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Gordon Howes

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Review of the genus *Brycon* (Teleostei: Characoidei)

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Contents

Introduction

As presently recognized *Brycon* is one of the largest neotropical characoid genera, containing over 60 nominal species—of which perhaps 40 or so are 'valid' species. The genus is ill-defined, being recognized by a combination of what are most likely plesiomorph characters, ie. the presence of two inner symphysial teeth in the lower jaw, 3 or 4 rows of premaxillary teeth, premaxillaries linked *via* a convoluted symphysial joint. These characters occur in other Neotropical and African characoids and, moreover, may be lacking in some species assigned to *Brycon*. There is a wide diversity of cranial and dental morphology within the genus and it is questionable whether *Brycon* as it now stands is a monophyletic unit. This is a question to which the author has addressed himself and although some progress toward an answer has been made, it is clear that before any polarity can be applied to the salient characters identified, many more in-and out-group comparisons have yet to be made. Thus, study of phylogenetic relationships of *Brycon* will not be completed for some years.

During the course of this phylogenetic study most of the literature concerning the genus has been consulted and indexed together with data on many type specimens examined. Since no revision of *Brycon* has ever been published nor (since Eigenmann, 1910) has a complete list of species been compiled, I felt it opportune to present these collected data in the form of a review in the hope that it will serve as the basis for a future revision.

For the purpose of this review, a broad generic concept of *Brycon* is retained, viz: fishes possessing a rhinosphenoid; a single medial symphysial tooth in each dentary; 3 or 4 rows of premaxillary teeth (sometimes modified so as to appear as two rows) with the two teeth forming the inner row enlarged; principal jaw teeth tri-quinquicuspid but sometimes with the lateral cusps reduced so as to appear virtually unicuspid; the premaxillaries joined at the symphysis by a convoluted interlocking joint (with a single exception); maxillary valve tissue often papillate and convoluted; posterior myodome open ventrally with part of the eye musculature taking its origin from the basioccipital rim; frontal and parietal fonantelle present—at least in juveniles; coracoid not enlarged; supramaxilla absent (the absence of

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these two latter characters exclude, respectively, *Triportheus* and *Chalceus* which share all the other characters).

The nominal species are arranged in alphabetical order; all known references are cited together with locality. Where possible the dental pattern of each species is illustrated. The data for the type specimens examined are tabulated.

Notes on counts and measurements

SL = standard length (mm); D = maximum body depth; S–D = snout to dorsal, measured from the tip of the snout to the origin of the first unbranched dorsal fin ray; H = head length, measured from tip of the snout to the edge of the operculum; Sn = snout length, from the tip to anterior edge of the orbit; IO = least interorbital width; Ey = eye diameter; Mth = mouth width, taken between the coronoid processes of the dentary; CpL = caudal peduncle length; CpD = caudal peduncle depth; PL, VL & DL = respectively, the length of the longest unbranched rays of the pectoral, ventral and dorsal fins; AL = length of the anal fin base; P–V = distance between the origin of the pectoral and ventral fins; PP–V = the length of the pectoral fin expressed as a percentage of the pectoral-ventral distance; scales are counted from dorsal fin origin to lateral line/lateral line/below lateral line to ventral midline; gill-raker count is given as epibranchial/ ceratobranchial; vertebrae are counted as abdominal (including the 4 Weberian elements) + caudal (including fused 1st ural and preural centra), the caudal vertebrae are counted from the first to bear a haemal spine; supraneurals (predorsal bones), all elements are counted.

The proportions are shown as percentages of the standard length excepting those for the snout, interorbital, eye and mouth width which are shown as percentages of the head length.

Dental formulae

Böhlke (1958) pointed out the difficulty of interpreting in *Brycon* just which teeth belong to which row and how many rows there are. Various authors have had different opinions. Fowler (1923) for example, recognized 5 rows of premaxillary teeth in *B. guatemalensis* whereas other authors recognize 3 or 4. Böhlke (1958) identified 3 rows of teeth in *B. alburnus* (*B. acutus* of Böhlke). He interpreted the elongate tricuspid series as the outer row, the middle (2nd row) as 2 or 3 tricuspids and the inner series (3rd row) as 7 or 8 quinquicuspid-tricuspid teeth. However, Böhlke suggested that a more correct interpretation would be to consider the 3rd row as being the two enlarged teeth near the symphysis and the 2nd row as numbering 8 or so teeth. It is this latter interpretation which I have accepted, partly for convenience of description and partly from ontogenetic evidence (unpublished), and use in the following descriptions (see Figs 1, 2, 15 & 16).

The counts for the teeth are given as of one side of the jaw. If a fish has more teeth in one side than the other, then it is the maximum figure that is given. The counts are shown as: Pmx 1 = premaxillary outer row, 2 = 2nd row, 3 = 3rd, inner row; Max = maxillary; Dent = dentary teeth; formula given as 7/9/1 would read 7 large anterior teeth, 9 small posterior teeth, 1 tooth at the symphysis, forming the inner row.

Catalogue of nominal species

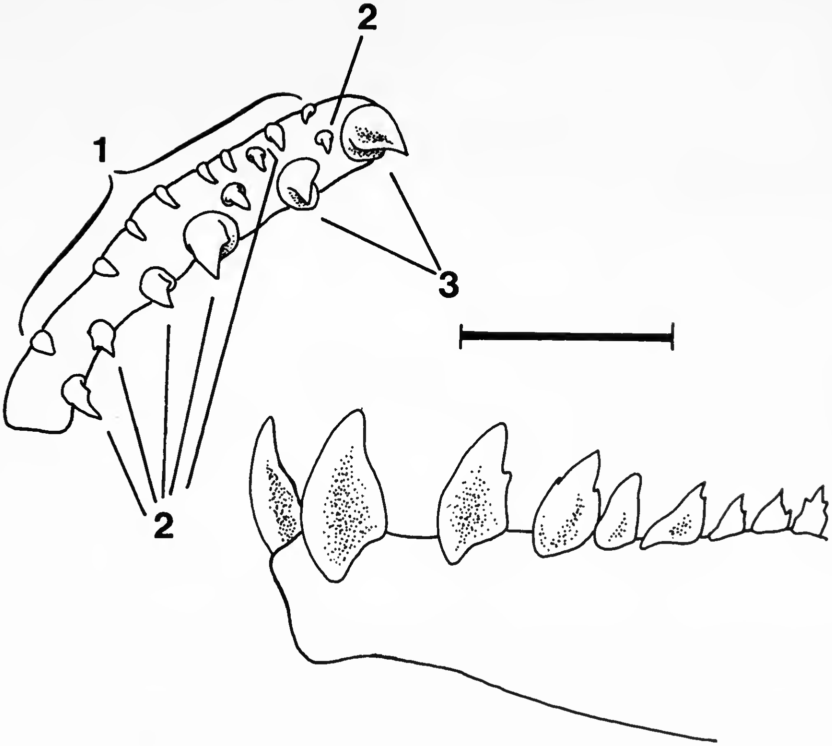
BRYCON Müller & Troschel, 1844

Arch. Naturgesch (1): 90

TYPE SPECIES. *Brycon falcatus* Müller & Troschel, 1844, *Arch. Naturgesch* (1): 90.

ETYMOLOGY. Gr. *brykon* = gnasher of teeth.

SYNONYMY. .*Chalcinopsis* Kner, 1863
Megalobrycon Günther, 1869



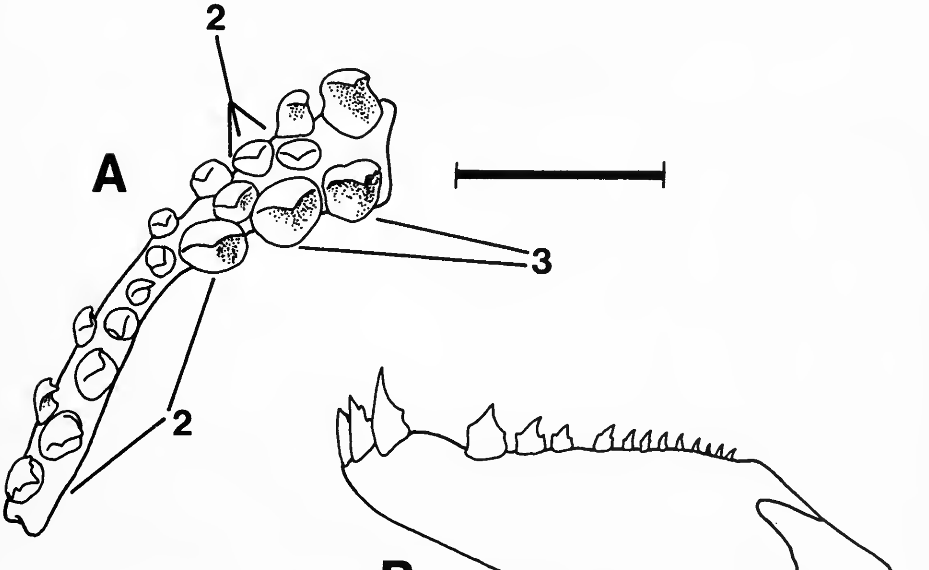


Fig. 1 (upper) *Brycon acuminatus* A, right premaxilla; B, left dentary (specimen ZUSP 1533, 140 mm SL. **Fig. 2** (lower) *Brycon alburnus* A, right premaxilla; B, left dentary (specimen BMNH uncat. 167 mm SL). The numbers indicate the row to which various teeth belong. 1 = 1st, outer row; 2 = 2nd, medial row; 3 = 3rd, inner row. Scales: solid = 3 mm, divided = 10 mm.

Catabasis Eigenmann & Norris, 1900
Bryconodon Eigenmann, 1903
Othonophanes Eigenmann, 1903
Triurobrycon Eigenmann, 1909
Holobrycon Eigenmann, 1909

Brycon acuminatus (Eig. & Norris, 1900)

Catabasis acuminatus Eigenmann & Norris, 1900, *Revta Mus. Paulista* **4**: 349–362 (description; type locality, Rio Tiete, Parana basin); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 447 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 367 (reference); Roberts, 1969 *Proc. Calif. Acad. Sci.* **36** (15): 437 (description of holotype, comments on dentition); Gery, 1972, *Zool. Verh.* **122**: 55 (reference in key); Gery, 1977, *Characoids*: 331 (comments on relationships).
?*Brycon ferox* Steindachner, 1876, *Sber. Akad. Wiss. Wien* **74**: 538, pl. 4 (see note on p. 28).

DISTRIBUTION. Rio Tietê, Parana basin.

COMMENTS. *Catabasis* is included in the synonymy of *Brycon* by virtue of its possessing those characters here used to define *Brycon*, see below and p. 1.

To my knowledge, only two specimens of *B. acuminatus* are known; the holotype in the California Academy of Sciences (CAS 11894) collected from the Rio Tietê by von Ihering and another in the Museu de Zoologia da Universidade de São Paulo (MZUSP 1533).

Concerning the second specimen which forms the basis of the following description, I am informed by Dr N. Menezes that it is recorded as being collected from Taubata close to Rio Paraíba. However, there is some doubt as to the correctness of this locality. It appears that the specimen was part of a collection loaned to the California Academy in *c.* 1930 and was returned to São Paulo in 1949. The specimen was catalogued by CAS as 11867 and determined as *Acestrorhamphus brachycephalus*. Dr Menezes has pointed out to me that despite extensive collecting in both the Rio Tietê and Rio Paraíba, no further specimens have been obtained and that it seems unlikely that *B. acuminatus* occurs in both rivers which have differing ichthyofaunas.

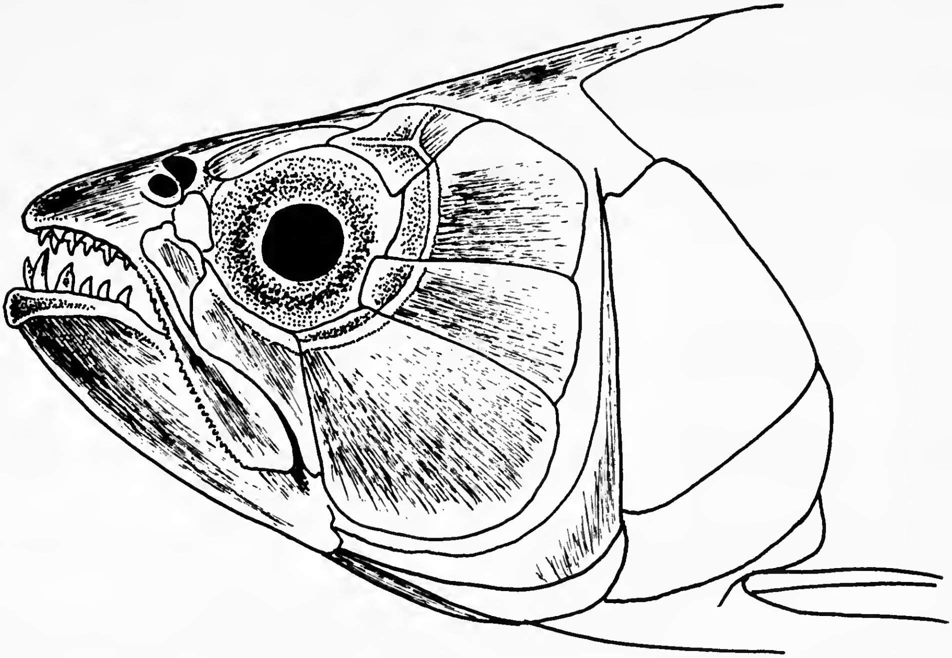
Roberts (1969) examined the holotype but because of damage to the specimen was unable to determine the character of the lower jaw dentition. He found that all the jaw teeth lacked cusps. In specimen MZUSP 1533 minute cusps are present on both upper and lower jaw teeth (Fig. 1). The outer row premaxillary teeth are unicuspid, there are 8 on the right and 9 on the left premaxilla. Forming what I interpret as the 2nd row are 7 teeth, all somewhat larger than those of the outer row. These 2nd row teeth are virtually unicuspid, having only small basal lateral cusps; the 3rd tooth—from the symphysis—in this row is larger than the others. The '3rd row' is comprised of two enlarged, unicuspid teeth close to the symphysis. The maxillary teeth number 19–20 and are downwardly curved unicuspids. The right dentary bears 12 outer and 27 inner teeth. The teeth on the left dentary number 14 and 23 respectively. On both sides of the jaw the inner row extends as far forward as the 6th outer row (counting from the symphysis). There is a single recurved unicuspid tooth behind the first outer tooth on each dentary.

Only the first gill arch on the left-hand side remains intact; the gill-rakers number *ca* 12/13, those on the ceratobranchial are long and spinous.

The superficial resemblance between *B. acuminatus* and *B. alburnus* is striking (cf. Figs 3 & 4). Both species have the same type of elongate snout and lower jaw, and shallow 4th infraorbital. There are, however, differences in dental morphology. Whereas in *B. alburnus* the inner row premaxillary teeth are readily recognizable as typically *Brycon*-like (i.e. as in *B. falcatus*) in morphology and arrangement, in *B. acuminatus* a triserial arrangement is barely discernible (Figs 1 & 2).

Another species from South-east Brazil, *Brycon ferox* may prove to be the senior synonym of *B. acuminatus* (see p. 28).

Proportions and counts of the specimen of *B. acuminatus* MZUSP 1533 are given in Table 1.



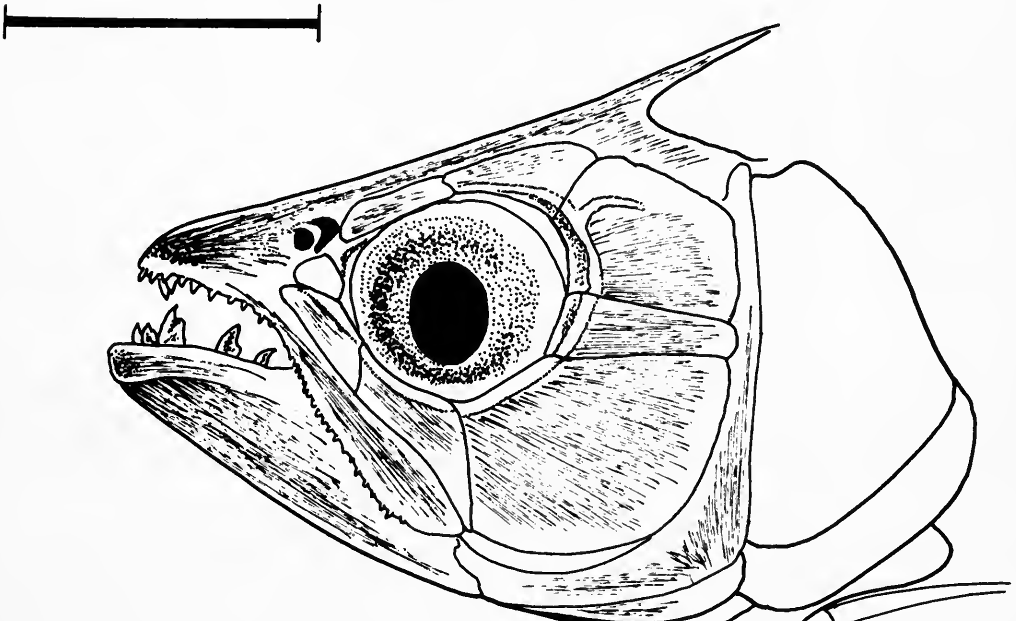


Fig. 3 (upper) *Brycon acuminatus,* head of specimen ZUSP, 140 mm SL. **Fig. 4** (lower) *Brycon alburnus*, head of specimen 1920.12.20 : 63–64, 148 mm SL. Scale = 20 mm.

Table 1 *Brycon acuminatus* counts and proportions of specimen MZUSP 1533.

SL (mm) 140			
D	29·3	Scales	10/51/6
S–D	55·7	Dorsal	ii 9
H	31·8	Anal	iv 24
Sn	30·5	Pectoral	i 13
IO	29·3	Ventral	i 7
Ey	19·0	Gill-rakers	12/13
Mth	23·6	Vertebrae	21 + 24
CpL	8·9	Supraneurals	10
CpD	10·0	Teeth:	
PL	18·5	Pmx 1	9
VL	15·0	2	7
AL	25·3	3	1
DL	22·5	Max	19–20
P–V	21·5	Dent	12–14/23–27/1
PP–V	87·0		

Brycon acutus Böhlke, 1958

A synonym of *B. alburnus.*

Brycon alburnus (Günther) 1859

Chalceus alburnus Günther, 1859, *Proc. Zool. Soc. Lond.*: 149 (description; type locality, Western Andes, Ecuador).

Chalcinopsis alburnus, Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 318 (description; type locality); Steindachner, 1892, *Denkschr. Akad. Wiss. Wien* **59**: 374–375 (description; Guayaquil); Gery, 1972, *Rev. Suisse Zool.* **79** (2): 931–932 (description; Sapo Guyas Province, Ecuador).

Brycon alburnus, Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Boulenger, 1898, *Boll. Musei Zool. Anat. comp. R. Torino* **13** (329): 4 (Rio Peripa & Rio Vinces); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 130–131 (Rio Daule, R. Vinces, R. Barranca); Rendahl, 1937, *Ark. Zool.* **29**A (11): 5–7 (Rio de Clementina, Babahoyo); Ovchynnyk, 1968, *Zool. Anz.* **181**: 245 (reference and Ecuadorian localities); Gilbert & Roberts, 1972 *A preliminary survey of the freshwater food fishes of Ecuador*: 16 & 36 (Rio Guyas drainage); Gery, 1972, *Acta Humboldtiana* no. 2: 8–9 (Rio Pilalo). Gery, 1977, *Characoids*: 335 (reference).

Brycon acutus Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.*, **110**: 67, pl. 4, fig. 1 (description; type localities, Rio Quininde & Rio Cupa, Esmeraldas Province); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Ovchynnyk, 1968, *Zool. Anz.* **181**: 245 (reference, Ecuadorian localities); Roberts, 1969, *Proc. Cal. Acad. Sci.* (4) **36** (15): 438 (description of dentition); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Esmeraldas and Guyas regions of Ecuador, ?Andean east slope.

COMMENTS. *Brycon alburnus* differs from other species currently assigned to the genus in lacking a premaxillary symphysial joint. The premaxillaries are separated by the elongate supraethmoid and are joined syndesmotically. The species also possesses a dental morphology different from its congeners, with the exception of *Brycon acuminatus*; see p. 4. The dentition of *Brycon alburnus* has been described by Böhlke (1958) and Roberts (1969) as *Brycon acutus*, and is illustrated here in Fig. 2.

Gery (1972; 1977) placed *B. alburnus* in the genus *Chalcinopsis* Kner considering (1972) that the type of that genus, *B. striatulus* was a close relative of *B. alburnus*. My observations indicate that these two species share no characters that I would consider to be derived ones.

The five type specimens of *Brycon alburnus* are in a poor state of preservation. In three the caudal fins are missing and in another the last three or four caudal vertebrae, together with the hypurals, are also missing and thus it has not been possible to use this particular specimen for proportional measurement. Another of these three specimens (100 mm SL) has the ventral part of the body, including the pelvic fins, cut away. The only complete specimen is the largest of the five, 119 mm SL.

Colouration. On the type specimens a dense distribution of melanophores is visible on the edges of the pectorals, ventrals and across the dorsal fins. There is also a dark band along the anal fin.

In a non-type specimen from Barranca Alta (BMNH 1920.12.20: 63–4) the colour pattern is particularly well-marked. The paired fins are very dark, the pigment extending almost to their bases. The dorsal fin is crossed by a wide band which fades distally. The anal is plain along a narrow basal region, the remainder is dark, the pigment becoming intensified between the first 7 or 8 rays. The edges of the caudal fin are dark. The caudal spot extends anteriorly to a vertical extending from the last anal ray.

Synonymy: Böhlke (1958) described *Brycon acutus* from the Esmeraldas drainage. I have examined a paratype of this taxon (ANSP 75929) and find that the proportions of this

Table 2 A comparison of counts and proportional measurements between the types of *Brycon alburnus* and *B. acutus*.

B. alburnus, syntypes BMNH 1860.6.16 : 167; 180; 201–202; 204			*B. acutus*, paratype ANSP 75929
SL (mm), 119, 103, 100, 94.			85
	Range	Mean	
D	26·0–27·5	27·1	27·0
S–D	57·0–58·5	57·8	55·6
H	27·7–32·0	30·1	29·0
Sn	30·0–32·0	31·0	31·0
I.O.	24·5–25·5	24·8	24·0
Ey	24·5–27·0	25·3	24·0
Mth	22·5–25·0	23·6	24·0
CpL	10·0–13·5	11·9	13·0
CpD	8·5–9·3 (f3)	8·6	7·1
PL	18·0–24·5	22·1	20·0
VL	9·7–17·0	16·8	15·4
AL	29·5–33·0	31·2	23·5
DL	19·5–23·0	21·7	20·0
P–V	21·0–23·0 (f3)	22·2	22·5
PP–V	100·0–108·0 (f3)	104·0	89·5
Scales	12/57/7 (f2); 11/63/7 (f1)		10/56/7
Dorsal	ii 9		ii 9
Anal	iv 28 (f2), iv 30 (f1)		iv 28
Pectoral	i 12 (f3), i 13 (f1)		i 13
Ventral	i 7		i 7
Gill-rakers	9/13 (f1), 9/14 (f4)		9/13
Vertebrae	23 + 20 (f2), 23 + 21 (f1)		24 + 21
Supraneurals	11		11
Teeth:			
Pmx 1	6–7		7
2	8–10		8
3	2		2
Max	22 (f2), 23 (f1), 25 (f1)		18
Dent	7–10/9–17/1		8/14/1

NB: The fifth type specimen of *B. alburnus* (the smallest) was not used for measurement owing to loss of the caudal skeleton, but was used for fin ray and tooth counts.

specimen, together witn those of the other type specimens given by Böhlke (1958) are within the ranges of those for *B. alburnus*. There are, however, slight differences in tooth counts. Böhlke (1958) states that there are 7–9 teeth in the outer premaxillary series of *B. acutus* and from 19–21 maxillary teeth (1 count 18 on the paratype examined). In *B. alburnus* there are never more than 7 (mean 6) teeth in the outer premaxillary series and 22–25 (mean 24) on the maxilla. It seems likely that this character may reflect populational variation.

Table 3 A comparison of counts and proportional measurements between *Brycon alburnus* from the Guyas and Esmeraldas regions of Ecuador.

BMNH 1920.12.20 : 61–62; 63–64 Guyas (R. Barranca Alta & R. Daule)			BMNH 1898.11.4 : 78–9; 2 uncat. Esmeraldas (R. Vinces; Naranjito)	
SL (mm)	173, 148; 107, 85		243, 154; 160, 157	
D	23·7–27·0	26·1	23·2–28·5	27·0
S–D	56·0–59·0	56·8	46·0–61·0	55·5
H	28·0–30·5	28·7	23·3–28·5	26·9
Sn	30·5–32·0	31·1	30·5–34·0	31·6
IO	23·0–30·5	26·5	25·5–29·5	27·0
Ey	21·3–29·0	24·8	17·7–22·0	20·9
Mth	23·0–26·5	25·0	24·5–26·5	25·2
CpL	9·4–11·5	10·5	7·8–10·8	10·0
CpD	7·6–9·5	8·5	6·5–8·9	8·3
PL	20·0–22·0	21·2	18·2–21·9	20·6
VL	14·1–15·5	14·9	12·6–15·2	13·7
AL	26·0–29·0	27·5	20·0–28·0	25·3
DL	18·5–19·0	18·7	16·9–19·6	18·6
P–V	19·5–23·5	22·2	17·5–22·0	20·8
PP–V	90·0–97·5	99·7	95·0–108·0	100·5
Scales	12/59/7 (f1); 12/60/7 (f1); 12/61/7 (f2)		13/58/7 (f1); 13/60/7 (f2); 13/62/7 (f1)	
Dorsal	ii 9		ii 9	
Anal	iv 32; iv 31; iv 30; iv 28		iv 29 (f2); iv 28 (f2)	
Pectoral	i 12 (f2); i 13 (f2)		i 12	
Ventral	i 7		i 7	
Gill-rakers	9/15 (f3); 10/14 (f1)		9/13 (f2); 9/14 (f1); 9/15 (f1)	
Vertebrae	23 + 22 (f2); 24 + 21 (f1); 24 + 20 (f1)		24 + 22; 24 + 20; 24 + 21; 23 + 22	
Supraneurals	11 (f2); 12 (f1); 13 (f1)		11 (f1); 12 (f3)	
Teeth:				
Pmx 1	6		6–7	
2	8–11		8–11	
3	2		2	
Max	23, 24, 25, 26		24 (f1); 25 (f2); 23 (f1)	
Dent	8/12–15/1		9–11/8–11/1	

Böhlke (1958) mentions an undescribed *Brycon* species from the R. Santiago (Andean east slope) which he considers as related to *B. acutus* but '. . . not as well marked a form' as that species. Again, this species may represent a populational variant of *B. alburnus* (see p. 10).

Counts and proportions for the type series of *B. alburnus* are listed in Table 2 together with those of the examined paratype of *B. acutus*. In Table 3 are listed the ranges and means of other specimens of *B. alburnus* in the BMNH collections which are representative of populations from the Rio Esmeraldas and Guyas drainages.

Brycon amazonicus (Spix) 1829

Chalceus amazonicus Spix, 1829, in Spix & Agassiz, *Selecta genera et species piscium ... Brasiliam*: 68 (description; type locality, Amazon).
Characinus amazonicus, Spix, 1829 *ibid*, pl. 35.
?*Brycon amazonicus*, Müller & Troschel, 1844, *Arch. Naturgesch.* (1): 90; Müller & Troschel, 1845, *Horae Ichth.* 1–2: 15 (both works carry the same brief description; locality, Brasil).

DISTRIBUTION: ?Amazon.

COMMENTS. Valenciennes (1849) considered this species a synonym of *Brycon opalinus* (Cuvier). He further noted that the *Brycon amazonicus* of Müller & Troschel should probably be referred to *Brycon hilarii.*

Günther (1864) placed *B. amazonicus* tentatively in the synonymy of *Brycon opalinus*, noting the discrepancy, according to Cuvier's figure, in the size of the scales between the two species (45 lateral line scales in *B. opalinus* cf. 56–58 in *B. amazonicus*). Eigenmann & Eigenmann (1891) and Eigenmann (1910) placed *B. amazonicus* in the synonymy of *B. opalinus* without comment, a practice followed by Fowler (1950).

There is a close resemblance between Spix's (1829) description and *B. carpophagus*. It is noted that there is a discrepancy between the text and the figure in the number of branched anal fin rays. According to Spix's description they number 24 but the figure shows only 18. Since *B. amazonicus* is known only from an iconotype and Spix's description is too inadequate to identify the species with any other, the best course of action would be to regard *B. amazonicus* a *nomen dubium*.

Brycon argenteus Meek & Hildebrand, 1913

Brycon argenteus Meek & Hildebrand, 1913, *Fieldiana Zool.* **10** (8): 84 (description; type locality, Rio Aruza, Panama); Meek & Hildebrand, 1916, *Fieldiana Zool.* **10** (15): 295, pl. 25 (Rio Chorrera, Bayano and Tuyra basins); Breder, 1927, *Bull. Am. nat. Hist.* **57**: 156–163 (reference in check-list and key; Tuyra); Hildebrand, 1938, *Fieldiana Zool.* **22** (4): 285 (description and discussion); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION: Pacific slope of Panama.

Brycon atrocaudatus (Kner & Steindachner) 1863

Chalceus atrocaudatus Kner & Steindachner in Kner, 1863, *Sber. bayer Akad. Wiss. Munchen* **2**: 227 (description; type locality, 'Westabhange der Andes im Staate Ecuador'); Kner & Steindachner, 1865, *Abh. bayer Akad. Wiss. Munchen* **10** (1): 44, pl. 4, fig. 3 (description; Western Ecuador).
Brycon atricuadatus, Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 336 (description copied from Kner & Steindachner); Starks, 1906, *Proc. U.S. natn Mus.* **30**: 777 (Peru); Pellegrin, 1912, *Miss. Geod. de l'Equateur* **9**: 135 (no locality stated); Eigenmann 1922, *Mem. Carnegie Mus.* **9** (1): 131–133, pl. 23, fig. 3 (synonymy, description; Ecuadorian and Peruvian localities); Pearson, 1937, *Proc. Cal. Acad. Sci.* (4) **22**: 90 (Jequetepeque R., Pacasmayo and Chilete, Peru); Thormählen de Gil, 1949, *Revta. Mus. La Plata* ns **5**, Zool.: 364 (reference; distribution); Hubbs, 1953, *Copeia* (3): 142 (note concerning authority).
Brycon atrocaudatus, Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.* **110**: 62 (synonymy; Ecuadorian localities; discussion); Ovchynnyk, 1968, *Zool. Anz.* **181**: 245 (reference; Ecuadorian localities); Gery, 1972, *Acta Humboldtiana* **2**: 6–7 (Esmeraldas, Rio Pilalo); Gery, 1977, *Characoids*: 339 (reference in key)
Brycon scapularis Fowler, 1911, *Proc. Acad. nat. Sci. Philad.* **63**: 502, fig. 3 (description: type locality, affluent of Chimbo, near Bucay, Ecuador); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference).
Brycon ecuadoriensis Eigenmann & Henn in: Eigenmann, 1917, *Proc. Amer. Philos. Soc.* **56** (7): 687 (description; type locality, Rio Barranca Alta at Naranjito, Ecuador); Tortonese, 1939, *Boll. Musei Zool. Anat. comp. R. Univ. Torino* **47** (3) no. 89: 48 (description; Rio Mira, Ecuador).

DISTRIBUTION. Northern and southern Ecuador into Peru.

COMMENTS. Boulenger (1898) considered *Brycon moorei* to be a synonym of *B. atrocaudatus*. Eigenmann (1922) thought that the variation in scale counts as given by Boulenger indicated that he had in fact misidentified some of his specimens, namely, those from the Rio Mira, Rio Peripa and Rio Zamora, and that these represented *B. oligolepis* Regan 1913. Eigenmann was correct in his surmise as was shown by Tortonese (1939) who re-determined the Festa material that Boulenger had used as *B. oligolepis*. Furthermore, the specimens in the BMNH collections cited by Boulenger as *B. atrocaudatus* from Paramba (Rio Mira) collected by Rosenberg form part of the type series of *B. oligolepis*.

Pearson (1937) recorded the species from the mouth of the Jequetepeque on the Pacific slope of Peru.

Eigenmann (1922) included *B. scapularis* Fowler in the synonymy of *B. atrocaudatus*, an action confirmed by Böhlke (1958) who, in turn, synonymised *B. ecuadoriensis* Eigenmann & Henn.

All the specimens in the BMNH collections previously identified as *B. atrocaudatus* have been re-determined as either *B. oligolepis* or *B. moorei*.

The synonymy followed here is that of Böhlke (1958) but this may eventually prove incorrect. The type specimen of *B. atrocaudatus* cannot presently be located but a comparison of Kner & Steindachner's figure (1863, pl. 4 fig. 3) with that of Eigenmann's (1922, pl. 23, fig. 3) shows two different fishes. Differences lie in the shape of the head, length of the snout, and in colouration. There are differences also between the descriptions of Kner & Steindachner and Eigenmann. The specimen figured by Eigenmann (1922) is one of a sample from Naranjito, Ecuador which Eigenmann states 'are typical'. The Naranjito specimens differ both in colouration and meristics from the other specimens Eigenmann places in *atrocaudatus* which are from Paita. Indeed, the Paita specimens appear to more closely resemble the type specimen than do the Naranjito specimens.

I have examined a specimen from Naranjito which conforms with Eigenmann's figure and description of those specimens and I believe that it represents an undescribed taxon. It does not seem to resemble the unamed *Brycon* species of Böhlke (1958), having a longer snout and different colour pattern.

I am advised by Mr Harald Ahnelt of the Naturhistorisches Museum, Vienna, that a search has failed to trace the type specimen of *B. atrocaudatus*. Until such time as the type can be located and compared with the '*atrocaudatus*' of Eigenmann (1922) and Böhlke (1958) and with the type specimens of *B. ecuadoriensis* Eig. & Henn, which species also occurs in the Naranjito, then caution must be exercised in the application of this name.

Brycon bahiensis Günther, 1864

Brycon bahiensis Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 334 (description; type locality, Bahia); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION. Unknown.

COMMENTS. The type specimen is well-preserved and Günther's description is accurate and acceptable. However, the following notes are added together with the counts and measurements (see Table 4, and Fig. 5).

Dentition. The outer row of premaxillary teeth numbers 11–12, the teeth peg-like and feebly tricuspid. The second row has 8, and the third, 2 teeth. The teeth on the left premaxillary are erupting replacement teeth.

On the dentary there are 11 outer tricuspid teeth, those anteriorly display 4 cusps. There are 15–17 posterior conical teeth which pass medial to the outer row as far as the 8th outer tooth. There are 24 maxillary teeth. Both the upper and lower lips are papillate.

Colouration. There are indications of a dusky edge to the anal fin and of a bar across the dorsal fin. Humeral and caudal spots are faintly visible. Pigment is also present at the base of the caudal fin and along its posterior border.

