (M: 16·2, 0·15); *S. motacilla* 2; *Helmitheros vermivorus* 6; *Protonotaria citrea* 1; *Geothylpis trichas* 4 (M: 11·5, 0·09); *G. poliocephala* 1; *G. formosa* 20; *Wilsonia pusilla* 4; *Icteria virens* 4; *Coereba flaveola* 2.

Family Drepanididae (Hawaiian Honeycreepers)
MATERIAL EXAMINED. *Himatione sanguinea* 1; *Palmeria dolei* 1; *Vestiaria coccinea* 1; *Loxops virens* 1.

Family Vireonidae (Peppershrikes, Shrike-Vireos)

Subfamily Cyclarhinae
MATERIAL EXAMINED. *Cyclarhis gujanensis* 1.

Subfamily Vireolaniinae
MATERIAL EXAMINED. *Vireolanius pulchellus* 1.

Subfamily Vireoninae
MATERIAL EXAMINED. *Vireo griseus* 3; *V. flavifrons* 2; *V. solitarius* 2; *V. olivaceus* 3; *V. flavoviridis* 3; *V. gilvus* 1; *Hylophilus ochraceiceps* 4; *H. decurtatus* 1.

Family Icteridae (American Orioles and Blackbirds)

Subfamily Icterinae
MATERIAL EXAMINED. *Psarocolius montezuma* 2; *Amblycercus holosericeus* 1; *Icterus galbula* 1; *I. spurius* 2; *I. dominicensis* 1; *Agelaius phoeniceus* 26 ($\bar{x}$ of 16 M: 55·4, 0·17. $\bar{x}$ of 9 F: 42·8, 0·18); *Sturnella magna* 4 (M: 105·5, 0·11. F: 78·6, 0·13): *S. neglecta* 1; *Quiscalus mexicanus* 1; *Q. major* 23 ($\bar{x}$ of 14 M: 192·9, 0·17. $\bar{x}$ of 9 F: 91·0, 0·21); *Q. quiscula* 6 (M: 113·4, 0·16; 117·4, 0·14; 119·1, 0·14. F: 84·2, 0·17); *Euphagus carolinus* 1 (M: 66·0, 0·13); *Molothrus ater* 15 ($\bar{x}$ of 6 M: 47·5, 0·13. $\bar{x}$ of 8 F: 37·3, 0·14).

Subfamily Dolichonychinae
MATERIAL EXAMINED. *Dolichonyx oryzivorus* 12 ($\bar{x}$ of 10 M: 39·0, 0·09).

Family Fringillidae

Subfamily Fringillinae (Chaffinches and Brambling)
MATERIAL EXAMINED. *Fringilla coelebs* 1; *F. montifringilla* 1.

Subfamily Carduelinae (Serins, Goldfinches, et al.)
MATERIAL EXAMINED. *Serinus mozambicus* 14; *Carduelis pinus* 2 (M: 10·5, 0·10); *C. tristis* 1; *Carpodacus purpureus* 2 (M: 26·2, 0·03); *C. mexicanus* 2 (F: 23·2, 0·11); *Pinicola enucleator* 4 (F: 55·2, 0·06; 56·8, 0·05; 60·2, 0·03); *Coccothraustes vespertinus* 1 (M: 56·6, 0·05).

Family Estrildidae (Waxbills, Grass Finches, and Mannikins)
MATERIAL EXAMINED. *Pytilia melba* 2; *Uraeginthus angolensis* 8; *Estrilda caerulescens* 1; *Poephila acuticauda* 1; *P. cincta* 1; *Chloebia gouldiae* 1; *Lonchura cucullata* 1; *Amadina fasciata* 7.

Family Ploiceidae

Subfamily Viduinae (Indigo-birds and Whydahs)
MATERIAL EXAMINED. *Vidua paradisaea* 1.

Subfamily Passerinae
Material examined. *Passer domesticus* 14 (M: 24·5, 0·09; 24·8, 0·20. F: 22·3, 0·18; 25·1, 0·18); *P. griseus* 3.

Subfamily Bubalornithinae
Material examined. *Dinemellia dinemelli* 1.

Subfamily Ploceinae
Material examined. *Amblyospiza albifrons* 1; *Ploceus subaureus* 3; *P. xanthops* 1; *P. velatus* 4; *P. cucullatus* 25; *Euplectes hordeaceus* 1; *E. orix* 11.

Family Sturnidae (Starlings)

Subfamily Sturninae
Material examined. *Sturnus vulgaris* 5 (M: 78·3, 0·11; 80·5, 0·13; 89·7, 0·11); *Sarcops calvus* 1; *Gracula religiosa* 1.

Subfamily Buphaginae
Material examined. *Buphagus erythrorhynchus* 2; *Buphagus* sp. 1.

Family Oriolidae (Orioles)
Material examined. *Oriolus oriolus* 1; *O. chinensis* 1; *O. xanthornus* 1.

Family Dicruridae (Drongos)
Material examined. *Dicrurus remifer* 1; *D. hottentottus* 1; *D. paradiseus* 1.

Family Callaeidae (New Zealand Wattlebirds)
Material examined. *Callaeas cinerea* 1; *Creadion carunculatus* 1; *Heteralocha acutirostris* 1.

Family Grallinidae (Australian Mud Nest Builders)

Subfamily Grallininae
Material examined. *Grallina cyanoleuca* 1.

Subfamily Corcoracinae
Material examined. *Corcorax melanorhamphos* 1; *Struthidea cinerea* 2.

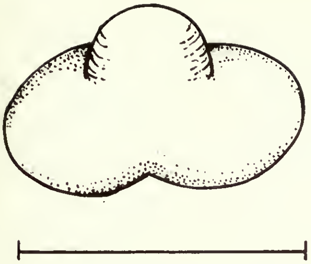
Family Artamidae (Wood-swallows)
Material examined. *Artamus fuscus* 1; *A. leucorhynchus* 1; *A. superciliosus* 1; *A. cinereus* 1; *A. minor* 1.

Family Cracticidae (Australian Butcherbirds)
Material examined. *Cracticus nigrogularis* 1; *Gymnorhina tibicen* 1; *Strepera graculina* 1.

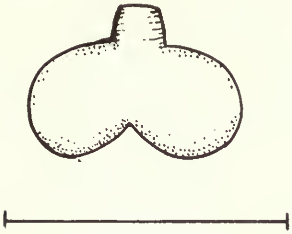
Family Ptilonorhynchidae (Bowerbirds)
Material examined. *Ailuroedus crassirostris* 1; *Amblyornis macgregoriae* 2; *Sericulus chrysocephalus* 1; *Ptilonorhynchus violaceus* 1; *Chlamydera nuchalis* 2.

Family Paradisaeidae (Birds of Paradise)
Material examined. *Manucodia comrii* 1; *Semioptera wallacei* 1; *Astrapia stephaniae* 1; *Lophorina superba* 1; *Cicinnurus regius* 1; *Diphyllodes respublica* 1; *Paradisaea apoda* 1.

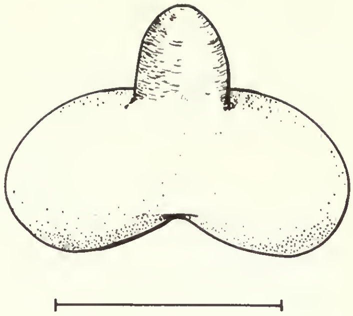
Family Corvidae (Crows, Magpies, Jays)
Material examined. *Cyanocitta cristata* 14 (M: 77·7, 0·20; 78·4, 0·10. F: 59·4, 0·08); *Aphelocoma coerulescens* 2 (M: 70·3, 0·11; 72·0, 0·07); *Garrulus glandarius* 1; *Pica pica* 2; *Corvus monedula* 1; *C. frugilegus* 2; *C. brachyrhynchos* 39 ($\bar{x}$ of 14 M: 563·1, 0·05. $\bar{x}$ of 11 F: 495·7, 0·05); *C. ossifragus* 4 (M: 330·0, 0·15. F: 232·0, 0·13); *C. corone* 2.



Dendrocolaptes certhia



Cinclus mexicanus



Corvus brachyrhynchos

Weights and sizes of glands

Early accounts of uropygial glands included brief comments about relative size ('small,' 'large,' 'smaller than'; Willughby 1678; Burton 1822, Macgillivray 1837, Bartlett 1861). Such relative adjectives and phrases persist in the more contemporary literature (Austin 1961, Thomson 1964, Shortt 1977). Edwards Crisp (1860, 1862) was probably the first person to publish gland weights, and, by weighing birds and their glands separately, he presented the relative proportion of gland weight to the bird's body weight. He (1860: 258) presented data on 34 species of aquatic and terrestrial birds, showing relatively lightest glands in pigeons and heaviest ones in *Cinclus aquaticus* (*C. cinculus aquaticus* of Peters) and six species of waterfowl. The frequent assertion that the preen gland of water-birds is relatively larger than that of land-birds (e.g., Kennedy 1971) is probably derived from Crisp's results (see also Coues 1890), even though Frederick II in 1260 reported large glands in aquatic species (Wood and Fyfe 1943).

Subsequent authors have presented absolute or relative gland weights for many more species (Kossman 1871, Paris 1913, Kar 1947, Grassé 1950, Elder 1954, Kennedy 1971, Johnston 1979, Jacob & Ziswiler 1982). In these reports, differences in relative gland weights have variously been attributed to season (Kossman 1871, Kennedy 1971), habitat (Crisp 1860, Jacob & Ziswiler 1982), intergeneric body weight (Johnston 1979), nutrition (Kossman 1871), individual variation (present study and others), and sex (Groebbels 1932). Although Elder (1954) suggested that glands of diving ducks (*Aythya*) are relatively heavier than those of dabbling ducks (*Anas*), some of Jacob & Ziswiler's data (1982: 214) 'clearly refute this hypothesis.' Subsequently I compared relative gland weights from 7 species of dabbling ducks ($N = 21$, $\bar{x} = 0{\cdot}30\%$, $SD = 0{\cdot}047$) with weights from 5 species of diving ducks ($N = 20$, $\bar{x} = 0{\cdot}29$, $SD = 0{\cdot}065$); the differences were not statistically significant (d.f. = 40, $t = 0{\cdot}7560$, $p > 0{\cdot}05$).

Jacob & Ziswiler (1982) presented gland weights from 574 individuals in 183 species, and I obtained gland weights from 544 individuals in 200 species. All these weights are presented in Table 1. A comparison of these two data sets shows reasonable agreement for the same taxon especially as regards mean values. Also apparent are variations in relative gland weights within and between species, variations that I attribute largely to individual body weight differences. The latter are probably due to sexual differences (see, for example, data for three species of Icterinae in the Systematic accounts) and variations in the amounts of subcutaneous fat.

From their analysis of relative gland weights, Jacob & Ziswiler concluded that 'the only thing that can be said with certainty regarding the size of the uropygial gland is that birds that swim and dive have, without exception, a large uropygial gland' (1982: 214). This statement should be expanded to include the earlier demonstrated correlations with season, nutrition, and sex by the other authors mentioned above.

I was able to examine the habitat-habit issue more thoroughly because of a much larger sample size, including birds living in most major habitat types. By grouping relative weights of birds at the family level and to broad habitat-habit categories (Fig. 2), I found that the largest (relative) glands

Table 1
Summary of uropygial gland weights

	PRESENT STUDY			JACOB & ZISWILER (1982)		
	No. of species	No. of glands	Relative gland weight*	No. of species	No. of glands	Relative gland weight*
Tinamidae				1	12	0·18
Diomedeidae				1	1	0·30
Procellariidae	5	9	0·46 (0·30–0·67)	2	4	0·24–0·27
Hydrobatidae	4	6	0·16 (0·07–0·37)			
Spheniscidae	1	2	0·08 (0·06–0·12)	2	3	0·21–0·26
Gaviidae	4	9	0·18 (0·09–0·30)	2	3	0·14–0·20
Podicipedidae	2	6	0·26 (0·19–0·42)	2	7	0·48–0·61
Phaethontidae	1	1	0·43			
Fregatidae	1	3	0·07 (0·06–0·07)			
Phalacrocoracinae	1	10	0·25 (0·20–0·35)	3	12	0·21–0·31
Anhinginae	1	8	0·15 (0·12–0·17)			
Sulidae	1	1	0·38	1	2	0·35
Pelecanidae	2	4	0·36 (0·30–0·43)	1	1	0·19
Ardeidae	9	20	0·14 (0·01–0·42)	3	7	0·05–0·07
Ciconiidae	1	1	0·05	1	2	0·08
Threskiornithidae	3	4	0·15 (0·11–0·19)	3	4	0·03–0·11
Phoenicopteridae				2	4	0·18–0.21
Cathartidae	2	10	0·04 (0·01–0·05)			
Pandioninae	1	2	0·25 (0·18–0·31)	1	1	0·36
Accipitrinae	11	25	0·06 (0·01–0·13)	7	17	0·04–0·22
Falconidae	4	15	0·07 (0·03–0·09)	1	4	0·08
Anatidae	25	55	0·26 (0·10–0·42)	15	55	0·08–0·54
Anhimidae	1	1	0·13			
Megapodiidae				1	1	0·18
Tetraonidae	6	7	0·05 (0·02–0·18)	3	11	0·09–0·15
Phasianidae	8	17	0·07 (0·02–0·16)	5	12	0·08–0·11
Meleagrididae	1	3	0·03 (0·02–0·04)	1	2	0·05
Numididae				2	3	0·05–0·18
Gruidae	1	4	0·05 (0·03–0·05)	1	1	0·05
Aramidae	1	7	0·28 (0·17–0·42)			
Rallidae	6	27	0·19 (0·11–0·34)	5	14	0·09–0·24
Haematopodidae				1	1	0·20
Charadriidae	2	4	0·18 (0·07–0·22)	1	2	0·16
Scolopacidae	9	25	0·12 (0·05–0·20)	4	5	0·11–0·18
Recurvirostridae	1	1	0·24			
Phalaropodidae	2	4	0·59 (0·42–0·79)			
Burhinidae				1	1	0·09
Chionididae				1	1	0·17
Stercorariidae	2	3	0·29 (0·28–0·37)			
Larinae	3	5	0·20 (0·13–0·29)	4	19	0·12–0·20
Sterninae	9	20	0·33 (0·18–0·57)	4	5	0·19–0·44
Rynchopidae	1	1	0·20			
Alcidae	5	7	0·27 (0·18–0·47)	3	7	0·17–0·29
Pteroclididae				1	1	0·02
Columbidae	5	11	0·04 (0·01–0·10)	4	5	0·02–0·04
Psittacidae	2	1	0·11 (0·05–0·16)	41	125	0·04–0·19
Cuculidae	2	2	0·06 (0·03–0·09)	2	4	0·12–0·16
Tytonidae	1	4	0·09 (0·04–0·12)	1	7	0·08
Strigidae	6	22	0·07 (0·03–0·11)	4	9	0·04–0·09
Steatornithidae				1	1	0·22
Caprimulgidae	3	11	0·01 (0·01–0·02)	1	1	0·01
Apodidae				2	11	0.04–0·05
Alcedinidae	1	2	0·24 (0·22–0·25)	1	2	0·18
Upupidae				1	2	0·14
Meropidae				1	1	0·11
Bucerotidae				2	4	0·08–0·11

Ramphastidae	1	2	0·13 (0·12–0·14)	2	5	0·08–0·10
Picidae	5	13	0·12 (0·08–0·14)	4	9	0·09–0·12
Tyrannidae	2	2	0.09 (0·08–0·10)			
Alaudidae				1	1	0·28
Hirundinidae	1	1	0·03	1	6	0·21
Motacillidae	1	1	0·13	1	2	0·27
Bombycillidae	1	1	0·10			
Cinclidae	1	3	0·61 (0·48–0·71)			
Troglodytidae				1	3	0·58
Mimidae	2	4	0·14 (0·07–0·18)			
Prunellidae				1	1	0·28
Turdinae	3	6	0·09 (0·07–0·12)	2	7	0·08–0·14
Aegithalidae				1	2	0·21
Paridae				2	23	0·14–0·15
Sittidae				1	1	0·12
Emberizinae	2	3	0·20 (0·12–0·26)	2	6	0·26–0·31
Cardinalinae	2	4	0·09 (0·07–0·09)	1	2	0·18
Thraupinae	1	1	0·06			
Parulidae	2	2	0·12 (0·09–0·15)			
Icterinae	6	55	0·15 (0·11–0·24)			
Dolichonychinae	1	10	0·09 (0·06–0·13)			
Fringillidae	5	7	0·06 (0·03–0·11)	3	26	0·22–0·25
Estrildidae				6	24	0·17–0·23
Passerinae	1	4	0·16 (0·09–0·20)			
Ploceidae				3	17	0·19–0·28
Sturnidae	1	3	0·12 (0·11–0·13)	1	8	0·10
Corvidae	4	32	0·10 (0·04–0·20)	7	40	0·08–0·12

*gland weight as percent of body weight; mean (extremes)

are found in nonpasserines that swim, dive or rest on water (N = 18 families, $\bar{x}$ = 0·28%). The smallest glands occur in terrestrial (non-aquatic) birds: nonpasserines (N = 15, $\bar{x}$ = 0·07%) and passerines (N = 16, $\bar{x}$ = 0·04%).

I found the largest relative gland weights in the Procellariidae (*Oceanodroma melania,* 0·69% *Fulmarus glacialis,* 0·67%) Phalaropodidae (*Phalaropus fulicarius,* 0·79%), Sterninae (*Sterna albifrons,* 0·57%), and Cinclidae (*Cinclus mexicanus,* 0·71%). The largest glands reported by Jacob & Ziswiler (1982) were for *Tachybaptus ruficollis* (0·61%) and *Troglodytes troglodytes* (0·58%). Because of its habit of plunging into water for fish, the Osprey expectedly has a larger (0·25%) gland than any other of the Falconiformes (Accipitrinae, 0·06% and Falconidae 0·07%). The smallest glands, which could be accurately weighed in the present study, were found in Caprimulgidae (11 individuals averaging 0·01%), Meleagrididae (3 individuals, $\bar{x}$ = 0·03%) and Columbidae (11 individuals, $\bar{x}$ = 0·04%).

Burton (1822: 4; and quoted by Murphy 1936) reported that the uropygial gland of *Fregata aquila* is a 'trifling size.' In my study, fresh weights of birds and glands of Fregatidae were available only for *F. magnificens,* so I could not compare relative gland weights among frigatebirds. However, the length of glands (sans feathers) were as follows: *F. magnificens,* 15 mm; *F. aquila,* 13 mm; *F. ariel,* 13 mm. The gland of *F. aquila* is thus no smaller than that of *F. ariel* which is the smallest species of *Fregata* (Nelson 1975). Frigatebirds have smaller glands relative to body weight (0·07%) than other nonpasserine birds that live on or in water (e.g., Procellariidae, 0·44%; Phaethontidae, 0·30%; Pelecanidae, 0·28%; Anatidae, 0·27%) with the exception of Spheniscidae (0·08%). The putative relationship between a small, 'insufficient' gland and feathers becoming so wet that frigatebirds drown (first proposed by Burton in 1822 and paraphrased by Welty 1962) lacks scientific verification (see related discussion on spread-wing posture in Clark 1969).

My findings enable me to correct several unverified statements in the literature on gland sizes. Gurney's (1913) assertion, paraphrasing Ticehurst, that the gland of *Sula bassana* 'is the largest proportionally' of all birds, now turns out to be incorrect. One relative gland weight for this species was only 0·38% (present study), compared with relatively much heavier glands in procellarids,

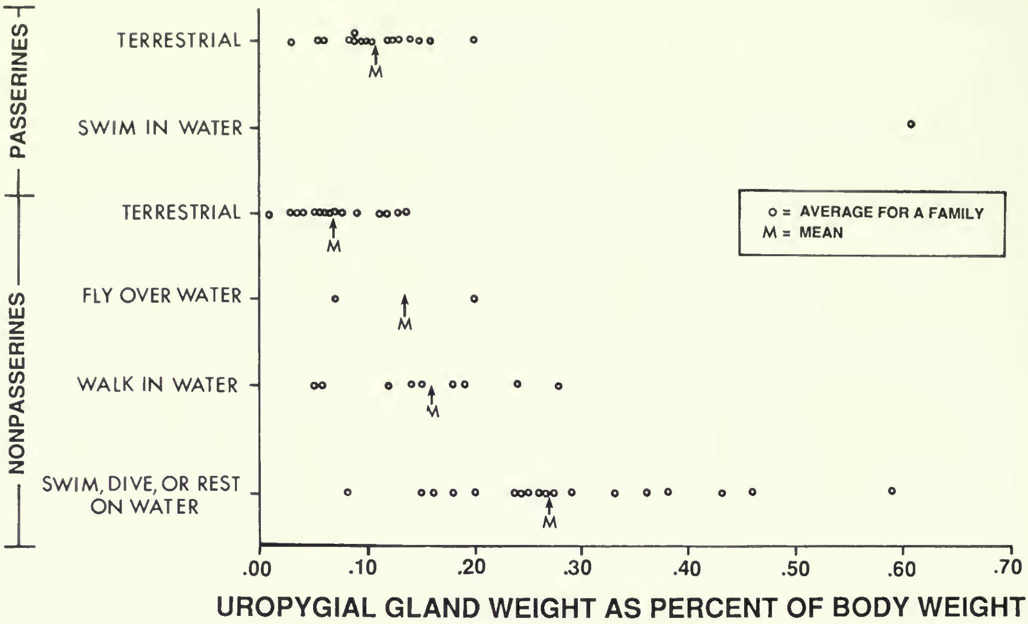


Fig. 2 Relationships between uropygial gland weights and avian habitat-habits.

anatids, phalaropes, and others (above). Austin (1961) (see also Shortt 1977) wrote that dippers (Cinclidae) have a 'tremendous preen gland, ten times the size of that of any other passerine bird.' To be sure, the gland of *Cinclus mexicanus* ($\bar{x}=0{\cdot}61$; 0·48–0·71%) is the largest yet reported for any passerine, but other passerine families (e.g., Emberizidae, Icteridae) have glands as large as 0·24–0·26% and *Troglodytes troglodytes* has a large gland (0·56–0·58%, Kennedy 1971; Jacob and Ziswiler 1982).

My data show that large (i.e., heavy) birds have absolutely large uropygial glands. For 670 individuals, representing 61 families of passerine and nonpasserine birds, I found a significant correlation between body weight and gland weight ($r=0{\cdot}694$, $P\leqslant 0{\cdot}01$). This correlation is important especially because of the inverse relation of plumage weight (as a percent of body weight) with body weight *per se* (Kossman 1871, Turcek 1966). Kennedy (1971: 370) correctly cautioned that 'this parallel could result from a functional connection between the preen gland [size and] secretion and the area of feathers which require anointing with it. Additionally, it is possible that relative to body weight, water-birds have a larger area of feather surface requiring anointing with secretion than land-birds of similar size, which may partly explain their larger glands.'

Conclusions drawn from size and weight relationships of glands must still be tentative. Despite the large numbers of weights and broad taxonomic coverage presented in this study and others (Kennedy 1971, Jacob & Ziswiler 1982), gland weights have never been reported from many birds—e.g., Apterygidae, wild Psittacidae, Trochilidae, Coliidae, most of the coraciiform and piciform families, and most of the passerines.

Feathers on uropygial glands

Feathers attached to the papilla at the end of the uropygial gland are collectively termed *circulus uropygialis* by Lucas & Stettenheim (1972) and Baumel *et al.* (1979). Through the years these feathers have been variously described in different birds as 'contour' (Nitzsch 1867), 'down' or 'downy' or 'modified down' (Nitzsch 1867, Newton 1893–1896, Beddard 1898, Verheyen 1956*f*, 1958*c*, *d*, Grassé 1950, Lucas & Stettenheim 1972, Baumel *et al.* 1979), 'semiplumes' (Nitzsch

1840), 'plumules' or 'plumulets' (Paris 1913), 'plumes' (Beddard 1898), with or without a rachis and/or hyporachis (Paris 1913, Verheyen 1959*c*). Some of the earlier publications (e.g., Nitzsch 1867) even described 'fine hairs' at the tip of certain glands. Miller (1924) was apparently the first investigator to use magnification in determining the number and type of feathers on a gland.

The number of feathers per gland ranges from 1 (minute) to 90 (Jacob & Ziswiler 1982, the present study). Jacob & Ziswiler provided a thorough discussion of the number, arrangement, density, and length of the feathers. Because of some individual variation in number of feathers and other considerations, Jacob & Ziswiler (correctly in my opinion) cautioned against the use of feather number for taxonomic or diagnostic criteria. Rather, from a functional standpoint, they noted a general tendency for waterbirds to have more and longer feather tufts than landbirds. They also believed that the proportional length of the papilla to that of the tuft is taxonomically specific (see also Schumacher 1919).

Lucas and Stettenheim (1972) classified uropygial gland feathers as 'modified down,' defining down as feathers with a rachis shorter than the longest barbs and semiplumes having a rachis that exceeds the longest barbs. My microscopic study of gland feathers from 70 families containing tufted glands revealed the presence of three feather types (Fig. 3). Most of the family representatives (62) had feathers of type I which, by the definition of Lucas & Stettenheim (1972), are down.