Another specimen in the BMNH collection is identified as *Brycon bahiensis* (BMNH 1912.11.21 : 1, 157 mm SL, Porto Real, Rio Janeiro; Collected by Dreneuf). This fish has similar proportions to the type but differs in its dentition, possessing only 14 maxillary teeth, 8 outer dentary and 8 outer premaxillary teeth.

Table 4 Counts and proportional measurements for the holotype of *Brycon bahiensis* BMNH 1862.11.23 : 26.

SL (mm) 125			
D	30·4	Scales	8/43/5
S–D	53·5	Dorsal	ii 9
H	24·9	Anal	iv 21
Sn	32·0	Pectoral	I 13
IO	42·0	Ventral	I 7
Ey	29·0	Gill-rakers	12/13
Mth	32·0	Vertebrae	23 + 21
CpL	12·0	Supraneurals	10
CpD	9·5	Teeth:	
PL	20·0	Pmx 1	12
VL	16·7	2	8
AL	29·0	3	2
DL	17·6	Max	24
P–V	23·5	Dent	11/15/1
PP–V	80·5		

Brycon behreae Hildebrand, 1938

Brycon behreae Hildebrand, 1938, *Fieldiana Zool.* **22**: 278 (description and figure; type locality Rio Chiriqui basin and Rio Chagres basin, Panama); Thormählen de Gil, 1949, *Revta. Mus. La Plata* ns. **5**: 359 & 364 (reference, distribution); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Miller, 1966, *Copeia* (4): 785 (reference, distribution); Gery, 1977. *Characoids*: 339 (reference).

DISTRIBUTION. Pacific slope of western Panama.

COMMENTS. Specimens in BMNH collection: 1925.3.6 : 18–27. Rio Chirique del Tire, Pacific slope, Panama. Presented by Dr. Behre. (These had previously been identified as *Brycon striatulus*.)

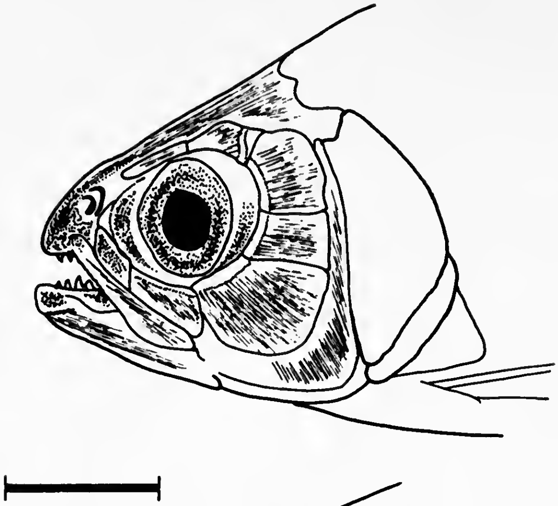
Brycon bicolor Pellegrin, 1909

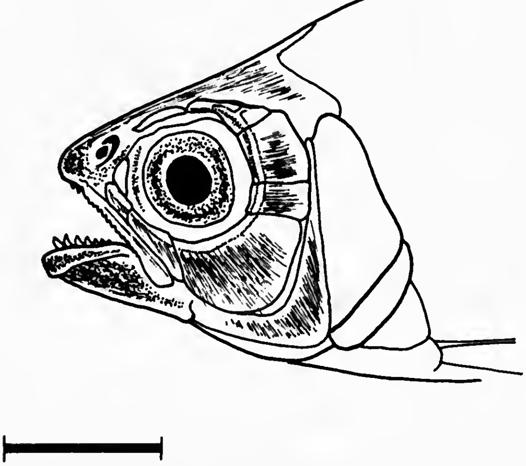
Brycon bicolor Pellegrin, 1909 *Bull. Mus. Hist. nat. Paris* **15** (1): 12 (description; type locality, Orinoco); Myers & Weitzman, 1960, *Stanford ichthyol. Bull.* **7** (4): 103 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Orinoco.

COMMENTS. *Brycon bicolor* has not been recorded as being collected since Pellegrin's original description of 1909. I have examined the three syntypes of this species and find that it is a very characteristic taxon hardly to be confused with any other *Brycon* species.

The most characteristic feature of the species is the colour pattern on the caudal and anal fins (Fig. 8). A dark bar extends diagonally from the base of the caudal peduncle across the upper lobe of the caudal fin. Pigment on the anal fin begins from about the base of the 9th ray and increases to cover the remainder of the fin. In two of the specimens there is a light line extending from the base of the dorsal fin to the supraoccipital process; this may, however, be an artefact of preservation.





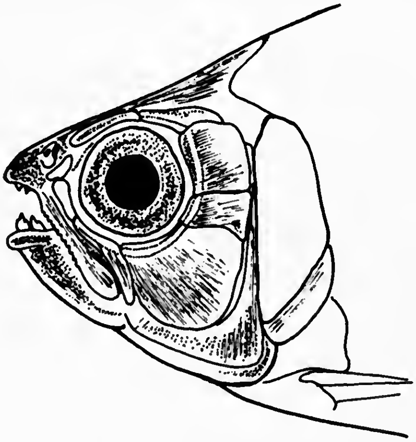


Fig. 5 (upper) *Brycon bahiensis*, head of holotype specimen BMNH 1862.11.23 : 26, 125 mm SL. **Fig. 6** (centre) *Brycon brevicauda*, head of syntype specimen BMNH 1849.4.8 : 42, 91 mm SL. **Fig. 7** (bottom) *Brycon falcatus* head of specimen BMNH 1972.10.17 : 1398–1411. Scales = 10 mm.

Table 5 Counts and proportional measurements for the syntypes of *Brycon bicolor* MNHN 87–746–748.

SL (mm) 111, 114·5, 118·5

	Range	Mean
D	35·2–41·0	38·4
S–D	53·0–55·0	54·2
H	28·0–29·0	28·2
Sn	25·2–26·8	25·4
IO	40·0–44·5	41·5
Ey	26·2–30·0	28·8
Mth	25·0–39·0	37·0
CpL	9·2–10·8	10·2
CpD	10·9–11·3	10·7
PL	19·7–20·7	23·0
VL	16·5–17·8	17·0
AL	22·5–25·2	23·6
DL	22·2–25·1	23·3
P–V	23·5–25·8	25·0
PP–V	76·5–88·0	82·0
Scales	15/57–61/9	
Dorsal	ii 9	
Anal	iv 22 (f2), iv 23 (f1)	
Pectoral	i 13	
Ventral	i 7	
Gill-rakers	15/16, 14/14, 14/15	
Vertebrae	20 + 22	
Supraneurals	8	
Teeth:		
Pmx 1	8–10	
2	8–9	
3	2	
Max	24–27	
Dent	8–11/18–22/1	

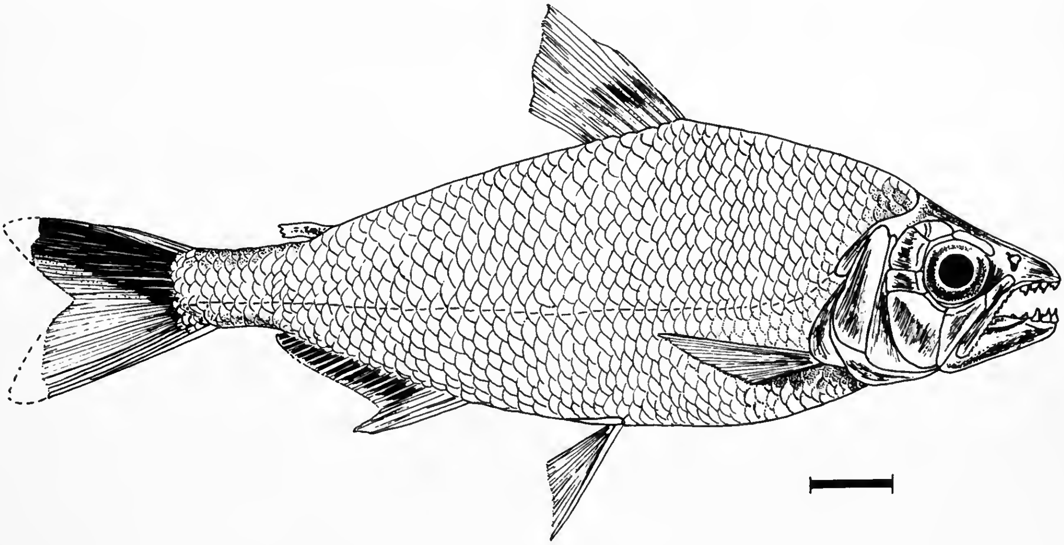


Fig. 8 *Brycon bicolor*, holotype MNHN 87746. Scale = 10 mm.

Other distinctive features are the large number of maxillary and inner dentary teeth (23–27 and 18–22 respectively) and the high number of scales between the dorsal fin and the lateral line (15).

Proportions and counts for the type specimens of *B. bicolor* are given in Table 5.

Brycon bolivarensis (Dahl) 1942

Synonym of *Brycon moorei moorei.*

Brycon brevicauda Günther, 1864

Brycon brevicauda Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 335 (description; type locality, Rio Tocantins, Rio Capin); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Boulenger, 1897, *Ann. Mag. nat. Hist.* (6) **20**: 297 (Marajo Island, specimen not in BMNH collections); Goeldi, 1898, *Boln. Mus. Paranense* **2**: 483 (Upper Tabajos); Fowler, 1950, *Archos Zool. Est. S. Paulo* **6**: 333 (reference and synonymy); Gery, 1964, *Vie et Milieu* (17): 448 (description, Ilha do Bananal, Brasil); Gery, 1977, *Characoids*: 338 (reference).

Brycon brevicaudus, Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference).

?*Brycon matrinchao* Fowler, 1941 (see p. 33).

DISTRIBUTION. Amazon, southern tributaries, R. Capin & R. Tapajos and Mato Grosso.

COMMENTS. The type specimens are a half-skin, 225 mm SL (270 mm total length), and two alcohol preserved specimens 91 & 87 mm SL, the head of the larger specimen is shown in Fig. 6.

The skin is still in a reasonable condition, except that the fin rays are somewhat broken and a few scales are missing. The jaws of the right side are present, but the teeth are badly damaged and an accurate count of those on the premaxilla is not possible.

The two alcohol specimens are well preserved and the colour patterns described by Günther are still present.

The skin is labelled as 'holotype'. This has not, however, been written by Günther and there seem to be no grounds for considering this specimen to be the holotype. The two other specimens are labelled as 'syntypes'. All the specimens appear to be conspecific.

Brycon brevicauda is a member of the *B. falcatus*-group (see p. 46) and indeed appears to 'replace' *B. falcatus* south of the Amazon. A comparison between the two species reveals differences in dentition and meristic characters. In *B. brevicauda* the teeth in the outer premaxillary row number 10–12 cf. 8–9 in *B. falcatus.* The dentary teeth are rather narrow and separated by a distinct gap from one another whereas in *B. falcatus* the teeth are stout and are contiguous. The lower jaw is also longer and shallower in *B. brevicauda* than in *B. falcatus.* Lateral line scales number 54–55 in *B. brevicauda* compared with 46–52 in *B. falcatus*, and mean body depth is 36·3% cf. 38% for the species respectively.

Both species share a similar type of colour pattern i.e. interrupted dark horizontal lines running through the middle of the scales along the dorsal and flanks; well-developed humeral spot (rather more elliptical in *B. brevicauda* than *B. falcatus*) and a black V-shaped caudal fin band. In addition both species possess the same kind of maxillary valve tissue pad and the same low number of vertebrae (total 40). Counts and proportions of the type specimen are given in Table 6. Specimens in BMNH collection:

Syntype	1842.4.20 : 13	Rio Jocantins	Pres. Gardiner
Syntypes	1849.4.8 : 42; 49	Rio Capin	Purch. Stevens (no doubt collected by Bates)

Brycon capito Cope, 1871

Brycon capito Cope, 1871, *Proc. Acad. nat. Sci. Philad.*: 261 (description; type locality, Rio Ambyiacu,

Table 6 Counts and proportional measurements of the syntypes of *Brycon brevicauda*.

BMNH 1864.4.20 : 13		BMNH 1849.4.8 : 42; 49	
SL (mm)	225 Half-skin	SL (mm) 91	87·5
D	37·5	36·0	35·5
S–D	49·0	51·5	52·5
H	21·0	29·5	28·5
Sn	–	29·5	28·0
IO	–	39·0	36·0
Ey	–	31·5	32·0
Mth	–	35·0	34·0
CpL	6·7	14·9	10·8
CpD	10·3	11·0	9·7
PL	17·7	19·7	19·4
VL	13·5	17·6	18·3
AL	25·0	25·4	24·0
DL	–	23·0	24·0
P–V	30·0	25·8	26·5
PP–V	61·0	74·0	76·5
Scales	10/55–56/?6	10/55/6	10/54/6
Dorsal	ii 9	ii 9	ii 9
Anal	iv 24	iv 24	iv 23
Pectoral	i 12	i 13	i 12
Ventral	i 7	i 7	i 7
Gill-rakers	–	12/14	14/14
Vertebrae	–	21 + 20	21 + 20
Supraneurals	–	8	8
Teeth:			
Pmx 1	–	11	12
2	–	9	9
3	2	2	2
Max	15	21	21
Dent	5/10/1	9/14/1	11/15/1

Ecuador); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Fowler, 1906 (1907) *Proc. Acad. nat. Sci. Philad.* **58**: 446, fig. 42 (description of type); Eigenmann & Allen, 1942, *Fishes of Western South America*: 253 (reference); Fowler, 1942, *Boln. Mus. Hist. nat.* Javier Prado, (22–23): 372 (reference); Fowler, 1945. *Los Peces del Peru*: 149 (reference); Thormãhlen de Gil, 1949, *Revta Mus. La Plata* **5**: 364 (reference, distribution); Fowler, 1950, *Archos Zool. Est. S. Paulo* **6**: 334 (reference); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Upper Amazon.

COMMENTS. The type specimen would appear to be the only known example of this species. The type is stated by Fowler (1906) to be 2¼ inches long. His figure shows a fish with a very long head and with pectoral fins extending as far as the ventrals. The fish is obviously a juvenile, and possibly of a species already known from this region.

Brycon carpophagus (Valenciennes) 1849

Chalceus carpophagus Valenciennes in Cuvier & Valenciennes, 1849, *Hist. Nat. Poiss.* **22**: 252 (description, type locality, Essequibo; Amazon); Castelnau, 1855, *Exped. Amer. Sud., Poiss.* **2**: 68, pl. 34, fig. 3 (Rio Sabará, Minas Gereas). ?Kner, 1860, *Denkschr. Akad. Wiss. Wien* **18**: 12 (Irissanga, Rio Parana).

Brycon carpophagus, Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 336 (reference); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference): Fowler, 1950, *Archos Zool. Est. S. Paulo* **6**: 334 (reference). Schubert, 1962, *Atas Soc. Biol. Rio de J.* **6** (3): 27; Godoy, 1975, *Peixes do Brasil* **2**: 287 (description).

?*Salmo matrincham* Natterer in Kner, 1860, *Denkshr. Akad. Wiss. Wien* **18**: 12 (name included in synonymy).

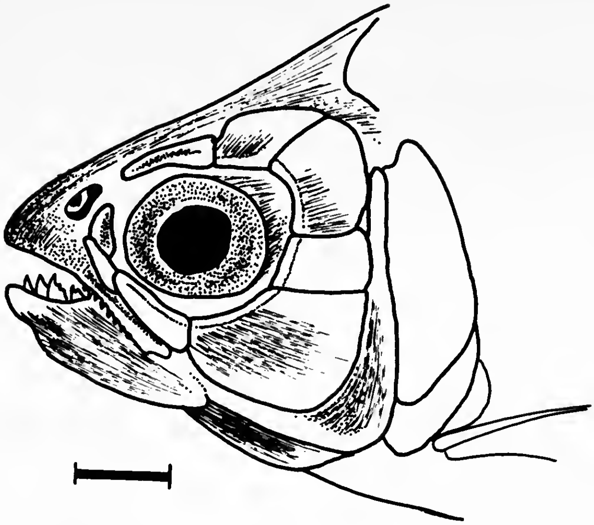
DISTRIBUTION. Amazon, Essequibo.

COMMENTS. I have examined two of the syntypes of *Brycon carpophagus* (proportions and measurements given in Table 7), namely those from the Essequibo and the Amazon, Schomburgk's (Fig. 9) and Montravel's specimens. Both specimens certainly appear to be conspecific and represent a taxon distinct from any other I have examined.

Lütken (1875) thought that *B. carpophagus* might prove to be the senior synonym of *B. orthotaenia* or *B. lundii*. *Brycon orthotaenia* is certainly not conspecific with *B. carpophagus*. As well as the evident differences in meristic and morphometric characters (cf. Tables 7 & 14) there are distinct differences in dental morphology, particularly in the premaxillary teeth (cf. Figs 10 & 22B). In *B. carpophagus* the tooth rows are more narrowly separated than those in *B. orthotaenia* and the teeth of the 3rd inner row are less strongly developed. There are differences also in the size and shape of the infraorbitals, and the

Table 7 Counts and proportional measurements for the syntypes of *Brycon carpophagus*.

MNHN A9832 Essequibo		MNHN A98 Amazon
SL (mm) 280		SL (mm) 255
D	34·0	29·7
S–D	53·0	50·0
H	24·0	25·6
Sn	30·0	29·0
IO	48·5	47·5
Ey	23·2	24·2
Mth	36·0	41·0
CpL	11·6	13·3
CpD	10·5	9·2
PL	18·7	Broken
VL	17·5	Broken
AL	23·0	23·0
DL	19·3	Broken
P–V	25·0	24·0
PP–V	75·0	–
Scales	12/58/9	12/58/8
Dorsal	ii 9	ii 9
Anal	iv 23	iv 24
Pectoral	i 15	i 14
Ventral	i 8	i 7
Gill-rakers	17/17	17/17
Vertebrae	22 + 25	21 + 26
Supraneurals	10	9
Teeth:		
Pmx 1	13	12
2	8	9
3	2	2
Max	22	21
Dent	10/19/1	11/13/1



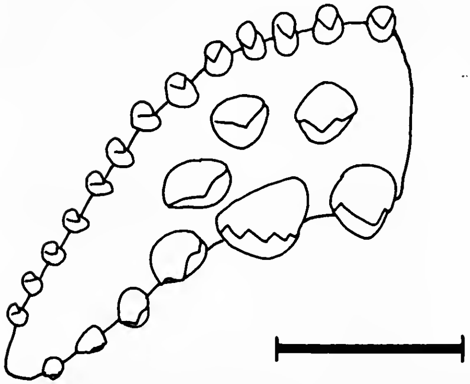


Fig. 9 (upper) *Brycon carpophagus*, head of syntype MNHN 9832. Scale = 10 mm. **Fig. 10** (lower) *Brycon carpophagus*, right premaxilla of syntype MNHN 9832. Scale = 5 mm.

border of the posterior cleithral lamina is extended caudad far more in *B. orthotaenia* than in *B. carpophagus*.

Brycon lundii is considered as possibly synonymous with *B. orthotaenia* (see p. 33).

The third syntype of *B. carpophagus* is a skin collected by Castlenau from the Rio Sabara (MHNH 81.25.3.2 A8615). However, from Castelnau's (1855) illustration (his description is only that of the coloration), and from an examination made on my behalf by Dr K. E. Banister, it is doubtful that the specimen is conspecific with the other two syntypes. From the illustration the scale counts are 9/51–52/?8 and prominent branching of the lateral line tubercles is shown, a feature which does not occur in the other syntypes. Banister (pers. comm) makes the scale count 11/50/6–7; the outer premaxillary teeth 8 (cf. 12–13 in the other syntypes) and those of the dentary 7/10 (cf. 10/19 in the other syntypes). These characters are more in accordance with *Brycon orthotaenia*.

Lütken (1875) notes that Natterer's specimen from Irisinga identified by Kner (1860) as *B. carpophagus* does not correspond with either Valenciennes or Castelnau's description of that species. The scale count given by Kner (1860) as 12/61/7 most closely matches that of *B. orbignyanus*.

Finally, the possibility remains that *B. carpophagus*, as represented by the Schomburgk and Montravel specimens, is a junior synonym of *B. amazonicus* known only from the iconotype (see p. 9).

Brycon cephalus (Günther) 1869

Megalobrycon cephalus Günther, 1869, *Proc. Zool. Soc. Lond.*: 423, fig. 1. (description, type locality, Upper Amazon); Regan, 1905, *Proc. Zool. Soc.*: 190 (Rio Negro; reference to a drawing by Wallace).

Brycon cephalus, Steindachner, 1876 (1877), *Sitz. Akad Wiss. Wien* **74** (9): 590 (synonymy of *Megalobrycon* with *Brycon*); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 56 (reference). Eigenmann, 1910. *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Eigenmann & Allen, 1942, *Fishes of Western South America*: 253 (reference); Fowler, 1942, *Boln. Mus. Hist. nat. Javier Prado* (22–23): 369 (reference); Fowler, 1945, *Los Peces del Peru*: 149 (reference); Thormählen de Gil, 1949, *Revta. Mus. La Plata* ns. **5** Zool.: 364 (reference, distribution); Fowler, 1950, *Archos Zool. Est. S. Paulo* **6**: 334 (reference); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Amazon.

COMMENTS. The type specimens are in a poor and fragile condition. There are virtually no scales left on the bodies and the fins are badly damaged. The cranial bones of one specimen (BMNH 1869.5.21 : 1) are exposed and partly disarticulated.

Counts and proportions for the types are listed below.

Apart from the types, the following specimens identified as *Brycon cephalus* have been examined:

BMNH 1893.4.24 : 37	Loc: Manaus, Coll. Antony (190 mm SL)
BMNH 1925.10.28 : 90	Loc: Manacapuni, Solimões. Coll. Erhardt (235 mm SL)
BMNH 1926.10.27 : 7	Loc: Monte Alegre, Amazon. Coll. Ternetz (180 mm SL)

The proportions and counts of these specimens conform to those of the types. The lateral line scale count ranges from 60–64. Günther, in his description of the types gives a count of *c.* 70, but I can count only approximately 58 scale pockets.

Günther (1869) distinguished his genus *Megalobrycon* from *Bryconops* but did not compare it with *Brycon*. This was presumably on the grounds that he thought there to be no inner row of mandibular teeth and thus it was immediately excluded from such a comparison. Steindachner (1876) pointed out that these specimens were probably aberrant in lacking the two inner teeth, and placed the species in the genus *Brycon*.

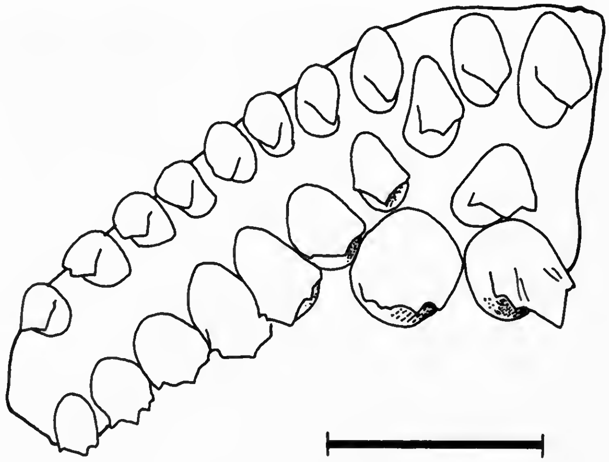


Fig. 11 *Brycon cephalus*, right premaxilla of syntype BMNH 1869.5.21 : 2, 305 mm SL. Scale = 5 mm.

In the larger specimen the two inner teeth are absent, but in the other they are present, although extremely small. These had obviously been overlooked by Günther. In the non-type specimens the inner teeth are very reduced as compared with those in other species. Premaxillary dentition resembles that of *B. falcatus* (Fig. 18).

Table 8 Counts and proportional measurements for the syntypes of *Brycon cephalus*.

	BMNH 1869.5.21 : 1	BMNH 1869.5.21 : 2
SL (mm)	287	305
D	31·5	29·5
S–D	51·0	50·0
H	24·0	24·5
Sn	29·0	30·5
IO	36·0	35·0
Ey	26·8	25·0
Mth	35·0	38·5
CpL	10·1	11·5
CpD	10·5	10·5
PL	broken	17·7
VL	broken	13·0
DL	broken	20·5
AL	22·4	25·3
P–V	24·0	24·0
PP–V	–	74·0
Scales	?13/58/?12	?
Dorsal	ii 9	ii 9
Anal	iv 22	iv 23
Pectoral	i 12	i 12
Ventral	i 7	i 7
Gill-rakers	10/14	15/16
Vertebrae	26 + 21	26 + 22
Supraneurals	10	9
Teeth:		
Pmx 1	10	10
2	8	9
3	2	2
Max	19	19
Dent.	12/6/1	9/11/0

Günther (1869) describes the colouration as appearing to be uniform, but in fact dark pigment still remains on the pectoral fins. Two of the non-type specimens display the colour pattern very well (Fig. 12). The posterior edges of the scales are dark, particularly at the overlapping edges, which gives the effect of zig-zag longitudinal lines. There is a dark humeral patch extending over 5 scales just above the lateral line. A dark band extends across the membrane of the dorsal fin; the pectoral fins are dusky, with a darker band extending across the middle of the fin; the ventral fins are dusky with a lighter edge but the tips of some rays are black. The membrane of the anal fin is very dark, becoming intensely black posteriorly. This darker region appears to extend along the scales at the base of the fin. The ventral surface of the caudal peduncle is black, this colouration extending as an oblique band to cover most of the peduncle and then continuing, still as an oblique band, across the upper lobe of the caudal fin. Some of the pigment runs onto the centre and lower rays of the fin.

The specimen figured by Goulding (1980, fig. 4.7) is undoubtedly *B. cephalus*.

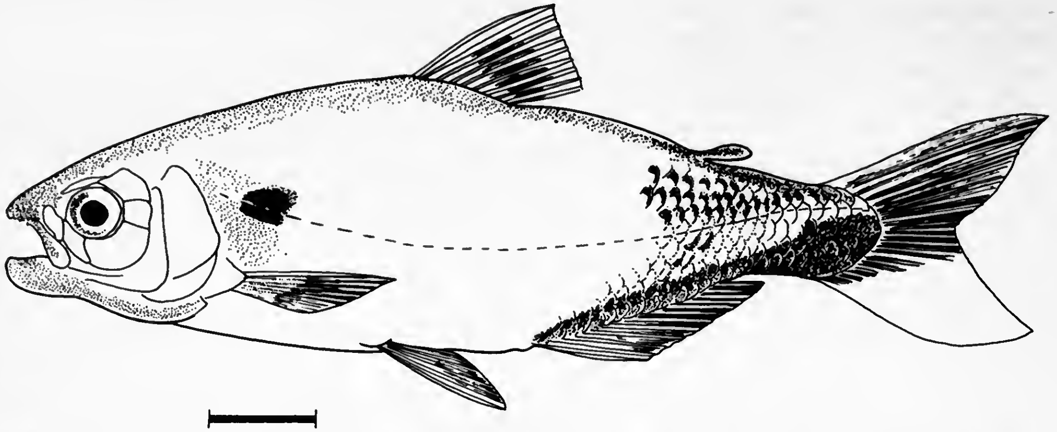


Fig. 12 *Brycon cephalus* (BMNH 1926. 10.27 : 7) showing characteristic body markings. Scale = 20 mm.

Brycon chagrensis (Kner & Steindachner) 1863)

Chalcinopsis chagrensis Kner & Steindachner in Kner, 1863, *Sber bayer Akad. Wiss. Munchen* **2**: 226 (description; type locality, 'Neu-Granada'); Kner & Steindachner, 1865, *Abh. bayer Akad. Wiss. Munchen* **10** (1): 42–43, pl. 5, fig. 3 (description; Rio Chagres); Wagner, 1865, *Abh. bayer Akad. Wiss. Munchen* **10** (1): 91 (reference to distribution); Regan, 1908, *Biologia Centrali Americana* Pisces: 169 (placed in synonymy of *B. striatulus*); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (placed in the synonymy of *B. striatulus*).

Chalcinopsis chagresensis (misspelling), Jordan & Evermann, 1896, *Bull. U.S. natn. Mus.* **47** (1): 337 (placed in the synonymy of *B. striatulus*).

Brycon chagrensis, Steindachner, 1876, *Sber. Akad. Wiss. Wien* **74** (1): 590 (synonymised with *B. striatulus*); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Meek & Hildebrand, 1916, *Fieldiana Zool.* **10**: 295 (description; Chagres basin); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 139 (description; Chagres basin); Behre, 1928, *Ann. Carnegie Mus.* **18**: 317 (placed in synonymy of *B. striatulus*); Hildebrand, 1938, *Fieldiana Zool.* **22**: 276 (discussion of the distinctness of *B. striatulus* and *B. chagrensis* with a note on distribution); Thormãhlen de Gil, 1949, *Revta Mus. La Plata* **5** Zool.: 359 & 364 (reference and note on distribution); Hubbs, 1953, *Copeia* (3): 143 (note on authorship); Miller, 1966, *Copeia* (4): 785 (reference, distribution); Menezes, 1969, *Papéis Dep. Zool. S. Paulo* **22** (20): 218–220 (notes on food); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Central Panama, Atlantic slope.

Brycon coquenani Steindachner, 1917

Brycon coquenani Steindachner, 1917, *Denkschr. Akad. Wiss Wien* **93**: 37, pl. 1, figs 1 & 2 (description; type locality, Rio Coquenan, Venezuela); Schultz, 1944, *Proc. U.S. natn. Mus.* **95**: 307 (description in key); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* 7 (4): 103 (reference); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION. Rio Coquenan, Venezuela.

Brycon coxeyi Fowler, 1943

Brycon coxeyi Fowler, 1943, *Notul. nat.* (119): 3, fig. 2 (description; type locality, Hacienda Los Mascota on Rio Pastaza, Rio Marañon basin, Ecuador, Amazon drainage); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 334, fig. 391 (reference); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* 7 (4): 103 (reference); Ovchynnyk, 1968, *Zool. Anz.* **181** (3–4): 245 (reference); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION. Rio Pastaza, Upper Amazon.

COMMENTS. Possibly synonymous with *B. melanopterus*.

Brycon dentex Günther, 1860

Brycon dentex Günther, 1860, *Proc. Zool. Soc. Lond.*: 240 (description; type locality, Esmeraldas, Ecuador); Eigemann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Boulenger, 1898, *Boll. Musei Zool. Anat. comp. R. Univ. Torino* **13**: 329 (Rio Peripa); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 134, pl. 22, fig. 1 (synonymy, description; Rio Daule, Guayaquil); Rendahl, 1937, *Ark. Zool.* **29A** (11): 6 (Rio de Clementina, Ecuador); Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.* **110**: 70 (measurements tabulated and discussion); Ovchynnyk, 1961, *Zool. Anz.* **181** (3–4): 245 (reference, Ecuadorian localities); Gilbert & Roberts, 1971, *Preliminary survey of the freshwater food fishes of Ecuador*: 26 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

Chalcinopsis dentex (part), Günther 1864, *Cat. Fish Brit. Mus.* **5**: 337 (description, Esmeraldas).

DISTRIBUTION. Ecuador, Pacific drainage.

COMMENTS. *Brycon dentex* is a distinctive species characterized by a long snout which projects well beyond the lower jaw (Fig. 13), leaving nearly all the upper jaw teeth exposed. The outer row teeth are not covered by the lip. The premaxillary has a wide dentigerous surface with the teeth arranged in four rows. The premaxillary symphysial joint is weakly

Table 9 Counts and proportional measurements for the syntypes of *Brycon dentex* BMHN 1860.6.16 : 156–159.

SL (mm) 116, 128·5, 148·2, 198·5

	Range	Mean
D	31·0–33·5	32·2
S–D	51·5–56·0	53·6
H	23·2–24·0	23·9
Sn	31·5–28·2	28·6
IO	31·5–37·0	34·6
Ey	27·0–30·5	29·1
Mth	24·9–28·5	26·7
CpL	11·5–13·4	12·7
CpD	8·5–9·0	8·7
PL	19·7–20·0	19·8
VL	13·7–15·6	14·7
AL	31·0–34·0	32·1
DL	19·0–19·8 (f3)	19·5
P–V	20·5–24·5	22·7
PP–V	83·0–96·0	87·0
Scales	10/47–51/8	
Dorsal	ii 9	
Anal	iv 31 (f3), iv 32 (f1)	
Pectoral	i 11 (f1), i 12 (f3)	
Ventral	i 7	
Gill-rakers	23/23–24	
Vertebrae	23 + 23 (f1), 23 + 24 (f1), 24 + 23 (f2)	
Supraneurals	10 (f1), 11 (f3)	
Teeth:		
Pmx 1	8–9	
2	8–9	
3	8	
4	2	
Max	9 (f1), 11 (f1), 15 (f2)	
Dent.	6–8/7–10/1	

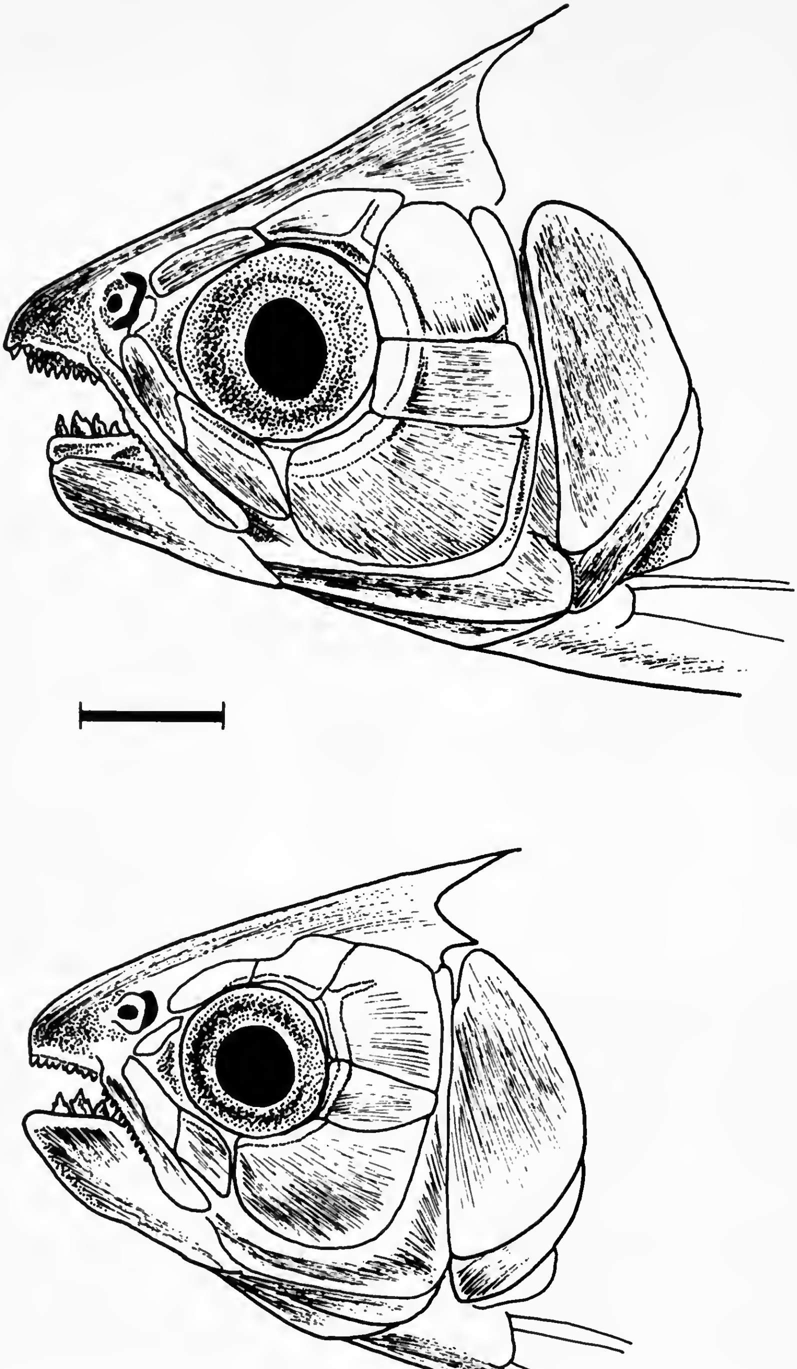
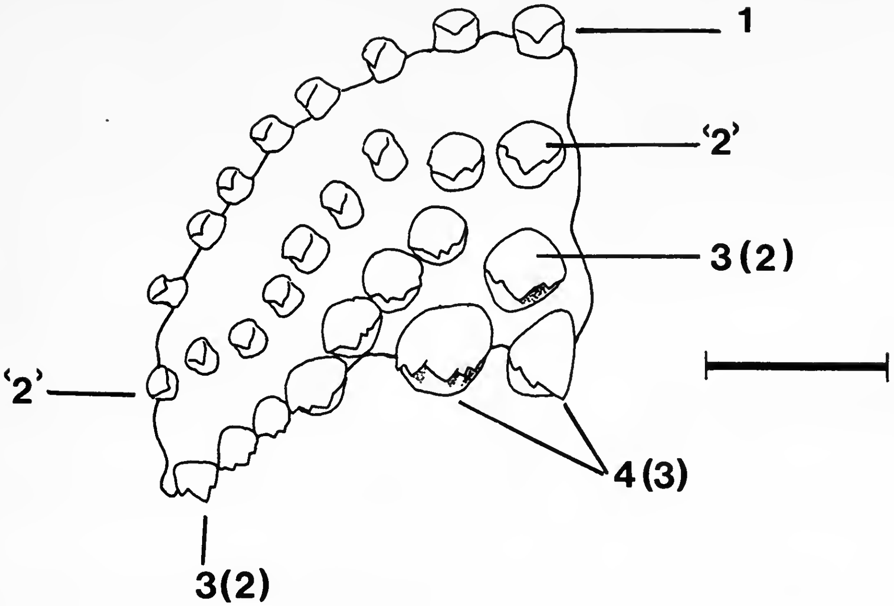


Fig. 13 (upper) *Brycon dentex*, head of syntype BMNH 1860.6.16 : 156, 198·5 mm SL. **Fig. 14** (lower) *Brycon oligolepis*, head of syntype BMNH 1914.5.18 : 5. 157 mm SL. Scale = 10 mm.



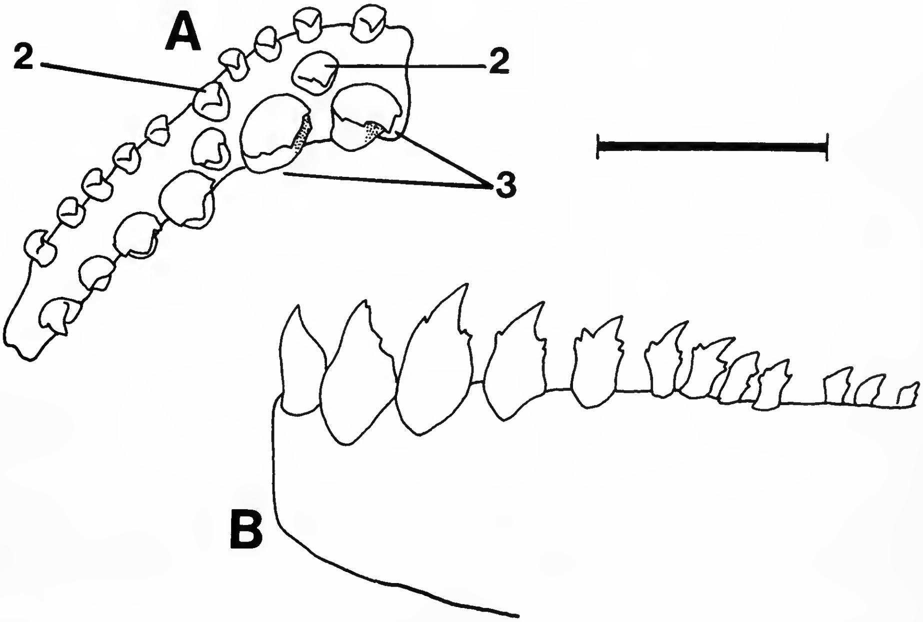


Fig. 15 (upper) *Brycon dentex*, right premaxilla. 1 = 1st, outer row; '2' refers to what is descriptively accepted as the 2nd row, but which ontogenetically is an almagamation of 1st and 2nd row teeth; 3(2) indicates the descriptive 3rd row but which ontogenetically is the 2nd row, and 4(3) refers to the descriptive 4th but ontogenetic 3rd row. **Fig. 16** (lower) *Brycon devillei* A, right premaxilla of syntype MNHN 4517; B, anterior part of left dentary in lateral view. Scale = 5 mm.

developed. Böhlke (1958) stresses that the 'Esmeraldas portion of the type series of *B. dentex* should be compared with the "Western Ecuadorian" specimens of *B. oligolepis* Regan'. In fact all the specimens constituting the type series are from the Esmeraldas. *Brycon dentex* differs from *B. oligolepis* in the arrangement of its teeth (cf. Figs 15 & 21) and in the number of lateral line scales and anal fin rays (cf. Tables 9 & 13). Specimens in the BMNH collections:

1860.6.16 : 156–159 (Syntypes)	Esmeraldas	Pres. Fraser
1976.7.5 : 20	Rio Jubones, near Pasaje	Coll: Bray
1978.7.14 : 18–19	Azuay region, south Ecuador	Coll: Lownie

Brycon devillei (Castelnau) 1855

Chalceus devillei Castelnau 1855, *Exped. Amer. Sud. Poiss.* **2**: 69, pl. 36, fig. 2 (description; type locality, Bahia); Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 333 (reference); Steindachner, 1879, *Denkschr. Akad. Wiss. Wien* **41** (1): 50 (*B. insignis* included in synonymy).

Brycon devillei, Eigenmann & Eigenmann 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Amaral-Campos, 1950, *Papéis Dep. Zool. S. Paulo* **9** (10): 140 (Rio Doce); Fowler, 1950, *Archos Est. Zool. S. Paulo* **6**: 335 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

?*Brycon insignis* Steindachner, 1876, *Sber. bayer Akad. Wiss. Wien* **74** (1): 587; Thormãhlen de Gil, 1949, *Revta Mus. La Plata* ns. **5** Zool.: 360 (reference).

DISTRIBUTION. Bahia, ?Jequitinhonha, ?R. Doce.

COMMENTS. I have examined the holotype of *Brycon devillei* and find this to represent a very distinctive taxon (Fig. 1). The most characteristic features are the length of the jaws and the nature of the dentition. The number of maxillary teeth are the highest for any *Brycon* species (30) and the 2nd row of premaxillary teeth is only narrowly separated from the outer row. The small teeth in the dentary occurring posterior and medial to the outer row number up to 37, again, the highest of any *Brycon* species.

The outer row premaxillary teeth have the central cusp strongly elongate and recurved (Fig. 16). The teeth of the second row are tri- to quadricuspid. Those in the 3rd row are quinqicuspid with the median cusp well-developed. The outer dentary teeth are quadricuspid with the 2nd cusp strongly triangular and recurved. The small medial dentary teeth extend as far forward as the 3rd outer tooth. The inner pair of symphysial teeth are strongly recurved unicuspids.

Many of the scales on the flanks are lost and little colour is present on the body save for a slightly darker dorsum. The dorsal fin is strongly pigmented between the 3rd and 6th rays; the anal fin bears a dark middle band extending posteriorly to the 19th ray; the bases of the upper and lower lobes of the caudal fin are dark and pigment extends along the principal rays of both lobes; both the pectoral and ventral fins are pigmented at their edges.

The general condition of the holotype is good and apart from the loss of scales the only damage is to the upper lobe of the caudal fin, which is missing (Fig. 17).

In overall appearance and dental morphology *B. devillei* most closely resembles *B. acuminatus* and *B. reinhardti*.

Concerning *Brycon insignis*, a direct comparison between Steindachner's (1876) figure and the type of *B. devillei* indicate that they are similar but that the 4th infraorbital of *B. insignis* is narrower than that of *B. devillei*, and that there are more branched anal fin rays (26 cf. 23).

If the taxa described by Steindachner (1876) and Amaral-Campos (1950) are conspecific with *B. devillei* then the distribution of this species is from Bahia to the Rio Jequitinhonha and south to the Rio Doce.

Counts and proportions for the holotype of *B. devillei* are given in Table 10.

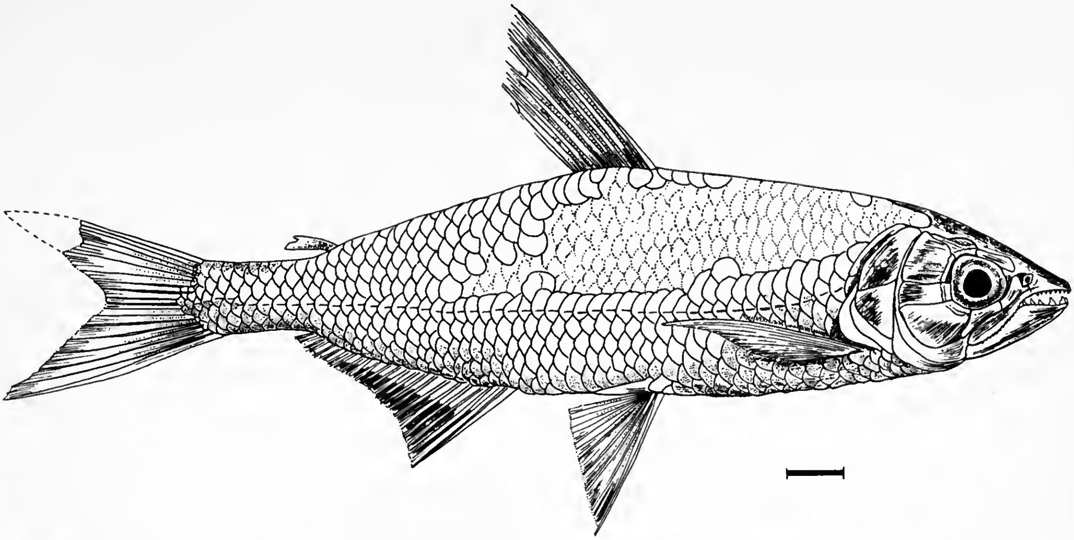


Fig. 17 *Brycon devillei*, syntype MNHN 4517. Scale = 20 mm. The dashed scale margins indicate those scales that are missing.

Table 10 Counts and proportional measurements for a syntype of *Brycon devillei* MNHN 4517, SL (mm) 143.

D	28·0	Scales	12/48/6
S–D	56·5	Dorsal	ii 9
H	28·0	Anal	iv 23
Sn	27·5	Pectoral	i 14
IO	31·2	Ventral	i 7
Ey	26·1	Gill-rakers	13/14
CpL	9·8	Vertebrae	20 + 24
CpD	9·2	Supraneurals	10
PL	22·0	Teeth:	
VL	17·5	Pmx 1	8–9
AL	27·0	2	6–7
DL	24·0	3	2
P–V	20·0	Max	25 (left) 30 (right)
PP–V	110·0	Dent	14–15/35–37/1

Brycon ecuadoriensis Eigenmann & Henn, 1917

Considered to be conspecific with *B. atrocaudatus* by Böhlke (1958: 62–63), but probably a distinct species. See comments on p. 10.

Brycon erythropterum (Cope) 1871

Megalobrycon erythropterum Cope, 1871 (1872), *Proc. Acad. nat. Sci. Philad.* **23**: 263 (description; type locality Rio Ambyiacu).

Megalobrycon erythropterus, Cope, 1871 (1872) *op. cit.* pl. 10, fig. 2.

Brycon erythropterus, Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Gery, 1977, *Characoids*: 335 (?synonym of *B. cephalus*).

Brycon erythropterum, Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 56 (reference); Fowler, 1939, *Proc. Acad. nat. Sci. Philad.* **91**: 263 (Contamana, Peru); Eigenmann & Allen, 1942, *Fishes of Western South America*: 254 (list of Peruvian localities): Fowler, 1942, *Boln. Mus. Hist.*

nat. Javier Prado (22–23): 170 (Peru); Fowler, 1945, *Los Peces del Peru*: 149 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 335 (reference).

DISTRIBUTION. Rio Ambyiacu, eastern Ecuador (Amazon drainage).

COMMENTS. Cope (1871) separated this species from *B. melanopterum* on the basis of colour pattern, position of dorsal fin, number of anal rays and differences in dentition. The differences as given by Cope appear to be those within the range of variability for a single species and it may eventually prove that both *B. erythropterum* and *B. melanopterum* are conspecific. Gery (1977), considered—probably correctly—that *B. erythropterum* may be a synonym of *B. cephalus*.

Brycon erythrura Fowler, 1941

Brycon erythrura Fowler, 1941, *Proc. Acad. nat. Sci. Philad.* **93**: 191, fig. 101 (description; type locality, Rio Jaguaribe, Oros, Russas); Thormãhlen de Gil, 1949, *Revta Mus. La Plata*, ns. **5** Zool.: 359 & 364 (reference and distribution); Fowler, 1950, *Archos Esta Zool. S. Paulo*, **6**: 335, fig. 392 (reference); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference and comment). Gery, 1977, *Characoids*: 651 (reference in index).

DISTRIBUTION. Rio Jaguaribe, Ceara, S.E. Brazil.

COMMENTS. As noted by Myers & Weitzman (1960) this species appears, at least from the figure, to be a *Salminus*. However, the description of the dentition and of the gill-rakers does not quite agreee with that of any species of *Salminus*. Gery (1977) refers this species to *Salminus hilarii*. This must remain a *species inquirenda*.

Brycon falcatus Müller & Troschel, 1844

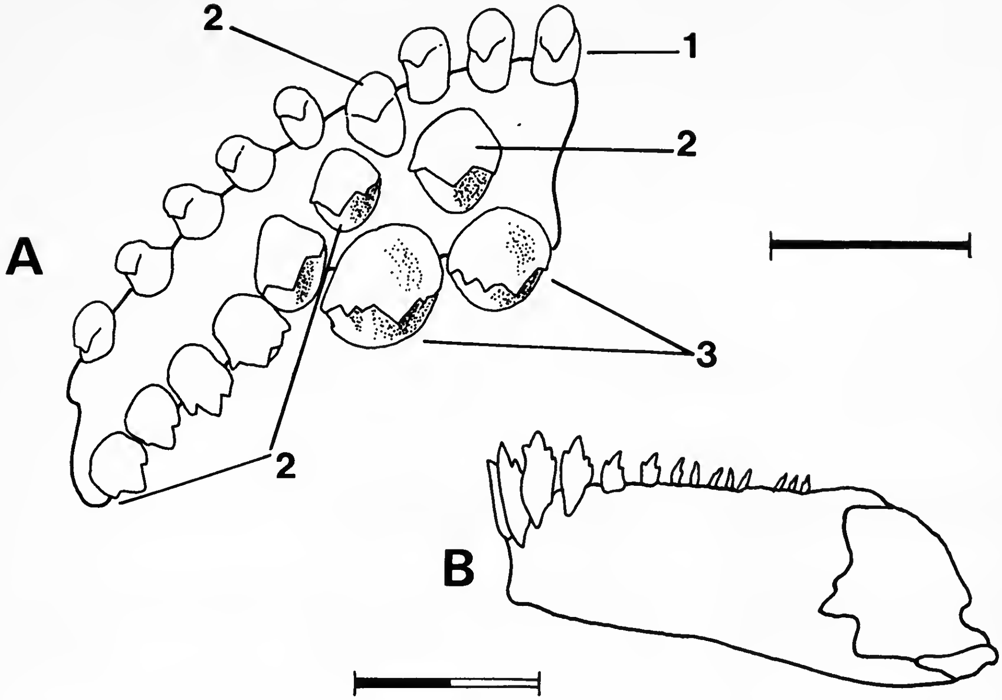
?*Chalceus labrosus* Schomburk, 1841, *Fish Brit. Guiana* **1**: 212.

Brycon falcatus Müller & Troschel, 1844, *Arch. Naturgesch* (1): 90 (brief description; type locality, Guiana; Surinam); Müller & Troschel, 1845, *Horae Ichth.* (1–2): 29, pl. 6, fig. 1 (description; Rivers of British Guiana and Surinam); Müller & Troschel, 1848 in Schomburgk, *Reisen in British-Guiana* **3**: 635; Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 334 (Essequibo; Surinam); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Goeldi, 1898, *Boln. Mus. Paranense* **2**: 483 (Capim); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Eigenmann, 1912, *Mem. Carnegie Mus.* **5**: 371, pl. 54, fig. 2 (synonymy, description, Guiana localities); Steindachner, 1917, *Denkschr. Akad. Wiss. Wien* **93**: 36 (Rio Surumu, Rio Branco); ? Nakashima, 1941, *Boln. Mus. Hist. nat. Javier Prado* ano 5 **16**: 70 (Iquitos); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 335 (reference); Thormãhlen de Gil, 1949, *Revta Mus La Plata*, ns. Zool. **5**: 360 (reference); Gery, 1964, *Vie et Milieu* (17): 450 (reference in key); Gilbert & Roberts, 1971, *Preliminary survey of the freshwater food fishes of Ecuador*: 26 (Amazon drainage); Gery, 1977, *Characoids*: 338 (reference in key).

Brycon schomburgki Müller & Troschel, 1844, *Arch. Naturgesch* (1): 91 (description; Guiana); Müller & Troschel, 1845, *Horae Ichth.* **1**: 29, pl. 6, fig. 2 (description; type locality, Essequibo); Müller & Troschel, 1848 in Schomburgk, *Reisen in British-Guiana* **3**: 96 (lower Essequibo); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1912, *Mem. Carnegie Mus.* **5**: 371 (included in synonymy of *B. falcatus*).

DISTRIBUTION. Amazon; Guyana; Surinam.

COMMENTS. In their original description Müller & Troschel (1844) did not designate type specimens, the locality was simply stated as 'Hab. in Guiana et Surinam'. In 1845 the authors made a full description stating a measurement of 9 zoll which would appear to be applicable to the specimen illustrated in plate 6. The specimens deposited in Berlin were those collected by Schomburgk (Essequibo) and Diepering (Surinam) and it would appear that these were the only specimens used for the description. Günther (1864) notes that Schomburgk's specimens in the BMNH are the types of the species. However, there is no evidence to support this and it would appear that the type specimens are those in Berlin.



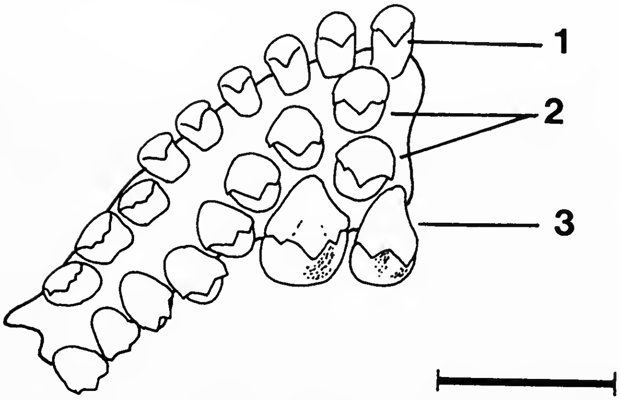


Fig. 18 (upper) *Brycon falcatus* A, occlusal view of right premaxilla. Scale = 3 mm; B, lateral view of left dentary. Scale = 10 mm. **Fig. 19** (lower) *Brycon guatemalensis*, occlusal view of right premaxilla. The 'misplaced' medial symphysial tooth is reckoned as belonging to the 2nd row (cf. Fig. 15). Scale = 5 mm.

Ontogenetic change is apparent in overall body proportions. Juveniles (less than 50 mm SL) are shallow bodied with a somewhat concave profile over the head. Larger specimens are deep bodied with a distinctly convex profile (Fig. 7). Premaxillary teeth are characteristically massive (Fig. 18).

Examination of stomach contents (pers. obs) show this species to be completely omnivorous. Contents include plant remains (stems and seeds); insects, (Coleoptera and Hymenoptera) and fish (catfish spines, possibly pimelodontid, and characoids, *Bryconops* sp.).

Brycon falcatus is recorded from the Amazon and Guianas. It apparently occurs in the Upper Amazon (Gilbert & Roberts, 1971) but the record from Iquitos of Nakashima (1941) must be regarded as dubious as this author gives a lateral line scale count of 68 (cf. 46–52 in specimens listed below).

Specimens in the BMNH collection:

1969.12.12 : 1–3 (previously unregistered)	British Guiana	Pres. Schomburgk
1864.1.21 : 35–36	Essequibo River, British Guiana	Pres. Erhardt
1870.3.10 : 28	Surinam	Pres. Kappler
1866.9.10 : 20	Surinam	Pres. Kappler
1866.9.10 : 23	Surinam	Pres. Kappler
1864.10.3 : 6	British Guiana	
1911.10.31 : 350	Turkeit, British Guiana	Pres. Eigenmann
1934.9.12 : 321–32	Upper Cuyuni, British Guiana	Pres. Carter
1972.7.27 : 52–76	Rupununi District, Guyana	Pres. Lowe-McConnell
1972.10.17 : 1398–1411	Moraballi, Essequibo, Guyana	Pres. Liley
1981.6.9 : 1–6	Nickerie district, Surinam	Pres. U.S. Natn. Museum

Brycon ferox Steindachner, 1876

Brycon ferox Steindachner, 1876, *Sber Akad. Wiss Wien.* **74**: 538, pl. 4, figs 1 & 1a (description; type locality, Rio Mucuri); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Thormãhlen de Gil, 1949, *Revta Mus. La Plata* ns. **5** Zool.: 360 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 337 (reference); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Rio Mucuri.

COMMENTS. From Steindachner's description and figures *Brycon ferox* appears to be closely related to, if not conspecific with *B. acuminatus*. Scale and fin ray counts match, as does the colour pattern. The elongate central cusps of the lower teeth shown in Steindachner's (1876) fig. 1a also closely resemble the tooth form of *B. acuminatus*. Steindachner (1876) points out the absence in one specimen of the two inner symphysial lower jaw teeth and it is presumably that specimen which he illustrates. Until such time as the holotypes of *Brycon ferox* and *B. acuminatus* can be compared directly then I retain both as separate taxa.

Brycon fowleri Dahl, 1955

Brycon fowleri Dahl, 1955, *Revista Linneana* **1**: 11–19; Myers & Weitzman, 1960, *Stanford Ichthyol. Bull* 7 (4): 103 (reference); Dahl, 1971, *Los Peces del Norte de Colombia*: 125, fig'd. (description).

DISTRIBUTION. Rio Sinu, Colombia (Caribbean slope).

COMMENTS. Original description of this species not seen. Dahl (1971) says that the species is endemic to the Rio Sinu. From the illustration the fish appears very like *B. oligolepis* but seems to possess a very short based dorsal fin.

Brycon guatemalensis Regan, 1908

Brycon guatemalensis Regan, 1908, *Biologia Centrali Americana,* Pisces: 168 (description; type localities, Rio Chisoy, R. Usumacinta, R. Motagua, Lake Yzabel, Guatemala); Meek, 1914, *Fieldiana Zool.* **10** (10): 108 (Costa Rican localities); Eigenmann, 1922, *Mem. Carnegie Mus.* **9**: 130 & 134 (reference and in key); Fowler, 1923, *Proc. Acad. nat. Sci. Philad.* **75**: 26 (description; Eden and Upper Tunky, Atlantic coast of Nicaragua); Hildebrand, 1938, *Fieldiana Zool.* **22** (4): 281 (description, distribution); Carr & Giovannoli, 1950, *Occ. Pap. Mus. Zool. Univ. Mich.* **523**: 10–11 (Rio Choluteca and tributaries, Honduras); Miller, 1966, *Copeia* (4): 785 (reference; distribution); Bussing, 1966 (1967), *Revta Biol. Trop.* **14** (2): 236 (reference; Costa Rica); Alvarez del Villar, 1970, *Peces Mexicanus*: 46 (description contained in key); Astorqui, 1971, *Revta Biol. Trop.* **19** (1–2): 27 Lake Nicaragua); Gery, 1971, *Aquarium* **4** (7): 49–50 (Punta Gorda, British Honduras); Bussing, 1976, in *Investigations of the Ichthyofauna of Nicaraguan Lakes* ed. Thorson T. B. Univ. of Nebraska: 160–161 (distribution); Gery, 1977, *Characoids*: 335, 339 (reference).

Chalcinopsis dentex (part), Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 337; Günther, 1868, *Trans. Zool. Soc. Lond.* **6**: 478 (Guatemalen specimens); Gill & Bransford, 1877, *Proc. Acad. nat. Sci. Philad.* **29**: 188 (description; Lake Nicaragua).

Brycon dentex (non Günther, 1860), Jordan & Evermann, 1896, *Bull. U.S. natn Mus.* **47** (1): 337 ('Yucatan to Ecuador'); Eigenmann & Ogle, 1907, *Proc. U.S. natn. Mus.* **33** (1556): 30 (Nicaragua); Meek, 1907, *Fieldiana Zool.* 7 (4): 109 (description; Lake Nicaragua).

DISTRIBUTION. Mexico, Guatemala, Honduras, Costa Rica, ?Nicaragua.

COMMENTS. This species is characterized by an almost straight dorsal profile. The pectoral, ventral and anal fin rays of two specimens (♂♂) bear denticulate protuberances. I have not found this feature in any other *Brycon* species examined (but see Kramer, 1978, cited under *B. petrosus*). The papillate lips are extremely well-developed.

The counts and proportions for the type specimens are listed in Table 11; all appear to be conspecific.

The species is reported as having a wide distribution, from Mexico to Guatemala (Miller, 1966). Jordan & Evermann (1896) give the range as from Yucatan to Ecuador but I have been unable to trace a reference to this species' occurrence in Yucatan. Regan (1908) noted that *B. guatemalensis* recorded from Lake Nicaragua by Gill and Bransford (1877) and Meek (1907), cited in those papers as *Brycon dentex*, was probably distinct from *B. guatemalensis*. Fowler (1923) thought there were no differences between his specimens from the Atlantic slope of Nicaragua, and those from Guatemala. Astorqui (1971) examined material from Lake Nicaragua but compared this only with the descriptions of Günther and Regan, and incorrectly synonymised *Brycon dentex* Günther 1860 (the Ecuadorian species) with *B. guatemalensis*. Regrettably I have no specimens available from Lake Nicaragua and am thus unable to confirm the opinion of Regan (1908) on the distinctiveness of the Nicaraguan taxon.

I have examined specimens determined as *B. guatemalensis* from Guarumo on the Atlantic slope of Panama collected by Dr. Behre. Hildebrand (1938, p. 281) states that he had not seen any of Behre's Panamanian specimens but on the basis of anal fin ray and scale counts considered them to belong to *B. guatemalensis*. The two specimens examined differ from the types in possessing slender bodies, M = 25·9% of SL cf. 31%; sloped dorsal profile cf. straight in *B. guatemalensis*; short caudal peduncle, M = 8·4% cf. 9·4%; shorter pectoral fin, M = 18·4% cf. 22·2%, and shorter anal fin, 25·1% cf. 31·2%. There are 8 scales above and 6 below the lateral line, cf. 10/8 in *B. guatemalensis*. The Panamanian specimens also exhibit a different preserved coloration in which the back is very dark, as are the pectoral fins. The type and arrangement of the dentition is almost identical in the two taxa (Fig. 19).

Behre (1928) also noted that his specimens differed from Regan's and quotes Eigenmann (a reference which I am unable to trace) to the effect that *B. argenteus* is identical with *B.*

guatemalensis. Hildebrand (1938) has shown that this is not the case. I have no specimens of *Brycon argenteus* to hand and am unable to say with certainty whether or not Behre's '*guatemalensis*' is conspecific with *B. argenteus*. Using Hildebrand's keys (1938, and in Eigenmann, 1922) these specimens do not key out satisfactorily to any of the Central American species but appear closer to *B. argenteus* than to any other species.

I would consider that this Atlantic slope form is not *Brycon guatemalensis* or *B. argenteus* and that it possibly represents a new species. However, only more extensive collections will resolve this problem and that concerning possible difference between lacustrine and fluviatile *B. guatemalensis*.

In Tables 11–12 the ranges are shown for the syntypical series from Rio Motagua, and individual proportions for those from the other type localities. The calculated means for the entire type series are compared with those of the two specimens from the Atlantic slope of Panama.

Brycon henni Eigenmann, 1913

Brycon henni Eigenmann, 1913, *Indiana Univ. Stud.* **18**: 36 (description; type locality, Upper Cauca and Dagua); Eigenmann, 1922, *Mem. Carnegie Mus.* **9**: 135, pl 22, fig. 2 (description; Colombian localities); Miles, 1947, *Los Peces del Rio Magdalena*: 160, fig. 114 (description; distribution); Myers

Table 11 Counts and proportional measurements for the syntypes of *Brycon guatemalensis*.

BMNH 1864.1.26 : 226–9 Rio Motagua		1864.1.26 : 387 Lake Yzabel	1869.2.23 : 8 Rio Chisoy	1865.4.29 : 40 R. Usumacinta
SL (mm) 214, 275, 341		72·5	177	231
	Range			
D	31·3–33·5	29·0	30·0	29·5
S–D	53·5–55·0	53·0	52·5	53·5
H	23·0–24·2	24·8	24·9	24·8
Sn	23·6–30·9	27·8	29·5	30·0
IO	38·0–46·0	27·8	34·0	40·5
Ey	22·0–25·0	33·3	25·0	24·5
Mth	27·0–32·0	27·8	29·5	30·0
CpL	11·3–11·7	12·4	11·9	10·8
CpD	9·5–9·8	9·6	9·1	9·1
PL	22·0–22·5	20·6	19·2	20·8
VL	15·5–16·7	15·3	13·5	16·0
AL	28·5–33·0	27·6	27·0	30·0
DL	18·4–20·9	20·0	18·0	19·0
P–V	21·0–24·0	19·4	25·0	26·0
PP–V	93·0–109·0	107·0	77·0	80·0
Scales	10/54/8	10/59/8	10/55/8	9/55/8
Dorsal	ii 9	ii 8	ii 9	ii 9
Anal	iv 30 (f1), iv 32 (f2)	iv 31	iv 30	iv 30
Pectoral	i 12 (f2), i 13 (f1)	i 12	i 12	i 12
Ventral	i 7	i 7	i 7	i 7
Gill-rakers	12/14, 14/15, 13/14	11/16	14/15	12/15
Vertebrae	23 + 22	23 + 22	23 + 22	24 + 22
Supraneurals	10 (f1), 11 (f2)	10	10	10
Teeth:				
Pmx 1	7–9	8	9	8
2	7–10	8	8	8
3	2	2	2	2
Max	13 (f1), 15 (f2)	11	15	13
Dent	8–11/8–9/1	7/8/1	9/7/1	9/10/1

Table 12 Comparison of the means for proportional measurements between all syntypes of *Brycon guatemalensis* and two specimens from Garurno, Panama.

B. guatemalensis mean of all syntypes		*Brycon 'guatemalensis'* Garurno, Panama BMNH 1925.3.6 : 16–17
		SL (mm) 215, 125
D	31·0	25·9
S–D	53·5	53·2
H	24·2	24·8
Sn	26·3	30·5
IO	37·8	34·5
Ey	25·3	25·8
Mth	29·4	26·2
CpL	11·5	12·4
CpD	9·4	8·2
PL	21·1	18·4
VL	15·5	14·2
AL	29·5	25·1
DL	19·2	18·1
P–V	22·9	21·8
PP–V	93·9	77·2
Scales	10/55/8	8/55/6
Dorsal	ii 9	ii 9
Anal	iv 30	iv 31
Pectoral	i 12	i 12
Ventral	i 7	i 7
Gill-rakers	13/15	12/15

& Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Dahl, 1971, *Los Peces del Norte de Colombia*: 124 (distribution; fig'd); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Colombia, Pacific drainage; R. Cauca, R. San Juan, R. Dagua, R. Patia and R. San Jorge.

Brycon hilarii Valenciennes) 1849

Chalceus hilarii Valenciennes in Cuvier & Valenciennes, 1849, *Hist. Nat. Poiss.* **22**: 246 (description; type locality, Rio San Francisco, Brasil); Castelnau, 1855, *Exped. Amer. Sud. Poiss.* **3**: 68, pl. 36, fig. 1 (Salinas).

Brycon hilarii, Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 336 (reference); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Boulenger, 1900, *Boll. Musei Zool. Anat. comp. R. Univ. Torino* **15** (370): 3 (Carandasiñho); Eigenmann & Ogle, 1907, *Proc. U.S. natn Mus.* **33**: 30 (Paraguay); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Bertoni, 1914, *Fauna Paraguaya,* Peces: 11 (Paraguay); Fowler, 1932, *Proc. Acad. nat. Sci. Philad.*: 357 (Descalvados, Mato Grosso); La Monte, 1935, *Am. Mus. Novit.* **784**: 7 (Rio Jurua); Bertoni, 1939, *Rev. Soc. Cient Parag.* **4** (4): 55 (Paraguay); Thormãhlen de Gil, 1949, Revta Mus. La Plata ns. **5**, Zool.: 360 (reference); Amaral-Campos, 1950, Papéis *Dep. Zool. S. Paulo* **9** (10): 140 (description; Para; Mato Grosso); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 366, fig. 393 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

Brycon hilarlii (misspelling), Eigenmann & Kennedy, 1903, *Proc. Acad. nat. Sci. Philad.* **55**: 523 (Arroya Trementina, Paraguay).

DISTRIBUTION. Amazon; R. San Francisco, Brasil; R. Paraguay.

Specimens in BMNH collection:

1910.5.26: 19–20 Paraguay R. (Pan de ezucar), Brazil. Pres. Tudor-Grant

Brycon insignis Steindachner, 1876

?Synonym of *Brycon devillei.*

Brycon iquitiensis (Nakashima) 1941

Holobrycon iquitiensis Nakashima, 1941, *Boln. Mus. Hist. nat. Javier Prado,* ano 5 (15): 72–73, fig'd.; Gery, 1977, *Characoids*: 651 (reference in index).

Distribution. ?Upper Amazon.