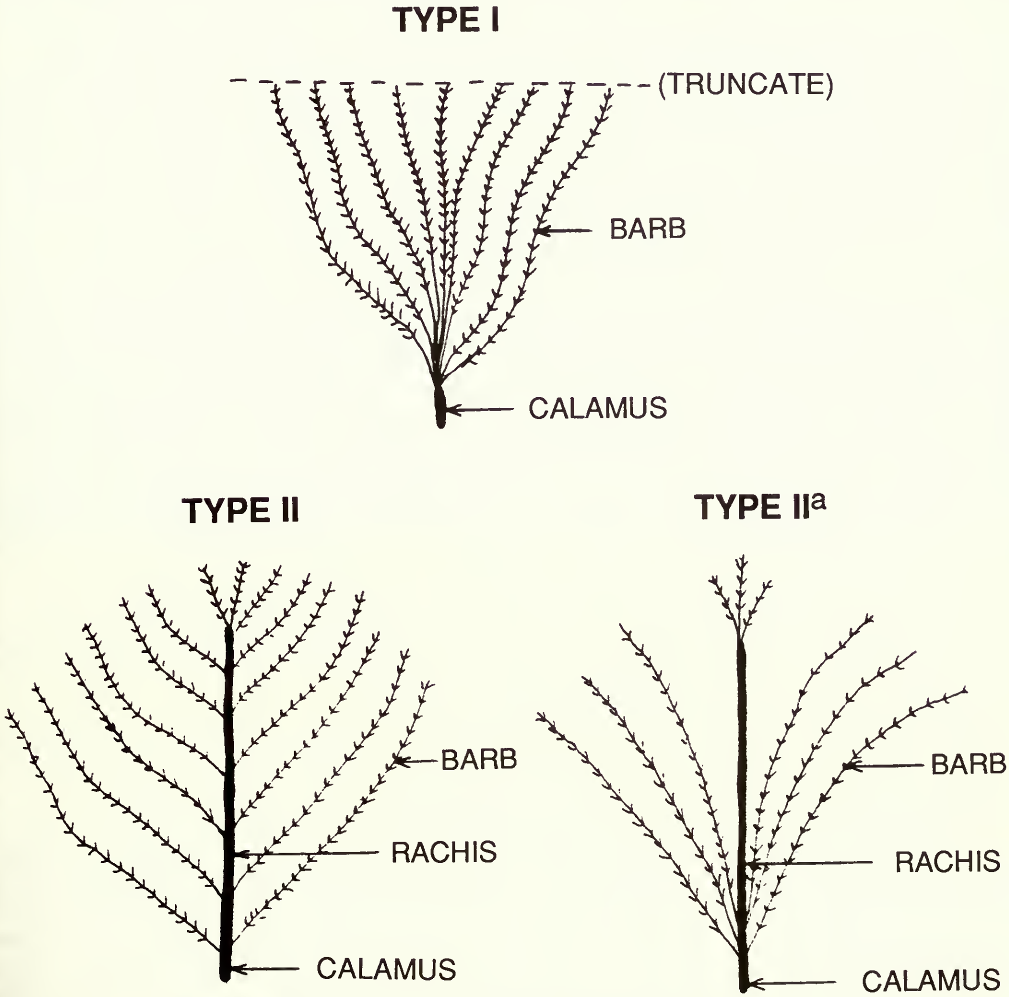


Fig. 3 Diagrams of typical uropygial gland feathers.

Three families each had feathers of Types II and IIa, both defined here as semiplumes. Nodal structures on barbules on these feathers differed from those on true down and contour feathers (Douglas Deedrick and Roxie Laybourne, pers. comm.). Therefore, the most appropriate terms for describing the *circulus uropygialis* are modified down or modified semiplumes.

Contrary to the reports of some other investigators (e.g., Lucas & Stettenheim 1972), I found no afterfeathers on any gland feathers. Even in groups (e.g., Galliformes) renowned for having afterfeathers on body contour feathers, afterfeathers were not found. This difference might be attributable to the criterion for identifying an afterfeather. Lucas & Stettenheim (p. 252) regarded any group of outgrowths on the rim of the superior umbilicus as an afterfeather; outgrowths were not identified in the present study.

Naked and tufted glands

Most early investigators such as Nitzsch (1867), Beddard (1898), and Paris (1913) generally categorized glands as either tufted or naked (nude, bare), that is, with or without feathers on the papilla. For the most part, the glands that they examined were 'obviously' (unmagnified) tufted or naked, although occasional references were made to a 'fine hair' at the tip of some glands (Nitzsch 1867). This dichotomous difference apparently served well until some putative 'naked' glands were examined with magnification by Miller (1924) and were found to possess 1–2 mm feathers.

It is now desirable to establish three categories of glands with respect to the degree of feathering on the papilla: naked (no feathers observable, even with magnification), minutely tufted (feathers detected only with magnification), and tufted (feathers observable without magnification). Glands previously considered to be naked by Paris (1913) and others but now known to be 'minutely tufted' include species in the families Apterygidae, Opisthocomidae, Tytonidae, Strigidae, and Momotidae. In each of these families, considerable individual variation has been found between the naked and minutely tufted conditions (see Systematic accounts).

Naked glands are also morphologically variable, particularly as regards the length and width of the papilla. In all passerine birds, for example, the papilla is distinct and well defined. Most nonpasserine naked glands, on the other hand, either have no papilla (Rhinochetidae, Columbidae, Hemiprocnidae, Galbulidae) or the papilla is so ill-defined and broad that it appears to be continuous with the glandular lobes (e.g., Apterygidae, Cathartidae, Cuculidae). Although I believe the passerine gland shape is distinctive, some nonpasserine glands superficially resemble the passerine type—Cariamidae, Steatornithidae, *Batrachostomus.* Close examinations of figures in the Systematic accounts will show the distinctiveness of the naked passerine gland as opposed to the several naked nonpasserine ones. Jacob & Ziswiler (1982) recognized different shapes among many passerine glands (heart-shaped, kidney-shaped, etc.), but these designations were so variable between and within families that I could not use them.

The majority of nonpasserines have obviously tufted glands, whereas passerine glands are uniformly naked. From an examination of all nonpasserine gland types, I conclude that the tufted gland is primitive. Derived types include those that are (1) minutely tufted, (2) naked (nonpasserine), and (3) naked (passerine).

Gland absence

The absence of uropygial glands in certain species of birds has been known at least since Nitzsch (1840). As more species were examined over the years, more were found to lack glands. For example, in the Columbidae, Garrod (1874*a*) noted gland absence in only 4 genera, Beddard (1898) and Grassé (1950) in 6 genera, and Verheyen (1957*a*) added 'new' species in *Treron* and *Goura.* I made a special effort to examine as many species and individuals as available in the Columbidae, Psittacidae, and Picidae because of earlier discrepancies in reports for genera and species in these families. Nearly every published account containing any information on the absence of uropygial glands (Beddard, Paris, Grassé, Elder, VanTyne & Berger, and others) include at least one factual error on the subject, sometimes simply by omission and frequently by uncritically copying a statement from an earlier author.

The glandless condition varies markedly at every taxonomic level: absent from entire orders, families, genera, species, and individuals. A gland might be present in some species of a genus, yet absent in others. At the individual level, for example in each of three species of *Ptilinopus* (*coronulatus, pulchellus, rivoli*), some individuals possess glands, whereas others do not. Darwin (1900) and Levi (1941) reported the gland's absence in certain varieties of *Columba livia*.

I found the gland to be absent in the following taxa (see Systematic accounts for details and pertinent comments): Struthionidae (all age groups), Rheidae (adults), Casuariidae (all age groups), Dromaiidae (adults), Mesoenatidae (all 3 species), Otidae (all 5 species examined), Columbidae (9 genera, 28 species), Psittacidae (6 genera, 31 species), *Podargus* (3 species examined), and Picidae (1 genus, 4 species).

Some minor discrepancies exist between my findings and earlier reports. Although Garrod (1874*b*) reported no gland in *Cacatua sulfur* (*Kakatoe sulphurea*), a live bird that I examined had a conspicuous, tufted gland. Nitzsch (1840), Beddard (1898), and others noted no gland in *Argusianus* (*Argus*); 5 specimens in the present study contained a gland. I suspect these discrepancies, as well as those in *Ara* and *Cacatua roseicapella*, can be attributed to individual variation among the specimens examined, most or all of them being captive birds.

Because the glandless condition is found in such a wide diversity of species and other taxa, a quest for causal relationships is appropriate. Why, for example, do some parrots have glands whereas others do not? No single attribute (distribution, climate, ecology, flight, etc.) has been found to be consistent as an explanation, a conclusion also reached by Kossmann (1871) who stated that he could find no relationship between gland absence and 'way of life of the bird.' Some flightless birds lack glands; others do not. Some insular pigeons have glands; others do not. Some neotropical parrots lack glands; others have well-developed glands. In my opinion, uropygial glands have apparently been secondarily and independently lost in a variety of birds, but these losses remain unexplained.

Although Beddard (1898: 232) stated that 'presence or absence cannot be made use of as a fact of great systematic importance,' he (pp. 313–314 and elsewhere) nonetheless used the 'fact' as a family characteristic. Similarly, Garrod (1874*b*), Nitzsch (1840), Paris (1913) and many others have used presence or absence of glands (in addition to naked vs. tufted conditions) as distinctive family and generic characteristics. This is a valid use of uropygial gland data except in cases of known individual variation. Gland absence in all species of the Mesoenatidae is just as good a family characteristic as is their singular limited distribution. On the other hand, in the Picidae, and especially in only a few species of *Campethera*, gland absence is probably of little taxonomic importance at the family level.

Glands in flightless birds

Because some authors (e.g., Elder 1954) have suggested relationships among uropygial gland secretions, normal feather functions, and flight capabilities, an analysis of gland presence/absence in flightless birds is desirable. Elder's experiments on ducks essentially showed that gland extirpation resulted in reduced feather waterproofing, thus rendering the birds flightless.

The first consideration has been to determine if a relationship exists between a flightless condition and gland presence in nature. In Table 2, flightless species identified from several literature sources are listed along with the presence or absence of the gland. Except for most of the ratites (Struthionidae, Rheidae, Casuariidae, Dromaiidae), only one other taxon (all three species of Mesoenatidae) is known wherein flightless species lack a gland. Overall, this analysis reveals virtually no correlation between a flightless condition and gland absence: for 42 flightless species examined, only 8 lacked a gland in the adult.

Table 2

The Relationship between the flightless condition*
and presence of uropygial glands

- Struthionidae**
  - *Struthio camelus*—absent in adult
- Rheidae**
  - *Rhea americana*—absent in adult
  - *Pterocnemia pennata*—absent in adult
- Casuariidae**
  - *Casuarius bennetti*—unavailable
  - *Casuarius casuarius*—absent in adult
  - *Casuarius unappendiculatus*—unavailable
- Dromaiidae**
  - *Dromaius novaehollandiae*—absent in adult

- Apterygidae
  - *Apteryx australis*—gland present, essentially naked (but see Beddard 1898, 1899)
  - *Apteryx owenii*—gland present, naked
  - *Apteryx haastii*—gland present, naked
- Spheniscidae
  - 16 species—gland present and tufted in all 10 species examined
- Podicipedidae
  - *Rollandia microptera*—gland present, tufted
  - *Podilymbus gigas*—gland present, tufted
- Phalacrocoracidae
  - *Phalacrocorax harrisi*—gland present, tufted
- Anatidae
  - *Tachyeres pteneres*—gland present, tufted
  - *Tachyeres brachypterus*—gland present, tufted
  - *Anas aucklandica*—gland present, tufted
  - *Mergus australis*—gland present, tufted (but perhaps capable of flight, see Weller 1980)
- Mesoenatidae
  - *Mesoenas variegata*—gland absent
  - *Mesoenas unicolor*—gland absent
  - *Monias benschi*—gland absent
- Rallidae***
  - *Rallus owstoni*—gland present, tufted
  - *Rallus wakensis*—gland present, tufted
  - *Cabalus modestus*—unavailable
  - *Atlantisia rogersi*—gland present, tufted or naked
  - *Tricholimnas lafresnayanus*—unavailable
  - *Tricholimnas sylvestris*—gland present, tufted
  - *Dryolimnas cuvieri aldabranus*—gland present, tufted
  - *Cyanolimnas cerverai*—gland present, tufted
  - *Nesoclopeus poeciloptera*—unavailable
  - *Gallirallus australis*—gland present, tufted
  - *Habropteryx insignis*—unavailable
  - *Habroptila wallacii*—unavailable
  - *Megacrex inepta*—unavailable
  - *Porzanula palmeri*—gland present, tufted
  - *Pennula sandwichensis*—unavailable
  - *Aphanolimnas monasa*—unavailable
  - *Tribonyx mortierii*—gland present, tufted
  - *Porphyriornis nesiotis*—gland present, tufted
  - *Porphyriornis comeri*—gland present, tufted
  - *Notornis mantelli*—gland present, tufted

Rhynochetidae
  Rhynochetos jubatus—gland present, naked
Alcidae
  Pinguinus impennis—gland present, tufted
Psittacidae
  Strigops habroptilus—gland present, tufted
Acanthisittidae
  Xenicus lyalli—unavailable (see Systematic accounts for other species).

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*Flightless species names taken from Thomson (1964), Greenway (1958), Austin (1961), Van Tyne & Berger (1976), Olson (1973*a*, *b*), Weller (1980), and Mlikovsky (1982).

**Several authors (e.g., Beddard 1898, Jacob 1978) have reported the absence of a gland in all ratites except *Apteryx*, although the species examined were usually not identified by the author.

***Opinions differ on the flight capability of some of these species. Ripley and Beehler (1985: 7), for example, reported that *Rallus owstoni* 'can fly as high as one or two meters above the ground, but they seldom do so.'

A second consideration concerns a possible relationship between gland size and a flightless condition. Although fresh gland weights from flightless species were unavailable to me, sizes (linear measurements) of glands of flightless species in the Podicipedidae, Phalacrocoracidae, Anatidae, and Rallidae were compared with glands from closely related (often congeners) species that fly. These comparisons revealed no major size differences in glands between flightless and flying birds.

General taxonomic considerations of glands

The use of the uropygial gland as a character in avian systematics has been both commonplace and controversial for many years. As early as 1840, Nitzsch identified general gland features (e.g., tufted vs. naked conditions) as characteristics of different avian taxa, and the gland was subsequently much used in classification by ornithologists such as Coues (1890) and Beddard (1898). This use in taxonomy has continued to date by some investigators (e.g., Olson & Steadman's 1981 characterization of *Pedionomus*), but others have excluded gland morphology in taxonomic considerations (e.g., Cracraft, 1985). Thomson (1964) stated that the gland is 'unsatisfactory as a taxonomic character,' and Jacob & Ziswiler (1982) noted that the gland 'has little systematic importance. . . .'

From the systematic accounts of this monograph, it can be seen that the gland's presence or absence, tufted vs. naked condition (and variations thereof) might vary at any taxonomic level: intraspecific to interordinal. At the ordinal level, the gland is present and naked (with distinctive papilla) in all the Passeriformes, thus adding, as it were, another passerine characteristic. On the other hand, the several morphological variations in glands of the piciform families lend credence, I believe, to Olson's (1983) suggestion for a polyphyletic origin of the Piciforms (see also Burton 1984).

The morphological gland characteristics that could be used in taxonomic analyses are:

1. ontogeny—e.g., gland present in embryos and young of some ratites, but absent in all age groups of other ratites.
2. presence or absence of the gland—e.g., absent from families (Mesoenatidae in the Gruiformes) and genera (*Amazona* in the Psittacidae).
3. lobe shape—e.g., cf. Apodidae and Trochilidae in the Apodiformes.
4. tufted vs. naked condition—
    a. degree of feathering (cf. Momotidae and Meropidae)
    b. shape, size, and length of papilla (cf. Leptosomatidae and Coraciidae).
5. histology—little is known about histological variations, but features such as the number of gland openings are mentioned by Jacob & Ziswiler (1982).

The value for a cladistic taxonomic scheme would depend on the number of variable features of the gland that could be analyzed and the incidence of multiple evolutions of those features. The recent chemo-taxonomic approach of Jacob & Ziswiler (1982), based on chemical differences in uropygial secretions among different taxa, has as yet received little attention in avian taxonomic schemes.

I believe that gland morphology is just as important a diagnostic taxonomic character as are muscle variations, osteological minutiae, incubation patterns, syringeal structures, and the like. The question is, of course, the degree of importance that one assigns to gland morphology in a large suite of taxonomic characters. Because of significant variations in gland morphology in different taxa, as identified in the present study, the least that could be said here is that gland morphology should be considered especially in cladistic taxonomic approaches.

Functions of glandular secretions

Uropygial gland functions (actually, the functions of glandular secretions) have been controversial ever since the gland was first described in the 13th century. Form and function of glands are biologically interrelated features, but, because the present report concentrates on gland morphology, only a brief summary of secretion functions is included here. (More detailed accounts can be found in Law (1929), Elder (1954), Thomson (1964), and Jacob & Ziswiler (1982)). At least 8 functions have been ascribed to the gland, and the interested reader is referred to the appropriate publications:

1. water-repellent action (Stubbs 1910, Elder 1954, Rijke 1970),
2. preserve physical structure of feathers (Rutschke 1960),
3. maintain horny sheath of bill (Thomson 1964),
4. as a scent organ (Giebel 1857, Jackson 1938, Mackworth-Praed and Grant 1970),
5. pheromone-producing (Balthazart and Schoffeniels 1974),
6. antirhachitic action (Hou 1928),
7. prevent growth of skin microorganisms (King and McLelland 1984),
8. dislodge feather lice (Morris 1836*a*).

Apparently any one or some combination of these functions could be ascribed to the secretions of an individual species but also the functions might not be identical for all birds. Most of the research on water-repellency ('waterproofing') has been appropriately conducted on aquatic birds, but virtually nothing is known about 'waterproofing' in landbirds. Indeed, Rutschke (1960) believed that the gland is only indirectly involved in 'waterproofing' of plumage in aquatic birds (see also Clark 1969), and Spearman (1971) made the unsupported comment that the glandular products are 'not essential for terrestrial birds.' Hou's studies (1928) on rickets and vitamin D were conducted only on chickens, pigeons, and, later, ducks. A scent-organ function for the gland has been reported for a variety of birds (e.g., *Anas moschata, Phoeniculus bollei*), but it is not clear how the 'foul-smelling' (to humans) secretions actually function. Contrary to the research reported by Elder (1954) on ducks, a number of reports have indicated that some birds from which glands had been surgically removed nonetheless had 'normal, bright plumages' (Arnall and Keymer 1975). As early as 1910, Pycraft expressed 'grave doubts' as to the function of the gland primarily because (1) he believed that some birds (e.g., *Anastomus*) presumably could not remove oil from the gland because of their peculiar bill structure and (2) birds lacking glands presumably keep their feathers in as good condition as those species possessing those glands.

Throughout much of the literature on uropygial glands, one finds the recurring suggestion that powder down somehow fulfills the function of oil from glands in those species where the gland is small or absent (Bartlett 1861, Nitzsch 1867, Newton 1893–1896, Verheyen 1956*f*, Voitkevich 1966, Jacob 1978, Goodwin 1983). This presumed correlation arose, I believe, because observers were seeking functional replacements in those birds either lacking glands or possessing small glands. Goodwin (1983: 27), for example, reports for pigeons, 'The powder down . . . appears to function in lieu of preen oil to aid in waterproofing of the feathers.' Verheyen (1956*f*, 1957*a*) variously describes the glands of Psittaciformes and Columbidae as being in a 'phase of regression' or 'deficient,' somehow compensated by 'a lot of powder.' This correlation argument contains a number of basic flaws, i.e., unproven assumptions (1) that a small gland produces insufficient oil and (2) that the oil and powder down are used more or less interchangeably for waterproofing feathers especially in land birds. It should be emphasized that virtually nothing is known about the quantity, rate of production, or rate of secretion of uropygial oils. Without experimental documentation, it cannot be assumed that small glands have any reduction in rate or quantity of secretion, whether the bird has powder down or not.

It is true that birds known to produce a significant amount of powder down (Gadow 1891, Chandler 1916, Thomson 1964, Jacob 1978, Baumel *et al.* 1979) tend to have relatively small glands: (gland weights as a percent of body weight) Ardeidae ($N=20$, $\bar{x}=0{\cdot}29\%$), Psittacidae ($N=41$, $\bar{x}=0{\cdot}10\%$, *fide* Jacob & Ziswiler 1982 for zoo birds), Ramphastidae ($N=3$, $\bar{x}=0{\cdot}12\%$), and Tinamidae ($N=1$, $0{\cdot}18\%$ *fide* Jacob & Ziswiler 1982). Relative gland weights are unavailable for other species that produce powder down: Podargidae, Cotingidae, Leptosomatidae, Artamidae, Ptilonorhynchidae, and others. The Mesoenatidae, which have five pairs of powder down patches (Olson 1978), lack a gland. According to Schuz (1927), 'powder downs are lacking, or nearly so, in ratite birds;' among the ratites, only *Apteryx* possesses a gland as an adult. Powder downs, produced in various amounts are known from a wide variety of other birds including Columbidae, Rhynochetidae, Eurypigidae, Podargidae, Otididae, and Accipitridae. This body of circumstantial evidence lends some support to the view that birds with well-developed powder down production have reduced (or no) uropygial glands.

A cause-and-effect functional relationship remains unproven, however. Furthermore, the function of powder remains conjectural probably because several types of powder (down) are known: as a waterproof dressing (Bartlett 1861), preserving feathers (Welty 1962), and cleaning feathers (Thomson 1964). Although the powder has a nonwettable property, it is composed largely of keratin, so its functional equivalence to uropygial oils must await experimental proof (see also Lucas & Stettenheim 1972).

All this information strongly argues that more research on functions of glandular secretions is badly needed before physiological generalizations can be asserted. Particularly open to question is the function of secretions in terrestrial birds and in bird taxa containing some glandless members (e.g., doves, parrots).

Future studies

Several biological aspects of uropygial glands merit further investigations because results therefrom could help to explain some of the morphological variations identified in the present monograph. Johansson's studies (1927) indicated a strong genetic component in the inheritance of uropygial glands in *Columba livia,* as is also suggested from the fact that certain varieties of this pigeon lack glands (Darwin 1900, Levi, 1941, Goodwin 1983). Hutt (1949) reported that mutation of a dominant gene in chickens causes bifurcation of the gland's papilla and that most heterozygotes have no uropygial gland at maturity. The rumpless chickens of Waterton (1836*a*) presumably had no glands and might have been genetic mutants. Inheritance of double gland papillae were discussed by Kessel (1945) for domestic fowl. Apparently these are the only investigations pertaining to the inheritance of uropygial glands, and further genetic studies might reveal biological relationships to the absence of glands in taxa of wild birds.

Another aspect in need of experimental studies is the physiology of gland production, secretion, and its relationship to preening. Nothing is known about either the quantity or rate of secretion of uropygial oils. Some information is available on histology, vascular supply and innervation (Kossman 1871, Paris 1913, Kanwar 1961). Many additional questions are unanswered, however: (1) do birds with large glands (e.g., waterbirds) produce more oil than birds with small glands (e.g., landbirds); (2) is gland oil production stimulated, and at what rate, by physical manipulation with the bird's bill; (3) is there either seasonal or daily variation in the quantity or rate of secretion?

Despite some papers that address preening activities in birds (e.g., in penguins, Bekoff *et al.* 1979, and references therein), little is known about the relationship between gland secretion and types or rates of preening activities that involve this gland. A case in point was the radical statement by Gurney (1913) that *Sula bassana* does not use its gland in preening, a statement since disputed by Nelson (1978).

As indicated in the previous account, attention should be given to functional attributes of glandular secretions, especially in terrestrial birds.

Little is known about any relationship between gland shape and the underlying muscles and rectrices. Future research could focus on explaining the several different gland shapes identified in this study especially as those shapes might be related to muscle differences or to placement of the rectrices.

A final research need is in embryology, especially post-hatching development as it might relate to function in certain species (a review of the gland's embryology is found in Jacob and Ziswiler 1982). Prior to the report by Pycraft in 1900, it was believed that ratites, with the exception of *Apteryx,* lack uropygial glands. He found, however, that in both *Dromaius novaehollandiae* and *Rhea americana,* a gland exists in both the embryo and nestling, but is absent in the adult. (Those conditions have been verified in the present study). Apparently no one has examined those embryonic glands histologically or functionally. Although no glands have been found in any age group of *Struthio* or *Casuarius*, might some trace or anlage be found by an embryonic-histological study? In other adult birds lacking glands (e.g., Mesoenatidae, Otidae) is there any early embryological development of a gland?

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Summary

The primary goal of this study has been to assemble a complete analysis of the uropygial gland's morphology in representatives of all bird families and subfamilies. Particular attention has been given to correcting erroneous information about glands in the existing literature. Morphological data are included from many avian taxa not previously reported.

The largest glands, relative to body weight, are found in birds that swim, dive or rest on water. Progressively smaller glands occur in birds that walk in water, those that habitually only fly over water, and lastly, terrestrial species. Glands are now known to be absent in the Struthionidae (all age groups), Rheidae (adults only), Casuariidae (all age groups), Dromaiidae (adults only), Mesoenatidae, Otidae, Columbidae (9 genera, 28 species), Psittacidae (6 genera, 31 species), *Podargus* spp., and Picidae (1 genus, 4 species). The absence of glands in these taxa is believed to be a secondary and independent loss. Because only 17 percent of flightless species lack a gland, this study revealed no significant correlation between gland absence and a flightless condition.

Many nonpasserine taxa possess tufted glands, whereas others have manifestly naked (non-tufted) glands. Apparently naked glands of others, e.g. Strigidae, actually might bear minute feathers. All species of the Passeriformes have naked glands. Feathers attached to the uropygial gland are more numerous in waterbirds than landbirds and are of two principal types, modified down or modified semiplumes. Only circumstantial evidence was found to support the oft-expressed hypothesis that power down is a substitute for gland secretions in glandless species.

The present complete study provides sufficient morphological characteristics for their consideration in avian taxonomic schemes.

Future investigations should focus on gland function, especially in terrestrial birds, the quantity and rate of secretion of uropygial oils, relationships between gland production and preening activities, details of feather structure, genetics, and embryological development.

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The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Miscellanea

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Contents

A review of the copepod endoparasites of brittle stars (Ophiuroida)

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Summary

A new family, the Chordeumiidae, is proposed for six genera of copepods that live as endoparasites of brittle stars. The status of these genera, *Chordeumium, Arthrochordeumium, Lernaeosaccus, Ophioicodes, Ophioika* and *Parachordeumium* is reviewed. The genera *Ophioithys* and *Amphiurophilus* are recognised as subjective synonyms of *Parachordeumium*. The sole species of *Lernaeosaccus* is reinterpreted and redescribed. Examination of the holotype of *L. ophiacanthae* revealed that it was originally described upside down. *Codoba discoveryi* is also redescribed from the types but cannot be placed in any of the existing families of the Siphonostomatoida at present.

Introduction

In his review of copepods associated with invertebrate hosts Gotto (1979) listed eight genera of endoparasites that utilise brittle stars as hosts. None of these has formally been placed in a family and even their ordinal placement is uncertain. There are obvious taxonomic problems concerning these genera which need to be resolved before their phylogenetic relationships with other copepods can be understood. Most of the species contained in these 8 genera have highly transformed females with bizarre body morphology in the adult and few, if any, recognisable limbs. However, in some genera either males or developmental stages are known and these provide more taxonomically useful information. The monotypic genus *Codoba* Heegaard is much less modified, still retaining a more-or-less cyclopiform facies in the adult female (Heegaard, 1951). *Codoba* is redescribed, based on the type material, and the taxonomic status and phylogenetic relationships of the other genera endoparasitic in ophiuroids are reassessed. The morphology of the monotypic genus *Lernaeosaccus* Heegaard is reinterpreted and a new description and diagnosis of the genus is provided.

Descriptions

Genus ***CODOBA*** Heegaard, 1951

DIAGNOSIS. Adult female prosome 4-segmented, slightly swollen; urosome 5-segmented. Caudal rami distinct, bearing 6 setae. Antennule 20-segmented, lacking aesthetascs. Antenna reduced to unarmed process. Mouth tube well developed. Mandible stylet-like, without teeth; palp absent. Maxillule bilobed, inner lobe with 1, outer with 2 setae. Maxilla with distal recurved claw. Maxilliped 3-segmented. Legs 1–4 biramous, rami medially directed, intercoxal sclerites absent. Leg 5 lacking. Male unknown.

TYPE SPECIES. *Codoba discoveryi* Heegaard, 1951 by monotypy.

Codoba discoveryi Heegaard, 1951

ADULT FEMALE. Body (Fig. 1A) slightly transformed cyclopiform, but with distinct segmentation. Prosome swollen, comprising cephalothorax incorporating first pedigerous somite, and 3 free pedigerous somites. Total body length of figured syntype 1·97 mm. Each free pedigerous somite with a pair of posterolaterally directed epimeral processes. Urosome short (Fig. 1B), comprising

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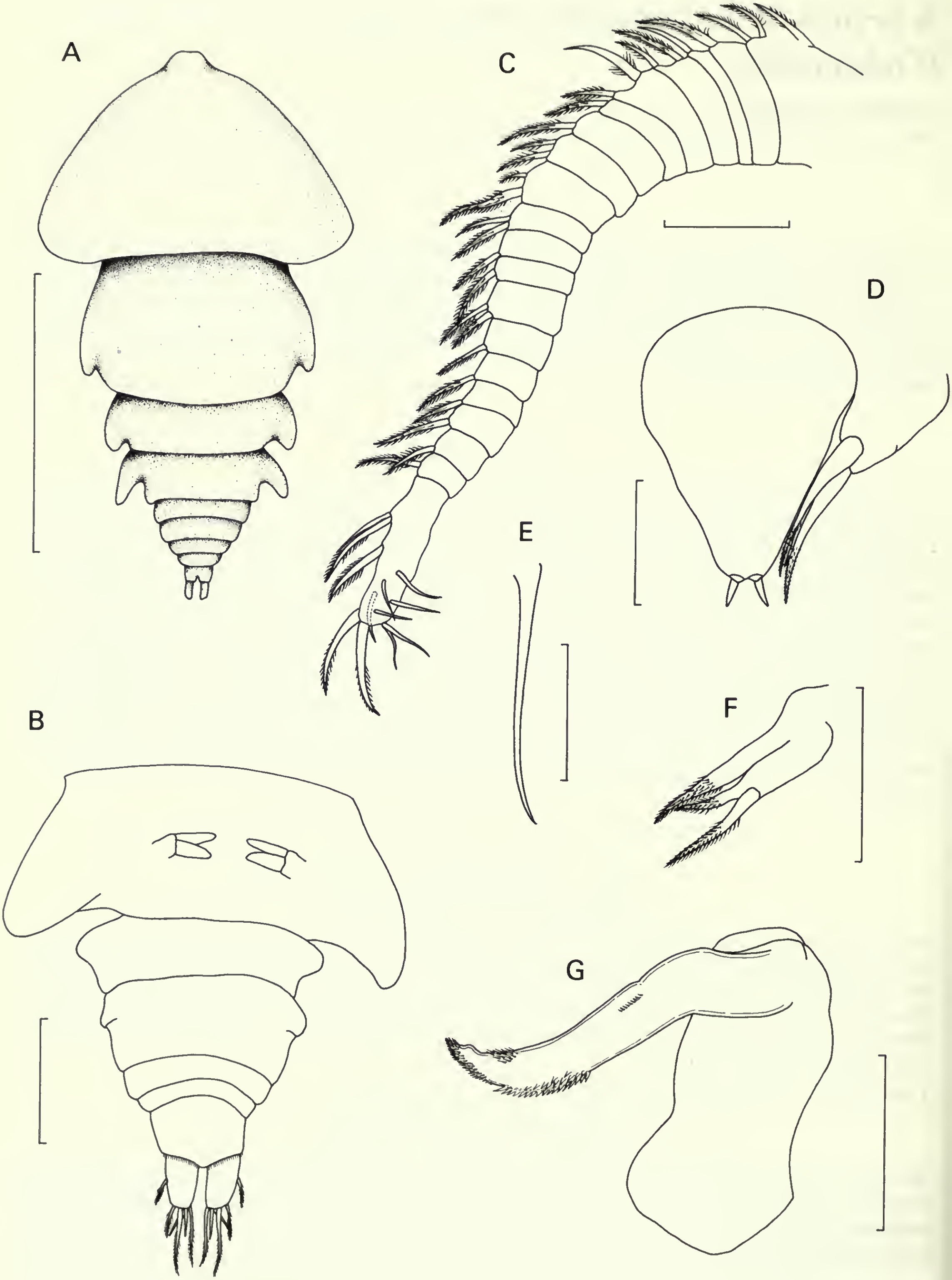
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somite of leg 5 (95 × 398 μm), the genital complex (130 × 130 μm), 2 postgenital somites (40 × 235 μm, 25 × 190 μm) and the anal somite (115 × 150 μm). Genital apertures unarmed; located ventrolaterally on genital complex. Anal somite with row of spinules along posterior margin. Caudal rami (Fig. 1B) about 1·5 times longer than wide (80 × 53 μm); armed with a lateral seta about at midlength, a naked dorsal seta and 4 distal margin setae, 3 of which are pinnate.

Antennule (Fig. 1C) 20-segmented; lengths of segments measured along posterior margin 13, 9, 5, 10, 11, 10, 13, 12, 12, 9, 9, 9, 18, 15, 14, 11, 15, 14, 11 and 61 μm; armature elements as follows: I—3, II—1, III—1, IV—2, V—2, VI—1, VII—1, VIII—2, IX—2, X—2, XI—1, XII—1, XIII—2, XIV—1, XV—1, XVI—1, XVII—1, XVIII—1, XIX—1, XX—12. No aesthetascs present. The size and number of armature elements on the apical segment indicate that it is derived by fusion of 2 or more segments. Antenna vestigial; reduced to small unarmed process located between base of antennule and mouth tube (Fig. 2F).

Mouth tube (Fig. 1D) well developed, formed from labrum and labium. Mandible (Fig. 1E) stylet-like, unarmed; palp lacking. Maxillule bilobed (Fig. 1F); inner lobe represented by single hirsute seta; outer lobe short, armed with 2 hirsute setae. Maxilla (Fig. 1G) comprising unarmed syncoxa and distal basis. Basis drawn out into recurved claw, armed distally with patches of denticles as figured. Maxilliped (Fig. 2A) 3-segmented; basal segment armed with a row of spinules; second segment elongate, armed with a single seta and several rows of spinules; third segment bearing a tiny seta proximally on outer margin, a small inner seta and 2 unequal apical spines. Spines dentate, 51 μm and 41 μm in length. Fine spinules present around apex.

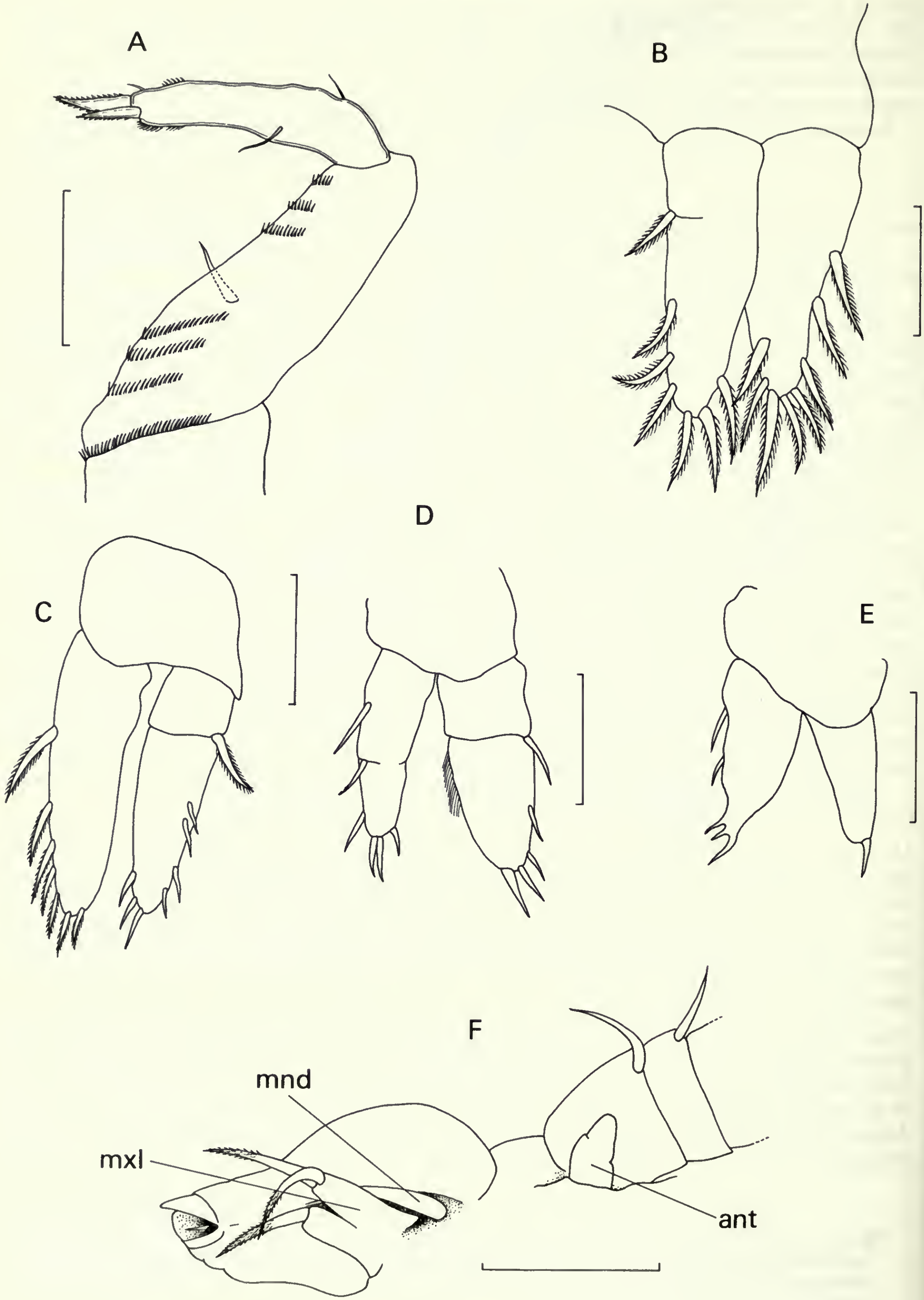
Swimming legs 1 to 4 biramous, positioned on ventral surface of somite with rami directed medially (Fig. 1B); intercoxal bars (sclerites) absent. Leg 1 (Fig. 2B) with unarmed protopod; exopod unsegmented, bearing 4 pinnate setae along outer margin, 2 at apex and 2 distally on inner margin; endopod indistinctly 2-segmented, bearing 4 pinnate setae along inner margin, 2 at apex and 1 distally on outer margin. Leg 2 (Fig. 2C) with unarmed protopod. Exopod 2-segmented; first segment with outer pinnate seta, second with 4 naked setae on outer margin, 1 at apex and 2 on inner margin. Endopod unsegmented; with 5 pinnate setae along inner margin and 2 at apex. Leg 3 (Fig. 2D) with unarmed protopod; both rami indistinctly 2-segmented. Exopod with outer seta on first segment, second with 2 outer and 2 apical setae, and a row of spinules medially; endopod with 2 inner margin setae on first segment; second with 1 inner, 1 outer and 2 apical setae. Leg 4 (Fig. 2E) with unarmed protopod; exopod with single apical seta; endopod with 2 setae on inner margin and 3-branched spinous projection apically. Leg 5 lacking.

Egg sacs lacking, eggs loose inside capsule with adult female. Capsule of specimen 1987.244 containing 44 eggs; eggs large, lecithotrophic, diameter approximately 190 μm.

Material examined. Syntypes: Dissected syntype (BM(NH) No. 1987.243) collected from *Ophiura meridionalis* (Lyman) at *Discovery* Stn 123, in 230–250 m off South Georgia, 15.12.1926. Intact syntype (BM(NH) No. 1987.244) from *O. meridionalis* at *Discovery* Stn 156, in 236 m off South Georgia, 20.1.1927. Third syntype an empty capsule (BM(NH) No. 1987.245) collected from *Amphiura belgicae* Koehler at *Discovery* Stn 160, in 177 m off South Georgia, 7.2.1927. These are the data on the labels with the specimens and do not correspond in some details with those data published by Heegaard (1951).

Remarks. When Heegaard (1951) erected the genus *Codoba* he indicated that new families would probably have to be established to accommodate the copepods parasitic on echinoderms but felt that it would be premature to do so in view of the lack of knowledge of the group. The high number of antennulary segments in *Codoba* is a plesiomorphic character and is typical of the family Asterocheridae but the genus cannot be referred to the Asterocheridae as it lacks a mandibular palp and an aesthetasc on either the penultimate or antepenultimate segment of the antennule.

Fig. 1 *Codoba discoveryi* Heegaard, 1951. Adult female syntype. A, dorsal; B, Fourth pedigerous somite and urosome, ventral; C, Antennule, ventral; D, mouth cone and maxillule, anteroventral; E, Mandible, anterior; F, Maxillule, lateral; G, Maxilla, posterior. Scale bars 100 μm unless otherwise stated: A = 1 mm, B = 200 μm, c = 50 μm.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These are regarded as diagnostic characters for the Asterocheridae by Stock (1987). The very reduced antenna is rare in siphonostomatoids, occurring mainly in species of the Nicothoidae. However, *Codoba* is not related to the Nicothoidae which primitively have reduced antennules and a well developed antenna. The typical subchelate antenna of siphonostomatoids is primarily an organ for grasping the host and its reduction is here interpreted as an adaptation to endoparasitism. Subject to a full review of the families of siphonostomes parasitic on invertebrates, which is in progress, the genus *Codoba* is left unassigned to any of the families recognised at present.

Review of other endoparasitic genera and species

AMPHIUROPHILUS Delamare Deboutteville, 1962

In his revision of the members of the family Philichthyidae parasitic on European fishes Delamare Deboutteville (1962) correctly removed *Philichthys amphiurae* Hérouard, 1906 from the genus *Philichthys* Steenstrup, 1862 on the basis of differences in male morphology. He established a new genus, *Amphiurophilus*, to accommodate *Philichthys amphiurae. Amphiurophilus* is a junior objective synonym of *Ophioithys* which was established by Heegaard in 1951 with the same type species, *Philichthys amphiurae* of Hérouard (1906). It is a subjective synonym of *Parachordeumium* Le Calvez, 1938 (see below).

ARTHROCHORDEUMIUM Stephensen, 1918

DIAGNOSIS. Postmetamorphosis adult female highly transformed; body somewhat dorsoventrally compressed, indistinctly segmented and with short, paired lateral processes. Two pairs of limbs present; antennules and maxillae. Antennules unsegmented, bifid at tip. Maxillae 3-segmented, including terminal claw. Egg masses irregularly wrapped around body.

Male and copepodid unknown.

TYPE SPECIES. *Arthrochordeumium appendiculosum* Stephensen, 1918 (by subsequent designation, Stephensen, 1933).

This is a valid genus established by Stephensen (1918) for *A. appendiculosum.* A second species, *Arthrochordeumium asteromorphae,* was described by Stephensen (1933).

CHORDEUMIUM Stephensen, 1918

DIAGNOSIS. Postmetamorphosis adult female moderately transformed; body cylindrical with paired lateral swellings on genital complex only; segmentation distinct. Median process present posterodorsally on genital complex. Three pairs of cephalic appendages present. Antennules unsegmented, bifid at tip. Antennae reduced to papilliform processes. Maxillae 3-segmented, including terminal claw. Legs 1 to 4 represented by slender, laterally-directed processes. Egg mass extruded posteriorly into cyst surrounding parasite.

Adult male similar to female in general facies but with better defined segments. Posterodorsal median process absent. Testes paired.

Copepodid stage without discrete caudal rami, caudal setae located on margin of anal somite.

TYPE SPECIES. *Chordeumium obesum* (Jungersen, 1912).

This genus was proposed by Stephensen (1918) as a replacement name for *Chordeuma* of Jungersen (1912). *Chordeuma* was preoccupied for a genus of Myriapoda (Kock, 1847). The type species, *Chordeuma obesum*, described by Jungersen (1912, 1914) becomes the type species of *Chordeumium* by monotypy.

Fig. 2 *Codoba discoveryi* Heegaard, 1951. Adult female syntype. A, Maxilliped, posterior; B, Leg 1, ventral; C, leg 2, ventral; D, leg 3, ventral; E, leg 4, ventral; F. Area between mouth cone and antennule showing antenna (ant), mandible (mnd) and maxillule (mxl). All scale bars 100 μm.

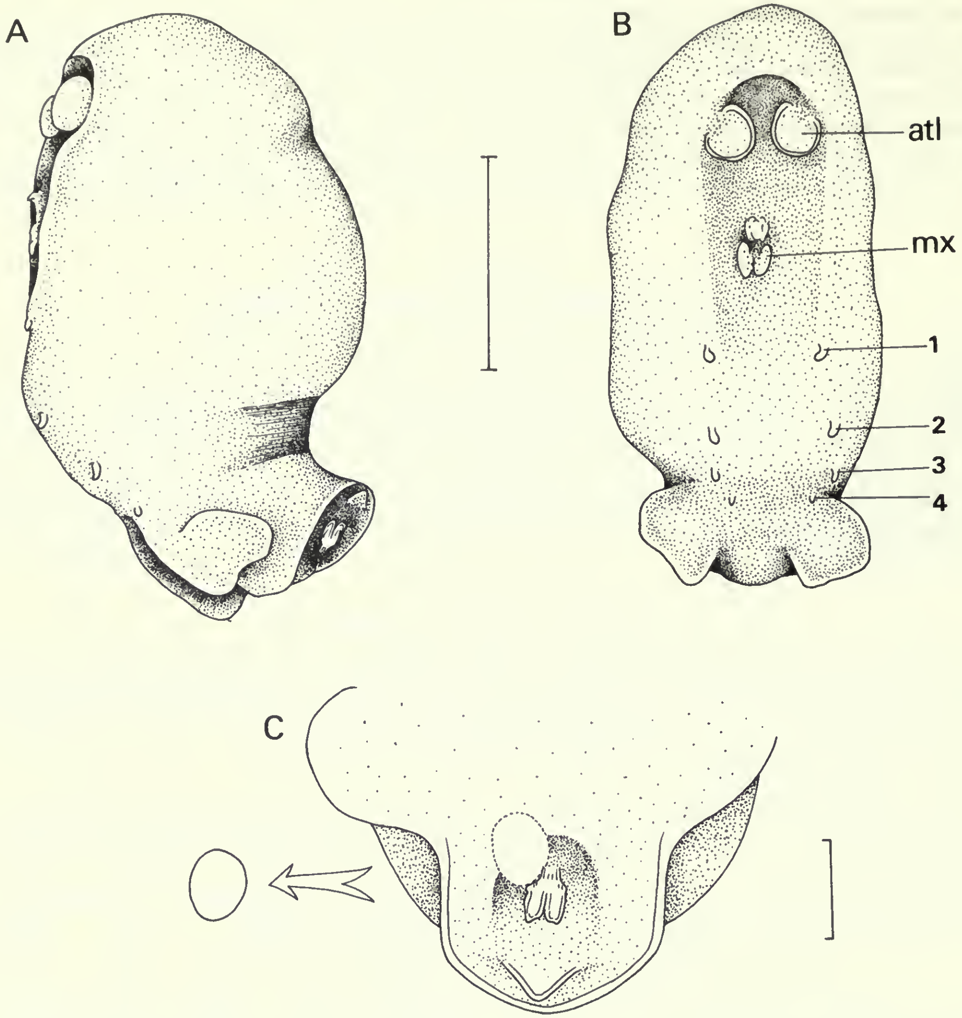

Fig. 3 *Lernaeosaccus ophiacanthae* Heegaard, 1951. Holotype female. A, lateral; B, ventral view showing antennules (atl), presumed maxillae (mx) and legs 1–4 (1–4); C, Posterior end of body, posterodorsal view showing median abdominal process and position of detached egg. Scale bars 1 mm unless otherwise stated: c = 0·25 mm.

LERNAEOSACCUS Heegaard, 1951

DIAGNOSIS. Postmetamorphosis adult female sac-like, lacking external segmentation. Single pair of lateral processes present on trunk. Posterior end concave containing a median posterior lobe. Lobate antennules and vestigial maxillae present anteriorly. Swimming legs 1–4 reduced to tiny, posteriorly directed lobes. Eggs large, released into masses surrounding female.

Male and copepodid stages unknown.

TYPE SPECIES. *Lernaeosaccus ophiacanthae* Heegaard, 1951 (by monotypy).

Lernaeosaccus ophiacanthae Heegaard, 1951

POSTMETAMORPHOSIS FEMALE. Body (Fig. 3A) highly transformed, lacking distinct segmentation and tagmosis. Body swollen, rounded anteriorly and dorsally, flattened ventrally and concave posteriorly. Total body length of holotype 2·87 mm. Posterior part of body of holotype reflexed dorsally, probably due to fixation. Single pair of lateral lobes present posteriorly behind fourth legs (Figs 3A–B). Concave posterior end containing genital openings, a median abdominal process and a median lobe. The median abdominal process originates close to the genital apertures (Fig. 3C). Eggs located at genital openings removed during examination. Eggs large; maximum diameter 173 µm. Egg masses not contained within sacs; wrapped around body within capsule produced by host.

Antennules represented by unarmed lobes (Fig. 3B, atl). Oral area obscured on holotype but apparently comprising a median structure and a pair of more posteriorly located limbs (probably maxillae, Fig. 3B, mx). Legs 1–4 present, reduced to unsegmented, unarmed and posteriorly directed lobes on ventral body surface (Fig. 3B, 1–4).

MATERIAL EXAMINED. Holotype: Adult female (BM(NH) No. 1982.242) collected from *Ophiacantha disjuncta* (Koehler) at Discovery Stn 190, in 316 m off the Palmer Archipelago on 24.03.1926. The depth and date on the label differ from those given by Heegaard (1951), which were 278 m and 14.03.1926 respectively.

REMARKS. This species was described by Heegaard (1951) upside down. The paired structures referred to by Heegaard as maxilliped 2 (Heegaard, 1951: Fig. 4b) are eggs. Dissected from the holotype, they were found to contain a nauplius at an early stage of development but with 3 recognisable pairs of appendages. The structure identified as a mouth cone containing mandibles is here reinterpreted as a median abdominal lobe. The thickening of the cuticle was misinterpreted by Heegaard as the paired mandibles. Close inspection of the trunk of the holotype revealed 4 pairs of posteriorly directed legs that were overlooked by Heegaard (1951). This parasite is closely related to *Chordeumium obesum*. The body morphology and appendage positioning are very similar. They are maintained as separate genera because of the differences in structure of the posterior part of the body.