Comments. The reason for placing this species in the 'genus' *Holobrycon* (see p. 41) is not clear and no justification for this action is made by Nakashima. No locality is stated nor is there indication of the number of specimens on which the description is based. This 'species' is probably one which is already known from the Upper Amazon. Gery (1977), refers the species to *Salminus hilarii.*

Brycon juanensis Rendahl, 1941

Synonym of *Brycon meeki.*

Brycon juradoensis Fowler, 1944

Synonym of *Brycon juanensis*, (see Böhlke, 1958), = *B. meeki* (see above).

Brycon labiatus Steindachner, 1880

Brycon labiatus Steindachner, 1880, *Denkschr. Akad. Wiss Wien* **42**: 75, pl. 3, fig. 1 (description; type locality, Cauca, Colombia); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Steindachner, 1902, *Denkschr. Akad. Wiss Wien* 72: 143 (Barranquilla; Barrancas, R. Lebrija).

Othonophanes labiatus, Eigenmann, 1903, *Smithson. misc. Collns.* **45**: 145 (brief description of the genus); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Eigenmann, 1922, *Mem. Carnegie Mus.* **9**: 139 (reference); Gery, 1977, *Characoids*: 335, 339 (reference).

Distribution. Cauca, Colombia.

Comments. The presence of an external mandibular flap in this species caused Eigenmann (1903) to assign it to a new genus, *Othonophanes.* There is some interspecific variability in the eversion of the lower lip and this cannot be regarded as a 'generic character'.

Brycon lineatus Steindachner, 1866

Synonym of *Brycon orbignyanus*, (see Ringuelet, Aramburu and Aramburu, 1967, pl. 35).

Brycon longiceps Steindachner, 1879

Brycon longiceps Steindachner, 1879, *Anz. Akad. Wiss. Wien* **16**: 150 (brief description, no type locality stated); Steindachner, 1879, *Denschr. Akad. Wiss. Wien* **41**: 156, pl. 1, fig. 5 (Ciudad Bolivar, Venezuela); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference; Orinoco); Schultz, 1944, *Proc. U.S. natn Mus.* **95**: 307 (reference); Gery, 1977, *Characoids*: 339 (reference).

Distribution. Apure—Orinoco, Venezuela.

Brycon lucidus (Kner)

This citation appears in Eigenmann, 1912, *Mem. Carnegie Mus.* **5**: 69 as a reference to the species occurring in the Rio Branco. It is obviously an error for *Bryconops lucidus* Kner, 1859.

Brycon lundii Reinhardt, 1874

Brycon lundii Reinhardt, 1874 in Lütken *Overs. K. danske Vidensk. Selsk. Forh.* (3): 135 (description; type locality, Rio das Velhas, Brasil); Lütken, 1875, *K. dansk. Vidensk. Selsk. Skr.* **12**: 221–223, fig'd. (discussion); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 54 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Steindachner, 1876, *Sber. Akad. Wiss Wien* **74** (9): 585 (description; R. Parahyba); Steindachner, 1917, *Denkschr. Akad. Wiss Wien* **93**: 38 (Barra); Amaral-Campos, 1950, *Papéis Dep. Zool. S. Paulo* **9** (10): 141 (description; R. San Francisco); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 337 (reference); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* 7 (4): 103 (reference); Gery, 1977, *Characoids*: 335, 339 (reference).

Triurobrycon lundii, Eigenmann, 1909, *Ann. Carnegie Mus.* **6** (1): 33; Godoy, 1975, Peixes do Brasil **2**: 288 (description).

Distribution. Rios das Velhas, São Francisco and Parahyba, S.E. Brazil.

Comments. Eigenmann (1909) erected the genus *Triurobrycon* to contain *B. lundii*. The basis for his generic separation was the elongate middle caudal fin rays of this species. This, however, is a feature of several other Amazonian species and by itself cannot be used to separate taxa. There are admittedly indications that the group of species with extended mid caudal rays share dental and other derived osteological characters (see p. 46) and it may be that when interrelationships of the various species groups are better understood generic status will have to be recognized.

Lütken (1875) compared *B. lundii* with *B. orthotaenia* and considered the possibility that they were synonymous. The only differences Lütken found between the species were the absence of inner symphysial teeth in the lower jaw of *B. orthotaenia*, and the difference in lateral line scale counts (59–61 in *B. lundii* cf. 53 in *B. orthotaenia*). Lütken used Günther's (1864) description for his data on *B. orthotaenia*.

The lack of inner teeth in the lower jaw of the type specimen of *B. orthotaenia* is an artefact, and the lateral scales number 48–49 in standard length (see p. 41). Lütken's lateral line count of 59–61 for *B. lundii* is obviously arrived at by extending the count to the base of the caudal fin. A standard length count of Lütken's figure gives 49–50 scales which is in accordance with that of *B. orthotaenia*.

Doubtless when direct comparison is made between the types of *B. lundii* and *B. orthotaenia* they will be found to be conspecific.

Brycon matrinchao Fowler, 1941

Brycon matrinchao Fowler, 1941, *Proc. Acad. nat. Sci. Philad.* **93**: 192, fig. 102 (description; type locality, Rio Parnaiba, Terezina, Piaui); Thormãhlen de Gil, 1949, *Revta Mus. La Plata* ns **5** Zool.: 360 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 337 (reference); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* 7 (4): 103 (reference); Gery, 1964, *Vie et Milieu* suppl. 17: 450 (in key); Gery, 1977, *Characoids*: 338 (in key).

Distribution. R. Parnaiba, Brazil.

Comments. This species is possibly conspecific with *Brycon brevicauda*.

Brycon medemi Dahl, 1960

Brycon medemi Dahl, 1960, *Caldesia* **8** (39): 461, fig'd. (description; type locality, Quebradas La Noche & Unguia, Upper & Lower Atrato, Colombia); Gery, 1977, *Characoids*: 339 (reference).

Distribution. Atrato, Colombia.

Comments. Dahl (1960) states that the dentition of this species is reminiscent of *B. alburnus* and *B. atrocaudatus*. His description would suggest closer affinity to *B. atrocaudatus*. He also mentions intraspecific variation between those specimens from lower and upper parts of the river.

Brycon meeki Eigenmann & Hildebrand, 1917

Brycon meeki Eigenmann & Hildebrand, 1917, *Proc. Amer. Philos. Soc.* **56** (7): 688 (description; type localities, R. San Juan, R. Dagua, R. Patia, Colombia); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 133, pl. 23, fig. 4 (Colombian localities); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Weitzman, 1962, *Stanford Ichthyol. Bull.* **8** (1): 1–77 (description of osteology); Gery 1977, *Characoids*: 339 (reference in key).

Brycon striatulus (*non* Kner), Regan, 1913, *Ann. Mag. nat. Hist.* (8) **12**: 462 (R. San Juan).

Brycon atricaudatus (*non* Kner), Eigenmann, 1913, *Indiana Univ. Stud.* **18**: 27 (R. Dagua).

Brycon juanensis Rendahl, 1941, *Ark. Zool.* **33A** (4): 10, figs 2 & 3 (description; type locality; Rio San Juan at Cabeceras, Colombia); Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.* **110**: 61 (reference and synonymy); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference).

Brycon (Chalcinopsis) juradoensis Fowler, 1944, *Proc. Acad. nat. Sci. Philad.* **96**: 232, figs 5 & 6 (description; type locality, R. Juradó, Chocó Province, Colombia.

DISTRIBUTION. Pacific Colombia.

Specimens in BMNH collection:

1924.3.3 : 4–6	Barbacoas	Pres: Rosenberg
1920.6.20 : 59–60	Barbacoas	Pres: Eigenmann
1910.7.11 : 191–92	Boca se Colima, Rio San Juan	Pres: Palmer

COMMENTS. Böhlke (1958) considered that *Brycon juanensis* was a possible synonym of *B. meeki*. I have examined two specimens of *B. juanensis* one of which is labelled as the type (110 mm SL, NRM 10688). Both specimens conform in every respect with the morphology and meristics of *B. meeki*.

Brycon melanopterus (Cope) 1871

Megalobrycon melanopterus Cope, 1871, *Proc. Acad. nat. Sci. Philad.* **23**: 262, pl. 13, fig. 1 (description; type locality, R. Ambyiacu).

Brycon (Megalobrycon) melanopterus, Steindachner, 1876, *Sber. Akad. Wiss. Wien* **74** (1): 590 (Amazonas).

Brycon melanopterum, Eigenmann & Eigenmann, 1892, *Proc. U.S. natn Mus.* **14**: 55 (reference); Fowler, 1906 (1907), *Proc. Acad. nat. Sci. Philad.* **58**: 447 (Peruvian Amazon); Fowler, 1942, *Boln. Mus. Hist. nat. Javier Prado* 22–23: 370, fig. 47 (R. Ambyiacu); Amaral-Campos, 1950, *Papéis Dep. Zool. S. Paulo* **9** (10): 142 (description; Tapajoz, Amazon).

Brycon melanopterus, Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 337–8 (reference and synonymy).

Brycon melampterum (misspelling), Eigenmann & Allen, *Fishes of Western South America*: 253 (Peruvian localities).

DISTRIBUTION. Upper Amazon.

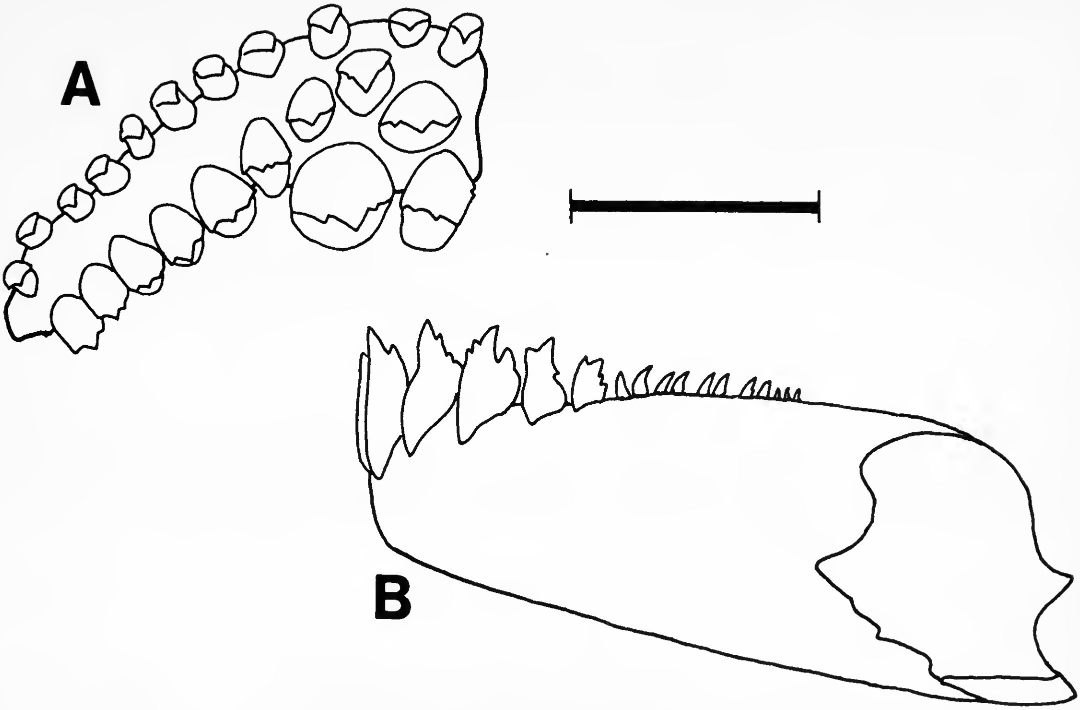
COMMENTS. Fowler (1950) includes, with a query, *Brycon siebenthalae* Nakashima, 1941; however, see remarks on p. 44.

Brycon melanoxanthus Heckel, 1860

Synonym of *Brycon orbignyanus*.

Brycon microlepis Perugia, 1897

Brycon microlepis Perugia, 1897, *Annali Mus. civ. Stor. nat. Giacomo Doria* **38**: 149 (description; type locality, Bahia Negra, Chaco boreal, Upper Paraguay); Eigenmann, McAtee & Ward, 1907, *Ann. Carnegie Mus.* **4**: 153 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Bertoni, 1914, *Fauna Paraguaya* Peces: 11 (reference; Paraguay); Bertoni, 1939,



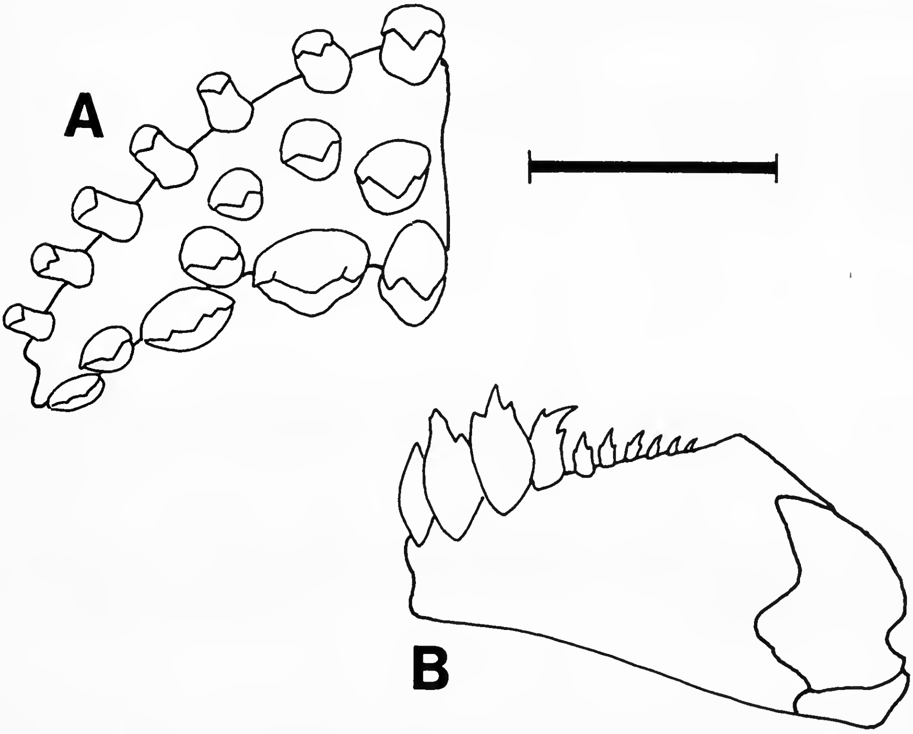


Fig. 20 (upper) A, *Brycon moorei*, occlusal view of right premaxilla; B, lateral view of left dentary. **Fig. 21** (lower) *Brycon oligolepis* A, right premaxilla; B, left dentary in lateral view. Scales = 5 mm.

Revta Soc. cient. Paraguay **4** (4): 55 (reference; Paraguay); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 338; Gery, 1977, *Characoids*: 338 (reference in key).

DISTRIBUTION. R. Paraguay.

Brycon moorei Steindachner, 1878

Brycon moorei Steindachner, 1878, *Denkschr. Akad. Wiss. Wien* **39**: 58, pl. 5, figs 2 and 2b (description; type locality, Rio Magdalena); Steindachner, 1880, *Denkschr. Akad. Wiss. Wien* **42**: 78 (Cauca R. near Caceres); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 138 (description); Miles, 1947, *Los Peces del Rio Magdalena*: 160–161, fig. 115 (description; Rio Magdalena; Upper and lower Cauca); Gery, 1977, *Characoids*: 339 (reference in key).

Two subspecies are recognized by Dahl:

Brycon moorei moorei, Dahl, 1971, *Los Peces del Norte de Colombia*: 123. *Othonophanes bolivarensis* Dahl, 1942, *K. fysiogr. Sallsk. Lund Forh.* **12** (18): 215–216 (description; Magdalena); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference). *Brycon bolivarensis*, Gery, 1977, Characoids: 339 (reference in key)

Brycon moorei sinuensis Dahl, 1955, *Rev. Linneana* **1**: 11–19 (not seen).

DISTRIBUTION. Magdalena and Cauca systems, Colombia.

COMMENTS. Dahl (1955; 1971) distinguishes two subspecies based on the number of lateral line scales (55–60 in *B. m. moorei* and 63–68 in *B. m. sinuensis*).

There are two specimens in the BMNH collections which display these differences. One from the Upper Cauca has 66 lateral line scales, the other from Barranquilla has 55. The former specimen is also more slender bodied, its depth being 28% of the standard length compared with 32% for the second specimen. Premaxillary dentition shown in Fig. 20. Specimens in BMNH collection:

1900.1.30 : 39	Barranquilla	Pres. K. Thomson	(250 mm SL)
1947.7.1 : 1	Upper Cauca	Pres. C. Miles	(180 mm SL)

Brycon nattereri Günther, 1864

Chalceus opalinus (non Cuvier) Kner, 1860, *Denkschr. Akad. Wiss. Wien* **18**: 10.

Brycon nattereri Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 334 (based on Kner's description, no specimen seen by Günther; type locality, Irisanga); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 431 (reference); Bertoni, 1914, *Fauna Paraquaya,* Peces: 11 (reference; Paraguay); Bertoni, 1939, *Revta Soc. cient. Paraguay* **4** (4): 55 (reference; Paraguay); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 338 (reference); Amaral-Campos, 1950, *Papéis Dept. Zool. S. Paulo* **9** (10): 139 (description; Rio Tiete); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Parana.

COMMENTS. The identity of this taxon must remain in doubt until Kner's specimen can be examined. It seems likely that *B. nattereri* represents either *B. orthotaenia* or *B.* '*orbignyanus*' (see p. 39).

Brycon obscurus Hildebrand, 1938

Brycon obscurus Hildebrand, 1938, *Fieldiana Zool.* **22** (4): 283, fig. 6 (description; type locality, El Valle, Pacific slope, Panama); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7**: 103 (reference); Miller, 1966, *Copeia* (4): 785 (reference, distribution); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. El Valle, Pacific slope of Panama.

COMMENTS. According to Hildebrand (1938) this species is closely related to *B. petrosus* of the Atlantic slope drainage.

Brycon oligolepis Regan, 1913

Brycon oligolepis Regan, 1913, *Ann. Mag. nat. Hist.* (8) **12**: 462 (description: type localities, Rio Condoto and Western Ecuador); Eigenmann, 1922, *Mem. Carnegie Mus.* **9**: 136, pl. 22, fig. 3 (synonymy, description, discussion and Colombian localities listed); Fowler, 1945, *Proc. Acad. nat. Sci. Philad.* **97**: 103 (description; Cauca, Colombia); Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.* **110**: 70 (discussion).

Brycon atrocaudatus (part), Boulenger, 1898, *Boll. Mus. Zool. Anat. comp. R. Torino* **13** (329): 3 (Rio Mira & Rio Peripa).

DISTRIBUTION. Pacific slope of Colombia and Esmeraldas region of Ecuador.

COMMENTS. The only specimens labelled as 'types' are two juveniles (BMNH 1913.10.1 : 8–9; 39·5 & 52·5 mm SL; Rio Condoto; collected by Spurrell). Regan (1913) based his description on 'Nine specimens, up to 220 mm total length, from the Rio Condoto (Spurrell) and Western Ecuador (Rosenberg)'.

In fact the total number of specimens deriving from these localities collected by Spurrell and Rosenberg totals only 7. These specimens I consider to constitute the type series.

Table 13 Counts and proportional measurements for 2 specimens of *Brycon orthotaenia*, including the holotype and 2 specimens of *Brycon 'orbignyanus'*.

	Brycon orthotaenia		*Brycon 'orbignyanus'*	
	Holotype (half-skin) BMNH 1861.5.16 : 71, SL (mm) 330	BMNH1924.6.2:3 SL 314 mm	BMNH1927.2.9:7 SL 248 mm	BMNH1876.6.8:22 SL 298 mm
D	33·0	37·0	33·0	32·0
S–D	53·0	52·0	50·0	54·0
H	21·0	24·0	23·0	22·0
Sn	27·0	33·5	30·0	31·0
IO	–	31·5	41·5	42·0
Mth	–	33·2	32·0	38·0
CpL	10·5	11·2	10·5	12·5
CpD	11·0	10·8	12·0	11·2
PL	Broken	19·4	19·3	19·6
VL	Broken	16·7	16·5	16·8
AL	24·0	26·0	22·6	22·9
DL	Broken	19·2	19·0	20·0
P–V	27·0	24·0	26·0	26·0
PP–V	–	81·0	81·0	75·0
Scales	10/48/8	11/49/9	12/52/9	12/51/10
Dorsal	ii 8	ii 9	ii 9	ii 9
Anal	iv26	iv 26	iv 25	iv 25
Pectoral	i 12	i 12	i 14	i 14
Ventral	i 7	i 7	i 7	i 7
Gill-rakers	–	13/16	15/15	15/15
Vertebrae	–	25 + 21	28 + 21	28 + 20
Supraneurals	–	9	12	12
Teeth:				
Pmx 1	11	10	10	14
2	7	8	10	13
3	2	2	2	2
Max	22	16	15	12
Dent	8/10	7/9	15/6	16/8

Böhlke (1958), stressed the need to determine the specific distinctness of *Brycon dentex* and *Brycon oligolepis*, believing that the type series of *B. oligolepis* 'is possibly a composite'. Although possibly a composite it does not include specimens of *Brycon dentex* which is a quite distinct species (see p. 21 and compare Figs 13, 14, 15 & 21).

The counts and proportions for the types are given in Table 14.

The type specimens from the Rio Condoto and Rio Paramba (N. Ecuador) appear to be conspecific but there are differences between these and a specimen from the Rio Durango (79° 45′ W, 1° 4′ N) a sub-tributary of the Rio Santiago, Esmeraldas Prov. This specimen has a wide interorbital (40% of the head length) and a long pectoral fin (96% of the pectoral-ventral distance). The dorsal surface and paired fins are very dark (although this may simply be the result of preservation). Böhlke listed a specimen of *Brycon posadae* Fowler from the Rio Durango which, as far as I can tell, shows close affinity to the BMNH specimen. Thus I would provisionally regard the Rio Durango specimen as being *B. posadae*.

Another specimen, from the Rio Mira (BMNH 1898.11.4 : 77), has a wide interorbital (40% of the head length), but in this case the pectoral fin is short being only 74% of the pectoral-pelvic distance.

The proportions for Rio Peripa specimens (BMNH 1898.11.4 : 75–76) fall within the ranges for the Colombian and Paramba specimens, except for the slightly longer head (with very narrow 4th infraorbital) and shorter caudal peduncle length. There is also a slight difference in colouration, in that the caudal peduncle blotch extends further forward than in other *B. oligolepis*. Until more material is available and the degree of variation known, these specimens are referred to *B. oligolepis*. Meanwhile I propose that the type locality of this species should be restricted to the Rio Condoto, Colombia. The type specimens from this locality appear to match well with other specimens from R. Telembi I have examined and with the descriptions of those specimens collected by Eigenmann (1922) from the same Colombian localities.

As pointed out by Böhlke, Tortonese (1939, *Boll. Mus. Zool. Anat. comp. Torino* **47**: 49) re-identified a specimen from the Rio Zamora as *Brycon oligolepis*, an identification that seems suspect.

Regan (1913) separated *B. oligolepis* from *B. atrocaudatus* on its fewer lateral line scales (44–48 cf. 54–55) and 'larger head'. However, Regan's comparative material of *B. atrocaudatus* has subsequently been determined as *B. moorei*.

Brycon opalinus (Cuvier) 1817

Chalceus opalinus Cuvier, 1817, *Mem. Mus. Hist. nat. Paris* **5**: 351, pl. 26, fig. 1 (description; type locality, 'Brasil'); Valenciennes in Cuvier & Valenciennes, 1849, *Hist. Nat. Poiss.* **22**: 244 (Rio Tiquilenhonha (= Jequitinhonha)).

Brycon opalinus, Müller & Troschel, 1844, *Arch. Naturgesch.* (1): 90 (brief description; Brasil); Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 334 (reference); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped.* **3** (4): 431 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 338 (reference, synonymy); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION. Uncertain.

COMMENTS. See remarks under *Brycon amazonicus*.

Brycon orbignyanus (Valenciennes) 1849

Chalceus orbignyanus Valenciennes, 1849 in Cuvier & Valenciennes, *Hist. Nat. Poiss.* **22**: 249 (description; type locality, La Plata).

Brycon orthotaenia Günther, 1864

Brycon orthotaenia Günther, 1864, *Cat. Fish Brit. Mus.* **5**: 335 (description; type locality, Rio Cipo, Brasil).

COMMENTS. These two species are treated together because in the past *Brycon orthotaenia* has been placed in the synonymy of *B. orbignyanus* along with *B. rodopterus* (Val.) 1849, and *B. lineatus* Steindachner, 1866. No synonymy is presented here because until the types of all these species have been compared any such compilation will be virtually useless.

Brycon orthotaenia is a species distinct from that described under the name of *B. orbignyanus* by various authors (Devincenzi, 1942 in Devincenzi & Teague, *An. Mus. Hist. nat. Montevideo* (2) **5** (4): 73; Thormählen de Gil, 1949, *Revta Mus. La Plata* ns **5** (35) Zool.: 355–364; Ringuelet, Aramburu & Aramburu, 1967, *Los Peces Argentinos de agua dulce*: 135–136). Amaral-Campos (1950, *Papéis Dep Zool. S. Paulo* **9** (10): 139) considered *B. orthotaenia* to be distinct from *B. orbignyanus*, although the characters he used to separate them were rather tenuous, being based only on Günther's description of *B. orthotaenia*.

The holotype of *B. orthotaenia* is a half-skin of approximately 330 mm SL. It is still in a reasonable condition; the scale rows are almost complete as is the dentition and skull bones of the left side. The distal margins of the fins are broken away and the caudal fin is almost parted from the body; however, the hypural bones are complete.

The type locality is the Rio Cipo, a tributary of the Itapicuru, eastern Brasil; a river system without connection to the Parana-Paraguay, the area of distribution of *B. orbignyanus*.

There are 22 teeth along the maxillary; the premaxillary count is 11/7/2 (Fig. 22B). The dentary possesses 8 large tri- or quadri-cuspid teeth followed by 10 small conical ones.

Another specimen in the BMNH collection (1924.6.2 : 3) from the Rio das Velhas, accords well with the proportions and other morphological features of the type. In this specimen there is a rather large horizontal oval humeral patch, which is only just visible on the type skin. A wide dark band extends along the lateral midline of the caudal peduncle from below the adipose fin to reach the edge of the medial caudal fin rays.

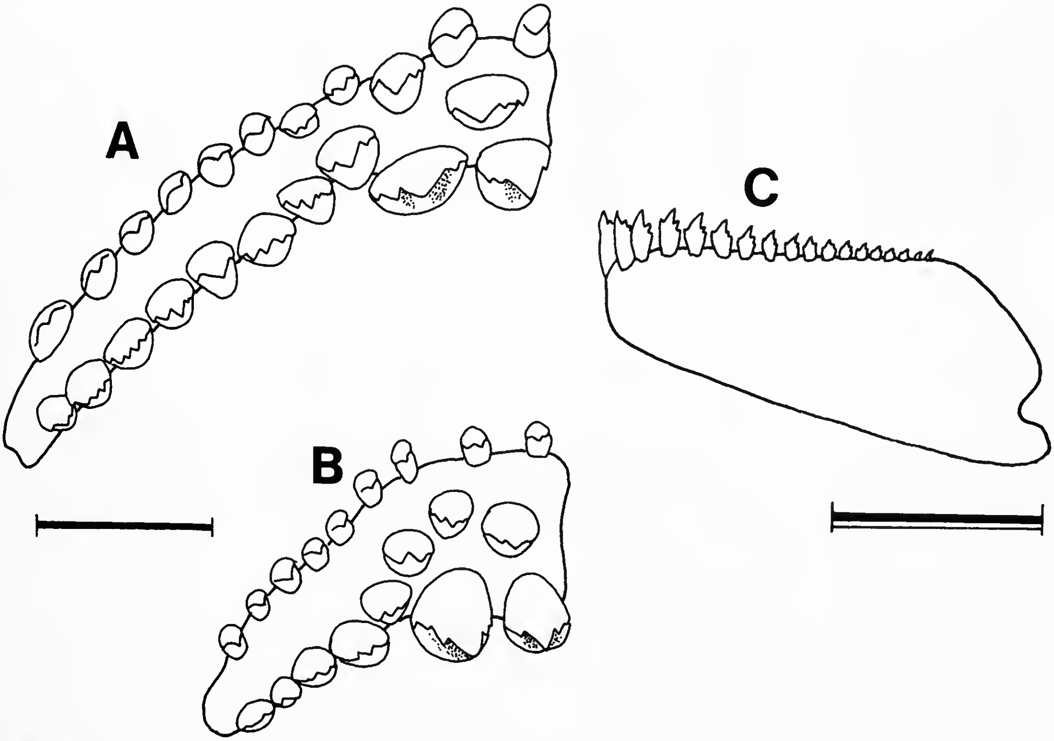


Fig. 22 A, *Brycon orbignyanus*, right premaxilla from specimen BMNH 1927.2.9 : 7–9, 248 mm SL; B, *Brycon orthotaenia*, right premaxilla from specimen BMNH 1924.6.2 : 3; 314 mm SL; C, *Brycon orbignyanus*, left dentary in lateral view from specimen BMNH 1927.2.9 : 7–9 (posterior border drawn from a radiograph). Scales: solid = 5 mm, divided = 10 mm.

Other specimens in the BMNH collections labelled as *B. orthotaenia* differ in several respects from the type and from the Rio das Velhas specimen. These I tentatively refer to *B. orbignyanus* (BMNH 1876.6.8 : 22; 1927.2.9 : 7; 1946.12.13 : 136–7).

In these specimens the body is less deep and the interorbital width narrower. The most noticeable difference is in the dentition where the 1st row of premaxillary teeth numbers 10–14, the 2nd row totals 10–13, and the dentary has 15–16. Although the total number of dentary teeth is the same as that in *B. orthotaenia*, they are gently graded instead of having the more abrupt gradation found in *B. orthotaenia* and other *Brycon* species (see Figs 22A & B). The lower jaw is long and shallow (Fig. 22C) and the upper and lower jaws are almost subequal whereas in *B. orthotaenia* the upper jaw strongly projects beyond the lower. In *B. orthotaenia* the maxillary valve tissue is thick and strongly folded as in *B. falcatus* thus contrasting with the highly convulted and papillose tissue of *B. orbignyanus*. In *B. orbignyanus* there is also a high number of abdominal vertebrae (28 cf. 25 in *B. orthotaenia*), of supraneurals (12 cf. 9) and of pectoral fin rays (14 cf. 12).

Further differences are seen in colouration. In *B. orbignyanus* dark bands run in zig-zag fashion between the scale rows. The paired fins and the dorsal and anal are all well-pigmented. The dark caudal band extends from a point posterior to the origin of the adipose fin.

Table 14 Counts and proportional measurements for the syntypes of *Brycon oligolepis*.

	BMNH 1913.10.1 : 8–9; BMNH 1914.5.18 : 5; Rio Condoto. SL (mm) 52·5, 39·5, 157		BMNH 1898.10.26 : 30–31; 1898.4.28 : 167; Rio Paramba. SL (mm) 146·5, 133, 70·5		BMNH 1902.5.27 : 50; Rio Durango. SL (mm) 180
	Range	Mean	Range	Mean	
D	31·0–33·0	31·8	29·5–31·0	30·0	30·5
S–D	54·5–56·0	55·0	53·0–55·0	54·3	53·0
H	24·5–27·0	26·1	24·5–28·2	26·6	25·0
Sn	23·3–28·5	26·4	25·0–26·2	26·3	29·0
IO	31·0–39·0	32·6	30·0–37·5	33·3	40·0
Ey	23·5–38·0	32·0	25·9–31·5	27·8	24·5
Mth	26·0–28·0	26·6	22·2–27·5	25·1	32·0
CpL	12·4–14·4	13·1	10·9–17·0	13·8	13·0
CpD	9·5–10·1	9·8	9·8–10·2	9·9	10·2
PL	18·5–19·5	19·0	20·0–23·1	21·5	19·8
VL	13·4–15·3	14·6	15·0–16·3	15·6	15·3
AL	25·9–28·0	26·2	22·6–26·2	24·6	27·0
DL	16·5–19·0	18·1	18·5–22·0	20·0	17·2
P–V	23·0–26·5	25·2	24·0–26·0	25·1	20·5
PP–V	83·0–91·0	76·3	83·0–91·0	86·0	96·0
Scales	9/45, 46, 49/7		8/45, 45, 46/7		8/45/7
Dorsal	ii 9		ii 9		ii 9
Anal	iv 25 (f2), iv 26 (f1)		iv 26 (f2), iv 28 (f1)		iv 26
Pectoral	i 12		i 12		i 12
Ventral	i 7		i 7		i 7
Gill-rakers	12/13		12/14		11/13
Vertebrae	24 + 19 (f2), 24 + 20 (f1)		23 + 21 (f2), 22 + 21 (f1)		23 + 21
Supraneurals	12		10		10
Teeth:					
Pmx 1	7–8		7–8		7
2	7		7–8		7
3	2		2		2
Max	13 (f2), 15 (f1)		14 (f2), 15 (f1)		18
Dent	6–7/6–8/1		7–8/6/10/1		9/10/1

Günther counted 53 scales in the lateral line on the type of *B. orthotaeniá* (that is, including those extending on to the caudal fin). Counting to the standard length, the total is 48 or 49. Counting to the standard length in *B. orbignyanus* the lateral line scales are 51–52 (cf. Thormãhlen de Gil, 1949 : 53–59). Günther (1863) also pointed out the marked ramification of the lateral line canal in those scales through which it passed. This character is not present in *B. orbignyanus.*

Boulenger (1897, *Boll. Mus. Zool. Anat. comp. Univ. R. Torino* **12** (279): 4) identified some specimens from Caiza, Bolivia as belonging to *B. orbignyanus*. However, these appear to represent a tetragonpterine species which as yet I have been unable to identify.

Brycon rodopterus was included in the synonymy of *B. orbignyanus* by Eigenmann (1910) and *B. lineatus* by Ringuelet, Aramburu & Aramburu (1967). The status of these species is yet to be confirmed.

The genus *Bryconodon* erected by Eigenmann (1903) to contain *B. orthotaenia* is not valid. Eigenmann gives no adequate definition of this genus nor why he considered it to differ from Brycon. In any case he may well have had *B. orbignyanus* in mind. Attention is drawn to the remarks concerning *Brycon lundii* and *Triurobrycon* (p. 33). Should *B. lundii* prove to be the junior synonym of *B. orthotaenia*, and *B. orthotaenia*, *B. orbignyanus* and *B. cephalus* are found to share derived characters which relate them at generic level, then the name *Megalobrycon* Günther, 1869 would have priority.

Counts and proportions of the type and one other specimen of *B. orthotaenia* are listed in Table 13 together with those of specimens of *B.* '*orbignyanus*'.

Brycon pellegrini Holly, 1929

Brycon pellegrini Holly, 1929, *Anz. Akad. Wiss. Wien* **66**: 208 (description; type locality, Manaus, Amazon); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 339 (reference); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Amazon.

COMMENTS. Possibly a synonym of *B. cephalus* Günther.