OPHIOICODES Heegaard, 1951

DIAGNOSIS. Postmetamorphosis adult female highly transformed; body asymmetrical, irregularly shaped and provided with numerous lateral and dorsal processes. No traces of segmentation visible. Female with midventral groove.

Male highly transformed; body elongate, unsegmented and with a pair of long, slender lateral processes. Testes paired. Male lies in midventral groove of female.

Copepodid stage unknown.

TYPE SPECIES. *Ophioicodes asymmetrica* (Pyefinch, 1940).

This is a valid genus. It was established by Heegaard (1951) on the basis of differences in male morphology between *Ophioica asymmetrica* Pyefinch, 1940 and the other 3 species of *Ophioika* Stephensen, 1933. He designated *Ophioica asymmetrica* Pyefinch, 1940 as type.

OPHIOIKA Stephensen, 1933

DIAGNOSIS. Postmetamorphosis adult female highly transformed. Body unsegmented, apparently globular due to positioning of about 5 pairs of long lateral processes which curve ventrally. Four to six egg masses held within space enclosed by processes. Pair of small anterior processes possibly representing antennules. No other limbs recognisable. Median conical process may represent oral cone.

Males degenerate body form with single well developed testis, male penetrating body of female.

Copepodid unknown.

TYPE SPECIES. *Ophioika ophiacanthae* Stephensen, 1933.

This genus was established by Stephensen (1933) to accommodate *Ophioika ophiacanthae*

Stephensen 1933. This becomes the type species by monotypy. Stephensen (1935) added a second species, *Ophioica appendiculata*, misspelling the generic name *Ophioika*. This is corrected here.

OTHER SPECIES. *Ophioikia appendiculata* Stephensen, 1935; *Ophioika tenuibranchia* Heegaard, 1951.

OPHIOITHYS Heegaard, 1951

Heegaard (1951) recognised the close relationship between *Philichthys amphiurae* and the genus *Ophioika*. He removed this species from *Philichthys* and proposed a new genus, *Ophioithys*, with *P. amphiurae* Hérouard, 1906 as type. This name is a senior objective synonym of *Amphiurophilus* as both genera have the same designated type species. This genus is, however, recognised herein as a synonym of *Parachordeumium* Le Calvez, 1938 (see below).

PARACHORDEUMIUM Le Calvez, 1938

DIAGNOSIS. Postmetamorphosis female highly transformed; body symmetrical, unsegmented, lacking limbs except for maxillae. Body with 4 pairs of major lateral processes, sometimes branched, forming enclosure containing egg masses; several paired and/or median papillae present dorsally; abdominal process well developed. Genital apertures paired. Maxillae 3-segmented, including terminal claw.

Adult male small, highly transformed, living in permanent association with female; body unsegmented, drawn out into long abdominal process posteriorly, anteriorly with pair of long lateral processes. Maxillae 3-segmented, including terminal claw.

Copepodid hatching with 3-pairs of developed biramous legs; lacking discrete caudal rami, caudal setae located on margin of anal somite. Antennules 5-segmented. Antenna 3-segmented, lacking exopod. Maxillae 3-segmented with terminal claw. Other cephalic appendages absent.

This is a valid genus established to accommodate a single species, *P. tetraceros* Le Calvez 1938, which was the type species by monotypy. The dorsal and ventral figures of the adult postmetamorphosis female *P. tetraceros* given by Le Calvez (1938) do not differ significantly from the figures in the detailed redescription of *Amphiurophilus amphiurae* by Goudey-Perrière (1979). Both these species inhabit the genital bursae of the *Amphipholis squamata* Della Chiaje in European waters and it is here proposed that they be synonymised. The oldest available name for this species is *Parachordeumium amphiurae* (Hérouard, 1906) and this is the type species of *Parachordeumium*.

TYPE SPECIES. *Parachordeumium amphiurae* (Hérouard, 1906) new combination. (syn. *P. tetraceros* Le Calvez, 1938).

The three new species described by Goudey-Perrière (1979) and placed within the genus *Amphiurophilus* are here transferred to the genus *Parachordeumium*. These new combinations are: *Parachordeumium bocqueti* (Goudey-Perrière. 1979); *Parachordeumium humesi* (Goudey-Perrière, 1979); *Parachordeumium hendleri* (Goudey-Perrière, 1979).

REMARKS. The third appendage of the copepodid stage of *P. amphiurae* (as *Amphiurophilus amphiurae* was identified as the mandible by Goudey-Perrière (1979). This limb is retained in the adult of both sexes. Its morphology (the segmentation and possession of a terminal claw) is most atypical for a mandible and this limb is here reinterpreted as the maxilla.

CHORDEUMIIDAE New Family

DIAGNOSIS. Copepods endoparasitic in ophiuroids; adult females more-or-less highly transformed typically losing external segmentation and often with paired lateral and median dorsal or posterior processes. Lateral processes where fully developed forming 'cage' enclosing egg masses. Cephalic appendages reduced or absent; antennules and maxillae typically retained in adult. Antenna sometimes present as vestige in adult. Maxillipeds absent. Legs 1–4 reduced to uniramous processes or absent. Eggs or eggs masses retained within cyst of host origin enclosing female. Adult male typically transformed, with at most one pair of lateral processes. Maxillae typically retained by adult male, sometimes antennules and antennae also. Copepodid larva lacking discrete caudal rami; caudal setae present on margin of anal somite.

TYPE GENUS. *Chordeumium* Stephensen, 1918.

OTHER INCLUDED GENERA. *Arthrochordeumium, Lernaeosaccus, Ophioicodes, Ophioika* and *Parachordeumium.*

Discussion

It is difficult to produce a meaningful diagnosis for the new family because so many of the species are extremely modified for their endoparasitic mode of life. Comparison between the better known species, *Chordeumium obesum* and *Parachordeumium amphiurae*, provides the best apomorphy for the family, based on the developmental stages. Both *C. obesum* and *P. amphiurae* lack discrete caudal rami in the copepodid stage (Jungersen, 1914; Goudey-Perrière, 1979). This character is rare in copepods and serves to link *Chordeumium* and *Parachordeumium.* This relationship is central to the definition of the family because the former genus shares several characters (the structure of the antennules and maxillae in the adult female, for example) with *Arthrochordeumium* and the latter, several characters of gross female morphology (the possession of paired lateral processes enclosing the egg masses, for example) with the genera *Ophioicodes* and *Ophioika.* The genus *Lernaeosaccus*, now reinterpreted, is apparently closely related to *Chordeumium.* Both genera have retained legs 1–4 as tiny lobes in the adult female, both have a pair of lateral processes posteriorly and both have a median abdominal process located just posterior to the gonopores.

The new family is placed in the order Siphonostomatoida on the basis of the reports of a mouth cone in *Ophioika* by Stephensen (1935). The mouth cone described by Heegaard (1951) in *Lernaeosaccus* is an abdominal process. It is probable that the highly modified female body from has been derived independently within the family, from a siphonostomatoid precursor that moved freely over the surface of the brittle stars. The species of the family Cancerillidae are typically ectoparasites of brittle stars (Emson *et al.*, 1985) and the family Asterocheridae contains species that live in the stomach of basket stars (Humes, 1986). A common ancestor shared with either of these families could have made the step towards a specialised endoparasitic existence. A relationship with the highly transformed families of fish parasites, such as the Chondracanthidae, Lernaeopodidae and Philichthyidae, is regarded as extremely improbable.

The endoparasitic *Cucumaricola notabilis* Paterson, 1958 may be closely related to the Chordeumiidae. The highly transformed morphology of the adult female, with its paired lateral processes, resembles that of the chordeumiids. Also, this species retains only the antennules, antennae and maxillae in the adult female (Paterson, 1958), as in *Chordeumium* itself. It differs from the new family in having discrete caudal rami in the copepodid stage, although the presence of 5-segmented antennules at this stage is another similarity between *Cucumaricola* and *Parachordeumium.*

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A new genus of tantulocaridan (Crustacea: Tantulocarida) parasitic on a harpacticoid copepod from Tasmania

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Introduction

There are now eleven described species of Tantulocarida placed in five genera (Boxshall & Lincoln, 1987). One of these, *Basipodella* Becker, contains two species both of which are parasitic on copepods. The other four genera parasitise tanaid, isopod, cumacean and ostracod hosts. *B. harpacticola* Becker was described from unidentified harpacticoid hosts caught at depths of 2000 to 5000 m in the Peru Trench in the eastern Pacific (Becker, 1975). *B. atlantica* Boxshall & Lincoln was found at a depth of about 3000 m in the North Atlantic to the southwest of the Azores, on a copepod belonging to the harpacticoid family Tisbidae (Boxshall & Lincoln, 1983). Whilst examining a collection of harpacticoids from the Bass Strait, off Tasmania, a single specimen of a *Stenhelia* species was found bearing a tantulocaridan on the side of its urosome (Fig. 1). This specimen, a tantulus larva containing a developing male, is described below as a new genus.

Description

AUSTROTANTULUS gen. n.

Diagnosis. Class Tantulocarida. Tantulus larva with first thoracic tergite partly concealed beneath posterior margin of dorsal cephalic shield; cephalic shield ornamentation comprising longitudinal lamellae and pores; thoracopods 1–5 of tantulus larva biramous, with well developed endites, uniramous leg 6 with coupling spines on protopod; abdomen of tantulus 2-segmented; adult male formed within trunk sac originating posterior to sixth thoracic tergite of preceding stage.

Type species. *Austrotantulus lincolni* gen. et sp. n.

Etymology. The generic name is derived from the Latin *australis* meaning South, and *tantulus* which forms part of the name of the class Tantulocarida.

Austrotantulus lincolni gen. et sp. n.

Tantulus Larva. The body (Fig. 2A) comprises the cephalic shield, 6 free thoracic somites and a 2-segmented abdomen. The body length is 125 µm, measured from the tip of the cephalic shield to the posterior margin of the abdomen, excluding the caudal setae. This may be an overestimate because expansion of the trunk sac may have caused separation of the thoracic tergites. The cephalic shield (Fig. 2B) is longer than wide (47 × 32 µm) and tapers anteriorly. The rostrum is absent. The oral disc has a diameter of about 15 µm and is positioned anteriorly so that it is visible in dorsal view. The surface ornamentation of the head, as seen by light microscopy, consists of longitudinal lamellae dorsally and oblique lamella on the downturned ventrolateral margins. Associated with these lamellae are at least 5 pairs of pores, as marked on Figure 2B. Internally a pair of chitinous bars leads towards the central pore of the oral disc. The cephalic stylet is very slightly curved and is about 22 µm long.

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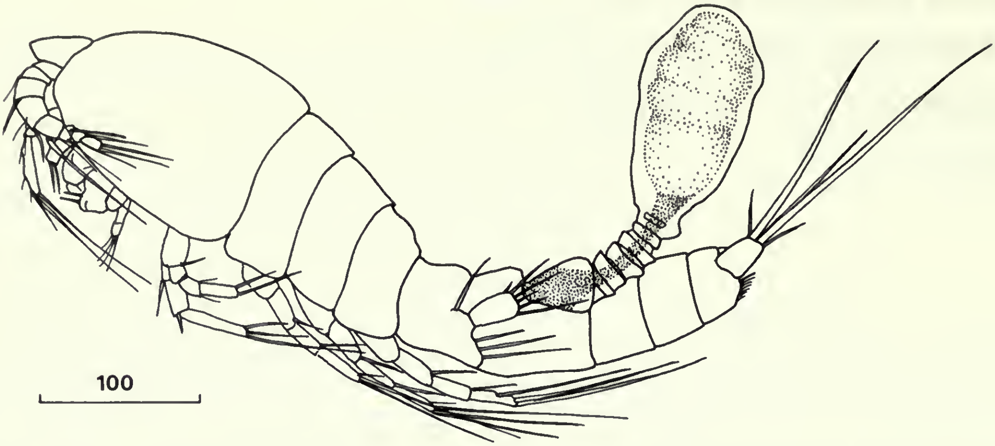

Fig. 1 *Austrotantulus lincolni* gen. et. sp. n. Holotype tantulus male undergoing metamorphosis attached to its harpacticoid host. Scale bar in µm.

The 6 free thoracic tergites are not conspicuously ornamented. The first tergite is partly concealed beneath the rear margin of the cephalic shield. Each thoracic somite bears a pair of well developed legs.

The 2-segmented abdomen is 27 µm in length (Fig. 2C) and is deflected ventrally by the expansion of the trunk sac posterior to the sixth tergite. The first abdominal somite is wider than long (5 × 13 µm), the second longer than wide (21 × 13 µm). The caudal rami are each represented by 1 short and 2 long setae arising from a common base.

There are no cephalic appendages. Thoracopods 1 to 5 have a large unsegmented protopod bearing a single endite which originates at the proximal rim of the limb. The armature of the endites cannot be discerned by light microscopy, but probably resembles that of *Deoterthron harrisoni* (see Boxshall & Lincoln, 1987). Thoracopods 1 to 5 are biramous. The exopod is 2-segmented and carries 2 apical setae in leg 1 (Fig. 2D). It bears 4 setae apically in legs 2 (Fig. 2E) to 5. The endopod is more than twice as long as the exopod and is indistinctly 2-segmented. The endopod of leg 1 is armed with 2 apical spines only. The endopods of legs 2 to 5 each have the 2 apical spines and, in addition, the proximal segment bears 2 long setae distally on its lateral margin. Leg 6 (Fig. 2F) is uniramous and has a large protopod armed with 2 complex coupling spines on the medial margin. There is no endite. The ramus is 1-segmented and armed with 2 long, curved setae.

MALE. The trunk sac of the holotype contained a male at an intermediate stage of development. This developing male was still attached via the umbilical cord. The tagmosis of the adult male could be discerned only in part, through the wall of the trunk sac. The first 2 pedigerous thoracic somites were fused to the head to produce a cephalothorax of 7 somites and there were 4 free thoracopod-bearing somites. However, the segmentation of the folded abdomen was not visible. A cluster of aesthetascs was present anteriorly on the cephalothorax, as described for the adult male of *D. harrisoni*. The male was not in a sufficiently advanced state of development for it to be dissected out of the enclosing trunk sac.

ETYMOLOGY. The species is named after Roger Lincoln in recognition of his work on the Tantulocarida.

MATERIAL EXAMINED. Holotype: ♂ tantulus, parasitic on the harpacticoid *Stenhelia* sp. from fine calcareous mud collected at about 22 m depth in the Bass Strait (at approximately 41°00′S 146°00′E), off Round Hill Point, near Burnie on the north coast of Tasmania. BM(NH) Registration No. 1987.418.

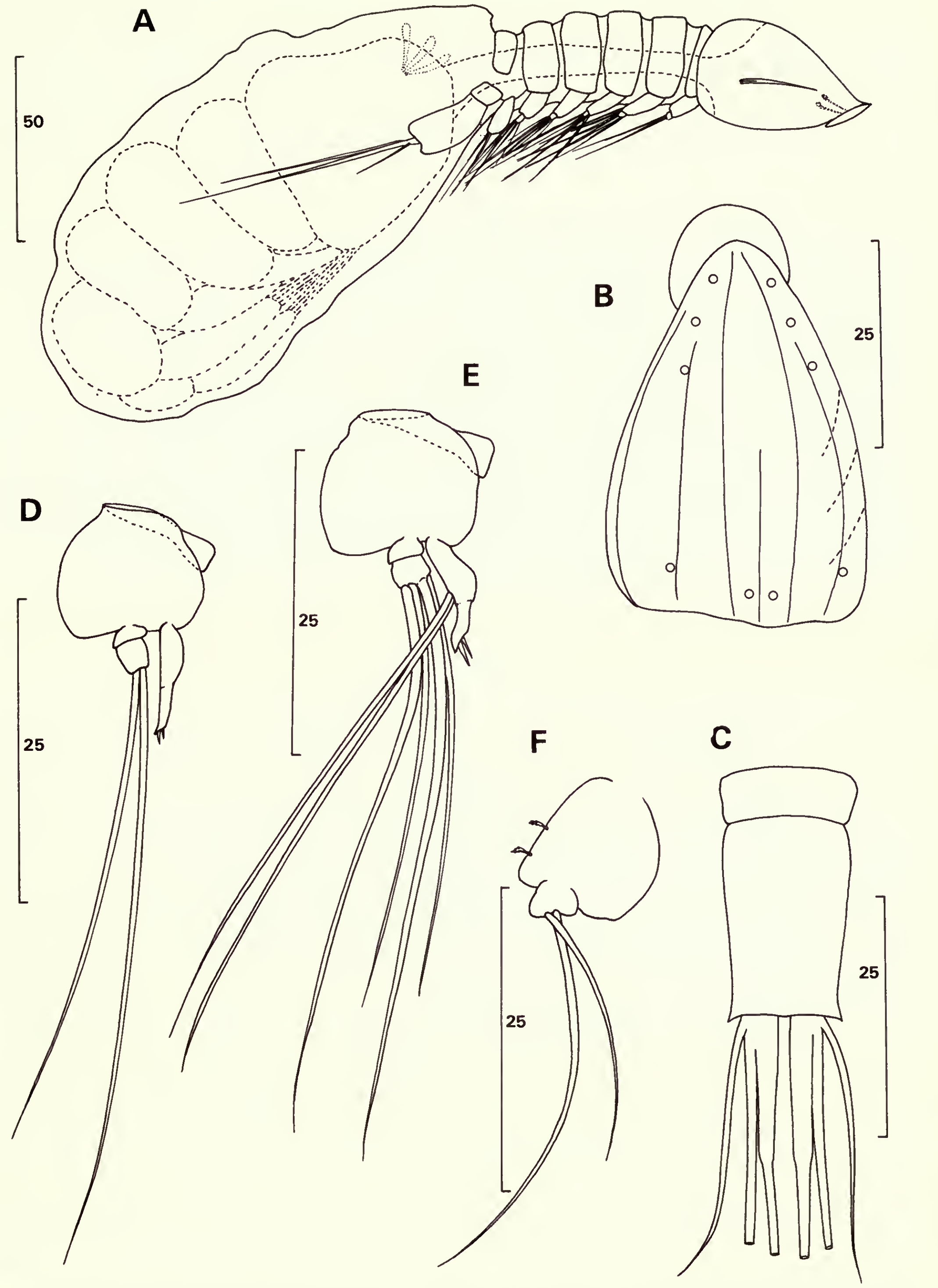

Fig. 2 *Austrotantulus lincolni* gen. et sp. n. A, Holotype, lateral view; B, cephalic shield, dorsal; C, abdomen, dorsal; D, leg 1, posterior; E, leg 2, posterior; F, leg 6, posterior. All scale bars in μm.

REMARKS. The new genus can be readily distinguished from *Basipodella* species, which are known to parasitise harpacticoids, by the segmentation of the abdomen. The abdomen is 2-segmented in the tantulus larva of the former and 6-segmented in the latter. Other differences include the general pattern of the surface ornamentation of the cephalic shield. In the new genus this basically consists of a system of longitudinal lamellae whereas in *Basipodella* species there are conspicuous transverse and longitudinal lamellae. The combination of 2-segmented abdomen in the tantulus, well developed endites and rami on the tantulus thoracopods, and of longitudinal ornamentation on the cephalic shield is found only in the family Deoterthridae, in species of *Deoterthron* Bradford & Hewitt. However, the familial position of *Austrotantulus* is problematical because, whilst the larval characters agree with the familial diagnosis of the Deoterthridae (Boxshall & Lincoln, 1987) the position of the male trunk sac (posterior to the sixth tergite) is typical for the families Basipodellidae and Microdajidae. The families Deoterthridae and Microdajidae may have been established prematurely by Boxshall & Lincoln (1987), formalising morphological gaps between taxa which represented a lack of data more than a phylogenetic reality. The new genus is provisionally placed in the family Deoterthridae, although as more taxa are discovered it may become necessary to revise the familial arrangement of the tantulocaridans.

The area around Tasmania and New Zealand is rich in tantulocaridans. *Deoterthron aselloticola* Boxshall & Lincoln was described from an isopod host, *Hydroniscus lobocephalus* Lincoln, caught at 3250–3340 m in the Tasman Sea (Boxshall & Lincoln, 1983) and *D. megacephala* Lincoln & Boxshall was also found on an isopod, *Haploniscus tangaroae* Lincoln, taken at 1386 m in the Tasman Sea (Lincoln & Boxshall, 1983). The genotype, *D. dentatum* Bradford & Hewitt, was reported from the ostracod *Metavargula mazeri* Kornicker collected in 384 m to the east of New Zealand (Bradford & Hewitt, 1980). It is probable that this apparent species richness compared to other geographical regions can be attributed to sampling effort in this recently discovered taxon, rather than to any distinct zoogeographical pattern.

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I would like to thank Dr Roger Lincoln for his comments on the manuscript.

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Unusual ascothoracid nauplii from the Red Sea

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Introduction

The study of larvae is important for elucidating the phylogenetic history of crustacean groups such as the maxillopodans where macroevolutionary events involving progenesis and neoteny may have occurred (Newman, 1983; Boxshall, 1983). It can also reveal homologies between apparently disparate structures such as the attachment disc on the antennule of a cirriped cyprid and the attachment claw on the same limb of an ascothoracid larva (Grygier, 1987*a*). One maxillopodan taxon, the Facetotecta, is still only known from larvae (see Grygier, 1985, 1987*b*). It is therefore, of interest when larvae with clear maxillopodan affinities are discovered which cannot easily be placed in a known group. Grygier (1987*a*) described a 'metanauplius incertae sedis' from the South China Sea which he tentatively identified as a postbrooding ascothoracid, possibly of a laurid (Ascothoracida: Lauridae). During recent plankton studies in the central Red Sea (Böttger, 1987) similar metanauplii were discovered in near surface waters, together with an earlier naupliar stage of what appears to be the same species. These and a similar metanauplius that clearly represents a related but distinct species are described in this paper.

Description

Nauplius type I

Body discoid (Fig. 1A), convex dorsally and concave ventrally; entirely covered with dorsal shield. Surface of shield (Fig. 1B) punctuated with pores arranged in bilaterally symmetrical pattern around lateral margins and in irregular rows either side of dorsal midline. Nauplius eye present. Conspicuous dorsal pore present on swelling about in middle of shield. Margins of shield downturned, provided with extensive ventral band of pores around entire circumference. Posteriorly shield drawn out into paired caudal processes each bearing a small ventral papilla. Papilla with apical pore. Caudal spine originating on ventral surface near posterior margin, 120 µm in length, armed with setules bilaterally. Body dimensions given in Table 1.

Paired frontal filaments simple, setiform but with a blunt tip (Fig. 1A, ff); positioned either side of midline just anterior to bases of antennules; median pore present between filaments.

Antennule (Fig. 1A, atl; Fig. 1C) uniramous, 4-segmented. First segment unarmed; second with 1 naked seta; third with 1 plumose seta; fourth segment showing some signs of subdivision near its apex, armed with 5 plumose and 2 naked setae on and around apex.

Labrum (Fig. 1A, la) an elongate muscular lobe extending posteriorly from between bases of antennae; bearing several rows of fine spinules around apex.

Antenna (Fig. 1A, ant; Fig. 2A) biramous, comprising protopod, 3-segmented endopod and 9-segmented exopod. Protopod with 3 endites; proximal endite small, armed with a few spinules; middle endite strongly developed, produced into 2 spiniform processes with 3 slender setae; distal endite strongly developed, produced into 2 divergent spiniform processes, each armed with spinules, 1 naked seta present on anterior surface and a slender plumose seta distally on medial surface. First endopod segment with 3 naked seta, second with 3, third with 4 at tip. First exopod segment unarmed, second to eighth each armed with a long naked seta, ninth segment with 2 setae, that on apex with a swollen base possible representing a tenth segment.

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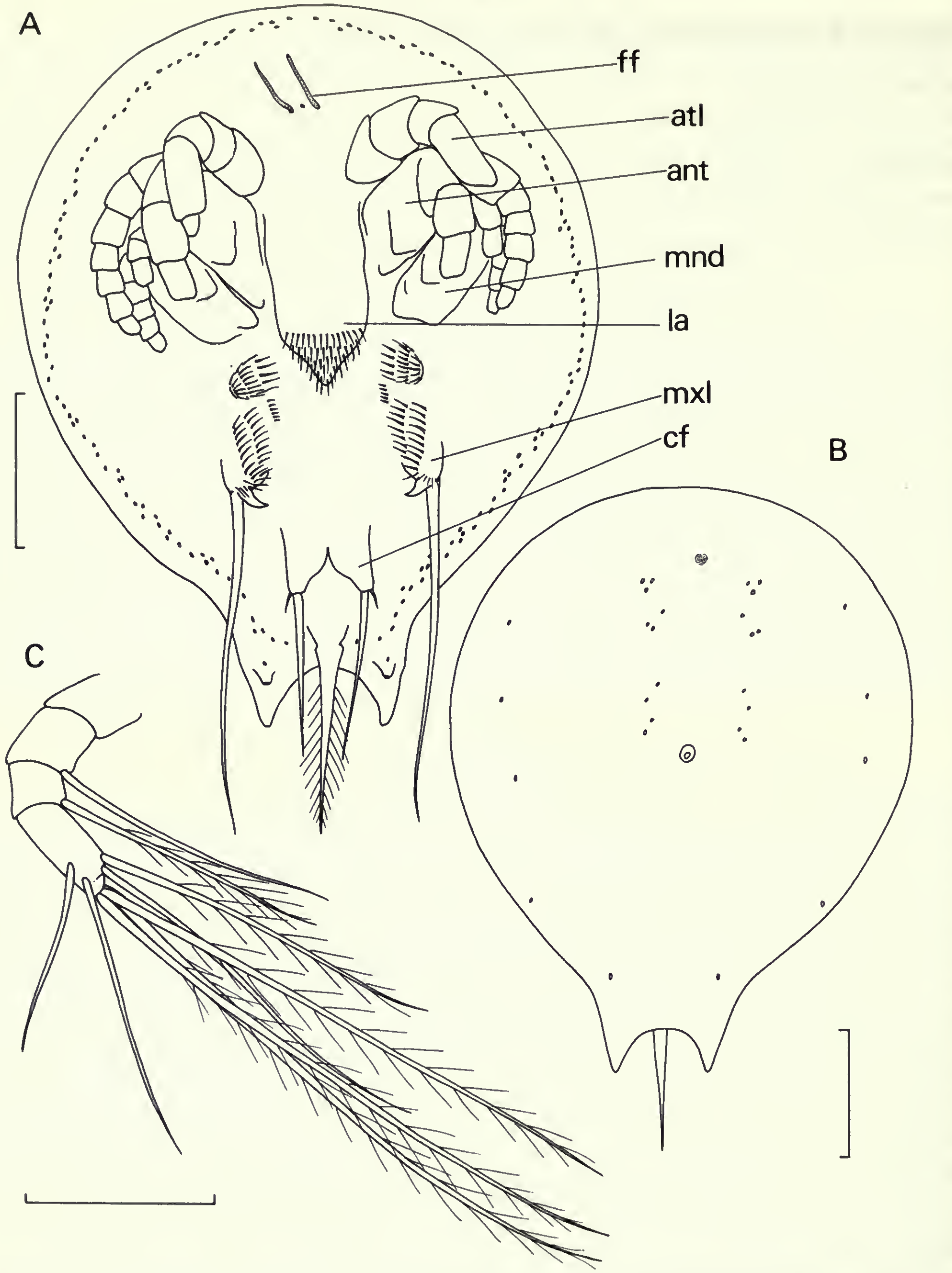

Fig. 1 Red Sea nauplius type I. A, ventral view, showing frontal filaments (ff), antennule (atl), antenna (ant), mandible (mnd), labrum (la), maxillule (mxl) and caudal furca (cf); B, dorsal view; C, antennule, ventral. All scale bars 100 µm.

Mandible (Fig. 1A, mnd; Fig. 2B) biramous, comprising protopod, 3-segmented endopod and 6-segmented exopod. Protopod with 2 endites; proximal endite armed with a large hirsute seta, a short spine and some spinules; distal endite armed with 4 stout setae, 3 of them plumose, and a row of long spinules. First endopod segment with 2 rows of long spinules, a naked seta and 2 stout setae bearing long setules, second with 3 naked setae, third with 4 naked setae. First to fifth exopod segments each with a single long seta, that on segment 4 being unusually robust and unilaterally spinulate; sixth segment with 3 naked apical setae.

Paired lobes located on ventral body surface just posterior to mandibles; armed with rows of medially directed spinules. Maxillule (Fig. 1A, mx1) represented by a small lobe bearing a long, posteriorly directed, apical seta, a short incurved spine and rows of medially directed spinules.

Caudal furca (Fig. 1A, cf) comprising paired lobes each bearing an inner naked seta and a short outer spine.

Table 1 Body dimensions and depth distributions of ascothoracid larvae type I in the central Red Sea.

STAGE	DEPTH (m)	DATE (time)	LENGTH (μm)	WIDTH (μm)
Nauplius	0–50	28.10.80(00:20)	443	350
	0–50	05.11.80(15:20)	463	370
	20–40	04.11.80(15:20)	468	344
mean			458	355
Metanauplius	0–50	27.10.80(11:00)	732	591
	0–50	05.11.80(00:13)	704	561
	0–50	05.11.80(00:13)	728	564
	50–100	27.10.80(11:00)	710	609
	50–100	19.10.80(13:00)	774	589
	50–100	05.11.80(00:13)	743	553
mean			732	578

Metanauplius type I

Body discoid (Fig. 2C) convex dorsally, concave ventrally; entirely covered with dorsal shield. Surface of shield ornamented with fine lamellae anteriorly and posteriorly, and punctuated with numerous pores arranged more or less symmetrically in an irregular row either side of the midline and over entire dorsolateral area. Tripartite nauplius eye well developed. Middorsal pore present but less conspicuous than in early nauplius. Posteriorly shield bearing 3 pairs of sensory setules. Equatorial ring of marginal pores on ventral surface of downturned shield margins present. Caudal processes bearing marked papillae both dorsally and ventrally; ventral papilla with an apical pore. Caudal spine 278 μm long. Body dimensions given in Table 1. Frontal filaments as in early nauplius.

Antennule (Fig. 3B) uniramous, 6-segmented. First segment unarmed; second and third each with 2 plumose setae, fourth with 3 plumose setae and a prominent angled spine passing obliquely across next segment; fifth segment with 4 long plumose setae, sixth with 4 long naked setae. Labrum as in early nauplius.

Antenna (Fig. 4A) biramous, comprising 2-segmented protopod, 3-segmented endopod and 12-segmented exopod. First protopodal segment (coxa) with single well developed endite bearing 2 slender naked setae basally and 2 curved spines apically, one of which is armed with small denticles distally. Second segment (basis) produced into strong endite bearing 2 setulate spines apically, 2 plumose setae present on anterior surface at base of endite. First endopod segment with 3 naked setae and a row of spinules; second with 7 marginal setae and a patch of spinules; third with 4 apical setae. First exopod segment unarmed, second to eleventh each with a long seta, twelfth segment with 1 medial and 1 apical seta, the latter with a swollen base probably representing a thirteenth segment.

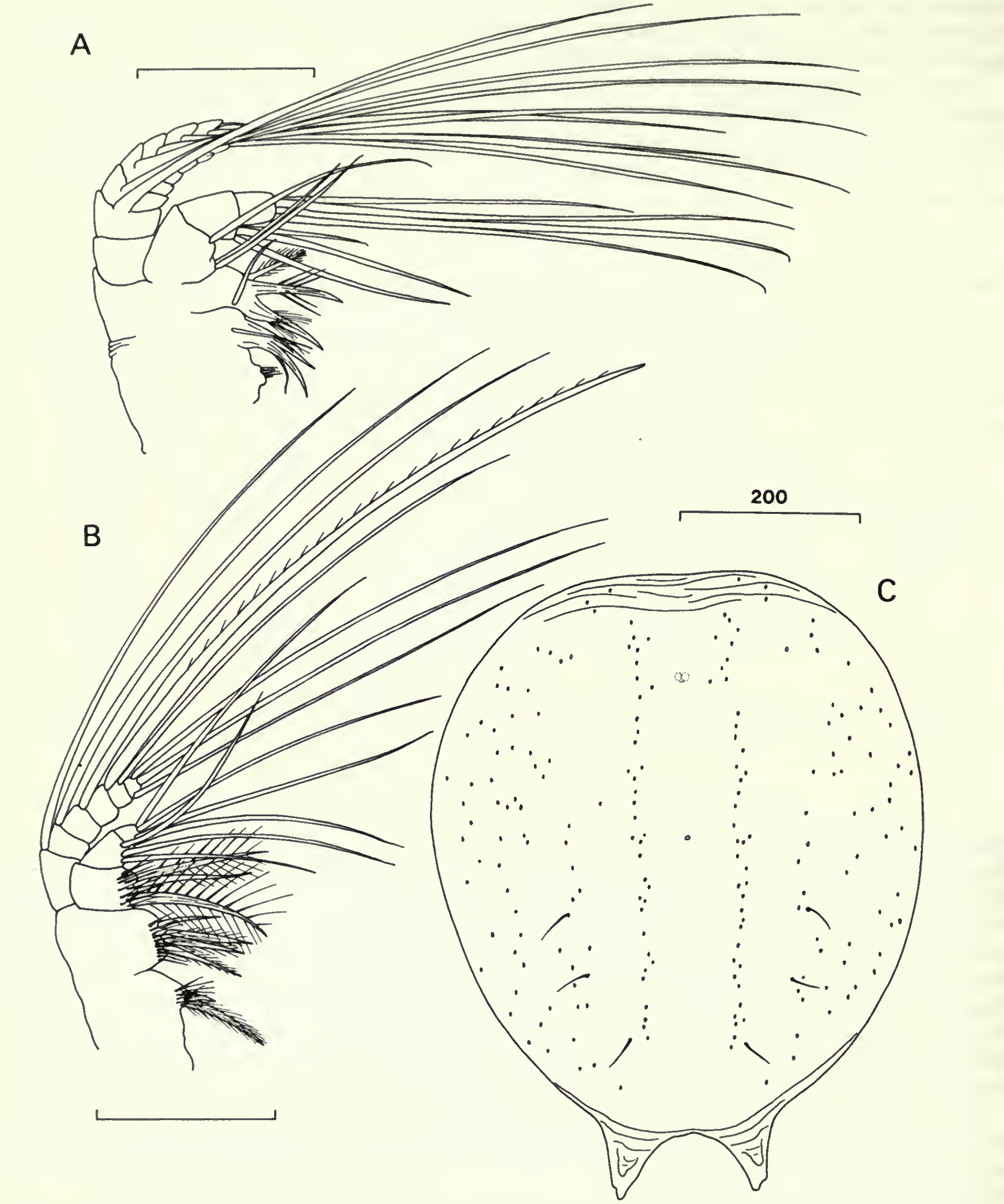

Fig. 2 Red Sea nauplius type I. A, antenna, medial; B, mandible, medial. Red Sea metanauplius type I. C, dorsal view. Scale bars 100 µm unless otherwise stated.

Mandible (Fig. 4B) biramous, comprising 2-segmented protopod, 3-segmented endopod and 7-segmented exopod. First protopod segment (coxa) armed with a large plumose seta, a short spine and some spinules; second armed with 5 stout setae, 4 of which are plumose, and some spinules. First endopod segment bearing 3 stout spinulate setae, second with 6 naked setae, third with 3 unilaterally plumose and 2 naked setae. First exopod segment unarmed; second to fourth each with a long seta; fifth with a robust, unilaterally spinulate seta; sixth with a plumose seta and seventh with 3 plumose setae.

Maxillule (Fig. 3C) 2-segmented; first segment fused with body surface, armed with rows of

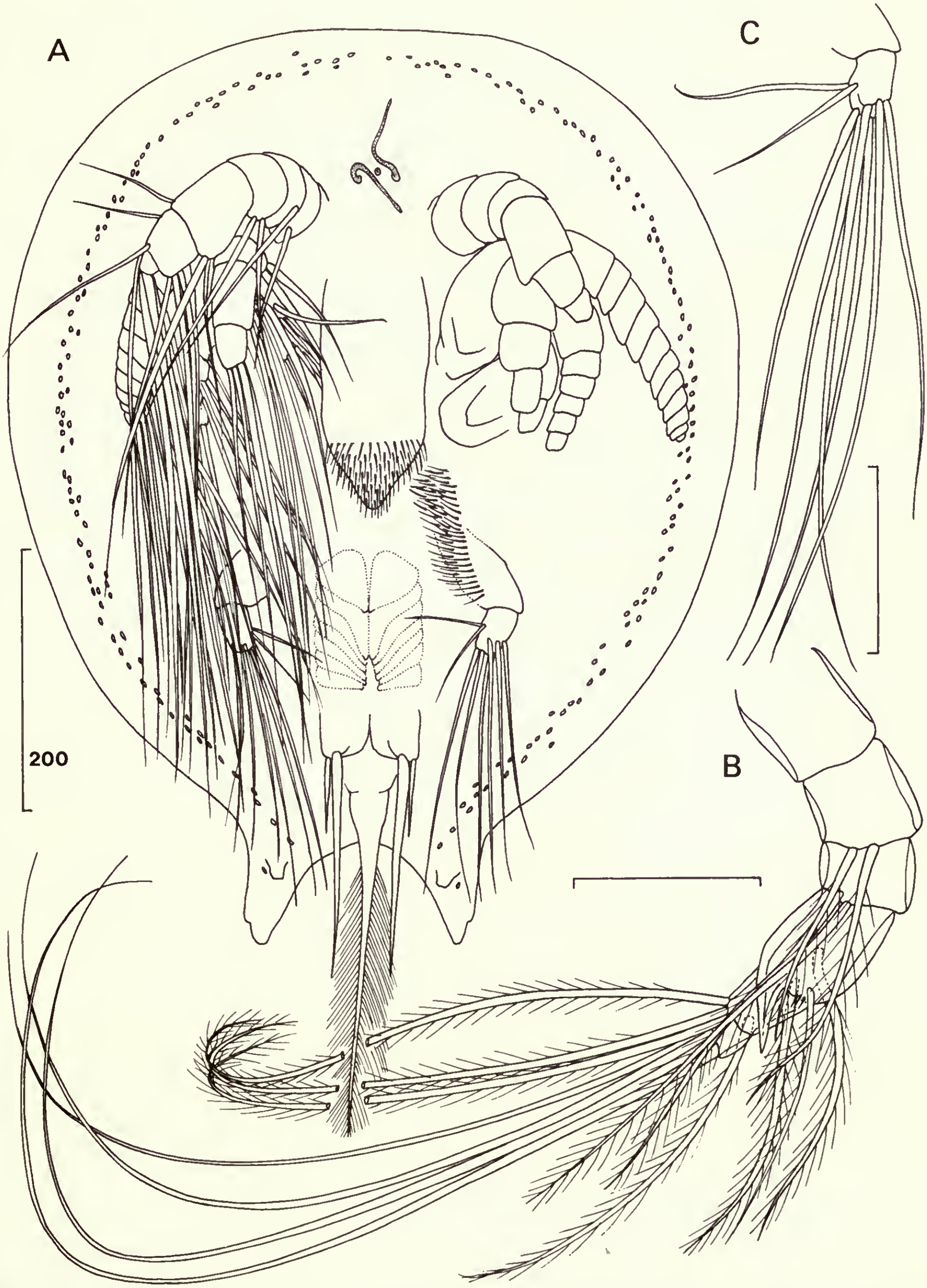

Fig. 3 Red Sea metanauplius type I. A, ventral view, with setae omitted from anterior limbs on left side; B, antennule, medioventral; C, maxillule, ventral. Scale bars 100 µm unless otherwise stated.

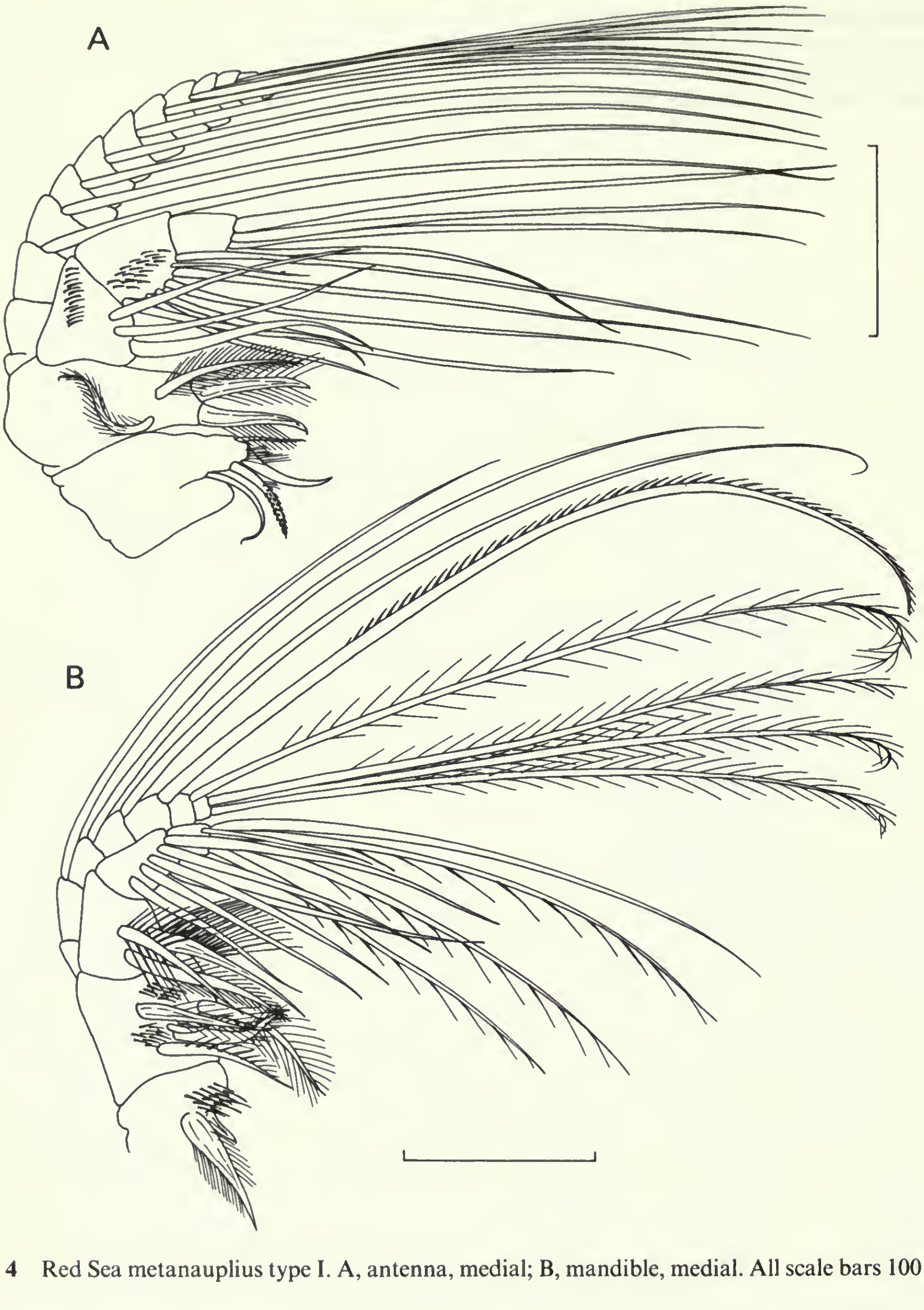

Fig. 4 Red Sea metanauplius type I. A, antenna, medial; B, mandible, medial. All scale bars 100 μm.

medially directed spinules that extend onto body; second segment bearing 2 short medial setae, 3 subapical setae on ventral surface and 3 distal margin setae.

Seven pairs of limb buds visible through body wall, marked externally only by tiny sclerotised lobes at the tip of each bud. Limb buds presumably representing maxillae and first to sixth thoracopods of subsequent stage. Caudal furca comprising paired lobes, each bearing a long inner seta and a shorter outer seta.

MATERIAL EXAMINED. 3 nauplii and 6 metanauplii collected at and around *Valdivia* Stn 177 (cruise 29) in the central Red Sea (21°25·96′N 38°04·22′E) between 0 and 100 m (see Table 1), in a multiple opening-closing net of mesh 0·1 mm. 1 nauplius and 2 metanauplii stored in the collections of the BM(NH), Reg. Nos 1988.100–102.

REMARKS. The metanauplius type I from the Red Sea is very similar to that described from the South China Sea by Grygier (1987*a*). There are small differences in the armature and segmentation of the antenna, mandible and maxillule, in the size of the caudal processes, and in the relative lengths of the caudal spine and setae on the lobes of the caudal furca. However, the basic organisation of these larvae is the same. As established by Grygier (1987*a*), their possession of rudiments of 6 pairs of thoracopods implies a maxillopodan affinity. The flattened, bowl-shaped dorsal shield is typical of the Ascothoracida and the possession of an equatorial ring of pores around the shield margin which is found only in some families of Ascothoracida (Grygier, 1987*a*) is here regarded as a derived character. These Red Sea larvae are referred to the Ascothoracida and, on the basis of similarities in the caudal region, possibly to the family Lauridae. Ascothoracid larvae of this type were distributed irregularly in small numbers in the upper 100 m (see Table 1) in the central Red Sea. None was found further north, above the Kebrit Deep.

The free swimming nauplius does not contain an obvious store of yolk. This, combined with its highly setose antenna and mandible each bearing well developed gnathobases, suggests that it is a planktotrophic feeder. The metanauplius is about 1·6 times longer than the nauplius and shows a marked increase in the numbers of limb segments. It is inferred from this that there is at least one stage, intermediate in size and limb segmentation, between the two stages described above. The metanauplius is clearly equivalent to the sixth nauplius (NVI) of cirripedes. The primordia of the 6 pairs of thoracopods visible through the integument indicate that the next moult will be to the equivalent of the cyprid stage of development. The presence of a well developed, setose maxillulary rudiment tends to confirm that the metanauplius is equivalent to the cirripede NVI which may have a similar maxillulary rudiment (Moyse, 1987).

The earlier nauplius is more difficult to equate precisely with a given nauplius stage of cirripedes. It appears to be a mid-development stage, most likely a NIV because it possesses 2 preaxial setae on the antennule. Whilst antennule segmentation varies within the cirripedes the sequence of appearance of preaxial setae on the antennule is remarkably constant. Typically the number of preaxial setae is 0 in NI-NII, 1 in NIII, 2 in NIV and 3 in NV–NVI. This pattern occurs repeatedly in both lepadomorph cirripedes, such as *Capitulum mitella* Linnaeus (Yasugi, 1937), and balanomorphs, such as *Balanus eburneus* Gould (Costlow & Bookhout, 1957) and *Tetraclita serrata* Darwin (Griffiths, 1979). Also the presence of 4 setae on the apical segment of the endopod of both the antenna and mandible is regarded as typical of the cirripede NIV, although this number does vary within the cirripedes.

Thus, the free-living, postbrooding phase of ontogeny appears to comprise 3 or more stages. The length of any brooded phase, prior to release of the larvae, is unknown but may be relatively short. This presumed ontogenetic pattern is much less modified than that of any other ascothoracid (data from Grygier, 1984). The discovery of the nauplius stage, probably equivalent to the cirripede NIV, confirms Grygier's (1987*a*) prediction that when ascothoracids release feeding naupliar stages these will resemble late instar cirripede larvae more closely than when nauplii are brooded.

Metanauplius type II

A single metanauplius (Fig. 5) was found which differed significantly from that described above. It is 808 μm in length and has the same basic organisation. The primordia of the maxillae and 6 pairs of thoracopods are visible through the integument but are smaller and more anteriorly located than in the above metanauplius. Other differences include: the limbs are relatively smaller, the antennary exopod is only 8-segmented, the mandibular exopod is only 5-segmented, the nauplius eye is lacking, the labrum is broader and truncate, the maxillules have 5 setae, the caudal processes are very small, the caudal furca bears 2 subequal pairs of setae, and there is no trace of any median caudal spine.

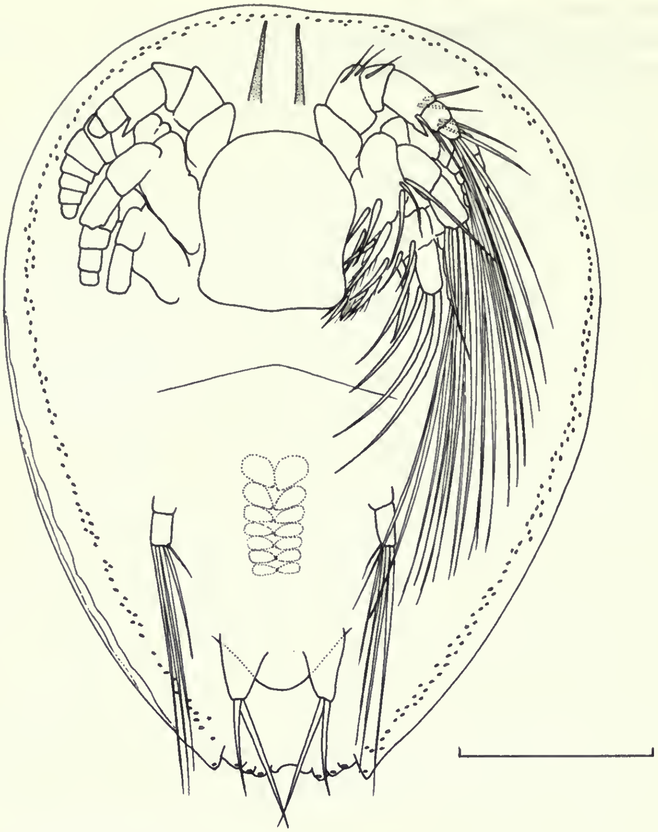

Fig. 5 Red Sea metanauplius type II, ventral view. Scale bar 200 μm.

MATERIAL. A metanauplius collected on 23 February 1981 in the central Red Sea (21°23·1′N 38°04·7′E) during *Valdivia* cruise 29 between 0 and 50 m, in a multiple opening-closing net of mesh 0·1 mm. Stored in the collections of the BM(NH), Reg. No. 1988.198.

REMARKS. This metanauplius is also identified as that of an ascothoracid probably of the family Lauridae, but there are sufficient differences to indicate that it represents a second species from the Red Sea. It differs from the Red Sea metanauplius type I and resembles the metanauplius described by Grygier (1987*a*) from the South China Sea in the following respects: the segmentation of the antennary and mandibular exopods, the maxillules have 5 setae, the caudal processes are small and the 2 pairs of setae on the caudal furca are subequal in length. It differs from the South China Sea specimen in the lack of a median caudal spine.