Brycon pesu Müller & Troschel, 1845

Brycon pesu Müller & Troschel, 1845 *Horae Ichth.* (**1–2**): 16, 30, pl. 7, fig. 1 (description; type locality, Guiana); Regan, 1905, *Proc. Zool. Soc. Lond.*: 190 (Rio Negro; reference to a drawing by Wallace); Steindachner, 1917, *Denkschr. Akad. Wiss. Wien* **93**: 35, pl. 1, fig. 3 (Surinam, Rio Purus, Rio Negro, Rio Branco, Rio Tapajos; reference to Haseman's collection); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 339 (reference and synonymy); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference).

Holobrycon pesu, Eigenmann, 1909, *Ann. Carnegie Mus.* 6: 33 (brief generic description; British Guiana localities); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Eigenmann, 1912, *Mem. Carnegie Mus.* **5**: 369, pl. 54, fig. 1; Gery, 1977, *Characoids*: 335 (reference, fig'd.: 320).

DISTRIBUTION. Guianas; ?Amazon.

COMMENTS. Eigenmann (1909) established the genus *Holobrycon* for *Brycon pesu.* His diagnosis of the genus was 'A *Brycon* without fontanels' (Eigenmann, 1912). In fact, fontanelles are present in this species and from a series of specimens the following observations were made:

Two specimens from Bartica, Guyana, BMNH 1911.10.31 : 347–349, 42 mm SL, fontanelles present; 85 mm SL, frontals closed, parietals open.

Seven specimens from Manaus, Amazon, BMNH 1897.12.1 : 324–331, 33–63 mm SL. Various degrees of separation of the frontals and parietals, but in the largest specimen both frontal and parietal fontanelles are present.

Three specimens from Mato Grosso, uncatalogued, 63, 105 & 117 mm SL, frontal and parietal fontanelles absent.

Regan (1911) commented on the presence of cranial fontanelles and indicated that such features were of very little taxonomic value and were usually absent in those characoids with flattened skulls. Weitzman (1962) found that in the Tetragonopterinae (Characinae of Weitzman), fontanelles became narrower with increased size. Roberts (1969) stated that 'Fontanels are apparently present in the young of all characoids'. If this is so, then open fontanelles may be considered a plesiomorph condition and their closure in *Brycon pesu* a derived feature. Vari, 1979 : 290 considered progressive reduction of the cranial fontanelle to be a derived feature amongst distichodontid characoids.

In dental morphology *Brycon pesu* appears to be a 'typical' *Brycon*, ie. of the *B. falcatus* group (see p. 46), but in general appearance and particularly in the red caudal fin it greatly resembles *Chalceus*.

Brycon petrosus Meek & Hildebrand, 1913

Brycon petrosus Meek & Hildebrand, 1913, *Fieldiana Zool.* **10** (8): 184 (description; type locality, Upper Chagres River, Panama); Meek & Hildebrand, 1916, *Fieldiana Zool.* **10** (15): 297, pl. 24; Hildebrand, 1938, *Fieldiana Zool.* **22** (4): 282 (description; Panamanian localities); Eigenmann, 1922, *Mem. Carnegie Mus.* **9**: 137, pl. 23, fig. 1 (brief description; localities); Myers & Weitzman, 1960, *Stanford Ichthyol Bull.* **7** (4): 103 (reference); Miller, 1966, *Copeia* (4): 785 (reference; distribution); Menezes, 1969, *Papéis Dep. Zool. S. Paulo* **22**: 217–218 (food; distribution given as Panama & Honduras); Gery, 1977, *Characoids*: 339 (reference in key); Kramer, 1978, *Copeia* (3): 535–537 (spawning habits).

DISTRIBUTION. Panama, Atlantic and Pacific slopes.

Brycon posadae Fowler, 1945

Brycon posadae Fowler, 1945, *Proc. Acad. nat. Sci. Philad.* **97**: 105, fig. 5 (description; type locality, Ricaurte, Rio Guebo, tributary of Rio Mira, Colombia); Böhlke, 1958, *Proc. Acad. nat. Sci. Philad.* **110**: 63 (description and discussion); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Ovchynnyk, 1968, *Zool. Anz.* **181**: 245 (reference; Ecuadorian localities).

DISTRIBUTION. Ecuador and southern Colombia (Pacific slope).

COMMENTS. Reference is made to this species on p. 38 under *Brycon oligolepis*.

Brycon reinhardti Lütken, 1874

Brycon reinhardti Lütken, 1874, *Overs. K. danske. Vidensk. Selsk Forh.*: 134 (description; type locality, central Brasil); Lütken, 1875, *K. dansk. Vidensk. Selsk. Skr.* **12**: 222 (description and discussion; Rio das Velhas); Steindachner, 1875, *Sitz. Akad. Wiss. Wien* **74** (1): 385, pl. 3, figs 3 & 3a (Campos, Juiz de Fora); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann & Ogle, 1907, *Proc. U.S. natn Mus.* **33**: 30 (Rio das Velhas); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference). Thormählen de Gil, 1949, *Revta Mus. La Plata* ns. **5** Zool.: 360 (reference); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 340 (reference); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Rio das Velhas; eastern Brasil.

COMMENTS. Lütken (1875) discussed this species and *Brycon lundii* at some length. He distinguished them from each other on differences in the depth of the body; length of the head; position of the eye; number of lateral line scales and the shape of the maxillaries. Lütken reported that he could find no 'essential differences' in dentition between the two species. Furthermore, he stated (correctly) that neither species could be confused with *Brycon hilarii* but that *B. lundii* could possibly be a synonym of *B. orthotaenia*, an opinion accepted here (p. 33).

Brycon reinhardti has been discussed in association with *B. devillei* and *B. acuminatus*, two species with which it is thought to be closely related.

Counts and proportions of the single specimen in the BM(NH) collection are given in Table 15. Premaxillary dentition is shown in Fig. 23.

Table 15 *Brycon reinhardti* counts and proportions of specimen BMNH 1876.1.10 : 36 (possibly a syntype).

SL (mm) 152·5			
D	28·9	Scales	8/45/5
S–D	57·0	Dorsal	ii 9
H	25·5	Anal	iv 20
Sn	27·0	Pectoral	i 14
IO	37·0	Ventral	i 7
Ey	24·2	Gill-rakers	11/14
Mth	33·2	Vertebrae	23 + 23
CpL	11·8	Supraneurals	10
CpD	9·8	Teeth:	
PL	17·6	Pmx 1	10
VL	15·4	2	9
AL	23·0	3	2
DL	16·4	Max	21
P–V	24·5	Dent	12/17/1
PP–V	72·0		

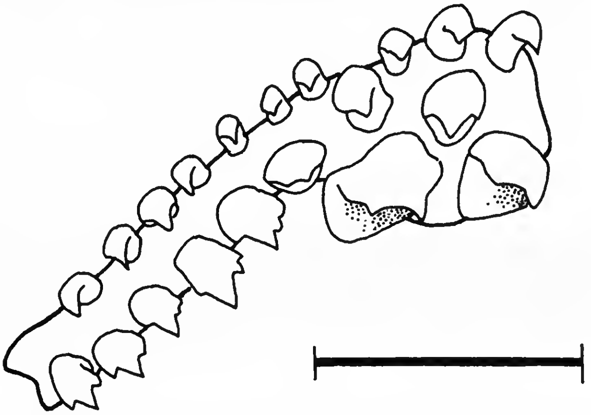


Fig. 23 *Brycon reinhardti*, right premaxilla from specimen BMNH 1876.1.10 : 36 Scale = 3 mm.

Brycon rodopterus (Valenciennes) 1849

Chalceus rodopterus Valenciennes, 1849 in Cuvier & Valenciennes *Hist. Nat. Poiss.* **22**: 249 (description; type locality, Buenos Aires).
Brycon rhodopterus, Eigenmann & Eigenmann, 1891, *Proc. U.S. natn. Mus.* **14:** 55 (reference).
Brycon rodopterus, Lahille, 1895, *Revta Mus. La Plata* **6**: 249 (Rio Santiago); Gery, 1977, *Characoids*: 651 (refers in index to *B. orbignyanus*).

DISTRIBUTION. La Plata.

COMMENTS. Status uncertain, possibly a synonym of *B. orbignyanus.*

Brycon rubricauda Steindachner, 1879

Brycon rubricauda Steindachner, 1879, *Sber. Akad. Wiss. Wien* **80** (1): 18 (description; type locality, Rio Cauca, Colombia); Steindachner, 1880, *Denkschr Akad. Wiss. Wien* **42**: 77, pl. 8, figs 1 & 1a (description Cauca near Caceres); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 135 (reference and comment); Miles, 1947, *Los Peces del Rio Magdalena*: 159 (Rio Magdalena and lower Cauca); Dahl, 1971, *Los Peces del Norte de Colombia*: 123 (description; distribution); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Magdalena and Cauca, Colombia.

COMMENTS. According to Eigenmann (1922) this species possesses four rows of premaxillary teeth and this caused him to place it near *B. dentex* and *B. meeki*. Possibly it is a synonym of *B. meeki*.

Brycon scapularis Fowler, 1911

Synonym of *B. atrocaudatus* (see Böhlke, 1958).

Brycon schomburgkii Müller & Troschel, 1844

Synonym of *B. falcatus* (see Eigenmann, 1912).

Brycon siebenthalae Eigenmann, 1912

Brycon siebenthalae Eigenmann, 1912, *Mem. Carnegie Mus.* **5**: 372, pl. 44, fig. 3 (description; type locality, Aruka River, British Guiana); Gery, 1977, *Characoids*: 338 (reference; fig. of tooth pattern).

DISTRIBUTION. Aruka River, Guyana.

COMMENTS. Nakashima (1941, *Boln. Mus. Hist. nat. Javier Prado* ano 5, **16**: 70) described two taxa which he named *B. siebenthalae* and *B. siebenthalae iquitensis* from the Upper Amazon; no exact locality was given. Eigenmann & Allen (1942, p. 254) treated these as *Brycon* sp.; Fowler (1950) tentatively placed them in the synonymy of *B. melanopterus*. The descriptions are too poor to allow identification. It is possible that these fish represent *B. stubelli*, but Nakashima gives a lateral line scale count of 72 cf. 57–58 for *stubelli*; the description is also at variance with the figure labelled as *B. siebenthalae*. In view of these and other errors (see under *B. falcatus* and *B. iquitiensis*) these taxa must remain *species inquirenda*.

Brycon stolzmanni Steindachner, 1879

Brycon stolzmanni Steindachner, 1879, *Denkschr. Akad. Wiss. Wien* **41**: 70, pl. 2, figs 6a & 6b (description; type locality, Chota, R. Marañon, Peru); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Pearson, 1937, *Proc. Cal. Acad. Sci.* (4) **22**: 90 (Paipay, Tingo de Paura, Pusoc, Peru); Fowler, 1942, *Boln. Mus. hist. nat. Javier Prado* ano 6 **22–23**: 372 (reference); Eigenmann & Allen, 1942, *Fishes of Western South America*: 254 (reference); Fowler, 1945, *Los Peces del Peru*: 150 (reference); Thormählen de Gil, 1949, *Revta Mus. La Plata* ns **5** Zool.: 364 (reference; distribution); Fowler, 1950, *Archos Esta Zool. S. Paulo* **6**: 340 (reference); Gery, 1977, *Characoids*: 342 (reference in key).

DISTRIBUTION. Peruvian Amazon and Pacific slope of Peru.

Brycon striatulus (Kner & Steindachner)

Chalcinopsis striatulus Kner & Steindachner, 1863 in Kner *Sber. bayer. Akad. Wiss. Munchen*: 226 (description; type locality, Panama); Kner & Steindachner, 1865 *Abh. bayer. Akad. Wiss. Munchen* **10**: 38–41, pl. 5, fig. 2 (description; locality 'Neu Granada & Panama').

Brycon striatulus, Steindachner, 1876, *Sitz. Akad. Wiss Wien* **74** (9): 590 (discussion of *Chalcinopsis*); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Jordan & Evermann, 1896, *Proc. U.S. natn. Mus.* **47** (1): 337 (description; distribution); Eigenmann & Ogle, 1907, *Proc. U.S. natn. Mus.* **33**: 30 (Aspinwall, Panama); Regan, 1908, *Biologia Centrali Americana*, Pisces: 169 (description; Costa Rica, Juan Vinas & El Poso del Rio Grande); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference); Meek, 1914, *Fieldiana Zool.* **10** (10): 109 (Costa Rican localities); Meek & Hildebrand, 1916, *Fieldiana Zool.* **10** (15): 294 (Rio Chorrera, R. Juan Diaz; R. Bayano; Tuyra basin); Eigenmann, 1922, *Mem. Carnegie Mus.* **9** (1): 139 (description; R. Frijoles; R. Fugra); Breder, 1927, *Bull. Am. Mus. nat. Hist.* **57**: 119 (reference: R. Tuyra); Hildebrand, 1938, *Fieldiana Zool.* **22**: 276 (reference and comment); Thormählen de Gil, 1949, *Revta Mus. La Plata* ns **5** Zool.: 359 & 364 (reference; description); Hubbs, 1953, *Copeia* (3): 142–143 (comment on authorship); Miller, 1960, *Copeia* (4): 785 (reference; distribution); Bussing, 1966, *Revta Biol. Trop.* **14** (2): 236 (reference: Costa Rica); Gery, 1977, *Characoids*: 339 (reference in key).

DISTRIBUTION. Central and eastern Panama, Pacific slope; Costa Rica, Pacific and Atlantic slopes.

COMMENTS. This species was made the type of the genus *Chalcinopsis* by Kner & Steindachner (1863), being distinguished from *Brycon* mainly by the shape of the ventral surface of the body. Günther (1864) followed this generic concept and included the species *dentex, chagrensis* and *alburnus* in that genus. Steindachner (1876) reduced *Chalcinopsis* to subgeneric status and mistakenly synonymised *B. chagrensis* and *B. striatulus.*

Chalcinopsis has been resurrected by Gery (1972); see p. 6.

Boulenger (1898, *Boll. Mus. Zool. Anat. comp. R. Torino* **13** (329): 4) recorded *Brycon striatulus* from Rio Santiago, eastern Ecuador, an identification confirmed by Tortonese (1939, *Boll. Mus. Zool. Anat. comp. R. Torino* **47** (3) n. 89: 50). These erroneus identifications were pointed out by Böhlke (1958). I am unable at this stage to say which species Boulenger's specimen represents.

Brycon stubelii Steindachner, 1882

Brycon stubelii Steindachner, 1882, *Anz. Akad. Wiss. Wien* **19** (18): 176 (description; type locality, Amazonas); Steindachner, 1882, *Denkschr. Akad. Wiss. Wien* **46** (1): 13, pl. 1, fig. 1 (Amazon at Iquitos); Eigenmann & Eigenmann, 1891, *Proc. U.S. natn Mus.* **14**: 55 (reference); Eigenmann, 1910, *Rep. Princeton Univ. Exped. Patagonia* **3** (4): 430 (reference, spelt as *stubeli*); Fowler, 1942, *Boln Mus. Hist. nat Javier Prado* ano **6** (22–23): 372 (reference; Iquitos); Eigenmann & Allen, 1942, *Fishes of Western South America*: 253 (reference); Fowler, 1945, *Los Peces del Peru*: 149 (reference); Thormählen de Gil, 1949, *Revta Mus. La Plata* ns **5** Zool.: 364 (reference; distribution); Gery, 1966, *Vie et Milieu* supple. 17: 450 (reference in key).

DISTRIBUTION. Peruvian Amazon.

COMMENTS. *Brycon stubelii* is possibly a synonym of *B. falcatus*. The major difference between the species appears to lie in the numbers of lateral line scales, given in Steindachner's description as 57–58. This count is made to the caudal base; a standard length count of Steindachner's (1882) illustration gives 52, and is thus in agreement with that of *B. falcatus*. Gilbert & Roberts (1971) have recorded *B. falcatus* from the Upper Amazon (see p. 28).

Brycon tovari Dahl, 1960

Brycon tovari Dahl, 1960, *Caldesia* **8** (39): 465 (description; type locality, R. Sando, tributary of R. Baudo, Colombia); Gery, 1977, *Characoids*: 339 (reference).

DISTRIBUTION. Western Colombia.

COMMENTS. Possibly a synonym of *B. meeki.*

Brycon travassosi Amaral-Campos, 1950

Brycon travassosi Amaral-Campos, 1950, *Papéis Dep Zool. S. Paulo* **9** (10): 141 (description; type locality, Bodoquena, Mato Grosso); Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* **7** (4): 103 (reference); Gery, 1977, *Characoids*: 338, 342 (reference, regarded as possible synonym of *B. lineatus*).

DISTRIBUTION. Mato-Grosso, Brasil.

COMMENTS. Possibly a synonym of *B. orbignyanus.*

Brycon whitei Myers & Weitzman, 1960

Brycon whitei Myers & Weitzman, 1960, *Stanford Ichthyol. Bull.* 7 (4): 99, fig. 1 (description; type locality, Rio Guaviare, Orinoco system, Colombia); Cala, 1977, *Lozania* (24): 1–21 (reference: Rio Guaviare, Colombia); Gery, 1977, *Characoids*: 335, 339 (reference).

DISTRIBUTION. Orinoco system, Colombia.

Species groups

Within *Brycon* as presently recognized, at least five species assemblages can be identified; these are:

1. *Brycon falcatus* group; characterized by a deep body; broad cranium; deep orbitosphenoid septum; small rhinosphenoid; posteriorly elongate epioccipital process; long maxilla with 19–24 teeth; premaxilla with wide dentigerous surface, the teeth in 3 rows, the 3rd row teeth large; lower jaw short and deep; lateral line scales 43–58; vertebrae 41–48; body markings usually as well-defined horizontal lines.
   INCLUDED SPECIES: *B. falcatus, B. brevicauda, B. bahiensis, B. cephalus, B. carpophagus, B. orthotaenia, B. siebenthalae, B. moorei, B. hilarii* and ?*B. bicolor.*
   DISTRIBUTION: Amazon basin.

2. *Brycon acuminatus* group; characterized by a slender body, long, rather pointed snout; narrow cranium; shallow orbitosphenoid septum; reduced rhinosphenoid; long maxilla with 20–30 teeth; premaxilla with narrow dentigerous surface, the teeth with modified triserial arrangement, inner teeth with elongate central, and reduced lateral cusps; lower jaw long and shallow; lateral line scales 45–51; vertebrae 44–48; body markings as humeral and caudal spots.
   INCLUDED SPECIES: *B. acuminatus, B. ferox, B. reinhardti, B. devillei.*
   DISTRIBUTION: South-east Brazil.

3. *Brycon orbignyanus* group; characterized by a long and deep body; long but blunt snout; broad cranium with anteriorly convex frontals; short maxilla with 12–15 teeth; premaxilla with wide dentigerous surface, outer row teeth numerous 12–15, cf. 6–10 in other species groups; lower jaw with regularly graded teeth; lateral line scales 50–52; vertebrae 48–49; supraneural 12; body marked with horizontal or zig-zag lines, a caudal spot and central caudal fin bar.
   INCLUDED SPECIES: *B. orbignyanus*, and ?*B. microlepis.*
   DISTRIBUTION: Parana-Paraguay.

4. *Brycon alburnus* group; characterized by a slender body; elongate pointed snout; narrow cranium; shallow orbitosphenoid septum; small rhinosphenoid; long maxilla with over 20 teeth; premaxilla with narrow dentigerous surface, teeth compressed with elongate central cusp, modified triserial arrangement; premaxillary symphysial joint weakly developed or syndesmotic; lower jaw long and shallow; lateral line scales 56–63; vertebrae 43–46; high number of supraneurals, 10–13; body with humeral and caudal spots.
   INCLUDED SPECIES: *B. alburnus, B. atrocaudatus* and ?*B. ecuadoriensis.*
   DISTRIBUTION. Ecuador.

5. *Brycon guatemalensis* group; characterized by an elongate body; narrow cranium; tubular olfactory foramen in the lateral ethmoid; large rhinosphenoid; short maxilla with 10–15 teeth; premaxilla with wide dentigerous surface, teeth in 3 or 4 rows; lower jaw short and deep; gill-rakers usually numerous, 12–14 on ceratobranchial; anal fin long with 30–38 branched rays, cf. 21–32 in other groups; lateral line scales 50–70, cf. 45–46 in other groups; vertebrae *ca* 45.
   INCLUDED SPECIES: *B. guatemalensis, B. striatulus* and all Panamanian, Central American and Pacific Colombian species (eg. *B. meeki, B. oligolepis, B. rubricauda*).

It must be pointed out that the above grouping does not imply that these are considered as monophyletic units. The characters used have yet to be assessed as plesio- or apomorphic. Furthermore, not all species possess characters which enable them to be included in the groups (eg. *B. dentex*) as here defined. However, it is hoped that this classification will serve as a framework for a more rigorous analysis.

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Frank J. Sulloway

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The *Beagle* collections of Darwin's finches (Geospizinae)

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Contents

Synopsis

In spite of the importance of the Geospizinae, or 'Darwin's finches', in evolutionary theory, the original type specimens from the *Beagle* voyage have long been a source of puzzlement to ornithologists. More especially, the localities recorded on the specimens do not seem to coincide, in a number of cases, with the various species and subspecies distributions observed today. The explanation for these anomalous specimens lies, in part, in Darwin's own collecting procedures while in the Galapagos. Darwin was initially misled by the divergent nature of these finch species, actually thinking them to be members of several different subfamilies. In addition (and contrary to the legend), Darwin did not begin to separate his ornithological collections by island while he was in the Galapagos Archipelago. Rather, whatever information he later provided in this connection was largely derived, after the *Beagle* voyage, from the carefully labelled collections of three other *Beagle* shipmates. It was at this time that Darwin, impressed by John Gould's (1837*a*) expert ornithological analysis of his Galapagos birds, finally became a convinced evolutionist and realized the closely related nature of the Geospizinae. Darwin's specimens, which were largely unlabelled by island, later acquired a number of erroneous localities as a result of Darwin's own incorrect guesses, as well as the efforts of later ornithologists to make Darwin's specimens agree with his published localities. As for the three other *Beagle* collections of Darwin's finches, these are accurately identified and described here for the first time. Moreover, these collections are shown to clarify a number of important problems bearing on the nomenclature and geographic distribution of Darwin's finches. In particular, hitherto unknown manuscript evidence establishes that a peculiarly large-billed form of *Geospiza magnirostris*, the Large Ground Finch, was collected on Chatham and Charles islands, where the form is now extinct. Another extinct form, *G. nebulosa*, the Sharp-beaked Ground Finch, was collected on Charles Island. *G. magnirostris magnirostris* and *G. magnirostris strenua* are therefore recognized here as valid trinomials, and the name *G. nebulosa* (Gould, 1837*a*) is recognized as having priority over *G. difficilis* (Sharpe, 1888). Finally, a summary table of specifications and measurements regarding the *Beagle* type specimens of Darwin's finches is provided in an appendix.

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Introduction

The Geospizinae, or 'Darwin's finches', have inspired an impressive body of scientific research ever since Charles Darwin first collected these birds during the voyage of H.M.S. *Beagle* (1831–36). As a miniature paradigm of evolution in action, the Geospizinae have few ornithological rivals, and they are rightly celebrated today as a classic case of adaptive evolutionary radiation.

Largely responsible for this special scientific status of Darwin's finches is the famous laboratory of evolution–the Galapagos Archipelago–where Darwin encountered these endemic birds in September of 1835. This oceanic archipelago comprises sixteen principal islands located on the equator some six hundred miles west of Ecuador (Fig. 1). Wholly volcanic in origin, the Galapagos Islands are several million years old and have never been connected to the South American mainland. Darwin's finches were evidently one of the earliest colonists of this archipelago, since their degree of evolutionary complexity (thirteen species belonging to four different genera) is unique among Galapagos birds. A fourteenth species belonging to yet another genus inhabits Cocos Island, four hundred miles to the northeast. Because Darwin's finches have no close ancestor on the American mainland, they are classified in their own separate tribe or subfamily, which is placed with the Emberizidae[1].

Being one of the earliest colonists of the Galapagos, the ancestral form of these birds must have encountered a sparsely tenanted environment possessing numerous vacant ecological niches. Through geographic isolation on the different islands, various finch populations gradually evolved reproductive isolation and hence status as separate species. Whenever these similar species were successful in recolonizing neighbouring islands, there ensued competition for scarce resources and eventually divergence and adaptive radiation into more specialized niches. Through this four-part process of geographic isolation, speciation, recolonization, and adaptive radiation, Darwin's finches have evolved a remarkable difference in the form of their beaks. Between the largest bill, which is shaped like that of a grosbeak, and the smallest, which resembles that of a warbler, graduated differences in beak structure are found with every species. There are three species of ground finches with large, medium, and small beaks; a fourth species of ground finch with a sharp, pointed beak; two species of cactus-eating finches; a vegetarian tree finch; large, medium, and small insectivorous tree finches; a mangrove finch; a finch that closely resembles a warbler in both its morphology and behaviour; and finally a tool-using 'woodpecker' finch, which extracts its prey from crevices in tree trunks by using twigs and cactus spines (Fig. 2). It was this striking degree of morphological differentiation that led Darwin to comment in his *Journal of Researches*: 'Seeing this gradation and diversity in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends' (1845 : 380).

Although research on Darwin's finches has continued to contribute in important ways to the understanding of evolutionary theory, there is one problem that has remained largely unresolved ever since Darwin collected these birds in 1835. This problem concerns the type localities of Darwin's own specimens, an issue that has been the subject of repeated discussion and debate in the ornithological literature. Not only have various doubts been expressed about the reliability of Darwin's collecting and recording procedures, but questions of proper nomenclature and even evolutionary issues have also been raised in this context. In addition, this problem is closely associated with a much-discussed historical question, namely, when was it that Darwin first realized the importance of geographic isolation as a key to species formation. Given the fame of this episode in Darwin's life, there has been a surprising degree of misunderstanding and misinformation regarding these issues. In fact, over the years Darwin's finches have become the focus of a considerable legend in the history of science, one that I have examined more extensively elsewhere (1982*a*). Here I shall confine myself to the problem of clarifying the type localities of the *Beagle* Geospizinae.

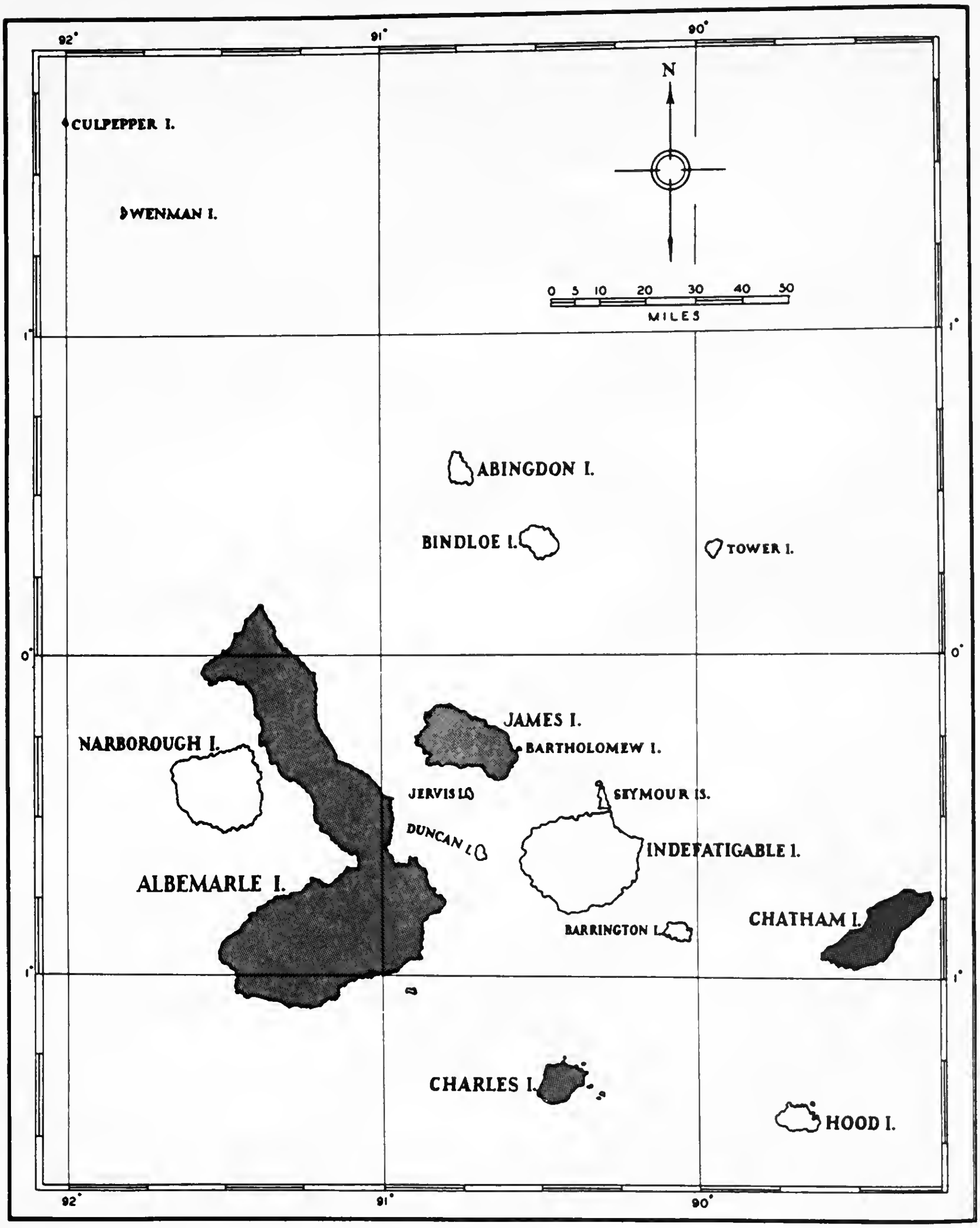


Fig. 1 The Galapagos Archipelago. Darwin visited the four shaded islands. (From Lack, 1945: Frontispiece.)

Darwin in the Galapagos

In his *Journal of Researches* Darwin later reported that the possibility of the different islands possessing separate forms was first brought to his attention by Nicholas O. Lawson, the vice-governor of the archipelago. Lawson, whom Darwin met on Charles Island, informed him that 'the tortoises differed from the different islands, and that he could with certainty tell from which island any one was brought' (Darwin 1845 : 394). This discussion took place sometime between 25 and 27 September 1835, during the second of Darwin's five weeks in the archipelago[2]. 'I did not for some time', Darwin commented, 'pay sufficient attention to

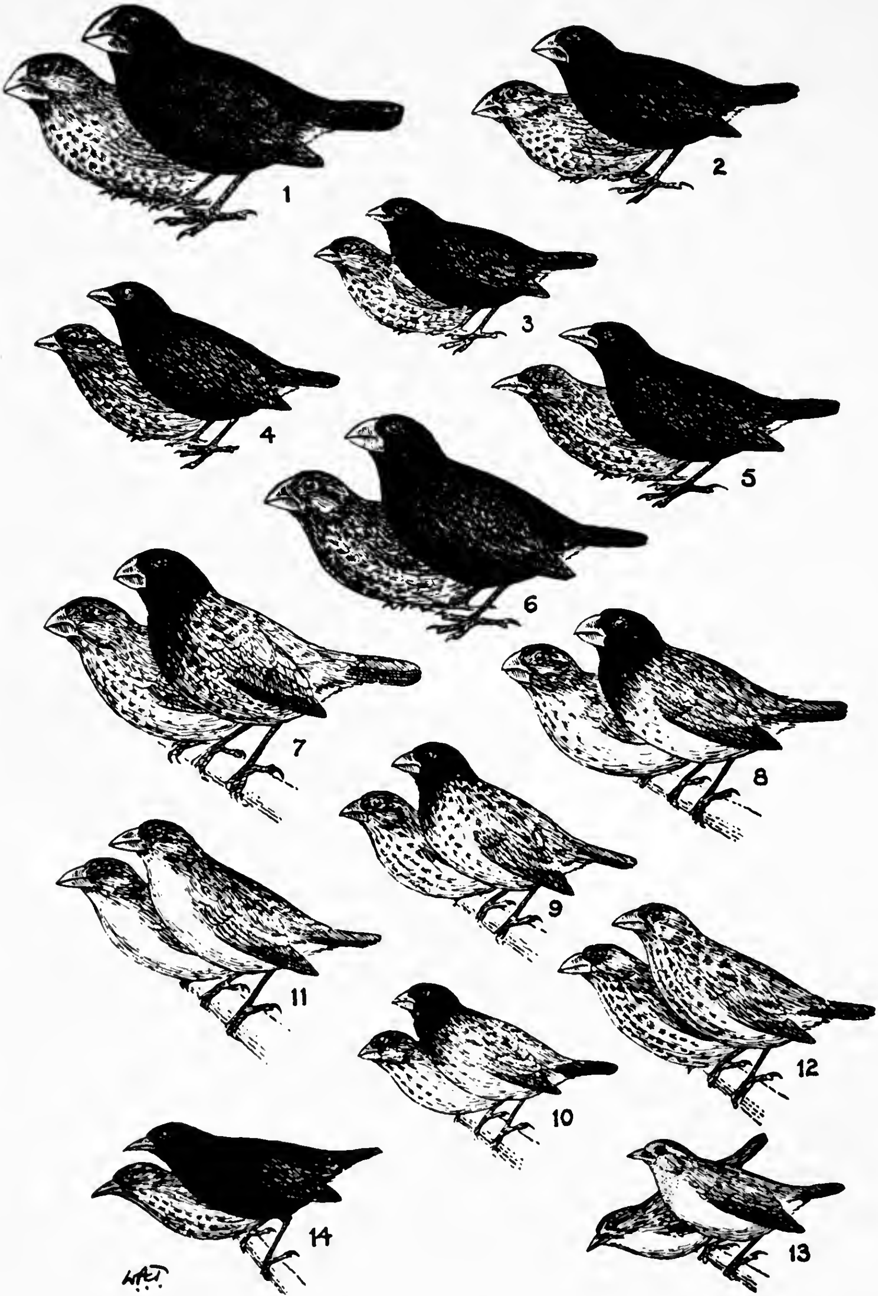


Fig. 2 Darwin's finches; the male (in dark plumage) and female of each species: *1, 2, 3,* the Large, Medium, and Small Ground Finches (*Geospiza magnirostris, G. fortis,* and *G. fuliginosa*); *4*, the Sharp-beaked Ground Finch (*G. nebulosa* [formerly *difficilis*]); *5* and *6*, the Cactus and Large Cactus Finches (*G. scandens* and *G. conirostris*); *7,* the Vegetarian Tree Finch (*Platyspiza crassirostris*); *8, 9,* and *10,* the Large, Medium, and Small Insectivorous Tree Finches (*Camarhynchus psittacula, C. pauper,* and *C. parvulus*); *11*, the Woodpecker Finch (*C. pallidus*); *12*, the Mangrove Finch (*C. heliobates*); *13*, the Warbler Finch (*Certhidea olivacea*); and *14*, the Cocos Island Finch (*Pinaroloxias inornata*). (From Lack, 1947 : 19.)

this statement, and I had already partially mingled together the collections from two of the islands. I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would have been differently tenanted ... [B]ut I ought, perhaps, to be thankful that I obtained sufficient material to establish this most remarkable fact in the distribution of organic beings' (1845 : 394).