Acknowledgements

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New Nicothoid copepods (Copepoda: Siphonostomatoida) from an amphipod and from deep-sea isopods

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Summary

One new genus, *Cephalorhiza*, and eight new species of parasitic copepods of the family Nicothoidae are described. One new species, *Sphaeronella australis*, is parasitic in the brood pouch of a lyssianasoid amphipod from southern Australia. All the other new taxa are parasites of deep-sea asellote isopods, from the North Atlantic and Indian Oceans. Two new species belong to the genus *Rhizorhina*, 4 belong to *Diexanthema* and one, *Cephalorhiza flaccida*, to the new genus.

Introduction

The family Nicothoidae contains eighteen genera of small, highly transformed copepods, all of which are parasitic on other crustaceans. Several of these genera are known either from amphipods (*Stenothocheres* Hansen) or from isopods (*Diexanthema* Ritchie, *Choniorhiza* Boxshall & Lincoln, *Nicorhiza* Lincoln & Boxshall), or from both amphipods and isopods (*Rhizorhina* Hansen, *Sphaeronella* Salensky). The present account describes a new species of *Sphaeronella* found in the marsupium of an amphipod from Australia and several new taxa from deep-sea asellote isopods collected in the North Atlantic and Indian Oceans. During an ecological study of the asellotes of the Rockall Trough, off the west coast of Scotland, about 15,500 asellote isopods were examined. Only four specimens harboured nicothoid parasites, which were found to represent four new species. Examination of additional material from the Porcupine Seabight and from the collections of the Centre National de Tri d'Océanographie Biologique (CENTOB, Brest) made off the island of Réunion in the Indian Ocean, revealed another three new species, one belonging in a new genus.

Descriptions

Family **NICOTHOIDAE**

Rhizorhina hystrix sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, simplified to a globular, almost spherical, trunk portion (Fig. 1B) and an intricate branching holdfast (Fig. 1A). Maximum width of globular trunk 859 µm, maximum length 788 µm; trunk featureless except for raised gonopores located about 353 µm apart on posterior surface. Small anterior swelling tapers towards branching holdfast. Holdfast 4-branched at origin, processes branching irregularly along length. Maximum extent of holdfast within host about 680 µm from origin. Arrangement of holdfast branches more or less 2-dimensional within host.

MATERIAL EXAMINED. Holotype ♀, parasitic on a preparatory female of *Eurycope complanata* Bonnier (*sensu* Wilson, 1982). Locality: *Discovery* Stn 50602 ♯ 2 in the Porcupine Seabight (51°1·0′N 13°7·2′W), depth 1955–1980 m, 07.vii.1979. Parasite located on arthrodial membrane between tergites of pereon segments 3 and 4. Holotype stored in BM(NH), Reg. No. 1987.435.

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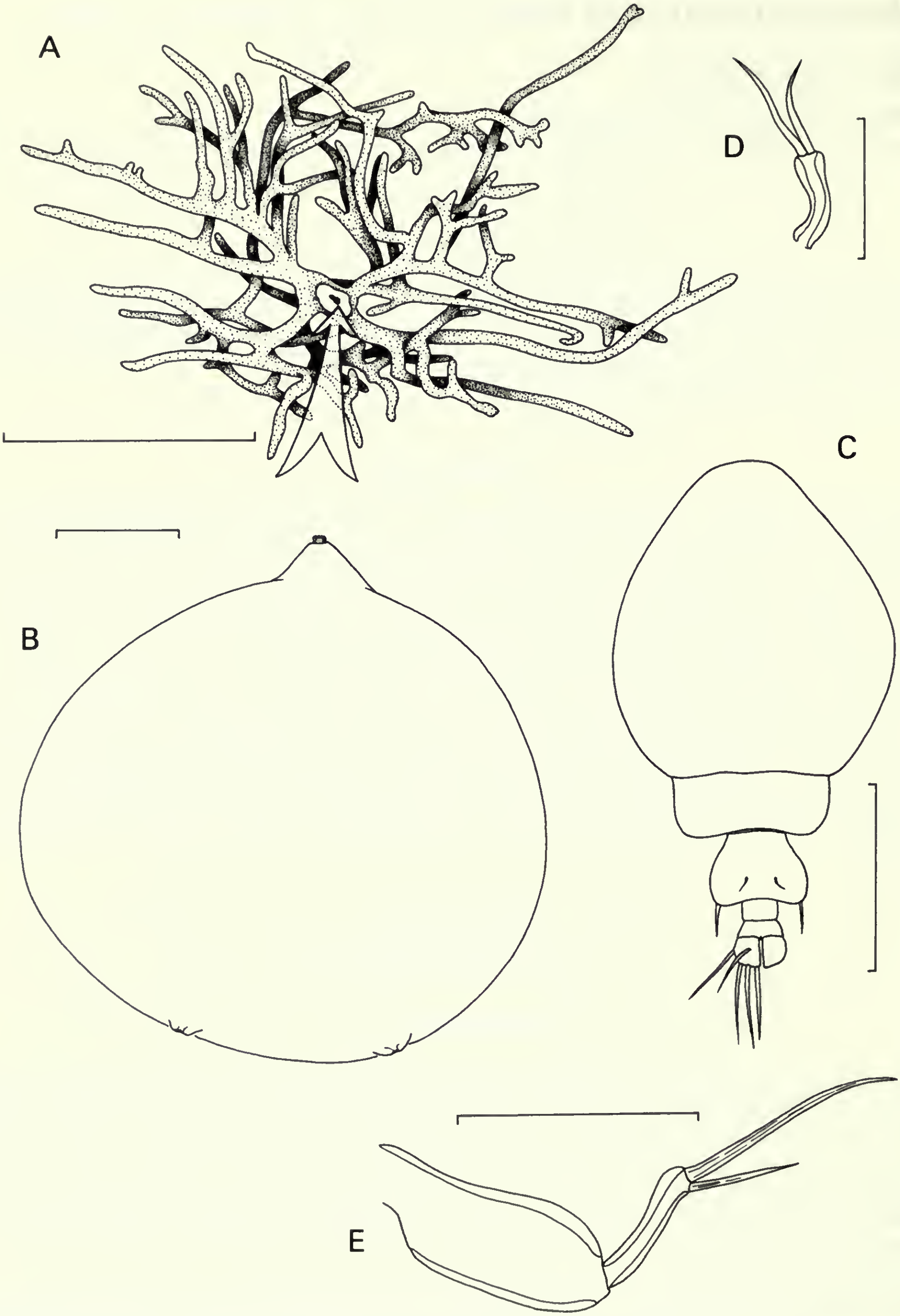

Fig. 1 *Rhizorhina hystrix* sp. n., Holotype female. A, Posterodorsal view of oral rootlet system; B, Trunk sac, showing point of attachment to rootlet system. *Rhizorhina aesthetes* sp. n., Holotype copepodid. C, Dorsal; D, Maxillule, lateral; E, Maxilla, posterior. Scale bars 200 µm, unless otherwise stated: C = 50 µm, D = 10 µm, E = 20 µm.

ETYMOLOGY. The species is named after the Porcupine seabight where it was collected.

REMARKS. It is difficult to characterise parasites that have undergone such a metamorphic reduction as *Rhizorhina* species. Four species of *Rhizorhina* have been described: *R. ampeliscae* Hansen from the amphipods *Ampelisca diadema* (Costa) and *A. brevicornis* (Costa), *R. serolis* Green from the isopod *Serolis bromleyana* Suhm, *R. leptostracae* Gotto from the leptostracan *Nebaliella caboti* Clark and *R. tanaidaceae* Gotto from the tanaid *Leviapseudes hanseni* (Lang). Small differences in size and shape of the trunk are given in Table 1. The new species is much smaller than *R. serolis* and also differs from this species in shape (Green, 1959). It is considerably larger than both *R. leptostracae* and *R. tanaidaceae*, which also differ in shape, the former being somewhat flattened dorsoventrally and the latter subquadrate in dorsal aspect (Gotto, 1984) in comparison with the almost spherical shape of *R. hystrix*. In size and shape the new species most closely resembles *R. ampeliscae* (Hansen, 1892). They can be distinguished on the basis of the much wider separation of the gonopores in *R. hystrix*. The branching holdfast system is probably not a good taxonomic character. It has rarely been described and may well vary according to position in the host, as has been described for the holdfasts of other mesoparasitic copepods (Fryer, 1961; Boxshall, 1989). It is noteworthy that the holdfast is basically 4-branched in both the new species and in *R. serolis* according to Green (1959). These branches are probably derived from the divided labrum and labium as found by Lincoln & Boxshall (1983) in the closely related *Nicorhiza*.

Table 1. Morphometrics of the adult females of *Rhizorhina* species.

	MAX. WIDTH	MAX. LENGTH	SHAPE	GONOPORES	
				POSITION	SEPARATION
R. ampeliscae	1·05 mm	0·96 mm	subspherical	posterior	187 µm
R. serolis	2·5 mm	2·0 mm	subrectangular	posterior	1·2 mm
R. leptostracae	552 µm	521 µm	discoid	posterior	205 µm
R. tanaidaceae	594 µm	500 µm	subquadrate	posterior	258 µm
R. hystrix	859 µm	788 µm	subspherical	posterior	353 µm
R. aesthetes	282 µm	304 µm	subspherical	ventral	132 µm

Rhizorhina aesthetes sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising globular trunk and branching holdfast. Trunk (Fig. 2A) subspherical, longer than wide; maximum width 282 µm, maximum length 304 µm. Trunk lacking appendages, featureless except for gonopores located 132 µm apart on ventral surface, just posterior to midlevel. Holdfast broken off in host.

COPEPODID STAGE. Body comprising 2-segmented prosome and 3-segmented urosome (Fig. 1C). Total body length 136 µm, maximum width 75 µm. First urosome somite bearing pair of setules dorsally and pair of setae posterolaterally representing the third swimming legs. Caudal rami about as long as wide; armed with a dorsal seta, lateral seta and 3 distal margin setae, all naked.

Antennules 3-segmented (Fig. 2B); armature as follows: I-1, II-1 + 1 aesthete, III-6 + 1 aesthete. Aesthete on second segment inflated proximally and distally, with mid-level constriction. All setae naked. Antenna absent. Mandible stylet-like, without apical teeth, palp absent. Maxillule (Fig. 1D) reduced to simple lobe bearing 2 apical naked setae. Maxilla (Fig. 1E) 2-segmented; basal segment unarmed, second segment bearing a terminal claw 19 µm long and seta 9 µm long. Maxilliped (Fig. 2C) 5-segmented, including terminal claw. Fourth segment bearing seta 7 µm long and the terminal claw 24 µm in length.

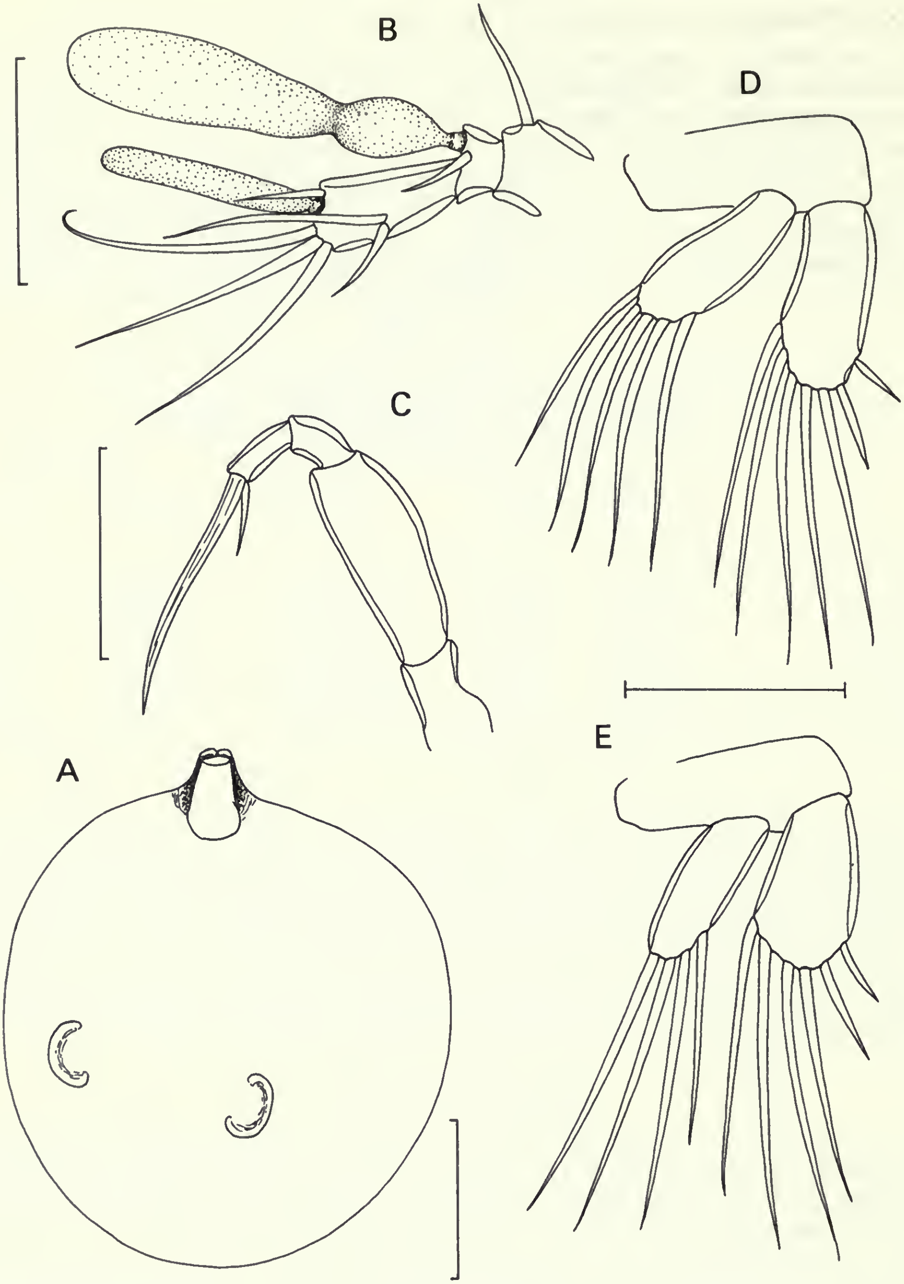

Fig. 2 *Rhizorhina aesthetes* sp. n. A, Paratype female trunk, ventral; B, Holotype copepodid antennule, ventral; C, Maxilliped, posterior; D, leg 1, anterior; E, leg 2, anterior. Scale bars 20 µm, unless otherwise stated: A = 100 µm.

Swimming legs 1 and 2 biramous, with 1-segmented rami. Leg 1 (Fig. 2D) exopod bearing 2 spines and 5 setae; endopod with 5 setae. Leg 2 (Fig. 2E) exopod bearing 2 spines and 4 setae, endopod with 4 setae. Leg 3 represented by posterolateral setae on surface of first urosomal somite.

MATERIAL EXAMINED. Holotype copepodid, 1♀ paratype. Parasitic on an unidentified ischnomesid (a fragment only). Locality: the Scottish Marine Biological Association's (SMBA) 'Permanent

Stn', sample ES172, in the southern Rockall Trough (54°39'N 12°17'W), depth about 2910 m, 27.v.1980. Adult female attached dorsolaterally to tergite of second pereon somite. Types stored in BM(NH), Reg. Nos 1987.436 (Holotype) and 1987.437 (paratype).

ETYMOLOGY. The species name refers to the large aesthete present on the second antennulary segment.

REMARKS. The new species is the only *Rhizorhina* described in which the adult female is longer than broad (see Table 1). This difference in shape, together with the small size of the trunk and the ventral position of the gonopores are sufficient to distinguish the female from other known species. The copepodid larva has 3-segmented antennules as in other species of *Rhizorhina* but, in addition to the usual apical aesthete, there is a conspicuous aesthete on the second segment.

Diexanthema nudum sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising a swollen, slightly dorsoventrally flattened prosome and an unsegmented urosome (Figs 3A, B). Total body length in ventral view 302 µm, maximum width 267 µm. Urosome length 75 µm, maximum width 86 µm. Prosome bearing well developed mouth cone anteroventrally containing stylet-like mandibles. Paired irregular lobes just anterior to base of mouth cone may represent modified antennae. Other mouthparts and legs 1–3 absent. Leg 4 represented by pair of minute papillae on ventral body surface.

Urosome bearing leg 5 ventrolaterally. Leg 5 comprising a simple unsegmented lobe armed with 3 distal spines (Fig. 3B). Gonopores large and unarmed, opening on posterior surface of urosome. Postgenital abdominal segments reduced to small, median lobe on posterior surface of urosome. Caudal setae lacking.

MATERIAL EXAMINED. Holotype ♀, parasitic on a species of the desmosomatid *Mirabilicoxa*, probably *M. acuminata* Hessler. Locality: SMBA Stn ES10 in the central Rockall Trough (56°37'N 11°04'W), depth about 2540 m, 04.vii.1973. Only one host specimen was infected out of a total of 61 examined from the Rockall Trough. Holotype stored in BM(NH), Reg. No. 1987.438.

ETYMOLOGY. The species name refers to the absence of cuticular hairs from the surface of the prosome.

REMARKS. The new species is closely related to *D. bathydiaita* Ritchie, a parasite of a species of *Nannoniscus* found in deep water off the western coast of Africa (Ritchie, 1975). The postmetamorphosis female of both species have the same gross morphology and both possess a mouth cone containing mandibles, an irregular branching structure derived from the antennae and a lobate fifth leg armed with 3 spines. The species differ in the presence of caudal setae and of a covering of minute hairs over the cuticle of the prosome in *D. bathydiaita* (Ritchie, 1975). The tiny papillae representing the fourth legs of the new species are not figured for *D. bathydiaita* but they may have been overlooked.

The host isopod is probably referable to *M. acuminata* described from the Gay Head-Bermuda transect off the eastern coast of the U.S.A. at depths of 3834 to 4800 m (Hessler, 1970). It differs only in having a lower pereopodal setal count in the preparatory female.

Diexanthema corrugatum sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising a swollen, globular prosome and a small unsegmented urosome (Fig. 3C). Total body length in ventral view 536 µm, maximum width 507 µm. Urosome length 107 µm, maximum width 134 µm. Oral area of holotype damaged, mouth cone not observed. Irregular branching structure present in a semicircle around oral area probably representing modified antennae. Other mouthparts absent. Leg 1 represented by pair of minute papillae on ventral surface of prosome posterior to oral region. Leg 3 represented by pair of naked setae located ventrolaterally. Leg 4 a free segment bearing 2 apical setae. Leg 5 absent. Gonopores unarmed, opening on posterolateral surface of urosome. Caudal setae lacking.

MATERIAL EXAMINED. Holotype ♀, parasitic on an as yet undescribed new species of the eurycopid *Acanthocope*. Locality; SMBA 'Permanent Stn' in the southern Rockall Trough (54°39'N12°17'W), depth about 2900 m, 07.iv.1977. Only one host specimen was infected out of a total of 111 examined from the Rockall Trough (84 from the Permanent Stn). Holotype stored in BM(NH), Reg. No. 1987.439.

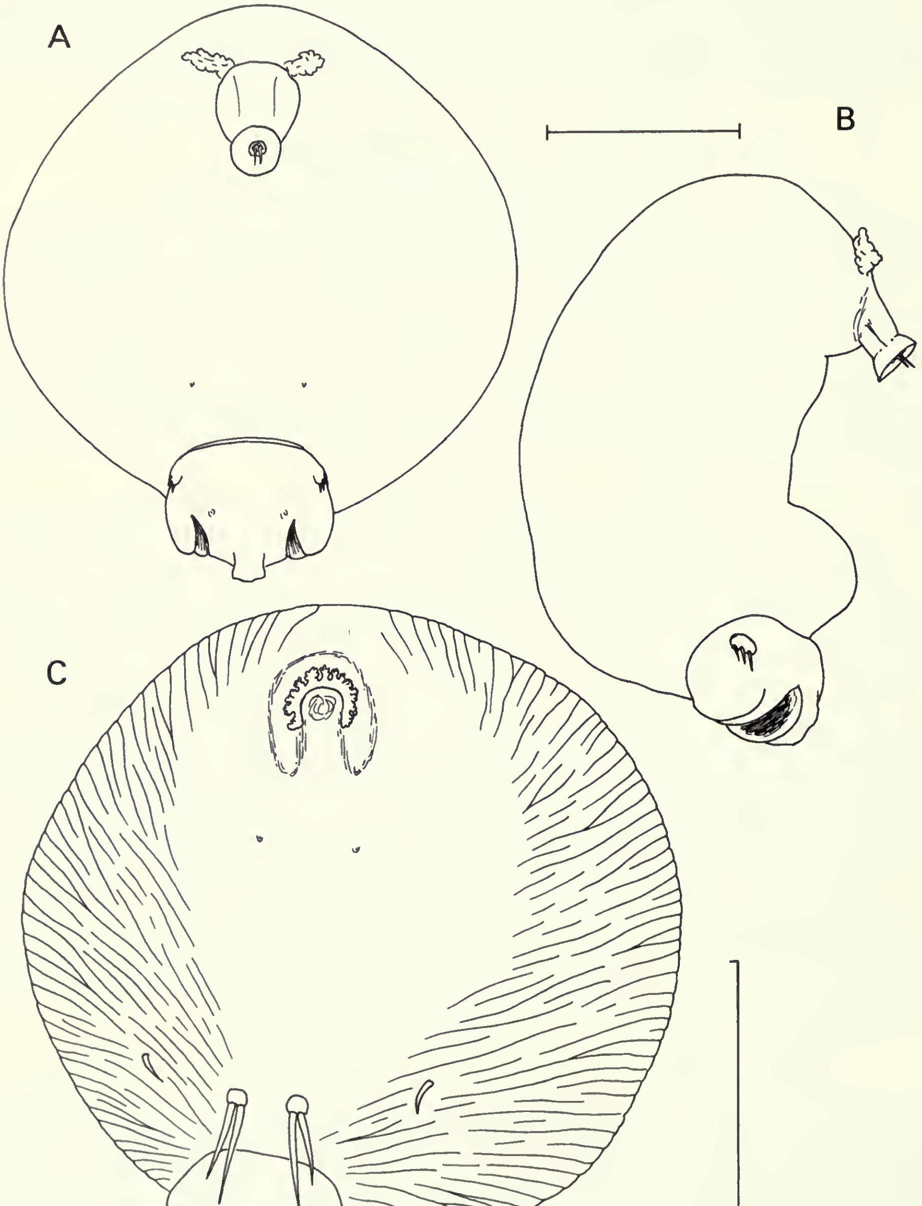

Fig. 3 *Diexanthema nudum* sp. n., Holotype female. A, Ventral view; B, Lateral view. *Diexanthema corrugatum* sp. n., Holotype female. C, Ventral view. Scale bars A, B = 100 µm, C = 200 µm.

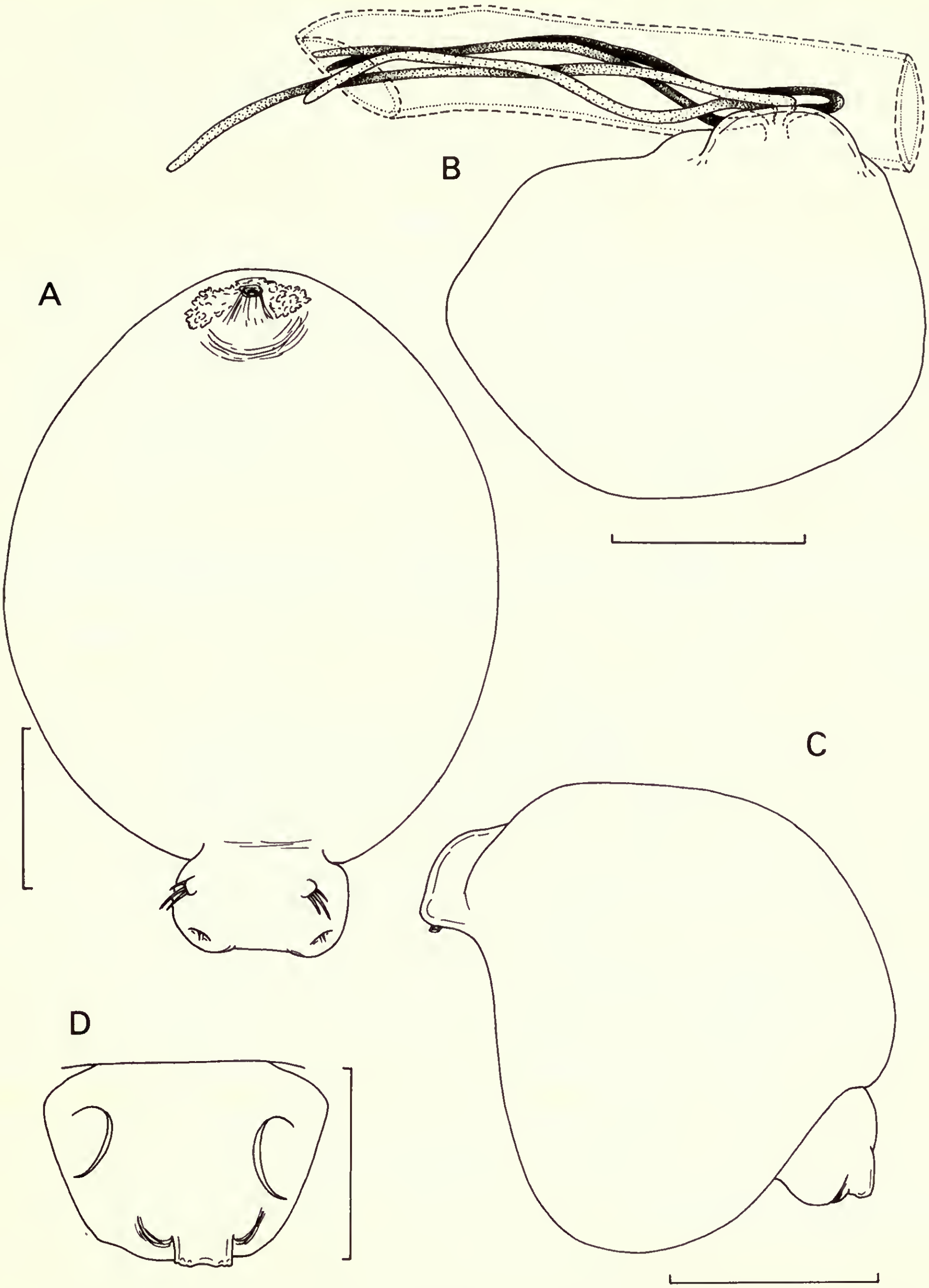

Fig. 4 *Diexanthema ritchiei* sp. n., Holotype female. A, Ventral view. *Diexanthema apoda* sp. n., Holotype female. B, Dorsal view of female attached to pereopod of host, showing 4 oral rootlets inside limb; C, Lateral view; D, Urosome, ventral. Scale bars A, D = 100 µm, B, C = 200 µm.

Etymology. The species name refers to the highly furrowed cuticle of the prosome.

Remarks. The new species is placed in *Diexanthema* because it possesses a globular prosome and an unsegmented urosome as in the preceding species. It differs from the three described species of *Diexanthema* in the structure of the third and fourth legs of the adult female. These legs are absent from *D. desistoma* Ritchie and *D. bathydiaita* (Ritchie, 1975) and absent (leg 3) or reduced to minute papillae (leg 4) in *D. nudum*. The third and fourth legs strongly resemble those of *Nicorhiza* species but the new species cannot be placed in this genus because of its truncated urosome. *Nicorhiza* species have a long, 4-segmented urosome (Lincoln & Boxshall, 1983).

The host occurs widely in the southern Rockall Trough between 2076 and 2925 m. It is clearly distinguishable from other described species of *Acanthocope*.

Diexanthema ritchiei sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising a swollen, globular prosome and an unsegmented, slightly dorsoventrally flattened urosome (Fig. 4A). Total body length in ventral view 426 μm, maximum width 307 μm. Urosome length 61 μm, maximum width 108 μm. Prosome without recognisable mouthparts or legs. Irregular branching structure present anterior to oral area may represent antennae as in other species of *Diexanthema*. Conical structure present in oral region interpreted as broken base of oral rootlets. Urosome bearing leg 5 anteroventrally. Leg 5 a simple lobe bearing 3 spines distally. Gonopores on posterolateral surface, each armed with 2 tiny setules. Posterior margin of urosome slightly concave, without trace of postgenital segments or caudal setae.

MATERIAL EXAMINED. Holotype ♀, parasitic on juvenile female of the ischnomesid *Haplomesus tenuispinus* Vanhöffen. Locality: *Discovery* Stn 50604 ♯ 1 in the Porcupine Seabight (50°6.2′N 13°52′W), depth 3490–3550 m, 04.vii. 1979. Holotype stored in BM(NH). Reg. No. 1987.440.

ETYMOLOGY. The species is named after the late Larry Ritchie, who established the genus *Diexanthema*.

REMARKS. The new species is placed in *Diexanthema* because of the gross body form, a swollen prosome and an unsegmented urosome. It possesses no obvious appendages on the prosome. The irregular branching structure anterior to the oral area is found in all other *Diexanthema* species except *D. desistoma*. *D. ritchiei* differs from other species in the structure of the feeding apparatus. *D. desistoma, D. bathydiaita*, and *D. nudum* all possess a typical nicothoid mouth cone containing stylet-like mandibles. The oral region of *D. corrugatum* was obscured (see above). The conical structure in the oral region of this species was not a typical oral cone. It appeared to be the broken stump of a rootlet system, as found in genera such as *Rhizorhina, Choniorhiza* and *Nicorhiza*. No rootlets were found in the host although this was in poor condition. The generic concept of *Diexanthema* is considerably broadened by the inclusion of this species as it now contains species with an oral cone and species with oral rootlets. The evolution of a rootlet system appears to have occurred independently several times within the Nicothoidae and, in our opinion, the presence of rootlets alone is insufficient to justify generic separation when the gross body morphology is the same.

The host, *H. tenuispinus*, was first described from the Davis Strait and from off the south coast of Greenland (Hansen, 1916). In the present study 228 specimens were examined from depths of 1993 to 2925 m in the southern Rockall Trough. None was infected. Only the specimen taken in the Porcupine Seabight was infected.

Diexanthema apoda sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising a swollen prosome and a small unsegmented urosome (Fig. 4B). Total body length in lateral view (Fig. 4C) 529 μm, maximum width 495 μm. Prosome extended anteriorly into a subrectangular 'hood'. Four oral rootlets originating on midventral surface of 'hood'. Rootlets unbranched, between 486 and 659 μm in length and about 12 μm in diameter. No other appendages or attachment structures present externally on prosome. Urosome (Fig. 4D) bearing unarmed gonopores ventrolaterally and small abdominal process posteromedially. Leg 5 absent. Caudal setae absent.

MATERIAL EXAMINED. Holotype ♀, parasitic on a preparatory male of the ilyarachnid *Bathybadistes spinosissima* (Hansen). Locality: SMBA 'Permanent Stn' in the southern Rockall Trough (54°39′N

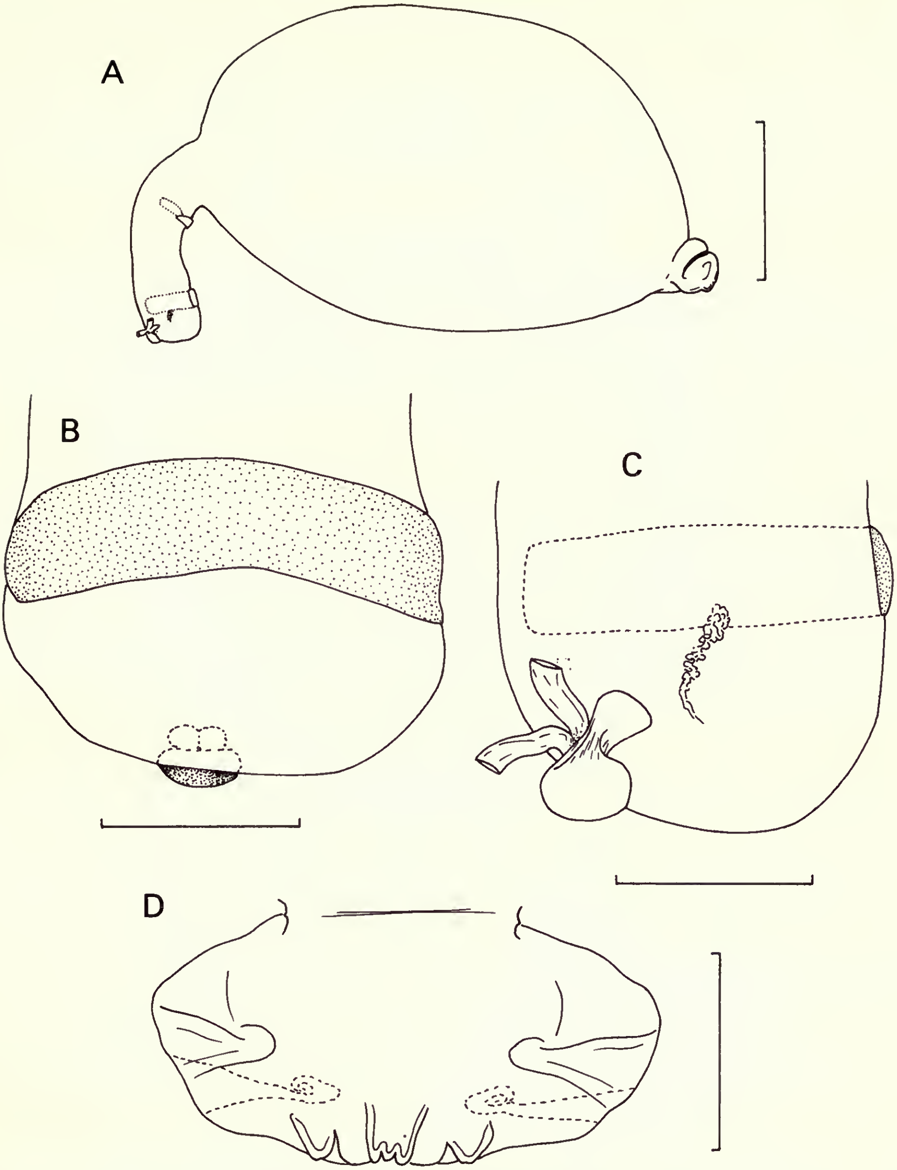

Fig. 5 *Cephalorhiza flaccida* gen. et sp. n., Holotype female. A, Lateral view; B, Tip of head process, dorsal; C, Tip of head process, ventrolateral; D, Urosome, ventral. Scale bars 100 µm, unless otherwise stated: A = 500 µm.

12°17′W), depth about 2910 m, 27.v.1980. A total of 839 specimens of *B. spinosissima* was examined from the entire Rockall Trough (783 from the 'Permanent Stn'), only 1 was infected. Holotype stored in BM(NH), Reg. No. 1987.441.

ETYMOLOGY. The species name refers to the complete absence of any recognisable limbs.

REMARKS. This species, like *D. ritchiei*, has rootlets instead of a typical siphonostomatoid mouth cone. It is even more reduced than *D. ritchiei* as it has lost the fifth legs but the general configuration of the urosome is the same as in other *Diexanthema* species. The fifth legs have also been lost in *D.*

corrugatum. *D. apoda* differs from all of its congeners in the presence of an anterior 'hood' distinct from the prosome.

The host, *B. spinosissima*, was first described from deep water (2702–3521 m) in and around the Davis Strait (Hansen, 1916). Chardy (1979) also recorded this species (as *Ilyarachna spinosissima*) from the Bay of Biscay. It occurred widely in the southern Rockall Trough between 1993 and 2925 m and at the 'Permanent Stn' it was the commonest of the 79 species of asellotes recorded, accounting for 14·7% of the asellote population.

Cephalorhiza gen. n.

DIAGNOSIS. Nicothoidae. Postmetamorphosis female highly transformed, comprising swollen prosome and small, unsegmented urosome. Prosome bearing stout, somewhat twisted, head process. Head process ornamented with 2 transverse chitinous lamellae dorsally. Oral apparatus carried distally on head process, apparently consisting of rootlets. No recognisable limbs present on prosome or urosome. Urosome unsegmented, bearing gonopores posterolaterally. Median abdominal process present but lacking caudal setae.

TYPE SPECIES: *Cephalorhiza flaccida* gen. et sp. n.

REMARKS. The new genus is the nineteenth in the family. It differs from all other genera in the possession of the stout head process which is embedded in the host up to the level of its base. It can be placed in the *Rhizorhina* group of genera identified by Boxshall & Lincoln (1983). This group now comprises five genera. *Rhizorhina, Choniorhiza, Nicorhiza, Diexanthema* and *Cephalorhiza*, and 14 species including those taxa described in the present account. Members of this group have highly transformed adult females and they exhibit the tendency to lose all cephalic appendages and develop oral rootlets. The structure of the urosome of the new genus is similar to that of some *Diexanthema* species and this is probably its closest relative within the group.

Cephalorhiza flaccida gen. et sp. n.

POSTMETAMORPHOSIS FEMALE. Body highly transformed, comprising swollen prosome and small, unsegmented urosome (Fig. 5A). Body length 2·34 mm, measured in lateral view round curve from tip of head process to end of urosome. Prosome globular with maximum diameter of 1·01 mm, bearing at its anterior extremity a stout, somewhat twisted, head process. Head process ornamented with 2 transverse chitinous lamellae dorsally (Fig. 5B). Oral apparatus carried distally on head process, apparently consisting of rootlets (Fig. 5C), but broken off in holotype. No recognisable limbs present on prosome or urosome. Irregular branching structure present near oral rootlets similar to the modified antennae of *Diexanthema* species but located posteriorly to oral region and unlikely to be homologous. Urosome unsegmented; maximum length 129 μm, maximum width 260 μm. Gonopores unarmed, opening on posterolateral surface (Fig. 5D). Median abdominal process present but lacking caudal setae.

MATERIAL EXAMINED. Holotype ♀, parasitic on preparatory female of *Ilyarachna antarctica* Vanhöffen; collected during the MD 32 cruise organised by the Terres Australes et Antarctiques Francaises (TAAF, Paris); chef de Mission Alain Guille and sorted by CENTOB, Brest. Locality: Marion-Dufresne Stn DS 106, off Réunion Island (20°47′5S 55°04′5E), depth 1710–1730 m. Holotype stored in Museum National d'Histoire Naturelle, Paris, No. MNHN Cp39.

ETYMOLOGY. The genus name is derived from the Greek *kephale*, meaning a head, and *rhiza*, meaning root. The species name, derived from the Latin *flaccidus* meaning flaccid, refers to the posture of the head process.

REMARKS. The host has the form of *Ilyarachna bicornis* as described by Hansen (1916). *I. bicornis* was synonymised with *I. antarctica* by Thistle (1980).

Sphaeronella australis sp. n.

ADULT FEMALE HOLOTYPE. Body subspherical (Fig. 6A) consisting of a small, somewhat dorsoventrally flattened head and a swollen, almost spherical trunk. Total body length 831 μm, maximum

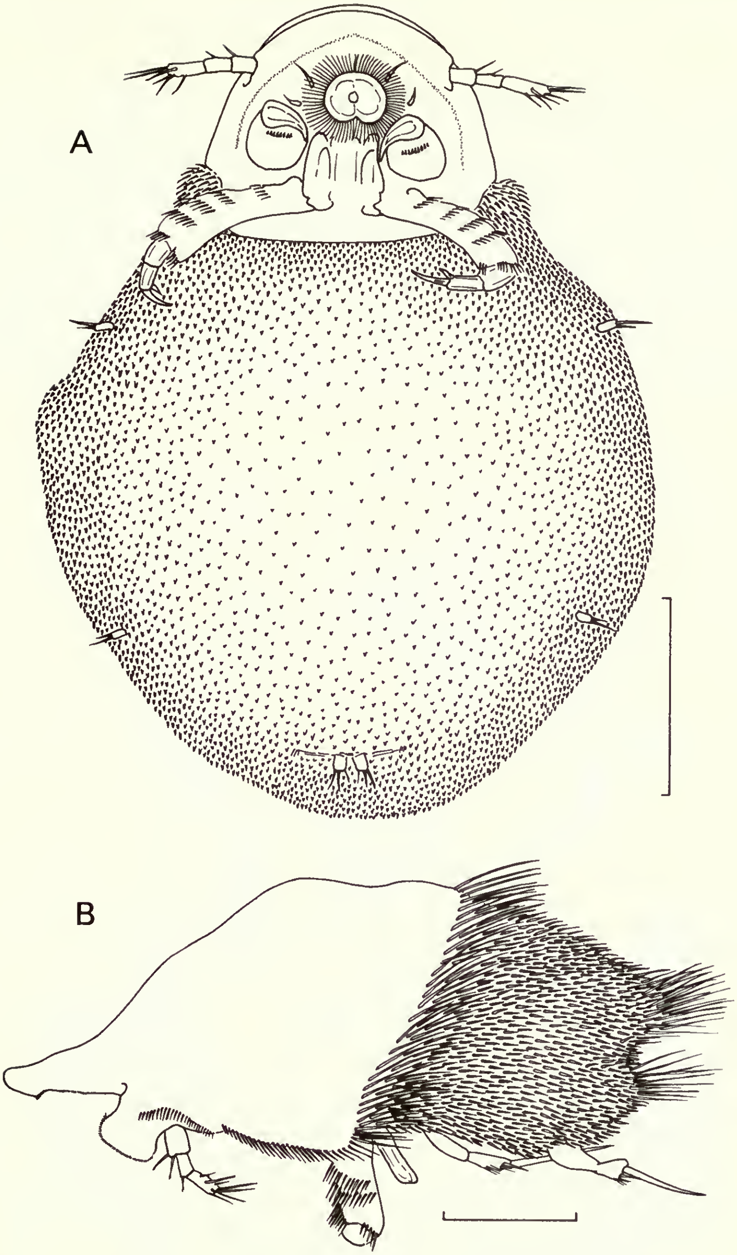

Fig. 6 *Sphaeronella australis* sp. n., A, Holotype female, ventral view; B, Paratype male, lateral view. Scale bars A = 200 μm, B = 100 μm.

width 623 μm. Size variable according to reproductive condition, trunk often much larger when fully gravid. Head dorsoventrally flattened, slightly concave ventrally. Anterior rim of head provided with fine marginal strip of hyaline membrane. Trunk covered with dense coat of tiny denticles.

Antennules, mandibles, maxillules and maxillae as for male (see below). Isolated seta present anterior to mouth cone may represent the antenna, absent in male. Ornamentation on surface of maxilliped arranged into rows on female, rather than irregular as in male. Legs 1–2 comprising a single free segment bearing 2 unequal setae apically. Caudal rami slightly longer than wide, bearing 3 distal setae.

ADULT MALE. Body highly transformed (Figs 6B, 7), dorsoventrally flattened, divided into head and small trunk. Body length 477 µm, maximum width 311 µm. Head naked dorsally and dorsolaterally, trunk covered with a dense coat of fine setules. Setules longer at junction between head and trunk, and at posterior extremity of trunk (Fig. 6B). Anterior margin of head (Fig. 7) complex, with deep indentations separating the median pseudorostrum from the lateral cephalic processes on either side. Margin of lateral cephalic processes armed with fine setules. Lateral margins of dorsal cephalic shield deflected ventrally, armed with row of submarginal setules.

Antennule (Fig. 8A) 3-segmented; first segment with 2 setae, second with 1, third segment with 9 simple setae and a double seta at the apex. Antenna absent. Mandible (Fig. 8B) a simple stylet armed with a marginal membrane distally; palp absent. Maxillule (Fig. 8C) comprising a simple

Fig. 7 *Sphaeronella australis* sp. n., Paratype male, ventral view. Scale bar 100 µm.

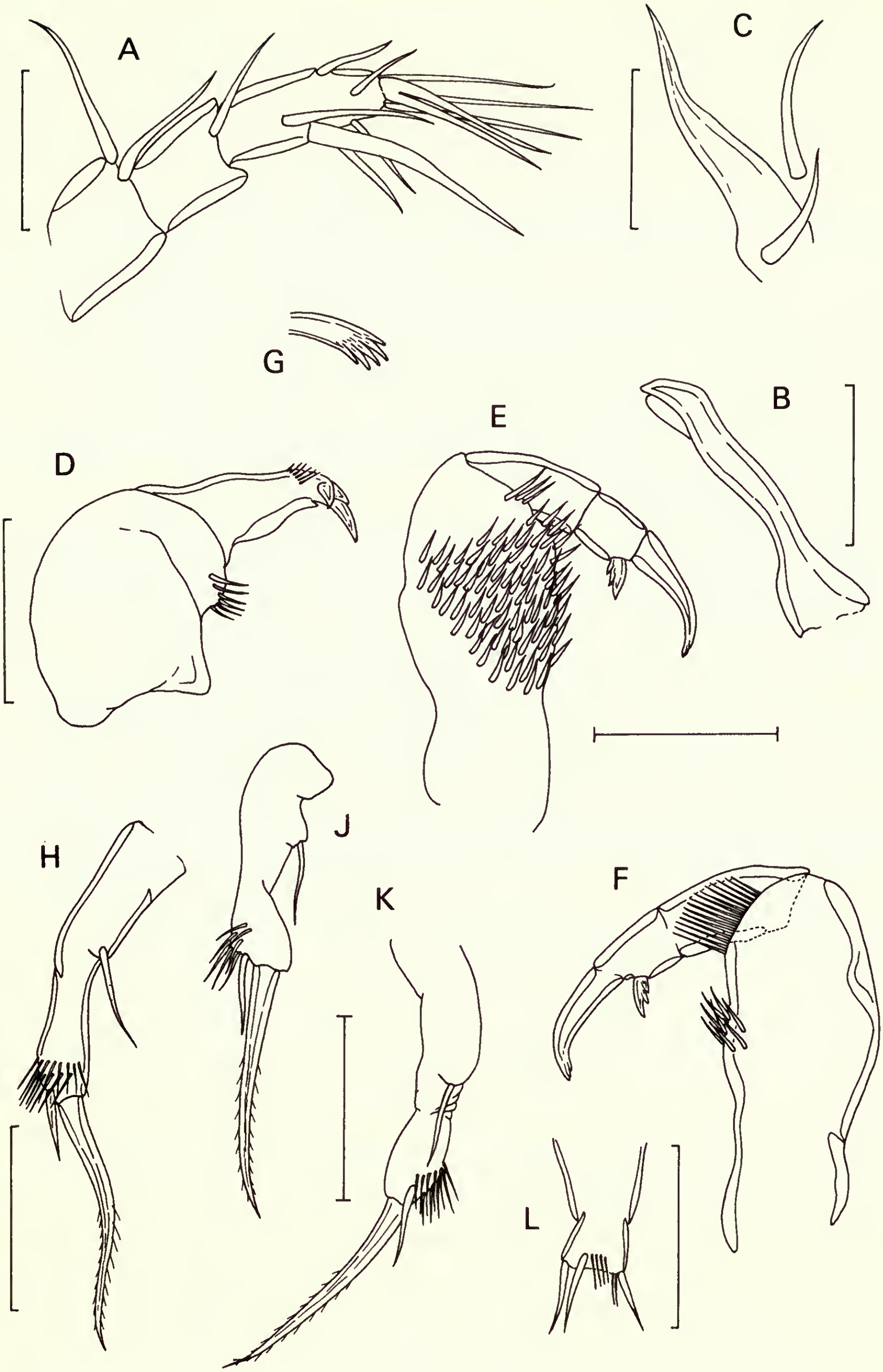

Fig. 8 *Sphaeronella australis* sp. n., Paratype male. A, Antennule, ventral; B, Mandible, posterior; C, Maxillule, ventral; D, Maxilla, posterior; E, Maxilliped, anterior; F, Maxilliped, posterior; G, Tip of maxillipedal claw, ventral; H, Leg 1, ventral; J, Leg 2, lateral; K, Leg 2, ventral; L, Caudal ramus, ventral. Scale bars 50 µm, unless otherwise stated: A–C = 25 µm.

tapering process, bearing a naked seta proximally, and an isolated seta situated on ventral surface of head near base of maxillulary process. Maxilla (Fig. 8D) 2-segmented; syncoxa robust, armed with single row of stout spinules, basis claw-like, bearing 3 teeth distally and a row of fine setules. Maxilliped (Figs 8E, F) 4-segmented, including the terminal claw; first segment robust armed with many stout spinules on anterior and medial surfaces, and a row of slender setules distally on posterior surface. Second segment unarmed, third bearing the terminal claw and a subapical tricuspid spine. Terminal claw 33 μm long, with complex quindentate tip.

Two pairs of uniramous swimming legs present. Leg 1 (Fig. 8H) slender, comprising 2 incompletely fused segments with the indentation at midlevel marking the line of fusion. Proximal segment bearing a naked seta, distal segment armed with 2 transverse rows of fine setules, a short (20 μm) subapical spine and a long (70 μm), sparsely pinnate, apical spine. Leg 2 (Fig. 8J, K) indistinctly 2-segmented, with deep indentation most apparent in lateral view (Fig. 8J). Proximal part bearing a single seta on a small ventral swelling; distal part with a patch of fine setules, a subapical seta (22 μm) and a long (68 μm), sparsely pinnate, apical spine. Caudal rami (Fig. 8L) bearing 3 naked setae and a few setules distally.

A large female paratype (Museum of Victoria J11809) had produced 19 egg sacs with a mean size of 795 × 681 μm (range 699 to 883 μm × 589 to 810 μm based on 19 measurements). Typical sac measuring 810 × 681 μm contained 216 eggs.

MATERIAL EXAMINED. Holotype ♀, 3♀♀ and 1♂ paratypes all parasitic in brood chamber of a species of the lysianassoid genus *Amaryllis*. Locality: Holotype ♀, Port Arthur, Tasmania (43°09′S 147°51E), 29 vii. 1909, Australian Museum (AM) No. P35852. Paratypes: 1♀ (AM No. P35853) off end of South Mole, Arthur Head, Freemantle, Western Australia, depth 6 m, 25.xii.1983, coll. J. K. Lowry; 1♀, 1♂ (Victoria Museum (VM) No. J11809), and 1♀ (J11810), FV 'Sarda', Bass Strait Stn 112 (40°22·2′S 145°17′E), depth 40 m, 3.xi.1980, coll. G. C. B. Poore.