Darwin did fortunately notice that the mockingbird he had collected on Charles Island differed from the form he had previously collected on Chatham Island. This discovery made him pay particular attention to their collection; and he subsequently made efforts to obtain, and to keep separate, specimens from the next two islands he visited (1841 : 63). These next two islands were Albemarle, where Darwin spent only part of a day, and James, where he spent a week. To Darwin's eyes, the mockingbird specimens from Chatham and Albemarle appeared to be the same, but those from James and especially Charles were noticeably different[3]. In his zoology notes Darwin commented about these specimens at the time: 'This bird which is so closely allied to the Thenca of Chili (Callandra of B. Ayres) is singular from existing as varieties or distinct species in the different Is^{ds}.—I have four specimens from as many Is^{ds}—There will be found to be 2 or 3 varieties.—Each variety is constant in its own Island.—This is a parallel fact to the one mentioned about the Tortoises.'[4] It was this singular fact in the distribution of the mockingbirds that subsequently prompted Darwin to write in his *Ornithological Notes*:

> When I recollect, the fact that from the form of the body, shape of scales & general size, the Spaniards can at once pronounce, from which Island any Tortoise may have been brought. When I see these islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware, is the constant asserted difference—between the wolf-like Fox of East and West Falkland Islds.—If there is the slightest foundation for these remarks the zoology of Archipelagoes—will be well worth examining; for such facts [would *inserted*] undermine the stability of Species. (1963[1836] : 262)

This famous statement, written approximately nine months after leaving the Galapagos Archipelago, is Darwin's first tentative admission of the possibility that species might be mutable[5].

To what extent, then, did the finches help to reinforce this insight? According to David Lack (1947 : 23), Darwin also began to separate the members of the finch tribe as a result of the vice-governor's remarks to him on Charles Island. Thereafter, Lack maintains, Darwin kept his ornithological collections from each island separate. Lack's assertion is based on a detailed examination of Darwin's type specimens, many of which are labelled as coming from the last island Darwin visited, and on the following statement made by Darwin in his *Journal of Researches*:

> Unfortunately most of the specimens of the finch tribe were mingled together; but I have strong reasons to suspect that some of the specimens of the sub-group Geospiza are confined to separate islands. If the different islands have their representatives of Geospiza, it may help to explain the singularly large number of the species of this sub-group in this one small archipelago, and as a probable consequence of their numbers, the perfectly graduated series in the size of their beaks. Two species of the sub-group Cactornis, and two of Camarhynchus, were procured in the archipelago; and of the numerous specimens of these two sub-groups shot by four collectors at James Island, all were found to belong to one species of each; whereas the numerous specimens shot either on Chatham or Charles Island (for the two sets were mingled together) all belonged to the two other species: hence we may feel almost sure that these islands possess their representative species of these two sub-groups. (1845 : 395)

Darwin's own testimony clearly implies that only the specimens from Chatham and Charles were mingled together, since he was later able to compare these specimens as a group with the specimens collected on James Island.

David Lack's insistence that Darwin began to separate and label his specimens by locality after leaving Charles Island is, nevertheless, called into question by the seemingly inaccurate nature of several of the island localities actually recorded by Darwin. Indeed, Darwin's type specimens have provided a considerable nightmare of taxonomic problems for subsequent ornithologists, based largely on their controversial localities. Darwin claimed, for example, that specimens of a peculiarly large-beaked form of *Geospiza magnirostris* came from Chatham and Charles islands. But after more than a century of subsequent collecting without finding any such large-billed specimens, ornithologists found themselves faced with a puzzle. Either this form had become extinct on Chatham and Charles islands, where no *magnirostris* specimens (large or small) had ever been found by other expeditions; or else Darwin's specimens must have come from islands other than those indicated. Swarth (1931 : 147–49), noting that the largest bills among *G. magnirostris* are found in the northern part of the archipelago, including James Island, believed that Darwin's specimens came from that island. Although Darwin's specimens are still somewhat larger than the present James Island race of this species, Swarth concluded that some evolution in bill size must have occurred since Darwin's visit. Darwin also reported taking specimens of the smaller-billed *G.* [*magnirostris*] *strenua* on Chatham Island, and these specimens as well have generally been thought to have come from James Island (Fig. 3)[6].

David Lack, who at first agreed with the judgment of Swarth and others[7], later changed his mind, given Darwin's testimony that only the specimens from the first two islands had been mingled together. Yet Lack himself distrusted other of Darwin's localities, including some involving specimens from the one island–James–where Lack claimed Darwin had kept his specimens separate. According to Lack (1945 : 14), one of Darwin's specimens of *Cactornis scandens,* labelled as coming from James Island, is actually an example of *Geospiza difficilis* (now *nebulosa*), the Sharp-beaked Ground Finch, and belongs to a form that is not found on James Island today. So either measurable evolution has occurred in the size of the beak, or, more probably, the specimen came from Charles Island, where FitzRoy collected a very similar specimen of this now extinct island race. Altogether, there is serious doubt about the accuracy of eight of the fifteen localities recorded on Darwin's Geospizinae type specimens[8].

Not only is the accuracy of Darwin's localities in doubt, but so is the means by which Darwin might have recorded this information. From his voyage specimen catalogues and other scientific notes it is very difficult to see how he could have supplied as much information as he later did in this regard. His *Ornithological Notes,* for example, lists localities for only three of his thirty-one Geospizinae, namely, for three specimens of a very distinctive species (*Camarhynchus psittacula*) that he recalled having seen on only one island–James. Moreover, this information was apparently recorded to indicate the rarity of the species rather than its locality per se. For the same reason Darwin also noted such information for two other Galapagos birds.

Darwin is known, of course, to have used FitzRoy's collections after the voyage to supplement his own record of localities. But this source of information still does not account for the localities entered on Darwin's own type specimens. Presumably, Darwin might have recorded localities on his specimen tags rather than in his catalogues. For this reason ornithologists have repeatedly bemoaned the fact that no original labels in Darwin's or John Gould's hand have ever been found among Darwin's type specimens at the British Museum. In the nineteenth century it was the custom of the museum curators to throw away the original collector's labels and to replace them with neatly printed museum labels. Information thought worthy of preserving was transferred to the new labels. But much valuable information, such as the original collector's numbers, was inevitably lost. George Robert Gray, who assisted Darwin with the *Birds* volume of the *Zoology of the Voyage of H.M.S. Beagle,* and who later received Darwin's types from the Zoological Society when it closed its museum, was a typical offender in this regard (Sharpe, 1906 : 84–85).

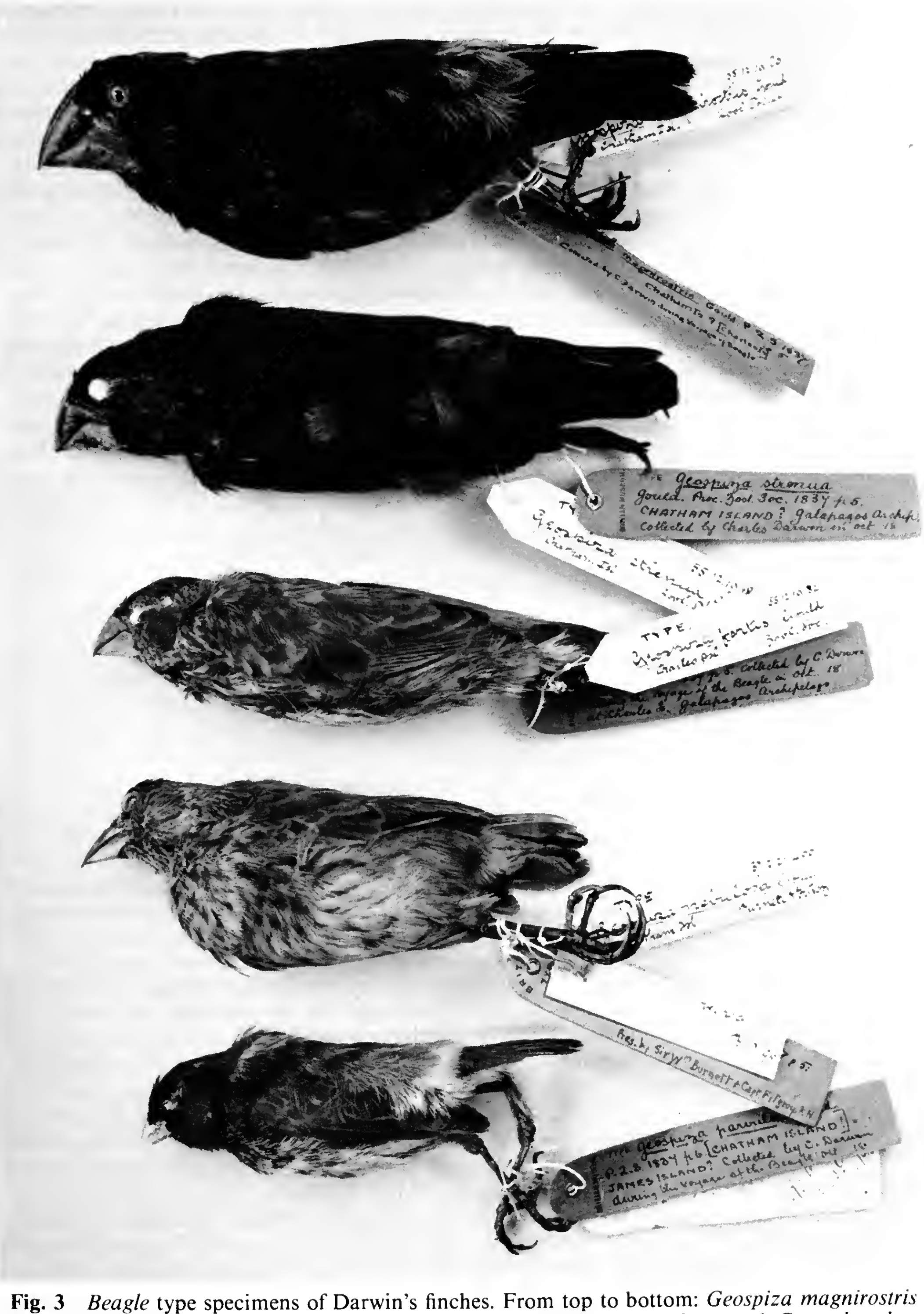


Fig. 3 *Beagle* type specimens of Darwin's finches. From top to bottom: *Geospiza magnirostris magnirostris*; *G. magnirostris strenua*; *G. fortis*; *G. nebulosa nebulosa*; and *Camarhynchus parvulus parvulus*. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

The question of whether or not Darwin recorded island localities directly on the specimen tags is largely resolved, however, by the fortunate discovery of one (and probably the only surviving) original label for his ornithological specimens. Having vainly sought, like previous investigators, for original labels among Darwin's type specimens, it occurred to me to examine all those Darwin specimens at the British Museum (Natural History) that are not endemic to the Galapagos. One such specimen was at last found (*Dolichonyx oryzivorus*–the American Bobolink), bearing what appears to be Darwin's original crude paper tag. Comparison of the specimen number (3374) with Darwin's manuscript catalogue shows that the number is indeed Darwin's, and that it is inscribed in his own hand (Fig. 4)[9]. On the reverse side of the tag the genus name, 'Dolychonyx', is written in pencil, in an unidentified hand, and below it, in ink, the species name, 'oryzivorus', appears, apparently in John Gould's hand. A second and smaller label, added when the specimen was presented to the Zoological Society in 1837, records Darwin's name, the date of accession, and, on the back, Darwin's original specimen number. The specimen was acquired by the British Museum in 1881, after Gould's death, along with many other birds from his huge personal collection. A third label (not shown) was attached to the specimen at this time.

Fig. 4 Darwin's specimen of *Dolichonyx oryzivorus*, with the only surviving label in Darwin's hand. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

Being a migrant species with an unusually wide range (from Canada to Chile), the Bobolink is an occasional visitor to the Galapagos in the autumn of each year. Coincidentally, in its autumn plumage the Bobolink is not unlike a Darwin's finch, although Darwin initially thought the bird was a pipit of very unusual structure[10]. When Gould first examined the bird in 1837, he thought it was a new species of finch. But he later discovered that it was an already described North American species and apparently decided to keep the specimen for his own collection[11]. This circumstance, together with the lack of scientific importance of the specimen, enabled its original Darwin and Zoological Society labels to survive.

What is particularly important about this specimen, with regard to Darwin's labelling practices, is that no island locality is recorded on either of the two earliest tags. Darwin did consider this information worth recording in his *Ornithological Notes,* however, since the bird had been encountered on one island only–James. Thus it appears that whatever island localities Darwin thought worth recording, such as those for three finch and four mockingbird specimens, were recorded in the master catalogue of specimens and in the *Ornithological Notes* rather than on the crude paper tags[12].

In short, Darwin does not appear to have altered his collecting or labelling practices while he was in the Galapagos Archipelago. After he left Charles Island, his collecting procedures continued to reflect the typological and creationist assumptions he had brought with him to that archipelago. What localities he did record were noted as largely incidental information to remind himself later of scarce species or noteworthy habitats. He continued, moreover, to collect only a few specimens of each species; and he entirely failed to collect finches on the third island he visited–Albemarle–even though almost every finch within miles was gathered in front of him at a spring near Bank's Cove[13]. Darwin thereby passed up the chance of collecting an additional species, and two endemic subspecies, of Galapagos finches. Even after leaving James Island and setting sail for Tahiti, Darwin apparently continued to treat the vice-governor's comment about the tortoises, and his own discovery with regard to the mockingbirds, as isolated anomalies. For if he had fully appreciated the revolutionary implications of these facts, he would never have allowed his *Beagle* shipmates to devour and discard all thirty adult tortoises brought on board ship as a source of fresh meat for the cruise across the Pacific (FitzRoy, 1839 : 498)[14].

These conclusions regarding Darwin's collecting procedures during his Galapagos visit bring us back once again to the problem of his finches and their dubious localities. In particular, if Darwin recorded only three island localities for these birds in his scientific notes, how and when did he derive the many additional localities that are now to be found on his type specimens? To answer this question I must take up the topic of what happened to Darwin and his finches after they returned from the *Beagle* voyage.

Darwin's return to England

After a voyage of nearly five years, the *Beagle* landed in Falmouth, England, on 2 October 1836. During the next several months Darwin arranged for the disposal and description of his collections within the various branches of natural history. His collection of birds and mammals, offered to the Zoological Society of London, was delivered on 4 January 1837[15]. The celebrated ornithologist John Gould, who was closely associated with the Zoological Society, lost no time in examining and naming the unusual finches that Darwin had brought back from the Galapagos Islands. At the very next meeting of the society (10 January), Gould described these birds as twelve new species, which he placed in one genus and two closely allied subgenera (*Geospiza, Cactornis,* and *Camarhynchus*). Moreover, he astutely realized the basic peculiarity of these finches, namely, that 'the bill appears to form only a secondary character'. Soon afterwards Gould recognized *Certhidea olivacea,* the Warbler Finch, as a thirteenth species of the group, belonging to yet another genus[16].

Darwin, who was at this time residing in Cambridge, did not learn of the details of Gould's analysis until he moved to London in early March of 1837 in order to have closer contact with the specialists working on his collections. Gould's findings, communicated to Darwin during a meeting with the eminent ornithologist, provided Darwin with a number of surprises[17]. While in the Galapagos, Darwin had been rather unclear about the precise relationship among the various finchlike species he had encountered there. In particular, he had misidentified several finch species as the forms that they, through extensive evolutionary radiation, now appear to mimick. For example, he had considered the Cactus Finch, *Cactornis scandens,* to be a member of the Icteridae (the family of the orioles and blackbirds); and he had classified the Warbler Finch, *Certhidea olivacea,* as a 'wren', or warbler. It appears, moreover, that Darwin initially distinguished as separate species of finches only 6 of the eventual 13 forms that Gould named in early 1837. Hence Darwin's finches only really became Darwin's *finches* after Gould rectified many of Darwin's earlier field misclassifications, and thereby clarified the unity and complexity of the group[18]. More important still for Darwin's evolutionary thinking, Gould (1837*d*) declared that 3 of the 4 island forms of Galapagos mockingbird brought to England by Darwin were distinct species, a possibility that Darwin had already asserted 'would undermine the stability of

Species'. For the Galapagos as a whole, Gould pronounced 25 of the 26 land birds as new and distinct forms found nowhere else in the world. Darwin was frankly stunned, not only by the realization that three separate species of mockingbirds indeed inhabited the different islands of the Galapagos, but also by the fact that most of these Galapagos species, even though new, were closely related to those found on the American continent[19]. His conversion to the theory of evolution, which took place shortly after his meeting with Gould in March of 1837, was a direct consequence of these two conclusions.

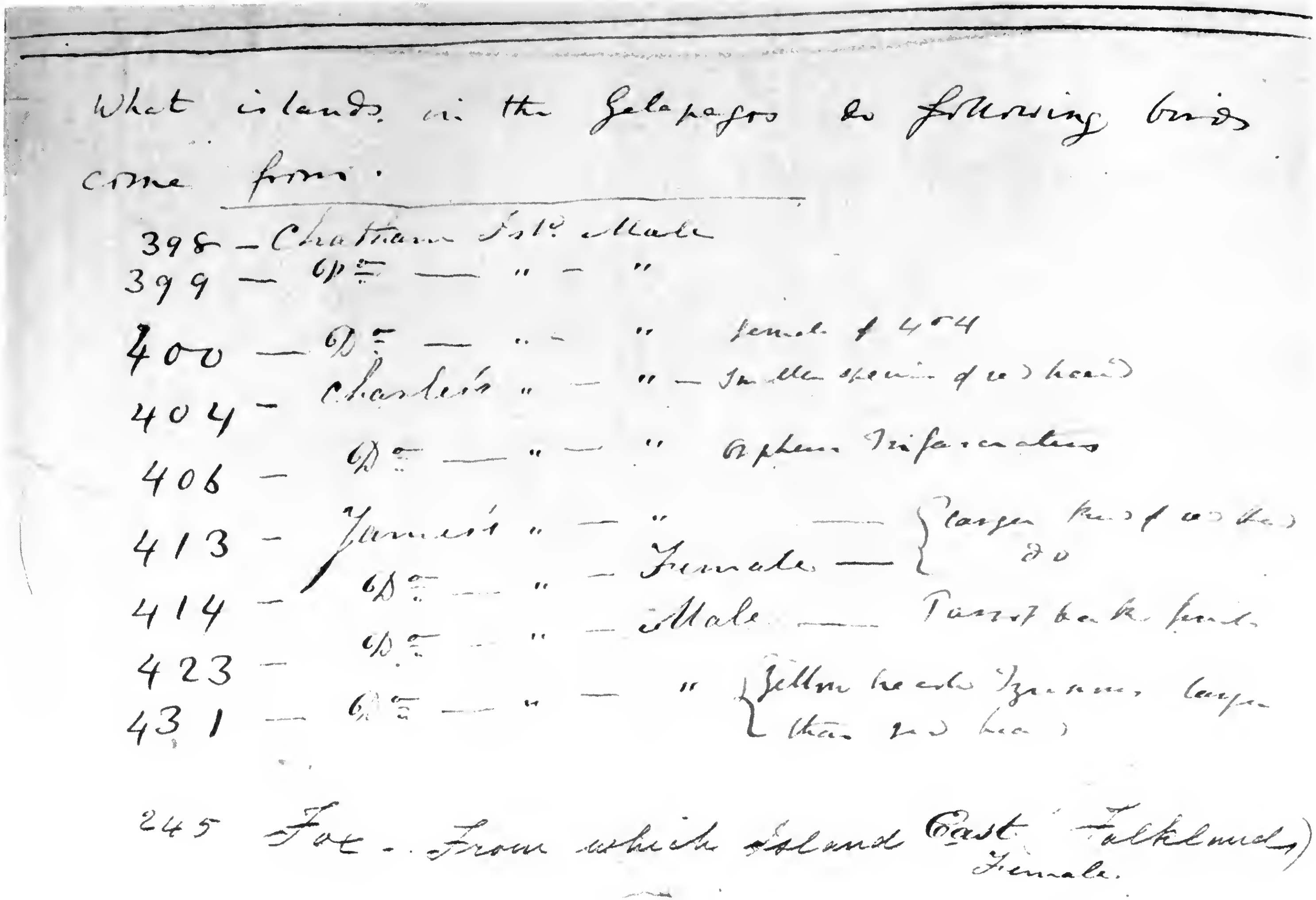
Reconstructing the finch localities

In the wake of Gould's taxonomic findings, many of them quite unexpected, Darwin soon realized that the unusual features of the Galapagos finches could be largely explained if they, like the mockingbirds, were confined to separate islands. He therefore began to solicit information from those shipmates on the *Beagle* who had made their own private ornithological collections and who, unlike himself, had fortunately kept accurate records of the islands from which they had procured their specimens. Captain FitzRoy's extensive collection, which had gone to the British Museum on 21 February 1837, offered relatively easy access, and Darwin later acknowledged his use of it in the *Zoology* (1841 : 99)[20]. What Darwin did not say in the *Zoology,* however, was that he also employed two other shipmates' collections, including that of his own servant, in attempting to reconstruct these island localities. The first of these sources of information came from Harry Fuller, who had spent a week collecting with Darwin on James Island. Altogether Fuller collected eight specimens of *Geospiza,* one from Chatham Island and seven from James. The collection of Darwin's servant, Syms Covington, was somewhat smaller and included only four finches, one from Chatham Island and three from Charles Island.

Records of Darwin's use of locality information from the collections of FitzRoy, Fuller, and Covington are among Darwin's manuscripts at Cambridge University Library (Figs. 5 & 6)[21]. There are four such sheets, in Darwin's hand. Although none of the sheets are dated, indirect evidence indicates that Darwin lost little time after he became an evolutionist in trying to reconstruct the Galapagos finch localities. One of the four sheets, which bears an 1836 watermark (manufacturer unknown), comprises a series of questions about Galapagos specimen localities evidently sent to FitzRoy and answered by an unidentified amanuensis or clerk (Fig. 5). On this same sheet an amanuensis, working for Darwin, also asked from what island of the Falklands a specimen of fox had come. Darwin mentioned the results of this latter inquiry in his *Journal of Researches* (1839 : 250–51), which was already in press by mid-August 1837. Similarly, Darwin's statement in his *Journal* (1839 : 475) that he 'very much suspect[ed]' that certain species of Galapagos finches were confined to separate islands corroborates the conclusion that he had already examined the various *Beagle* collections by the time his *Journal* went to press. Since Darwin had reached the Galapagos chapter of his *Journal* by late May or early June and since he had finished with the whole of the *Journal* by the end of June, his efforts to collate the various *Beagle* Geospizinae by locality probably date from June at the latest[22].

It was undoubtedly at this time, that is, sometime in the spring or early summer of 1837, that Darwin also tried to reconstruct the island localities of his *own* Galapagos specimens. For a few birds Darwin was able to infer from his notes or from memory that he had collected these specimens on one island only. This was the case, for example, for an owl, a swallow, a flycatcher, and for three finch specimens with a peculiar beak shaped like that of a parrot (*Camarhynchus psittacula*). In addition, from his *Beagle* shipmates Darwin apparently acquired several finch specimens that were lacking in his own collection, and at least one of these had a locality attached[23].

Unfortunately, certain of Darwin's attempts to reconstruct the island localities of his own specimens involved a bit of guesswork, and errors inevitably crept in. In his master catalogue of specimens, for example, he drew a line under the first eight Geospizinae and wrote

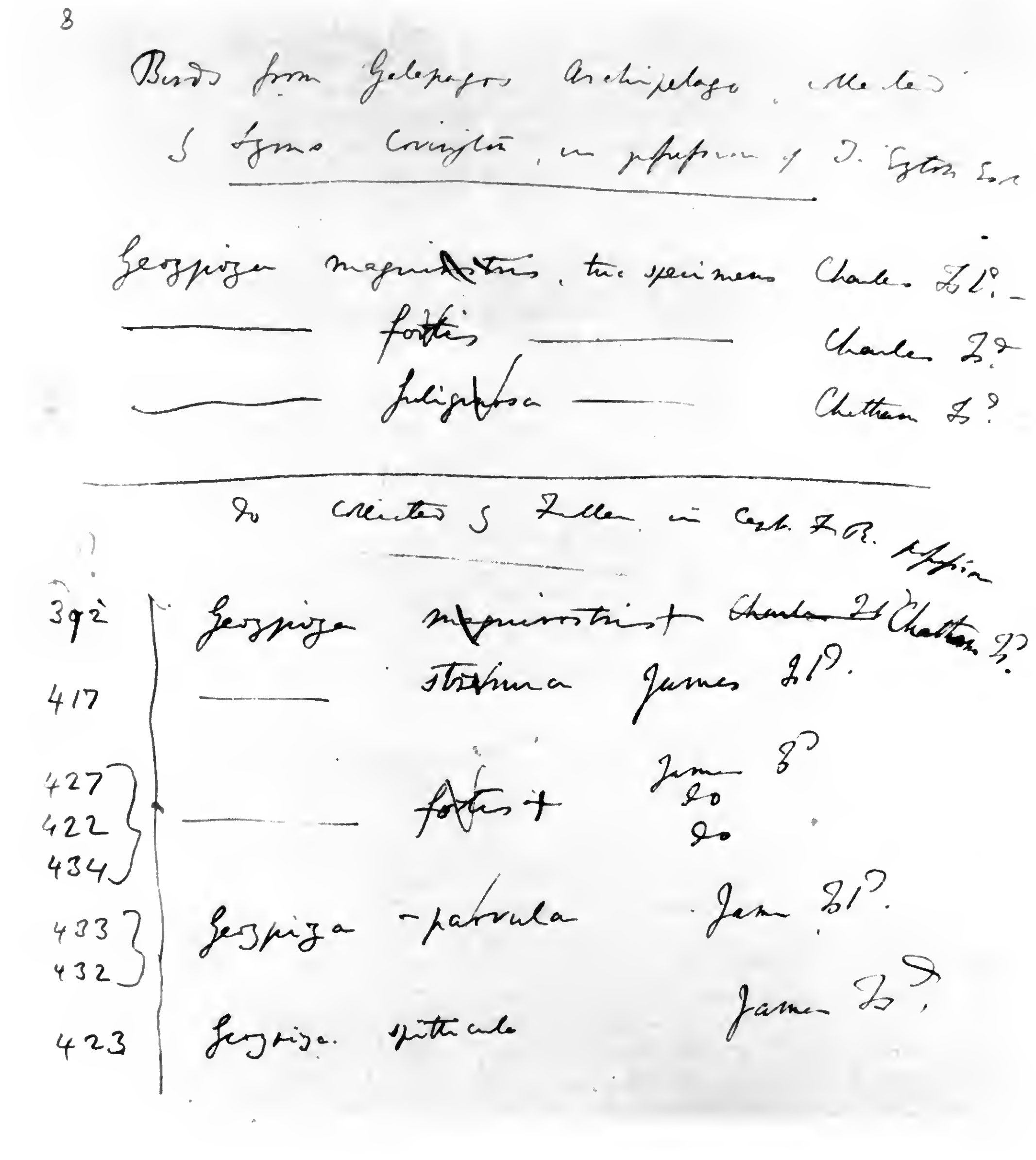


What islands in the Galapagos do following birds come from.

398 – Chatham Isld. Male
399 – Do — " – "
400 – Do — " – " female of 404
404 – Charles's " – " – Smaller species of red head
406 – Do — " – " Orpheus Trifasciatus
413 – James's " – " —— {larger kind of red head
Do — " – Female — {do
414 – Do — " – Male —— Parrot beak finch
423 – Do – " – " {Yellow headed Tyrannus larger than red head
431 – Do — " – "

245 Fox – From which island East Falklands)
Female.

Fig. 5 Darwin's request for information regarding the island localities of FitzRoy's Galapagos birds, with replies in the hand of an unidentified amanuensis. A second unidentified amanuensis, who is known to have worked for Darwin after the *Beagle* voyage, addressed the last question on the list, which was in turn answered by the first amanuensis. Additional memoranda, later added by Darwin, appear at the right of most of the entries. (Courtesy of the Syndics of Cambridge University Library.)



8

Birds from Galapagos Archipelago, collected by Syms Covington, in possession of [illegible] Esq

Geospiza magnirostris, two specimens Charles Isd. —
—— fortis —— Charles Isd.
—— fuliginosa —— Chatham Isd?

Do collected by Fuller in Capt. F.R. possession

392 Geospiza magnirostris ~~Charles Isd~~ Chatham Isd?
417 —— strenua James Isd.
427 422 434 —— fortis James Isd / Do / Do
433 432 Geospiza parvula James Isd.
423 Geospiza psittacula James Isd?

Fig. 6. Darwin's notes on the island localities of Covington's and Fuller's Galapagos finches. (Courtesy of the Syndics of Cambridge University Library.)

‘Chatham Is^{d}??’[24]. The reason Darwin surrounded this locality designation with three question marks is evident from the order of the catalogue entries as a whole. As may be seen from the number sequence assigned to his birds, Darwin ticketed, numbered, and catalogued the entire collection only after leaving the Galapagos Archipelago in late October 1835. Within the list of birds, the entries proceed topsy-turvy, with specimens from the different islands entered in no apparent order[25]. It is hardly surprising, then, that at least two of the eight specimens that Darwin later assigned to Chatham Island appear to have been mislabelled (see pages 63–64).

In the process of attempting to correlate the results from four different collections, Darwin inadvertently made other mistakes. In the *Zoology* (1841 : 101) he later gave the locality of *Geospiza fortis* as Charles and Chatham islands; but this was clearly an error, since the *Beagle* specimens all came from Charles and James[26]. Further inaccuracies are associated with Darwin's claim about geographic representation among the various species of the Geospizinae. Eager to squeeze whatever evolutionary evidence he could from these finches, Darwin systematically collated the island localities of the four *Beagle* collections to see if any of the species represented one another on the different islands. In two genera, *Cactornis* and *Camarhynchus,* he claimed this to be the case. Of the numerous specimens shot by four collectors at James Island, he reported, all belonged to *Cactornis scandens* and *Camarhynchus psittacula,* whereas the specimens collected either on Chatham or Charles were those of *Cactornis assimilis* and *Camarhynchus crassirostris.* 'Hence we may feel almost sure', he concluded, 'that these islands possess their representative species of these two sub-groups' (1845 : 395).

Darwin's analysis of these two genera was plagued by several errors. In actual fact, FitzRoy had collected a specimen of *Cactornis assimilis* on James, not Charles or Chatham islands, thus invalidating half of Darwin's claim. Furthermore, Darwin had not collected long enough on any of these islands to realize that the various finch species are by no means confined to single islands. *Camarhynchus crassirostris,* for example, is found not only on Charles Island, where Darwin believed his own specimens had probably been taken, but also on Chatham and James. Similarly, *Cactornis scandens* and *Camarhynchus psittacula* are not confined to James Island, as Darwin had thought, but are found on the other islands he visited. Thus Darwin's claim about geographic representation in this group of four species is not only wrong in every detail, but it is not even substantiated by the *Beagle*'s own collections. It is no wonder, then, that Darwin was so excited and relieved, in 1845, by Joseph Hooker's rigorous demonstration of representation in his several hundred species of Galapagos plants. To Hooker he wrote in July of that year, 'I cannot tell you how delighted and astonished I am at the results of your examination; how wonderfully they support my assertion on the differences in the animals of the different islands, about which I have always been fearful' (1887, **2** : 22). Darwin lost no time in adding Hooker's welcome results to his *Journal of Researches,* which he was then engaged in revising for the second edition[27].

Fortunately, the errors and uncertainties associated with Darwin's ornithological specimens did not affect the published results of the *Zoology of the Voyage of H.M.S. Beagle* that much. Of the seventeen localities that Darwin published for his finches, fifteen were either provided or corroborated by the other shipmates' collections. Darwin himself, employing an educated guess, was able to supply localities for two additional species that only he had collected. In the end only two species of finches remained without any locality whatsoever.

Unfortunately, what later ornithologists generally failed to appreciate was that Darwin's published localities were not necessarily those of his own specimens. In fact, the largely borrowed nature of Darwin's published localities for his Galapagos finches has had one curious repercussion that has confused even further the localities of the *Beagle* type specimens. A number of originally unlabelled Darwin specimens appear to have acquired island localities later in a completely circular fashion, based on the published information provided in the *Zoology of the Voyage of H.M.S. Beagle.* Curators at the British Museum apparently noticed that certain Galapagos species were indicated in the *Zoology* as coming from one island only. They therefore assumed that unlabelled Darwin specimens of these species must have come from those published localities. The specimens in question now carry these island localities on their labels; and in the British Museum's published list of type specimens there are notes to see the relevant pages of the *Zoology of the Voyage of H.M.S. Beagle*[28]. In certain instances (for example, in the case of Darwin's specimens of *Otus galapagoensis, Hirundo concolor,* and *Dolichonyx oryzivorus*), these derivative localities are indeed correct, since Darwin was the only person on the *Beagle* to collect these species, whose localities he was later able to recall. But this same process of circular relabelling is apparently what accounts for at least four of Darwin's finches being given localities that do not necessarily belong to them[29].

More ironically still, three of Captain FitzRoy's accurately labelled specimens have also suffered from this relabelling process, based once again on Darwin's published testimony. In one instance FitzRoy's specimen of *Camarhynchus psittacula,* which was procured on James Island, was relabelled as coming from Charles Island. This error was precipitated by the loss of Darwin's three type specimens of *C. crassirostris. C. crassirostris* and *C. psittacula* are somewhat similar species. FitzRoy's slightly aberrant specimen of *psittacula,* which was later thought to be the missing type of *crassirostris,* was accordingly reassigned to that species. But the island locality now had to be altered as well to agree with Darwin's dubious, but 'official', information for the type of *C. crassirostris*[30]! The classification error was eventually caught by Swarth (1931 : 208), but the specimen in question still bears two island localities. Similarly, two other FitzRoy specimens, one being the type of *Geospiza nebulosa*, were also relabelled incorrectly, owing once again to Darwin's published localities[31].

In short, the published designations of the *Zoology* were seen by later ornithologists and museum curators as more definitive than the accurately labelled FitzRoy specimens that had largely supplied this information. Swarth (1931 : 11) actually dismissed FitzRoy's localities wholesale, assuming his specimens could have come from practically anywhere in the archipelago[32]. David Lack (1945, 1947), although not going quite so far, assumed that all of FitzRoy's specimens were really Darwin's, and that those specimens labelled as coming from either Chatham or Charles Island could have come from either locality. With all of these confusions about the localities of Darwin's and FitzRoy's specimens, it is little wonder that the *Beagle* types have proved so problematical to ornithologists over the last hundred years.

Because there has been so much misinformation with regard to the various specimens of Geospizinae collected during the *Beagle* voyage, and because Darwin's published localities for these birds were largely derived from other *Beagle* collections, I have thought it worthwhile to present a brief history and description of all the known specimens. Altogether, there were between 56 and 58 Geospizinae collected by four different *Beagle* shipmates. Precise information regarding the collectors, the localities, and the sexes of many of these *Beagle* Geospizinae is provided here for the first time, based on hitherto unknown manuscript sources. In addition, I have supplied measurements of all the specimens (see the Appendix), and have reassigned several birds that appear to have been misclassified by Gould or later ornithologists. I shall begin with Darwin's collection, which was the largest.