REMARKS. *Sphaeronella* contains 76 species, the majority (42 species) parasitic on amphipod hosts. The new species belongs to the *S. leuckartii* group which Hansen (1897) recognised for the following 9 species, *S. antillensis* Hansen, *S. atyli* Hansen, *S. chinensis* Hansen, *S. danica* Hansen, *S. leptocheiri* Hansen, *S. leuckartii* Salensky, *S. elegantula* Hansen, *S. messinensis* Hansen, and *S. vestita* Hansen. This number was increased by the description of *S. aorae* by Scott (1905) and of *S. devosae* and *S. ecaudata* by Stock (*in* Stock & De Vos, 1960). Green (1958) regarded *S. elegantula* and *S. aorae* as synonymous with *S. leuckartii*. This group is characterised by the presence in the male of a conspicuous rectangular projection in the middle of the frontal margin of the head (here referred to as the pseudorostrum), by the rudimentary or absent antenna, and by the presence of a tuft of hairs at the base of the maxillule. Within the group the new species is most closely related to *S. chinensis* Hansen, which is known from the marsupium of *Corophium bonelli* Milne-Edwards from Hong Kong. The morphology of the males is very similar, especially in the configuration of the frontal margin of the head. However, the ventral sternal processes in the maxillipedal region of the male are better developed and more widely divergent in *S. australis* than in *S. chinensis*. Also the terminal seta on the apex of leg 2 is longer than the limb itself in *S. chinensis* but shorter than the limb in *S. australis*.

The oral area of the male of the new species had collapsed inwards, thereby retracting the mouth cone so that it is less visible in ventral view. In life it would protrude more, as in the lateral view of *S. chinensis* given by Hansen (1897).

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A new genus of Lichomolgidae (Copepoda: Poecilostomatoida) associated with a phoronid in Hong Kong

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Introduction

Copepods are rarely reported as parasites or associates of the lophophorate phyla Bryozoa, Brachiopoda and Phoronida. Two new harpacticoids, *Tegastes knoepffleri* and *Peltobradya bryozoophila*, were described by Medioni & Soyer (1967) as associates of the bryozoans *Schizobrachiella sanguinea* (Norman) and *Schizomavella linearis* (Hassall) respectively, at Banyuls-sur-Mer in southern France. Recently Humes & Boxshall (1988) described a new genus of the family Myicolidae which occurs on the intertidal brachiopod *Lingula anatina* Lamarck collected at Starfish Bay, New Territories, Hong Kong. This is the first known copepod associate of a brachiopod. Examination of other invertebrates collected at the same time in Starfish Bay has revealed a copepod associated with a phoronid, *Phoronis australis* Haswell, which is itself an associate of the burrowing anemone *Cerianthus filiformis* Carlgren. The phoronid lives embedded in the mucilaginous tube of the *Cerianthus* (Morton & Morton, 1983). Three copepods were found in the lophophore of the phoronid and are described below as a new genus of the family Lichomolgidae.

Material and Methods

The phoronid was collected by a diver at a depth of 3 to 5 m in Hoi Sing Wan (Starfish Bay). The phoronid was placed in a plastic bag, transported to the laboratory and examined live. The copepods were picked off and fixed in 70% ethanol. All figures were drawn with the aid of a camera lucida.

Descriptions

Genus *PHORONICOLA* gen. nov.

Diagnosis. Body cyclopiform. Urosome in ♀ 4-segmented, in ♂ 5-segmented. Caudal ramus with 6 setae. Rostrum broad. First antenna 7-segmented. Second antenna 4-segmented, with the formula 1, 1, 4 + 1 articulated claw, and 4 + 3 articulated claws.

Labrum incised medially. Mandible tapering smoothly into lash. Paragnath a small hairy lobe. First maxilla with 3 setae. Second maxilla with long slender lash, 2 setae near base of lash, and a short proximally directed seta. Maxilliped in ♀ 3-segmented with pointed tip, in ♂ 4-segmented.

Legs 1–4 with 3-segmented rami, except for leg 4 endopod which is 1-segmented. Leg 4 exopod armed I–0; I-1; I, I, 5: endopod armed with an apical serrate spine. Leg 5 with a free segment bearing 1 apical spine and 1 subapical seta. Leg 6 in ♀ represented by 2 setae situated on a small lobe at each genital aperture, in ♂ represented by single seta on genital flap.

Associated with Phoronids.

Bull. Br. Mus. nat. Hist. (Zool.) **54**(6): 301–307

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TYPE SPECIES. *Phoronicola spinulatus* gen. et sp. n.

ETYMOLOGY. The generic name is derived from *Phoronis*, the host genus, and the Latin *-cola*, meaning inhabiting.

Phoronicola spinulatus gen. et sp. n.

TYPE MATERIAL. 1♀ and 2♂♂ from 1 *Phoronis australis* collected in 3–5 m in Hoi Sing Wan (Starfish Bay), on the southern shore of Tolo Harbour, New Territories, Hong Kong by Dr P. G. Oliver on 3 April 1986. Holotype ♀ (BM(NH) Reg. No. 1987.415), and 2♂♂ paratypes (BM(NH) Reg. Nos 1987.416–417) deposited in the British Museum (Natural History), London.

FEMALE. Body (Fig. 1A) with stout prosome and slender urosome. Length (excluding caudal setae) 1·17 mm and greatest width 0·49 mm. Length to width ratio of prosome 1·41:1. First pedigerous segment fused with cephalosome. Ratio of length of prosome to that of urosome 1·47:1.

Segment bearing leg 5 (Fig. 1B) 62 × 139 μm. Genital segment elongate, 189 μm long, anterior half with convex lateral margins and broader (133 μm) than posterior half (straight sides and width of 80 μm). Genital areas located dorsolaterally about in middle of segment. Each area bearing a small process armed with 2 smooth setae (Fig. 1B), an apical seta 23 μm long and a subapical seta 29 μm long. Postgenital segment 52 × 72 μm, anal segment 82 × 65 μm.

Caudal ramus (Fig. 1A) 3·0 times longer than wide (84 × 28 μm), bearing 6 setae. Outer lateral seta 63 μm long, naked and positioned on mid-dorsal surface. Dorsal seta naked, 55 μm long. Outermost terminal seta 84 μm long, innermost terminal seta 106 μm and 2 median terminal seta 377 μm (outer) and 501 μm (inner); all 4 of these setae plumose.

Rostrum (Fig. 1C) broad based, moderately well defined. First antenna 7-segmented as in male (Fig. 1D); formula for armature: 4, 12, 6, 3, 4+1 aesthete, 2+1 aesthete and 7+1 aesthete. Two setae on first segment, 3 on fourth segment, 1 on sixth segment and 5 on seventh segment plumose. Second antenna (Fig. 1E) 4-segmented; armature 1, 1, 4+1 articulated claw, and 4+3 articulated claws.

Labrum (Fig. 1C) with 2 broad, tapering lobes. Mandible (Fig. 1F) with a slender base carrying distally a bipectinate blade. Paragnath a small hairy lobe. First maxilla (Fig. 1G) conical, with 3 elements. Second maxilla (Fig. 2A) 2-segmented. First segment unarmed. Second segment drawn out into a slender apical lash with a comb of strong spinules along outer margin, and fine spinules along inner margin. Second segment armed with a stout barbed spine on medial margin, a naked spine near its base and a fine, proximally directed setule near the base of the outer margin. Maxilliped (Fig. 2B) 3-segmented. First segment unarmed; second segment bearing a naked seta and a stout spinose seta. Third segment armed with a naked spine, terminating in slightly curved spiniform process bearing 3 spinules. Ventral area between bases of maxillipeds (Fig. 2C) and first legs only slightly protuberant.

Legs 1–4 (Figs 2D–F, 3A) biramous with 3-segmented rami except for endopod of leg 4 being 1-segmented. Spine and seta formula of legs as follows:

P1	coxa 0–1	basis 1–0	exp I–0; I–1; III, I, 4
			enp 0–1; 0–1; I, 5
P2	coxa 0–1	basis 1–0	exp I–0; I–1; III, I, 5
			enp 0–1; 0–2; I, II, 3
P3	coxa 0–1	basis 1–0	exp I–0; I–1; II, I, 5
			enp 0–1; 0–2; I, II, 2
P4	coxa 0–0	basis 1–0	exp I–0; I–0; I, I, 5
			enp I

Outer distal angle of legs 1–2 coxae with patch of fine spinules. Inner margin of basis of legs 3–4 with rows of long hairs. Rows of hairs present on inner margins of all exopod segments and outer margins of all endopod segments. Leg 4 (Fig. 3A) with 1-segmented endopod 42 μm in length, bearing a few spinules proximally on inner margin and a longer row of spinules on outer margin. Apical element spiniform, 62 μm long, armed with serrate membrane on both sides.

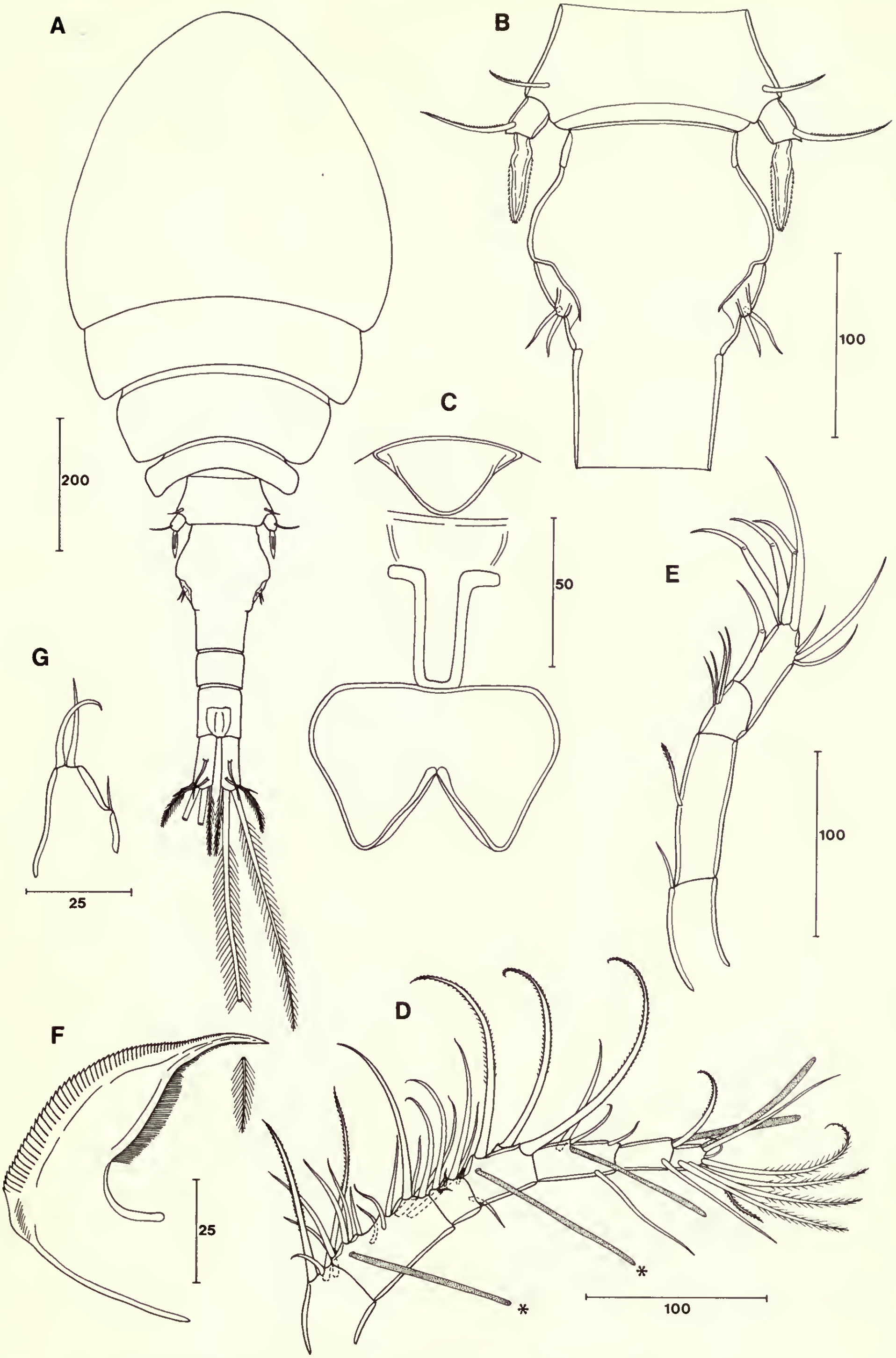

Fig. 1 *Phoronicola spinulatus* gen. et sp. nov. A, Holotype female, dorsal; B, Fifth pedigerous and genital segments, dorsal; C, Rostrum and labrum, ventral; D, Male first antenna, anteroventral (with aesthetes absent in female marked with asterisks); E, Female second antenna, posterior; F, Mandible, posterior; G, First maxilla, anterior. All scales in μm.

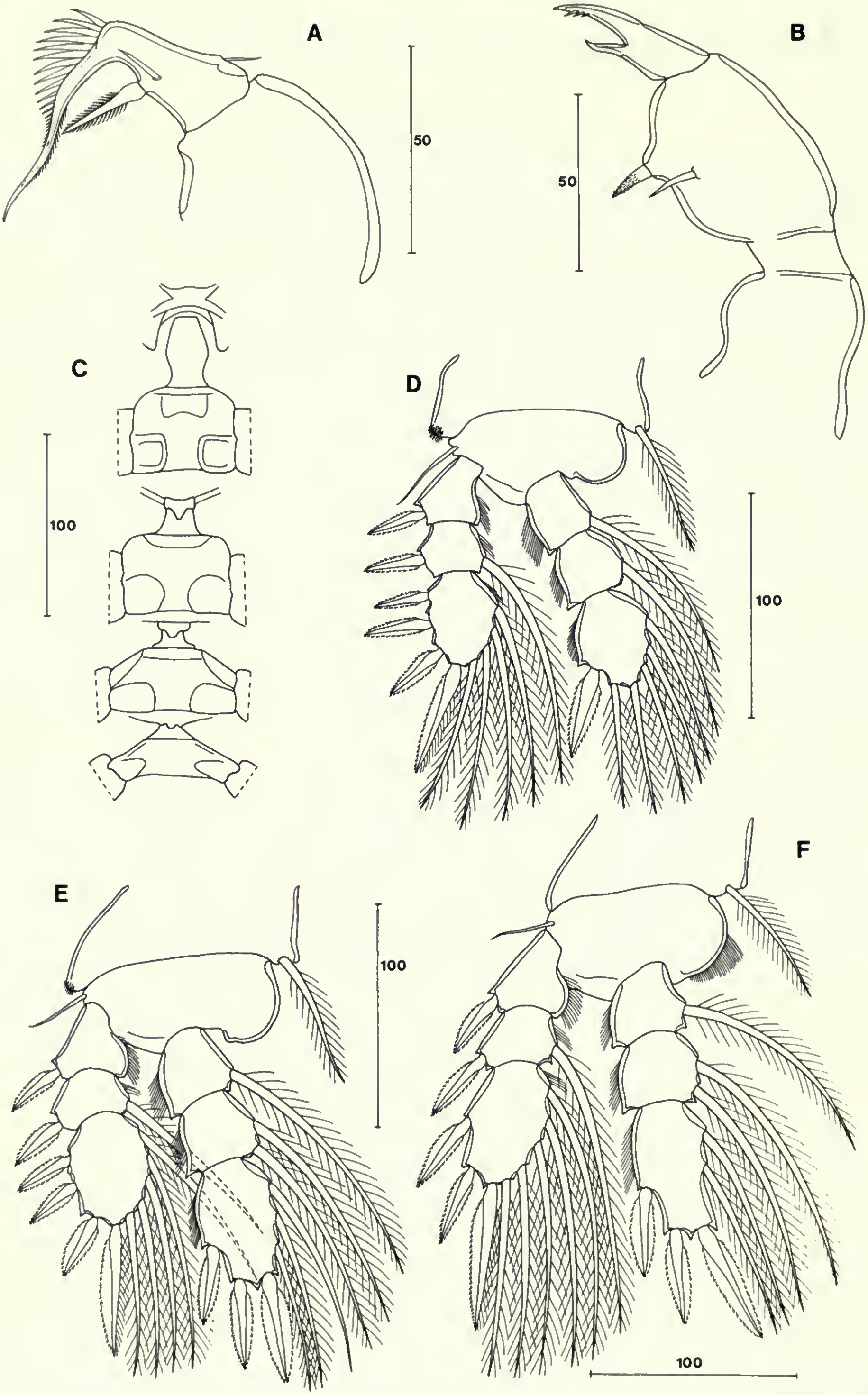

Fig. 2 *Phoronicola spinulatus* gen. et sp. nov. Female, A, Second maxilla, posterior; B, Maxilliped, posteromedial; C, Ventral body wall between maxillipeds and swimming legs; D, Leg 1, posterior; E, Leg 2, posterior; F, Leg 3, posterior. All scales in µm.

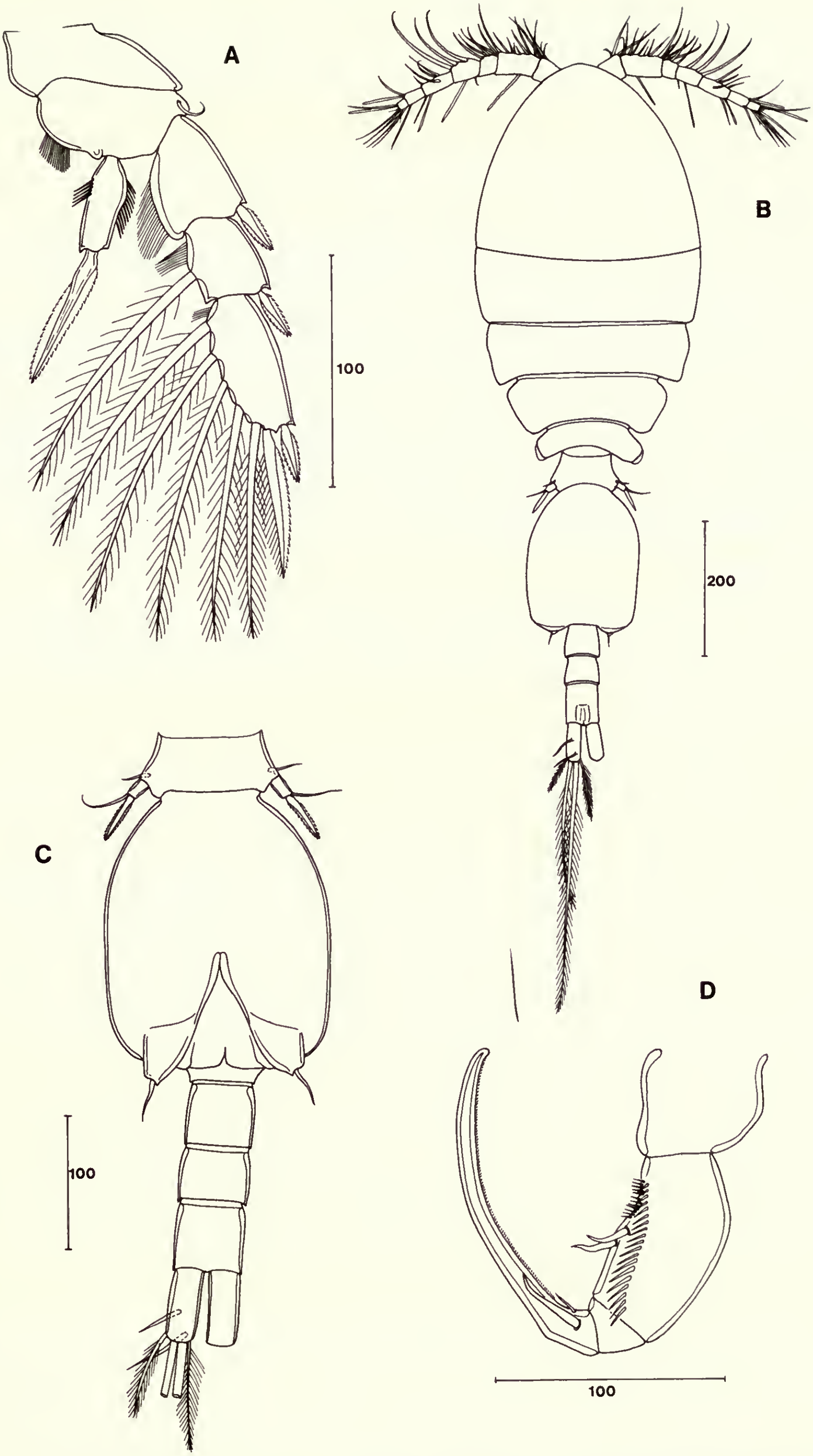

Fig. 3 *Phoronicola spinulatus* gen. et sp. nov. A, Female leg 4, posterior; B, Paratype male, dorsal; C, Urosome, ventral; D, Maxilliped, posteromedial. All scales in μm.

Leg 5 (Fig. 1B) free segment about 1·2 times longer than wide (21 × 18 μm), with a small spiniform projection at outer distal angle. Strong spiniform apical element 49 μm long, armed with serrate membrane both sides; subapical seta 56 μm long, with tiny spinules along anterior margin. Dorsal seta 35 μm. Leg 6 represented by process bearing 2 setae located in genital area (Fig. 1B).

Egg sacs not seen.

Colour of live specimen white.

MALE. Body (Fig. 3B) similar to that of female in general form. Length 1·04 mm excluding caudal setae, greatest width 0·33 mm; length to width ratio of prosome 1·73:1. Ratio of length of prosome to length of urosome 1·25:1.

Segment of leg 5 (Fig. 3C) 43 × 101 μm. Genital segment 214 × 166 μm. Three postgenital segments from anterior to posterior 49 × 51, 41 × 52 and 54 × 51 μm.

Caudal ramus similar to that of female but shorter, 56 × 20 μm, ratio 2·8:1.

First antenna (Fig. 1D) 7-segmented; lengths of segments measured along posterior border 26, 61, 19, 34, 44, 29 and 18 μm respectively. Armature formula as for female except for additional aesthetes on segments 2 and 4 (marked with asterisks on Figure 1D).

Rostrum, second antenna, labrum, mandible, paragnath, first and second maxilla like those of female. Maxilliped (Fig. 3D) slender, 4-segmented. First segment stout, unarmed. Second segment with 2 naked inner setae, a row of spinules along inner surface and a shorter row of fine spinules proximally. Third segment unarmed. Claw comprising short basal section representing the fourth segment, armed with 2 unequal setae. Claw curved, 146 μm in length, bearing a row of fine spinules along concave margin.

Legs 1–4 similar to those of female. Leg 5 (Fig. 3C) free segment more elongate than in female, 1·7 times longer than wide (17 × 10 μm). Apical serrate element 38 μm long, subapical seta 40 μm.

Leg 6 (Fig. 3C) forming the posteroventral genital flap closing the genital aperture, armed with a single apical seta 34 μm long.

Spermatophores not seen.

Colour of live specimens white.

ETYMOLOGY. The specific name *spinulatus* refers to the spiniform nature of the single serrate element on the endopod of leg 4.

REMARKS. The new genus belongs to the family Lichomolgidae. The lichomolgid genera *Aspidomolgus* Humes, *Haplomolgus* Humes & Ho, *Kelleria* Gurney, *Lichomolgella* Sars, *Octopicola* Humes, *Paramacrochiron* Sewell, *Pseudomacrochiron* Reddiah, *Sewellochiron* Humes and *Telestacicola* Humes & Stock share with the new genus the 1-segmented endopod of leg 4 (Humes & Stock, 1973). Most species of *Macrochiron* Brady also exhibit this 1-segmented condition. However, none of these genera has only a single apical element on the leg 4 endopod. *Aspidomolgus* (II, I), *Kelleria* (II, 1), *Octopicola* (2, 1) and *Telestacicola* (II, 1) all have 3 elements, *Lichomolgella* (II), *Macrochiron* (II), *Paramacrochiron, Pseudomacrochiron* (II) and *Sewellochiron* (II) have 2 apical elements and *Haplomolgus* has none.

The presence of one articulated claw on segment 3 and 3 claws on segment 4 of the second antenna is recorded in only a single species of *Acaenomolgus* Humes & Stock, within the Lichomolgidae. Members of this genus, however, have a 2-segmented leg 4 endopod. *Kelleria* has 1 and 2 articulated claws on the third and fourth segments of the second antenna respectively and has a 1-segmented endopod on leg 4 but differs from *Phoronicola* in possessing an additional urosome segment in both sexes and in the formula for the third exopod segment of leg 4 which is II, I, 5 compared with I, I, 5 in the latter.

No phoronid has previously been recorded as host to a copepod. *Cerianthus*, with which the *Phoronis* is associated, is host to the copepod *Boholia cerianthiphila* Kossmann in the Philippine Islands (Kossmann, 1877). This lichomolgid has not been recorded since its original description and was regarded as insufficiently described or of uncertain position by Humes & Stock (1973) in their revision of the family. The original description of *B. cerianthiphila* shows that it possesses 2 strong claws at the apex of the second antenna whereas *Phoronicola* has 3 slender articulated setiform claws. The segmentation of the body is also different in these two genera. These differences are sufficient to distinguish between them.

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We would like to thank Professor Brian Morton (University of Hong Kong) for the opportunity to collect this material during the Second International Workshop on the Flora and Fauna of Hong Kong and Southern China held during April 1986. We are also grateful to Dr P. G. Oliver (National Museum of Wales) who collected the phoronid host.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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