Darwin's collection

Darwin collected 31 specimens of Geospizinae in the Galapagos Archipelago (1963 [1836] : 262–64). These, along with the rest of his ornithological specimens, were presented to the Zoological Society of London on 4 January 1837. Most of the specimens were subsequently mounted and displayed in the society's museum, as was customarily done with type specimens in the nineteenth century. In 1855 the Zoological Society decided to close its museum, and the British Museum was given first pick of the specimens (Sharpe, 1906 : 251). Unfortunately George Robert Gray, who was then the curator in charge of birds, did not acquire all the *Beagle* type specimens, a fact that has been greatly regretted by subsequent ornithologists. Of Darwin's 31 specimens of Geospizinae, only 19 were included among the 403 birds purchased from the Zoological Society on 19 December 1855. A few months later Darwin presented the British Museum with 3 additional Galapagos birds, including a specimen of finch ('*Geospiza*'). The following year John Gould sold 2 more of Darwin's '*Geospiza*' to the museum, bringing the total to 22[33]. Three of these specimens appear to have been subsequently lost, so that the present total at the British Museum stands at 19 specimens (see note 84). None of these birds bear any indication of their sex on the old nineteenth-century labels. Although this information is presented here for most of the specimens, it is derived from Sharpe's (1888) and Swarth's (1931) sometimes conflicting inferences from plumage. These designations cannot therefore be regarded as entirely accurate, except in the case of adult males.

Geospiza magnirostris Gould = ***Geospiza magnirostris magnirostris*** Gould[34]

The British Museum has at least two Darwin specimens of this large-billed form of *magnirostris*. Specimen no. 1855.12.19.80 is an adult male and is labelled on its nineteenth-century tag as coming from 'Chatham Isl'. A newer red type specimen tag gives the locality as 'Chatham Is? [Charles Is.]'. The second specimen, no. 1855.12.19.113, is a female and is labelled as coming from 'Chatham'. Both of these specimens are undoubtedly among the eight that Darwin, after the voyage, guessed he had collected on '?Chatham Is^{d}??'[35]. It is possible that the specimen tags at the Zoological Society originally carried question marks after the locality designation. Both specimens were subsequently mounted, and the locality on the stands was probably given without a question mark. When the specimens were taken off the stands in 1855 and provided with British Museum labels, the uncertainty of the original locality information was doubtless forgotten[36]. The red type label on specimen no. 1855.12.19.80, which gives the locality as 'Chatham Is? [Charles Island]', dates from the early decades of this century, and reflects an attempt to second-guess the locality designation on the much older tag.

Geospiza strenua Gould = ***Geospiza magnirostris strenua*** Gould, ***Geospiza fortis*** Gould, and ***Geospiza nebulosa debilirostris*** Ridgway

There are four Darwin specimens of *Geospiza strenua* (*sensu* Gould) in the British Museum, an adult male (no. 1855.12.19.81) and three females (nos. 1855.12.19.83, 1855.12.19.114, and 1856.3.15.4). According to a note on the label of specimen no. 1855.12.19.83, Gould's (1841 : 101) description of the female of this species was taken from this individual. The specimen, which has a very small bill, was definitely not the bird figured by Gould in the *Zoology*. The male bears the locality 'Chatham Isl.' on its nineteenth-century tag and 'Chatham Island?' on the newer red type specimen tag. The first two females are indicated as coming from 'Chatham Isl.'. The other female specimen has no locality. The three specimens bearing a Chatham locality are undoubtedly among the eight that Darwin later assigned to '?Chatham Is^{d}??' in his master catalogue. If Darwin was correct about the locality of these three specimens, then two of them are extremely small examples of *G. magnirostris magnirostris*, which Fuller's collection conclusively establishes as the Chatham Island race of this species. On the other hand, the third and even smaller Chatham specimen (Gould's female type) must belong to a large example of *G. fortis*[37]. According to David Lack (1947 : 23), the fourth bird is a typical specimen of *G. difficilis* [now *nebulosa*] *debilirostris* and hence must have come from James Island[38].

There is very good reason to question the Chatham Island localities ascribed to specimens no. 1855.12.19.81 and no. 1855.12.19.114. First of all, the presence of such diminutive examples of *G. magnirostris magnirostris* on the same island as the largest known example of this species (see under Fuller's collection), implies an extraordinary degree of variation in this island form. But even granting that the character range for *G. magnirostris magnirostris* was extremely great on Chatham Island, Darwin's two small examples depart from the mean size of culmen, bill depth, and wing length for this subspecies by an average of 3·8 and 3·5 standard deviations. Such disparities are significant at the ·001 level[39]. (For the sake of argument, I have made this statistical comparison using the largest standard deviation that has ever been observed in *G. magnirostris*, anywhere in the archipelago, for each of the three characters involved in the computation.) Moreover, using culmen length in specimen no. 1855.12.19.81 and wing length in specimen no. 1855.12.19.114, the probability that either of these two birds came from Chatham Island is less than one in ten thousand. The probability that *both* birds came from Chatham is virtually nil. What therefore seems quite likely is that these two specimens are examples of *G. magnirostris strenua,* taken on James Island, where the subspecies overlaps with these specimens in all of their basic dimensions. In this connection, it should be remembered that Darwin's locality designations for these two specimens were retrospective guesses made almost two years after he had visited the Galapagos. That Darwin may have accurately remembered where he had collected specimens of *G. magnirostris magnirostris* is possible; but that he accurately distinguished the localities of all the specimens of the two *G. magnirostris* subspecies is more doubtful. Indeed, he probably grouped all the large-billed birds together when he entered them in his catalogue, just as he did with other clearly distinguishable finch species. This, in turn, must have made it even more difficult for Darwin, later, to differentiate the localities of his two *G. magnirostris* subspecies. Finally, it is highly unlikely that Fuller was the only person to collect *G. magnirostris strenua* on James Island, where Darwin did the bulk of his own collecting. Several specimens should also be present in Darwin's collection, and these two specimens, of dubious locality and extremely diminutive size, are therefore probably from James.

With regard to Darwin's apparent error about the locality of his two *G. magnirostris strenua* specimens, he may have been partially misled by Gould's misclassification of a FitzRoy specimen. FitzRoy's single Chatham Island specimen of '*G. strenua*' is either a very large example of *G. fortis* or, more probably, a hybrid between *G. fortis* and *G. magnirostris magnirostris* (see page 68). Hence no true specimens of *G. magnirostris strenua* were taken on Chatham Island.

If I am wrong about reassigning Darwin's two diminutive specimens of *G. strenua* to the James Island form of *G. magnirostris strenua,* then the possibility cannot be ignored that they, too, are hybrids between *G. magnirostris magnirostris* and *G. fortis* on Chatham Island. It is unlikely, however, that the *Beagle* collections would have included three hybrid specimens out of eight Chatham Island examples of *G. magnirostris* and *G. fortis,* so I am considerably more confident that Darwin's two specimens, given their dubious locality, belong to the James Island form of *G. magnirostris strenua.*

Geospiza fortis Gould

The British Museum possesses three Darwin specimens of *G. fortis.* Two of them, which were misclassified by Gould, are noticed separately under *Geospiza strenua* and *Geospiza dentirostris.* The other, a female from 'Charles Isl.' (no. 1855.12.19.82), was correctly identified by Gould. I strongly suspect that this specimen was originally collected by someone other than Darwin, to whom it must later have been given. In his *Ornithological Notes* and specimen catalogue, Darwin did not record a Charles Island locality for any of his birds, although he did later state that his three specimens of *Camarhynchus crassirostris* may have come from that island. Unlike *C. crassirostris,* however, *G. fortis* is not easily differentiated from other similar species. It is therefore extremely unlikely that Darwin could have reconstructed this locality from memory, especially since he was unable to do so for another specimen of this species (see under *Geospiza dentirostris*). Darwin's servant, on the other hand, did collect a specimen of *G. fortis* on Charles Island. Covington later gave or sold this specimen, along with three other Geospizinae, to Darwin's friend Thomas C. Eyton. All the Covington specimens, but his Charles Island *G. fortis,* eventually came into the possession of the British Museum in 1885. I believe that Darwin, who lacked a female of this species (*sensu* Gould), acquired this specimen from Eyton so that it could be described by Gould[40]. If I am wrong about the history of this specimen, then the locality on the tag is almost certainly a later addition by someone other than Darwin. Given the specimen's measurements, it could have come from any of the three islands on which Darwin collected finches (Chatham, Charles, and James). A jet black male, figured by Gould in the *Zoology,* has been lost.

Geospiza dentirostris Gould = *Geospiza fortis* Gould

The British Museum possesses one specimen (no. 1855.12.19.176) of this so-named form, which was the only example collected by Darwin. From dissection, Darwin thought it was a male, but Gould considered it a female on the basis of its plumage (Darwin, 1841 : 102). Darwin was unable to provide a locality for this specimen. Both Swarth (1931 : 153) and Lack (1945 : 12) have considered the bird to be an example of *G. fortis.* Given the diminutive size of this specimen, especially in bill depth, it almost certainly came from Charles Island.

Geospiza dubia Gould = *Geospiza fortis* Gould

The only type specimen for this species, a female, is lost. It was evidently not received by the British Museum in 1855, since it appeared in small type in Gray's *Hand-List* (1870 : 88). Based on Gould's description, Swarth (1931 : 155–56) considered this form to be an example of *G. fortis.* Darwin listed the locality as Chatham Island, and the specimen was undoubtedly one of the eight that, after the voyage, he guessed had come from that island.

Geospiza fuliginosa Gould

Two Darwin specimens of *G. fuliginosa* are in the British Museum (nos. 1855.12.19.44 and 1857.11.28.247). Both are adult males and are labelled as coming from Chatham Island. These are the last of the eight specimens that Darwin later assigned to '⸮Chatham Is^{d}??' in his master catalogue of specimens. Although the specimens could have come from any of the three islands on which Darwin collected finches (Chatham, Charles, and James), they approach most closely in their measurements the Chatham Island form of *G. fuliginosa.* The female specimen that Gould described in the *Zoology* (1841 : 102) is not in the British Museum collection.

Geospiza parvula Gould = *Camarhynchus parvulus parvulus* (Gould)

There are two specimens of *G. parvula* collected by Darwin (no. 1855.12.19.167, a female; and no. 1855.12.19.194, an adult male). Both specimens were evidently the models for Gould's coloured plate (1841 : Plate 39). They were at one time labelled as coming from Chatham Island (Sharpe, 1888 : 4), but neither specimen belongs to the distinctive Chatham Island form (*salvini*) of *C. parvulus* (Swarth, 1931 : 229–31)[41]. This Chatham Island designation has therefore been questioned on the labels and 'James Island' written on them as well. In the *Zoology* (1841 : 102), Darwin listed only James Island as the locality of this species, a designation undoubtedly based on the three FitzRoy and two Fuller specimens that did come from that island. I do not believe that Darwin gave his own specimens any locality. Warren & Harrison (1971 : 420) give James Island as the locality of type specimen no. 1855.12.19.194, relying solely on the information given in the *Zoology.* Both specimens surely acquired this 'James' locality on their labels by the same circular process of reasoning. Nevertheless, measurements of bill depth and wing length support the correctness of this James Island designation.

Cactornis scandens Gould = *Geospiza scandens scandens* (Gould) and *Geospiza nebulosa nebulosa* Gould

Darwin's specimens of *C. scandens* include an adult male (no. 1855.12.19.125), a female (no. 1855.12.19.20), and a third specimen noticed separately under *Cactornis assimilis.* The first two birds are labelled as coming from James Island, but this is almost certainly a later designation provided by reference to the *Zoology* (1841 : 104). Lack (1945 : 14–15) assigns specimen no. 1855.12.19.20 to *G. difficilis* (now *nebulosa*) and suggests that it belongs to the extinct form of this species that FitzRoy collected on Charles Island (see *Geospiza nebulosa,* under FitzRoy's collection). From Darwin's statement in the *Zoology* (1841 : 105) that he and two other collectors were daily looking out for jet black examples of the Cactus Finch, it seems likely that at least some of his specimens did come from James Island, where he, Bynoe, and Fuller spent a week collecting together. As Lack notes in this connection, the adult male specimen has 'so small a bill that it almost certainly came from James' (1945 : 16).

Cactornis assimilis Gould = ***Geospiza scandens rothschildi*** Heller and Snodgrass –a straggler?

Darwin collected one specimen of this form (no. 1855.12.19.15), which Sharpe (1888 : 18) considered an immature male but Swarth (1931 : 198) thought a female[42]. Darwin did not know from which island he had procured it. According to both Swarth (1931 : 198) and Lack (1945 : 16), Darwin's specimen agrees most closely with the Bindloe form (*rothschildi*) of *G. scandens.* FitzRoy's collection includes an almost identical specimen taken on James Island, however, and Darwin's specimen probably came from there as well. James Island is only forty miles from Bindloe, and stragglers, mostly juveniles, have frequently been reported over even longer distances (Lack, 1945 : 106)[43].

Camarhynchus crassirostris Gould = ***Platyspiza crassirostris*** (Gould)

Darwin collected three specimens, one male and two females, of *C. crassirostris,* but none of them were acquired by the British Museum in 1855. Darwin was unsure about which island of the Galapagos he collected these specimens on, but he guessed that it was probably Charles. Since *C. crassirostris* is common only in the transitional zone, Darwin would had to have collected this species either on Charles or James, the only two islands where he visited this zone. It is possible that he remembered taking *C. crassirostris* and *C. psittacula* on different islands. In this case, Charles Island is indeed the most likely locality for his *C. crassirostris* specimens, since he encountered *C. psittacula* only on James.

Camarhynchus psittacula Gould = ***Camarhynchus psittacula psittacula*** Gould

Darwin collected three specimens of *C. psittacula* on James Island, two males and one female (1963[1836] : 263). Only one of them, a supposed female (no. 1855.12.19.22), is now in the British Museum. Another specimen, also thought to have been a female, was acquired but has been lost (no. 1855.12.19.12). Since Darwin collected only one female of this species, the surviving specimen may well be a juvenile male. It is doubtful if the museum ever received the third specimen, since it was not recorded by Sharpe (1888 : 17). Darwin's locality for these specimens may definitely be trusted, since he explicitly noted in his *Ornithological Notes* that he had seen this well-defined species on one island only.

Certhidea olivacea Gould = ***Certhidea olivacea olivacea*** Gould

Three specimens of the Warbler Finch are credited to Darwin at the British Museum (no. 1855.12.19.126, a male, which is labelled as having once been Darwin's no. 3340; and two specimens of unknown sex, no. 1855.12.19.127 and no. 1855.12.19.164). The bird with the distinctive cinnamon throat, as figured by Gould, is no longer among the specimens at the British Museum (Swarth, 1931 : 255). Darwin believed his specimens came from Chatham and James islands and that the species was 'certainly found at the latter [island]' (1841 : 106). *Certhidea olivacea* shows distinctive variations by island, and Swarth (1931 : 255) confidently assigns Darwin's three specimens to James Island[44].

In his *Ornithological Notes* Darwin recorded collecting only two specimens of *C. olivacea* (nos. 3310 and 3340). On the back of manuscript page 74 of these notes he wrote, 'A number lost at the [Zoological] Society belong to Geospiza (certhidea) olivacea'[45]. Included among these lost specimens was probably the male in Gould's coloured plate. It would therefore seem that Darwin, after the voyage was over, acquired a minimum of one and perhaps two additional specimens of this species from other *Beagle* collections. The most likely source of such replacement specimens would have been the collections of Covington and Fuller, which are noticed separately.

Other Darwin specimens

The accessions catalogue for birds received by the British Museum records three specimens of Darwin's finches that I have been unable to locate[46]. The first is a specimen of *Camarhynchus psittacula* (no. 1855.12.19.12) that was seen by Swarth (1931 : 215) but that has since been lost. The second specimen, a '*Geospiza*' (no. 1855.12.19.43), was included like the first in the purchase from the Zoological Society. The third specimen, also a '*Geospiza*' (no. 1857.11.28.248), was purchased from John Gould along with no. 1857.11.28.247, a specimen of *G. fuliginosa* that is in the collection. In the British Museum's record of accessions, this third specimen is marked as having been destroyed. Several other missing Darwin specimens may now be at the Leiden Rijksmuseum van Natuurlijke Historie, and these specimens are discussed separately under that collection.

FitzRoy's collection

The captain of H.M.S. *Beagle,* Robert FitzRoy, possessed considerable interest in several branches of natural history. It was at his instigation that a naturalist was invited to accompany the *Beagle* on its voyage around the world. Since Darwin, as a condition of his appointment, had insisted upon the right to dispose of his voyage collections as he wished, FitzRoy apparently decided to undertake his own separate zoological collection for the benefit of the British Museum. When he was unable to leave the ship, he encouraged other officers of the *Beagle* to procure specimens for him. This occurred, for example, in the Galapagos, where Benjamin Bynoe, the surgeon of the *Beagle,* spent a week collecting for the captain on James Island. Another officer of the *Beagle,* Edward H. Hellyer, actually drowned while attempting to procure a specimen for FitzRoy's collection[47].

A copy of FitzRoy's manuscript catalogue of specimens is now at Cambridge University Library among Charles Darwin's papers[48]. This catalogue indicates that FitzRoy collected 447 zoological specimens during the *Beagle* voyage. Sixty of these (50 birds and 10 reptiles) were procured in the Galapagos Archipelago. Each Galapagos specimen was carefully dated and labelled by island. FitzRoy's catalogue also notes the sex and eye colour of each specimen, the latter being something Darwin generally did not record. At least 13, and perhaps as many as 26 of FitzRoy's 50 Galapagos birds, were collected by Harry Fuller, another *Beagle* shipmate. After the voyage, most of Fuller's specimens were separated from FitzRoy's collection and were subsequently acquired by the Haslar Museum in Plymouth. This portion of FitzRoy's collection is noticed separately.

The ornithological portion of FitzRoy's catalogue lists the following specimen numbers and localities for the Galapagos Islands: nos. 387–400 (Chatham Island), nos. 401–10 (Charles Island), and nos. 413–38 (James Island). To the feet of each specimen was originally attached a tiny paper tag (roughly 4·5 mm × 12 mm) recording one of these assigned numbers. Only Fuller's specimens have retained these tiny tags. When the British Museum received the bulk of FitzRoy's collection on 21 February 1837, all of his specimens were given new numbers. Fortunately the old numbers were recorded in the museum's register of accessions, along with the island locality of each bird[49]. There is accordingly no room for doubt about the island localities of any of FitzRoy's specimens at the British Museum. Later ornithologists, however, have rarely been aware of this fact.

Of FitzRoy's 50 Galapagos birds, only 24, including 13 Geospizinae, were presented to the British Museum. Fourteen of these specimens, including 8 Geospizinae, were evidently collected by Benjamin Bynoe[50]. Of the remaining 26 Galapagos birds in FitzRoy's collection, at least 8 were Geospizinae that later went to the Haslar Museum. These specimens are noticed separately under Fuller's collection. Hence 18 of FitzRoy's specimens still remain unaccounted for. Most of them were probably Fuller's, since Darwin commented in his *Ornithological Notes* (1963[1836] : 265) that Fuller possessed several wading birds that his own collection lacked. It is also possible that some of these missing specimens were collected by other *Beagle* shipmates who, like Fuller, may have taken charge of them after the *Beagle*'s return to England. Officers and ordinary seamen were under no obligation to collect for either FitzRoy or Darwin, and they were accordingly free to keep and sell in England whatever they procured. FitzRoy later reminded Darwin of this fact when he concluded, after seeing a draft of Darwin's acknowledgments section for the *Journal of Researches,* that Darwin had not given sufficient credit to the officers of the *Beagle* for assisting him in his collections[51]. Inasmuch as the officers generally made an effort to insure that Darwin and FitzRoy each received rare specimens, whatever these officers might have kept were undoubtedly duplicates or already described species[52].

Geospiza magnirostris Gould = ***Geospiza magnirostris magnirostris*** Gould

FitzRoy procured three specimens of this large-billed form of *magnirostris,* a female (no. 1837.2.21.398 = FitzRoy no. 403), an adult male (no. 1837.2.21.402 = FitzRoy no. 407), and a juvenile male (no. 1837.2.21.403 = FitzRoy no. 408). Sharpe (1888 : 8) gives the sex of this third specimen incorrectly. FitzRoy recorded that all three specimens were taken between 25 and 27 September 1835 on Charles Island, which should put an end to the many disputes about the locality of this form[53]. It has generally been thought that this form became extinct on Charles Island in the nineteenth century. In 1957, however, Robert Bowman collected on Charles Island an adult female of *G. magnirostris* that he claimed overlapped with some of the *Beagle* specimens. Other birds of this species were also observed by Bowman at this time (1961 : 271). No one has seen or collected specimens of *G. magnirostris* on Charles Island since Bowman's visit. In all likelihood, the specimens seen by him in 1957 were part of a small population that had recently recolonized Charles Island from the north and that subsequently became extinct. This supposition is supported, moreover, by the measurements of Bowman's specimen, which are: culmen from nostril, 15·7 mm; bill depth, 19·6 mm; and wing, 77 mm (University of California, Berkeley, Museum of Vertebrate Zoology, specimen no. 140985). There is no overlap between these measurements and any of the large-billed *Beagle* specimens of *G. magnirostris magnirostris* taken on Charles Island. Bowman's specimen is, in fact, a typical example of *G. magnirostris strenua,* and it accords most closely with the smaller forms of this subspecies found in the centre of the archipelago. Since 1888 there have been two other reports of isolated specimens of *G. magnirostris* taken on Charles Island[54]. Among Darwin's finches, colonizations of islands within the Galapagos group probably occur much more frequently than has hitherto been appreciated on the basis of collectors' evidence.

Geospiza strenua Gould = ***Geospiza magnirostris magnirostris*** Gould × ***Geospiza fortis*** Gould?

FitzRoy collected one specimen of *G. strenua,* an adult male from Chatham Island (no. 1837.2.21.396 = FitzRoy no. 397). This specimen is intermediate between *G. magnirostris magnirostris* and *G. fortis* on Chatham Island. The measurements of the specimen are slightly larger than for any known race of *G. fortis.* They are also within the range of the smaller forms of *G. magnirostris,* but not of the larger forms of that species[55]. Since the specimen is an adult male, and since its placement within the *G. magnirostris* group would require a variability in the exceptionally large Chatham Island race that would be fifty per cent greater than for any known form, the most reasonable assignment is to *G. fortis.* More plausible still is that the specimen is a hybrid between the two species. Hybrids are known to occur between these two forms in one or two per cent of all matings (Peter Grant, personal communication)[56].

Geospiza fuliginosa Gould

FitzRoy's collection included three specimens of *G. fuliginosa,* a male (no. 1837.2.21.417 = FitzRoy no. 436) and two females (1837.2.21.410 = FitzRoy no. 420; and

1837.2.21.411 = FitzRoy no. 421). They were all procured on James Island. The first of these three specimens is missing at the British Museum (Natural History) and has evidently been lost or destroyed. Darwin recorded in his manuscript notes on FitzRoy's collection that the two female specimens belonged to *G. parvula,* and this was apparently Gould's own designation[57]. As Swarth (1931 : 229) points out, the name *parvula* has commonly been applied to small examples of *G. fuliginosa.* In Gould's day it was not realized that males of *Camarhynchus parvulus,* unlike those of *G. fuliginosa,* are never fully black, and this circumstance added to the difficulty of distinguishing these two species.

Geospiza nebulosa Gould = ***Geospiza nebulosa nebulosa*** Gould

Gould gave the name *G. nebulosa* to at least two specimens, of which one, a female, was collected by FitzRoy on Charles Island (no. 1837.2.21.400 = FitzRoy no. 405). A male specimen, which provided the type description, came from Darwin's collection and has unfortunately been lost. Swarth (1931 : 153) synonymized FitzRoy's specimen with *G. fortis,* but the specimen has much too narrow and pointed a bill to accord with that species. Lack (1945 : 14–15), on the other hand, placed the specimen with the *G. difficilis* group and, following Swarth (1931 : 190), thought that one of Darwin's specimens of *Cactornis scandens* (no. 1855.12.19.20) should also be reassigned to this form. The bills of these two specimens are slightly larger than in any known forms of *G. difficilis,* and both specimens lack the chestnut on the wing bar and undertail coverts, as is found in some members of the *G. difficilis* group[58]. The only other species with which these two specimens exhibit even a slight overlap in measurements is *G. fortis,* which has, however, a larger average depth of bill than culmen, as measured from the nostril (Lack, 1947 : 174–76). In *G. difficilis*, as in the two *Beagle* specimens, the opposite is true. Moreover, *G. difficilis* and the two *Beagle* specimens possess a relatively straight culmen, whereas the culmen is definitely curved in the other species of *Geospiza.* Hence these two *Beagle* specimens agree most closely with the measurements and general characteristics of *G. difficilis,* and evidently constitute, as Lack himself concluded, an extinct race of this species from Charles Island.

Lack's opinion is reinforced by certain facts regarding the distribution of this species. *G. difficilis* is confined to the humid zone of those islands, like Charles, where *G. fuliginosa* is also present. Both Darwin and FitzRoy visited the highlands on Charles Island, and FitzRoy's specimen was shot on 27 September 1835, during the afternoon that Darwin and several *Beagle* officers made an excursion to the highest point on the island. Two specimens of the Galapagos Rail, which is also confined to the highlands, were procured for FitzRoy's collection during this same excursion. Another almost identical specimen of '*G. nebulosa*' was taken on Charles Island in 1852 by an expedition that also visited the highlands[59]. Although once found on all of the larger islands in the archipelago, *G. difficilis* has definitely become extinct on several of them, probably owing to ground clearing and cultivation in the humid zone. It is hardly surprising, then, that *G. difficilis* may have encountered this same fate on Charles Island, which was the first island to be settled, in 1832. Within just a few years, ecological disturbances associated with the settlement were already manifesting themselves. Darwin (1963[1836] : 264) specifically noted that the larger species of ground finches, which normally prefer the arid lowlands, were extremely common on Charles Island near the cleared tracts at the highlands settlement. Indeed, these ground finches had become quite troublesome to the settlers, eating seeds buried up to six inches in the cultivated fields. Thus, by the mid-1830s any endemic Charles Island population of *G. difficilis* would have been faced with two threats to its continued existence: a diminishing habitat and increased competition from other species of Darwin's finches that are normally restricted to the lower altitudes. Although the reasons for their disappearance are less clear, two other species of birds, *Geospiza magnirostris* and *Nesomimus trifasciatus,* became extinct on Charles Island during the nineteenth century.

Other ornithologists have generally accepted Lack's judgment that FitzRoy's specimen of *G. nebulosa* is an extinct form of *G. difficilis* (Bowman, 1961 : 270; Harris, 1974 : 36).

Although the name *nebulosa* has not been used for nearly a century, the law of priority in nomenclature insists that the name of the first described subspecies shall have precedence over all later described subspecies of the same species. Thus the name *nebulosa* should technically replace *difficilis,* which was first proposed by Sharpe (1888 : 12) for the Abingdon Island race of this species. Lack (1945 : 14–15) recognized the need for this substitution but was reluctant to institute it because he thought, erroneously, that Gould's *G. nebulosa* was known from only two specimens whose localities were not entirely certain. The type locality, however, is now definitely established as Charles Island. Gould, moreover, apparently had a third–and now lost–specimen in his possession when he described this species. Finally, a fourth specimen was collected on Charles Island in 1852. Based on these facts, together with the subsequent agreement of ornithologists that Gould correctly differentiated FitzRoy's specimen of *G. difficilis* as *G. nebulosa,* the name *nebulosa* appears to have legitimate priority over *difficilis* (cf. Paynter, 1970 : 162). The following names therefore have priority for this species: *G. nebulosa nebulosa* Gould (the extinct Charles Island form of the species); *G. nebulosa difficilis* Sharpe (Abingdon and Tower islands); *G. nebulosa debilirostris* Ridgway (Narborough, James, and Indefatigable islands); and *G. nebulosa septentrionalis* Rothschild and Hartert (Wenman and Culpepper islands).

The question of why the Charles Island subspecies of *G. nebulosa* possessed such a large bill can perhaps be answered, albeit somewhat speculatively, by considering the other finch species with which it would have been in competition for food resources. With the large average beak size of the ground finches on Charles Island, where *G. magnirostris magnirostris* was apparently the commonest bird in the lowlands, and with unusually small-billed tree finches in the highlands, the large bill of *G. nebulosa nebulosa* might plausibly be accounted for by the simultaneous operation of character release and character displacement in an upward direction. Indeed, Charles Island is unique in being the only island in the Galapagos on which the majority of resident Geospizinae have smaller bills than *G. nebulosa.* Hence a net upward displacement in bill size would be expected compared with other subspecies of this species.

Geospiza parvula Gould = ***Geospiza fuliginosa*** Gould and ***Camarhynchus parvulus parvulus*** (Gould)

FitzRoy collected three specimens of *G. parvula* (*sensu* Gould) on James Island. Two of these specimens have been correctly reassigned to *G. fuliginosa* by subsequent ornithologists and are separately noticed under that species. The third specimen, a female, is a valid example of *C. parvulus* (no. 1837.2.21.414 = FitzRoy no. 428). No specimen with this registration number actually exists at the British Museum. But there are two specimens bearing reg. no. 1837.2.21.411; and one of these, a female of *C. parvulus,* is evidently the missing specimen.

Cactornis scandens Gould = ***Geospiza scandens scandens*** (Gould)

FitzRoy collected one example of *C. scandens,* an adult male, on James Island (no. 1837.2.21.412 = FitzRoy no. 424). This specimen was the jet black one shot by Bynoe and mentioned by Darwin in the *Zoology* (1841 : 105). The specimen is missing from the British Museum collection.

Cactornis assimilis Gould = ***Geospiza scandens rothschildi*** Heller and Snodgrass –a straggler?

FitzRoy's collection included a single juvenile male specimen of this form, which was procured on James Island (no. 1837.2.21.415 = FitzRoy no. 430). Both Sharpe (1888 : 18) and Swarth (1931 : 198) give the sex incorrectly. For the identity of this specimen, see *Cactornis scandens,* under Darwin's collection.

Camarhynchus psittacula Gould = ***Camarhynchus psittacula psittacula*** Gould

There is a single individual of *C. psittacula* in FitzRoy's collection, a male that was procured on James Island (no. 1837.2.21.413 = FitzRoy no. 426). According to Darwin (1963[1836] : 264), this specimen was shot by Bynoe. The bird was originally designated *psittacula* by Gould, but it subsequently became confused with the type of *C. crassirostris,* acquiring that name and a Charles Island locality on the tag. Both Swarth (1931 : 208) and Lack (1945 : 16–17) concur that the specimen indeed belongs to *C. psittacula,* although it is perhaps slightly aberrant[60].

Certhidea olivacea Gould = ***Certhidea olivacea olivacea*** Gould

FitzRoy's collection included one specimen of *C. olivacea,* a female collected on James Island (no. 1837.2.21.408 = FitzRoy no. 416).

Fuller's collection

Harry Fuller, FitzRoy's personal steward on the *Beagle,* collected eight specimens of Geospizinae while in the Galapagos Archipelago[61]. These birds now reside at the University Museum of Zoology, Cambridge, England. The specimens may be identified as Fuller's by the tiny numbered tags, corresponding to FitzRoy's *Beagle* catalogue sequence, that still adhere to the feet[62]. Fuller spent a week collecting with Darwin, Bynoe, and Covington on James Island, and seven of his eight specimens came from that island.

Information on a later set of specimen tags allows us to reconstruct the following history for Fuller's birds. Seven of his eight specimens have the name 'Dr. Armstrong' on the labels. This is apparently the same Dr Armstrong mentioned by John Stevens Henslow, during the *Beagle* voyage, in an 1834 letter to Darwin[63]. Armstrong was in charge of the Haslar Museum (part of the Haslar Royal Naval Hospital in Plymouth), to which Fuller's specimens were either given or sold sometime after the *Beagle* voyage. In deciding whether Fuller had the right to dispose of his own specimens as he wished, it is relevant to note that the specimens that went to the Haslar Museum were not just duplicates but included some forms that FitzRoy's collection otherwise lacked. Given this fact, and given that only Fuller's specimens (and not Bynoe's) were subsequently withheld from the British Museum, it seems justified to speak of 'Fuller's collection' as a separate entity from FitzRoy's own official collection, to which Bynoe contributed[64].

In 1856, the Haslar Museum was closed down and its specimens were distributed to other museums and collections. In this connection, the Lords of the Admiralty presented a number of Haslar Museum mammals, birds, reptiles, fish, and molluscs to the British Museum on 12 January 1856[65]. None of the birds given to the British Museum included Galapagos specimens. On the other hand, at least seven Galapagos birds (Armstrong's finches) were acquired by Sir William Jardine, in whose hand the later specimen tags are written. Jardine's tags indicate that the specimens were procured on the voyage of the *Beagle,* but no name other than Dr Armstrong's appears on the labels. After Jardine died, his collection of 8542 ornithological specimens was sold by auction in 1886. His seven Geospizinae were purchased by Alfred Newton, who deposited them in the University Museum of Zoology, Cambridge. There is an auctioneer's catalogue of Jardine's collection (Anonymous, 1886).

The eighth Cambridge specimen (FitzRoy no. 433) has a different history. It was at one time owned by Hugh Edwin Strickland, an ornithologist and friend of Darwin's. The earliest specimen tag indicates that the specimen was 'Procured by C. Darwin Esq.'. Strickland may have acquired the bird through Darwin, which would account for its erroneous ascription to him. Darwin in turn must have obtained the specimen from FitzRoy or Fuller. Strickland's collection of 6006 skins was given by his widow to the University Museum of Zoology, Cambridge, in 1867. A catalogue of Strickland's collection was later prepared by Salvin (1882).

Because these eight specimens were apparently named by Gould and were later used by Darwin in supplying locality information for the *Zoology,* they may be considered syntypes. None of the specimens possess island localities on their labels, and most are lacking an indication of the sex. This information has been resupplied here, based on Darwin's manuscript notes and FitzRoy's catalogue.

Geospiza magnirostris Gould = ***Geospiza magnirostris magnirostris*** Gould

Fuller collected one specimen of this large-billed form of *magnirostris,* an adult male, on Chatham Island (no. 27/Fri[E]/26/e/2 = FitzRoy no. 392). Measurements of the bill exceed even the largest of the specimens procured by other *Beagle* collectors[66]. Fuller's specimen establishes that the large-billed form of *magnirostris* was once endemic to two islands in the Galapagos–Charles, where FitzRoy and Covington collected it; and Chatham, where Darwin guessed he had taken two other specimens (see page 63). Thus Darwin may have accurately recollected taking specimens on Chatham Island. The species is now extinct on that island.

Geospiza strenua Gould = ***Geospiza magnirostris strenua*** Gould

Fuller collected one specimen of this *G. magnirostris* subspecies, an adult male procured on James Island (no. 27/Fri[E]/26/e/1 = FitzRoy no. 417)[67].

Geospiza fortis Gould

Fuller's collection includes three specimens of *G. fortis,* all collected on James Island (no. 27/Fri[E]/26/b/2 = FitzRoy no. 427, an adult male; no. 27/Fri[E]/26/b/3 = FitzRoy no. 434, also an adult male; and no. 27/Fri[E]/26/b/4 = FitzRoy no. 422, a female). Although Gould's original designation for these specimens was *G. fortis,* Jardine was evidently at a loss as to how to characterize them. On the labels he therefore entered only the genus name. Subsequently he inserted *nebulosa* as the species name, and later this name was synonymized with *difficilis* on the tags. Measurements establish that the specimens are all clearly examples of *G. fortis.*

Geospiza parvula Gould = ***Geospiza fuliginosa*** Gould

Fuller procured two specimens of *G. parvula* (*sensu* Gould) from James Island (no. 27/Fri[E]/26/d/3 = FitzRoy no. 432, and later Jardine's specimen; and no. 27/Fri[E]/26/d/4 = FitzRoy no. 433, the specimen later acquired by Strickland). Both specimens are actually adult males of *G. fuliginosa* in black plumage and were incorrectly assigned by Gould[68]. Jardine also assigned his specimen to *G. parvula,* the name that appears on his tag. In addition to the indication provided by their telltale plumage, measurements of the specimens also support their reassignment to *G. fuliginosa.*

Fuller claimed that specimen no. 432 was a female. Darwin alluded to this fact in the *Zoology,* since he was much puzzled by the collection of a female in black plumage and rightly considered the case exceptional (1841 : 99). The specimen in question is almost certainly an adult male, incorrectly sexed by Fuller.

Camarhynchus psittacula Gould = ***Camarhynchus psittacula psittacula*** Gould

Fuller collected one specimen of *C. psittacula,* a male in juvenile plumage, on James Island (no. 27/Fri[E]/11/f/1 = FitzRoy no. 423). This specimen was previously thought to be a female, but FitzRoy's catalogue lists it as a male.

Covington's collection

Syms Covington, 'Fiddler and boy to Poop cabin' on the *Beagle,* became Darwin's servant and amanuensis during the second year of the voyage[69]. Darwin taught him how to shoot and skin birds, and Covington became a valuable assistant in all his collecting activities. How Covington came to have his own collection of birds from the Galapagos is something of a mystery, since he was employed to collect for Darwin. But he evidently possessed four Geospizinae and several other birds from the Galapagos that were not recorded as part of Darwin's own catalogue of specimens[70]. Soon after the voyage the Geospizinae and at least two other Galapagos birds became the property of Thomas C. Eyton, a naturalist and close friend of Darwin's[71]. Covington was fortunately later able to tell Darwin from which islands his finch specimens were procured, and Darwin subsequently made use of this information when collating the localities of all the *Beagle* specimens for the *Zoology* (see page 58 & Fig. 6).

After Thomas Eyton died in 1880, a portion of his ornithological collection was purchased by the British Museum. Included in this purchase of 205 skins in 1881 were 2 birds from the Galapagos, a mockingbird and a dove. Both birds are now credited to Darwin, but they were almost certainly collected by Covington[72]. Covington's Galapagos finches had a different history. After Eyton's death, 3 of the 4 specimens passed into the hands of Osbert Salvin and Frederick Godman, both of whom had a keen interest in Galapagos birds. In 1885 Salvin and Godman presented these 3 specimens, along with 51 other Geospizinae from the collections of Dr Habel and Commander A. H. Markham, to the British Museum[73]. There the 3 Covington specimens were erroneously presumed to be Darwin's, whose own name still appears on the labels. It is my belief that Covington's fourth finch is also in the British Museum collection, having been acquired and transmitted by Darwin at a much earlier date. Covington's specimens, which were undoubtedly seen by Gould, may be considered syntypes.

Geospiza magnirostris Gould = *Geospiza magnirostris magnirostris* Gould

Covington collected two specimens of this large-billed form of *magnirostris* (no. 1885.12.14.280, an adult male; and no. 1885.12.14.281, apparently a female). No island localities are given for these specimens, but Darwin recorded in his manuscript notes that Covington's specimens both came from Charles Island, where FitzRoy collected similar specimens.

Geospiza fortis Gould

At least one specimen of *G. fortis* was collected by Covington, on Charles Island. I strongly suspect that this specimen is no. 1855.12.19.82 at the British Museum, referred to separately under Darwin's collection. Darwin, who lacked a female of this species (*sensu* Gould), apparently borrowed it from Thomas C. Eyton in order that Gould might describe it (see page 64).

Geospiza fuliginosa Gould

Covington collected one specimen of *G. fuliginosa,* a female or juvenile male, on Chatham Island (no. 1885.12.14.320). The locality is given on the label.

The Leiden Rijksmuseum collection

Swarth (1931 : 12) has claimed that several Galapagos birds that he judged to be from the *Beagle* voyage, although he was not able to ascertain their history, exist at the Leiden Rijksmuseum van Natuurlijke Historie. There are seven possible *Beagle* specimens at the Leiden Rijksmuseum, including five Geospizinae. The Geospizinae were all purchased in 1863 from the well-known Amsterdam natural history dealer Gustav Adolph Frank. They include three specimens of *Geospiza fuliginosa* (one male and two females), a female of *Geospiza crassirostris* (= *Platyspiza crassirostris*), and a female of *Cactornis scandens* (= *G. scandens*). The other two Galapagos specimens are a male and a female of *Zenaida* *galapagoensis.* These last two specimens once possessed labels written in the hand of Coenraad Jacob Temminck, a director of the Rijksmuseum, who died in 1858. Hence the two doves arrived at the Leiden Rijksmuseum even before the five Galapagos finches.

There is good reason to believe that most of these Leiden specimens are indeed *Beagle* (and Darwin) specimens. The British Museum (Natural History) is missing Darwin type specimens in all four of the categories represented in Leiden. These missing specimens include one female and probably more specimens of *Geospiza fuliginosa*[74], a specimen of *Cactornis scandens,* all three type specimens of *Camarhynchus crassirostris* (a male and two females), and the male type of *Zenaida galapagoensis.* Gould's measurements for this last specimen agree very closely with male specimen in Leiden. In addition, one of the two female specimens of *G. fuliginosa* in Leiden matches the description of the female type given in the *Zoology* (1841 : 101).

Were it not for two inconsistencies between these missing Darwin specimens and those in Leiden, I would feel sure that they are the same. First, Darwin collected only one specimen of the Galapagos Dove, not two, as are present in Leiden. Nevertheless other *Beagle* shipmates, in particular Darwin's servant, undoubtedly collected additional specimens of this common species. This may account for the presence of the second specimen in the Leiden collection. The second inconsistency concerns the sex of Darwin's missing specimen of *C. scandens,* which appears to be a male, not a female[75]. But even if it is a male (and this is not certain), Darwin's missing specimen would be in a state of juvenile and hence 'female' plumage, so the possibility exists that the specimen in Leiden has been incorrectly sexed. According to Gerlof F. Mees, the sexes of the Leiden specimens were not originally entered on the labels but were later supplied around 1900 by estimation from the plumage[76]. It is also possible that Swarth's (1931 : 190) 'female' specimen of *C. scandens* at the British Museum is actually a juvenile male. In this case the missing Darwin specimen would have to be a female, in agreement with the estimated sex of the specimen in Leiden. In this connection it must be emphasized that none of Darwin's specimens at the British Museum carry the sex on their labels. Doubtless the Zoological Society specimens lacked this information as well. Moreover, it is very common for females and juvenile males of Darwin's finches to be confused when the original collector's designation of the sex is missing[77]. Measurements of the Leiden specimen of *C. scandens,* which has a small bill, establish that it came either from Chatham or, more probably, from James Island (in which case it must be a juvenile male). Both of these islands were visited by Darwin.

If the Leiden specimens are not Darwin's, the question arises as to who else might have collected them. It is virtually impossible that any of the Geospizinae in Leiden were collected by members of the *Beagle* voyage other than Darwin. He went to considerable trouble to track down all the other Geospizinae after the *Beagle* voyage, and all of these specimens are accounted for[78]. Additionally, Darwin was the only person on the *Beagle* to collect specimens of *C. crassirostris,* a species that was never received by the British Museum but that is present in Leiden.

The question arises, therefore, as to who else visited the Galapagos between 1835, when the *Beagle* made the first systematic collections, and 1863, when the Leiden Rijksmuseum acquired its five Geospizinae. The first collection after Darwin's visit was made in 1838 by Adolphe-Simon Néboux, surgeon of the French frigate *Vénus.* Néboux's collecting was done on one island only, Charles, where the *Vénus* spent eleven days[79]. Néboux collected specimens of the dove (*Zenaida galapagoensis*), swallow (*Progne modesta*), Medium Ground Finch (*Geospiza fortis*), and Cactus Finch (*G. scandens*), but he did not collect any other finches[80]. Néboux's specimens are now at the Museum d'Histoire Naturelle in Paris, where they were presented in 1839 (Prévost & des Murs, 1855 : 204–9; Swarth, 1931 : 102). Another *Vénus* officer, the assistant surgeon Charles-René-Augustin Léclancher, procured four specimens of the Galapagos Dove, one female specimen of the Cactus Finch, and one specimen of an unidentified species of *Camarhynchus*[81]. Léclancher's specimens were described by Lafresnaye (1840, 1843), who kept three of the doves and the one specimen of *Camarhynchus* for his own collection[82]. In 1865, two years after the Leiden

Rijksmuseum acquired its own Galapagos finches, Lafresnaye's entire collection, including all of his Galapagos specimens, was sold to the Boston Society of Natural History. The collection now resides at the Museum of Comparative Zoology, Harvard University. None of the Galapagos finches have survived. I have been unable to trace the whereabouts of Léclancher's fourth dove and his one specimen of the Cactus Finch.

There were two other expeditions to the Galapagos after 1838 and before 1863. The first was that of H.M.S. *Herald,* which visited the islands in January 1846 but spent only seven days there. Stops were made at Chatham, Charles, and James islands. The naturalist on board was Thomas Edmonston, who met with a tragic end shortly afterwards (Seemann, 1853, **1**: 67–69). Two specimens of Geospizinae, apparently collected by Edmonston, were later presented to the British Museum by Captain Henry Kellett and Lieutenant Wood of the *Herald* (Sharpe, 1888 : 11, 17).

The Galapagos Archipelago was visited again in May 1852 by the Swedish frigate *Eugenie,* which spent nine days there and visited Chatham, Charles, Indefatigable, Albermarle, and James islands. Dr Kinberg, the zoologist and surgeon of the expedition, collected 26 species of birds, including specimens of *Geospiza fuliginosa, G. nebulosa, G. scandens*, and *Zenaida galapagoensis* (Sundevall, 1871). He did not, however, collect specimens of *Platyspiza crassirostris.* Sundevall explicitly states that Kinberg provided an island locality for every specimen, but none of the specimens in Leiden possess this information. Moreover, Sundevall must have had the Kinberg collection in his possession after 1863 in order to write his later report. The birds from the *Eugenie* voyage are now at the Naturhistoriska Riksmuseet in Stockholm (Swarth, 1931 : 33).

What is noteworthy about all of these other expeditions to the Galapagos is that none of them reported collecting specimens of *P. crassirostris,* which lives in the transitional and humid zones and would not normally be collected by someone on a brief visit. Darwin is the only person known to have collected this species until the *Albatross* expedition procured specimens in 1888. Moreover, the Leiden specimen of *P. crassirostris,* which has a very small depth of bill, appears to have come from Charles Island, where Darwin reported taking his own specimens. All in all, Darwin's collection therefore remains the most likely source for the specimens in Leiden.

If the Leiden specimens are Darwin's, they may have been acquired by Gustav Adolph Frank, and then by the Leiden Rijksmuseum, through the agency of John Gould. Gould at one time owned at least four Galapagos specimens collected by Darwin, and these he probably acquired in 1855 at the dispersal of the Zoological Society's Museum. Gould was a shrewd dealer in specimens, always on the lookout for birds that could be sold or exchanged to his advantage. It is said that for many years not a hummingbird arrived in London without Gould getting to it first. Between 1857 and 1860 he sold three of Darwin's Galapagos specimens, including two Geospizinae, to the British Museum[83]. That Gould, during this same period, may have traded other Darwin specimens that eventually found their way to Leiden is certainly plausible. Of additional relevance is the fact that Gould maintained a lively correspondence with Temminck, the Leiden Rijksmuseum director, and exchanged numerous specimens with him over the years (Mees, 1964, 1967). The two Leiden specimens of *Zenaida galapagoensis,* which were acquired independently of the finches and prior to Temminck's death, may therefore have come directly from Gould.

Appendix:
Specifications concerning the *Beagle* collections of Geospizinae

The Table that follows presents a summary of measurements and other relevant information concerning the *Beagle* collections of Darwin's finches. In my measurements I have attempted to duplicate David Lack's (1945 : 76) procedures in order to facilitate comparison between the *Beagle* type specimens and Lack's extensive tables of measurements for each island population (1945 : 142–51; 1947 : 168–85). All bill measurements were made with either vernier or dial calipers accurate to better than 0·1 mm, a distance that is smaller than the normal range of error involved in duplicating these measurements. (The use of dividers is not recommended for fine measurements of this sort, since dividers, owing to their angular divergence, tend to overestimate distances.)

The culmen was measured from the anterior lip of the nostril to the tip of the bill. Insertion of calipers any distance into the nostril results in a larger and more variable measure, so all measurements were taken from just inside the most superficial portion of the nostril lip. There is occasionally some bilateral asymmetry in the culmen (from nostril) distance. All measurements given here were therefore taken from the right side of the specimen, as viewed from the dorsal side. For depth of bill, calipers were positioned to yield the largest possible measure between the base of the bottom mandible and the top of the upper mandible. This point on the upper mandible is usually not where the mandible meets the feathered skull, but rather somewhat anterior to this spot, before the curved culmen begins to descend. All bill measurements were taken six times. The high and the low measurements were then discarded, and the four remaining measurements averaged. Wing measurements were taken of both wings, when present, using a millimeter rule. The flattened wing was measured from the carpal joint to the tip of the longest primary, to the nearest 0·5 mm.

These various measurements are presented in the Table that follows, along with the name of the person who collected the specimen, the specimen's institutional location and registration number, its specific and subspecific identity, its sex, and the island from which it was procured. Under the heading *Form,* the correct classification is given first and is followed by the name on the label(s). Under the heading *Island,* the locality given on the label(s) is presented first, in quotation marks, and is separated from the real, or most probable, locality by a colon. Where an island name alone follows the colon, the locality provided is accurately established by manuscript evidence. Where the colon is followed by the expression '——form of subspecies' (indicating a particular island), the locality has been estimated on the basis of the specimen's measurements and plumage, which coincide with only one possible island form, given the various islands known to have been visited by the collector.

The Table includes all existing specimens, as well as the 5 British Museum (Natural History) specimens that have been lost or destroyed since 1837. Not included in the Table, except insofar as they may be represented among the 2 missing '*Geospiza*' listed on page 80 or among the Leiden Rijksmuseum collection, are 10 specimens already described under Darwin's collection that are not at the British Museum. These, in summary, seem to be: one adult male specimen of *Geospiza fortis,* one female specimen of *G. dubia,* one female specimen of *G. fuliginosa,* one male specimen of *G. nebulosa,* one juvenile male specimen of *Cactornis scandens,* one male and two female specimens of *Camarhynchus crassirostris,* one male specimen of *C. psittacula,* and one male specimen of *Certhidea olivacea.* All in all, at least 27 and possibly all 31 of Darwin's Geospizinae are accounted for as currently present at the British Museum (Natural History) and the Leiden Rijksmuseum, or as having been lost or destroyed since 1837[84]. Similarly, of the 25 to 27 specimens procured by other *Beagle* collectors, all but 2, both of which were among the 13 FitzRoy specimens that went to the British Museum in 1837, appear to have survived.

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Table: Specifications concerning the *Beagle* collections of Geospizinae*

				Bill	Wing			
Collector	Specimen	Form	Culmen	Depth	Left	Right	Sex	Island
Darwin	BM(NH) 1855.12.19.80	*Geospiza magnirostris magnirostris* (=‘*G. magnirostris*’)	17·7	21·8	90	90·5	ad. ♂	‘Chatham?’ and ‘Charles’: probably Chatham
Darwin	BM(NH) 1855.12.19.113	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	17·7	21·7	–	87·5	♀(?)	‘Chatham’: probably Chatham
FitzRoy	BM(NH) 1837.2.21.398	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	17·1	22·1	85	85·5	♀	‘Charles’: Charles
FitzRoy	BM(NH) 1837.2.21.402	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	18·9	22·3	90	91	ad. ♂	‘Charles’: Charles
FitzRoy	BM(NH) 1837.2.21.403	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	17·2	22·2	88	86	juv. ♂	‘Charles’: Charles
Fuller	UMZC 27/Fri(E)/26/e/2	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	18·2	23·8	91	92	ad. ♂	‘Galapagos’: Chatham
Covington	BM(NH) 1885.12.14.280	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	18·3	22·5	93	90·5	ad. ♂	‘Galapagos’: Charles
Covington	BM(NH) 1885.12.14.281	*G. magnirostris magnirostris* (=‘*G. magnirostris*’)	18·5	21·7	87·5	84	♀ (?)	‘Galapagos’: Charles
Darwin	BM(NH) 1855.12.19.81	*G. magnirostris strenua* (=‘*G. strenua*’)	13·9	17·8	79·5	79	ad. ♂	‘Chatham?’: James form of subspecies
Darwin	BM(NH) 1855.12.19.114	*G. magnirostris strenua* (=‘*G. strenua*’)	15·7	18·1	73·5	74·5	♀ (?)	‘Chatham’: James form of subspecies
Fuller	UMZC 27/Fri(E)/26/e/1	*G. magnirostris strenua* (=‘*G. magnirostris*’)	14·7	18·5	83	84	ad. ♂	‘Galapagos’: James
FitzRoy	BM(NH) 1837.2.21.396	*G. magnirostris magnirostris* × *G. fortis*? (=‘*G. strenua*’)	14·3	16·0	82·5	81·5	ad. ♂	‘Chatham’: Chatham
Darwin or Covington	BM(NH) 1855.12.19.82	*G. fortis* (=‘*G. fortis*’)	12·5	13·2	71	71	♀ (?)	‘Charles’: Charles?
Darwin	BM(NH) 1855.12.19.83	*G. fortis* (=‘*G. strenua*’)	14·0	14·8	75	74	♀ (?)	‘Chatham’: probably Chatham
Darwin	BM(NH) 1855.12.19.176	*G. fortis* (=‘*G. dentirostris*’)	10·3	10·1	–	67	juv. ♂ (?)	‘Galapagos’: Charles form of species

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**All measurements are in millimetres.*

				Bill	Wing			
Collector	Specimen	Form	Culmen	Depth	Left	Right	Sex	Island
Fuller	UMZC 27/Fri(E)/26/b/2	*G. fortis* (= '*G. difficilis*')	12·1	13·4	73	72	ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/b/3	*G. fortis* (= '*G. difficilis*')	12·2	12·1	67·5	68·5	ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/b/4	*G. fortis* (= '*G. difficilis*')	12·2	12·6	–	67	♀	'Galapagos': James
Darwin	BM(NH) 1855.12.19.44	*G. fuliginosa* (= '*G. fuliginosa*')	8·9	8·1	61·5	62·5	♀ (?)	'Chatham': probably Chatham
Darwin	BM(NH) 1857.11.28.247	*G. fuliginosa* (= '*G. fuliginosa*')	8·8	8·2	64·5	65	♀ (?)	'Chatham': probably Chatham
Darwin?	LRNH Cat. 2, pur. 1863	*G. fuliginosa* (= '*G. fuliginosa*')	8·5	8·0	66	65	ad. ♂	'Galapagos': locality uncertain
Darwin?	LRNH Cat. 3, pur. 1863	*G. fuliginosa* (= '*G. fuliginosa*')	8·7	7·5	63·5	63	♀ (?)	'Galapagos': locality uncertain
Darwin?	LRNH Cat. 4, pur. 1863	*G. fuliginosa* (= '*G. fuliginosa*')	8·5	7·6	62	62	♀ (?)	'Galapagos': locality uncertain
FitzRoy	BM(NH) 1837.2.21.410	*G. fuliginosa* (= '*G. parvula*')	8·0	7·1	58	60	♀	'James': James
FitzRoy	BM(NH) 1837.2.21.411 [i.e., 1837.2.21.414]	*G. fuliginosa* (= '*G. fuliginosa*')	8·4	8·0	61	60	♀	'James': James
FitzRoy	BM(NH) 1837.2.21.417	*G. fuliginosa* (= '*G. fuliginosa*')	Missing				♂	'James': James
Fuller	UMZC 27/Fri(E)/26/d/3	*G. fuliginosa* (= '*G. parvula*')	8·5	8·0	65	–	ad. ♂	'Galapagos': James
Fuller	UMZC 27/Fri(E)/26/d/4	*G. fuliginosa* (= '*G. parvula*')	8·0	8·1	64	65	ad. ♂	'Galapagos': James
Covington	BM(NH) 1885.12.14.320	*G. fuliginosa* (= '*G. fuliginosa*')	9·4	8·5	62	62	♀ (?)	'Chatham': Chatham
Darwin	BM(NH) 1855.12.19.20	*G. nebulosa nebulosa* (= '*C. scandens*')	11·0	10·4	71	72	♀ (?)	'James': extinct Charles subspecies
FitzRoy	BM(NH) 1837.2.21.400	*G. nebulosa nebulosa* (= '*G. nebulosa*')	10·8	10·2	71	72	♀	'Chatham' and 'Charles': Charles
Darwin	BM(NH) 1856.3.15.4	*G. nebulosa debilirostris* (= '*G. strenua*')	9·6	8·6	67	66·5	♀ (?)	'Galapagos': James form of subspecies

Darwin	BM(NH) 1855.12.19.125	*G. scandens scandens* (=‘*C. scandens*’)	12·3	8·5	66	68	ad. ♂	‘James’: James form of subspecies
Darwin?	LRNH Cat. 1, pur. 1863	*G. scandens scandens* (=‘*C. scandens*’)	11·6†	9·2	69	69	juv. ♂ (?)	‘Galapagos’: probably James form of species
FitzRoy	BM(NH) 1837.2.21.412	*G. scandens scandens* (=‘*C. scandens*’)	Missing				ad. ♂	‘James’: James
Darwin	BM(NH) 1855.12.19.15	*G. scandens rothschildi?* (=‘*C. assimilis*’)	14·4	10·1	72·5	71·5	juv. ♂ (?)	‘Galapagos’: probably James
FitzRoy	BM(NH) 1837.2.21.415	*G. scandens rothschildi?* (=‘*C. assimilis*’)	14·1	10·2	70·5	70·5	juv. ♂	‘James’: James
Darwin?	LRNH Cat. 2, pur. 1863	*Platyspiza crassirostris* (=‘*G. crassirostris*’)	10·5	11·6	87	86·5	juv. ♂ (?)	‘Galapagos’: probably Charles form of species
Darwin	BM(NH) 1855.12.19.12	*Camarhynchus psittacula psittacula* (=‘*C. psittacula*’)	Seen by Swarth (1931 : 215); now missing.				♀ (?)	‘James’: James
Darwin	BM(NH) 1855.12.19.22	*C. psittacula psittacula* (=‘*C. psittacula*’)	10·5	11·2	72·5	69·5	♀ (?)	‘James’: James
FitzRoy	BM(NH) 1837.2.21.413	*C. psittacula psittacula* (=‘*C. psittacula*’)	10·4	12·5	79	78	♂	‘Charles’ and ‘James’: James
Fuller	UMZC 27/Fri(E)/11/f/1	*C. psittacula psittacula* (=‘*C. psittacula*’)	10·1	10·4	70	72	juv. ♂	‘Galapagos’: James
Darwin	BM(NH) 1855.12.19.167	*C. parvulus parvulus* (=‘*G. parvula*’)	7·0	6·5	59·5	60	♀ (?)	‘Chatham’ and ‘James’: James form of subspecies
Darwin	BM(NH) 1855.12.19.194	*C. parvulus parvulus* (=‘*G. parvula*’)	4·9†	6·6	60	61·5	ad. ♂	‘Chatham’ and ‘James?’: James form of subspecies
FitzRoy	BM(NH) 1837.2.21.411	*C. parvulus parvulus* (=‘*G. parvula*’)	6·5	7·2	58·5	59	♀	‘James’: James
Darwin	BM(NH) 1855.12.19.126	*Certhidea olivacea olivacea* (=‘*C. olivacea*’)	7·3	5·0	56	55	♂	‘Galapagos’: James form of subspecies

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†*Denotes a broken culmen.*

Collector	Specimen	Form	Bill		Wing		Sex	Island
			Culmen	Depth	Left	Right		
Darwin?	BM(NH) 1855.12.19.127	*C. olivacea olivacea* (=‘*C. olivacea*’)	7·8	4·4	53·5	56·5	?	‘Galapagos’: James form of subspecies
Darwin?	BM(NH) 1855.12.19.164	*C. olivacea olivacea* (=‘*C. olivacea*’)	6·0†	4·7	53·5	53	?	‘Galapagos’: James form of subspecies
FitzRoy	BM(NH) 1837.2.21.408	*C. olivacea olivacea* (=‘*C. olivacea*’)	7·5	4·3	54·5	53·5	♀	‘James’: James
Darwin	BM(NH) 1855.12.19.43	‘*Geospiza*’	Missing					Unknown
Darwin	BM(NH) 1857.11.28.248	‘*Geospiza*’	Destroyed					Unknown

†*Denotes a broken culmen.*

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Notes

1. Darwin's finches have been the subject of numerous systematic treatments, of which the most important are by Gould (1837*a*, 1841, 1843), Salvin (1876), Ridgway (1890, 1897), Rothschild & Hartert (1899, 1902), Snodgrass & Heller (1904), Swarth (1931), Hellmayr (1938 : 130–46), Lack (1945, 1947, 1969), Bowman (1961, 1963), Paynter (1970 : 160–68), Harris (1974), and Steadman (in press). Monographic works, such as those by Swarth (1931) and Lack (1945, 1947), have usually given Darwin's finches family or subfamily status – the latter being the general consensus. Nevertheless, some authors have recommended that they be accorded only tribal status within the Emberizinae subfamily (Paynter & Storer, 1970 : vii). Differentiation between subfamilies and tribes is a subjective matter, and I have preferred to follow the monographic tradition on this point. Species and genus names of certain forms of the Geospizinae have changed over the years, making for some minor inconsistencies in terminology in discussions of the literature. For example, *Cactornis scandens* (Gould, 1837*a*) is no longer given separate generic status, but is classified instead with the other species of *Geospiza*. I have followed the policy of using the original names proposed by Gould (1837*a*, 1841) when discussing individual *Beagle* specimens or Darwin's views about them. Otherwise, the current nomenclature has been followed, with the exception that I recognize *Geospiza magnirostris magnirostris* and *G. magnirostris strenua* as valid trinomials and also recognize the name *G. nebulosa* as having priority over *G. difficilis*. See pages 69–70 and note 53.

2. According to FitzRoy (1839 : 490), Lawson came on board the *Beagle* on 25 September and then escorted a party, including Darwin and FitzRoy, to the settlement in the highlands. Darwin spent four days on Charles Island, the last being 27 September. See also Darwin's *Diary* (1933 : 336).

3. DAR 31·2: MS p. 342v (all DAR numbers refer to the Darwin MSS, Cambridge University Library): 'The Thenca of Albermale [*sic*] Island is the same as that of Chatham Is^{d}—'. Contrary to Darwin's voyage opinion, the mockingbirds from Albemarle (*Nesomimus parvulus*) and Chatham (*N. melanotis*) are now recognized as separate species by some ornithologists, whereas the James and Albemarle forms are both assigned to *N. parvulus*. Gould (1841 : 62–63), to confuse matters further, later synonymized the Chatham and James forms under the name *melanotis*, which merely goes to show that the Chatham, Albemarle, and James forms are all very similar in appearance and would be classified by many ornithologists as subspecies. The Charles Island form of the mockingbird (*N. trifasciatus*) is more noticeably distinct, but even this form would be ranked as a subspecies by some ornithologists. See Harris, 1974 : 128; and Davis & Miller, 1960 : 447–48.

4. DAR 31.2: MS pp. 341–42.

5. Toward the end of the voyage Darwin prepared a series of separate specimen catalogues for the use of the specialists who later took charge of his collections after the *Beagle*'s return to England. The *Ornithological Notes* (1963[1836]) constitutes one of twelve such catalogues. On the dating of these catalogues, see Sulloway (1982*b*).

6. See, for example, Rothschild & Hartert, 1899 : 155; Swarth, 1931 : 149; and Lack, 1945 : 9. Similarly, Hellmayr has concluded: 'There seems hardly any doubt that in the case of *G. strenua* and *G. magnirostris* the localities, as given . . . in the "Zoology of the Beagle", are altogether untrustworthy' (1938 : 130, n.3). As recently as 1973, Ian Abbott reached a similar conclusion (6 December 1973 letter to the British Museum [Natural History], Sub-department of Ornithology, Tring, excerpted on a typed sheet stored with the *Beagle* collections of *G. magnirostris*). Abbott believed these specimens were probably collected on Abingdon or Tower Island, which were briefly visited by some *Beagle* officers and crew.

7. See Lack, 1940 : 49; and 1945 : 9–10.

8. These doubtful localities involve the following birds: two specimens of *Geospiza magnirostris* (British Museum registry nos. 1855.12.19.80 and 1855.12.19.113, labelled as coming from Chatham Island but thought to have come from James); two specimens of *G. parvula* (British Museum nos. 1855.12.19.167 and 1855.12.19.194, labelled as coming from Chatham Island but elsewhere assigned to James [Darwin, 1841 : 102]); one specimen of *Cactornis scandens* (British Museum no. 1855.12.19.20, labelled as coming from James but assigned by Lack to an extinct race of *G. difficilis* [now *nebulosa*] on Charles or Chatham Island); and three specimens of *G. strenua* (British Museum nos. 1855.12.19.81, 1855.12.19.83, and 1855.12.19.114, labelled as coming from Chatham but thought to have come from James).

9. In addition, the paper is similar to that used by Darwin on the *Beagle* voyage. The registry number of this specimen at the British Museum is 1881.5.1.2394.

10. In his *Ornithological Notes* he wrote: 'Anthus. was shot by Fuller on James Isd: it was the only one specimen seen during our whole residence. It is described as rising from the ground suddenly & again settling on the ground—Showed in its flight long wings, like a Lark; uttered a peculiar cry.—Its structure appear[s] very interesting' (1963[1836] : 265).

11. Whether Gould acquired the specimen in 1837, or whether he perhaps acquired it as late as 1855, when the Zoological Society closed its museum and sold all its ornithological specimens, is not known. Gould also possessed other Darwin type specimens. In 1857 he sold 251 ornithological specimens to the British Museum, including 2 specimens of *Geospiza* that once belonged to Darwin (reg. nos. 1857.11.28.247 and 1857.11.28.248). See 'Zoological Accessions Aves, 1854–1873', p. 64, and 'Zoological Accessions Aves, 1880–1884', p. 106; British Museum (Natural History), Sub-department of Ornithology, Tring.

12. This conclusion is confirmed by an analysis of the locality information published by Waterhouse (1845) in his paper on Darwin's Galapagos insects. Of 29 species, 14 have island localities and 15 do not. Each of these 14 localities is recorded as well in Darwin's specimen catalogue; and the island and habitat information given by Waterhouse corresponds exactly to Darwin's own wording in that catalogue. Thus only where this information was recorded in Darwin's notes was it preserved for later use. Darwin apparently recorded such information incidentally as part of the habitat description. For example, specimens 3363 and 3364 are followed by the comment: 'Small insects, sweeping; high up, central parts of Charles Island' ('Printed Numbers 3345[–3907]', Down House). In his section on advice to collectors, which appeared only in the first edition of his *Journal of Researches* (1839 : 598–99), Darwin recommended that a number be placed on each specimen immediately after it was procured, and that this number be entered in the specimen catalogue 'during the very same minute' so that the locality would never be subject to doubt. If localities had been recorded on the numbered tags, this precaution would have been unnecessary. Finally, that none of Darwin's ornithological specimens had localities on the labels is reinforced by Gould's failure to provide any island designations for the Galapagos species he named in January and February of 1837. See 'Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840', pp. 120–21, 123–24, 129–30, 134; and Gould, 1837*a, b, c, d*.

13. In his *Diary,* Darwin wrote in this connection: 'To our disappointment the little pits in the Sandstone contained scarcely a Gallon [of water] & that not good. It was however sufficient to draw together all the little birds in the country; Doves & Finches swarmed round its margin' (1933 : 338; entry for 1 October 1835). Similarly, FitzRoy commented: 'Around this scanty spring draining continually through the rock, all the little birds of the island appeared to be collected, a pretty clear indication of there being then no other fresh-water within their reach . . .' (1839 : 495).

14. These tortoises, from Chatham Island, were brought on board the *Beagle* just five days before Darwin returned from James Island. FitzRoy had earlier embarked eighteen Chatham Island tortoises, and these were devoured as well. FitzRoy did, however, bring two Hood Island tortoises back to England ('Zoological Accessions, 1837', p. 1; British Museum [Natural History], Mammals Library, London). Two other very small tortoises also survived the *Beagle* voyage–apparently brought home as pets (DAR 29.3 : 40, MS p. 7v). When Darwin finally realized the significance of having an expert taxonomist decide whether the reported differences between the tortoises were of specific distinction, these four tortoises were the only ones available. Although they were from three different islands (Hood, Charles, and James), they were all too young to be of value (Darwin, 1839 : 465). Darwin also missed an opportunity to bring back an adult carapace of the unusual saddleback form of tortoise on Charles Island. According to FitzRoy (1839 : 492), numerous shells were lying around at the Charles Island settlement, where they were being used as flower pots. Within about ten years of Darwin's visit, the Charles Island tortoise was extinct. Zoologists had to wait nearly a century to find remains of this form in a lava cave (Broom, 1929).

15. Several of his specimens, including his Bobolink, still bear this date of accession on the labels. It seems likely that Darwin presented the specimens in person since he came to London from Cambridge that same day to deliver a paper before the Geological Society (Darwin, 1837*a*). He also wrote a letter dated 4 January that was read that afternoon at a meeting of the Zoological Society Council. According to the minutes of that meeting, Darwin's letter 'announced a present to the Society of his entire Collection of Mammalia and Birds made during His Majesty's Surveying Vessel Beagle. It was ordered that the best thanks of the Society be returned to Mr. Darwin for his liberal and valuable contribution to its preserved Collections: and that his wishes with respect to the disposal of the duplicate specimens in this Collection, and to the mounting and describing of the same be strictly complied with' (unpublished 'Zoological Society Minutes of Council', **5**: 79–80).

16. See 'Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840', p. 120; manuscript record of the meeting of 10 January 1837. For the number of finch species named by Gould on 10 January 1837, see Sulloway, 1982*a* & 1982*b*. On 10 May Gould again brought Darwin's finches before the Zoological Society, naming 14 species in 4 genera, including *Certhidea olivacea* (see 'Minutes', pp. 164–65). Gould's fourteenth species, *Geospiza incerta,* lived up to its name, for he subsequently synonymized it under one of the others. A curious remnant of this change of mind remains in the published *Proceedings of the Zoological Society,* for although it is said that 14 species were named, only 13 names and descriptions follow (Gould, 1837*a*). Also of interest is the fact that the published *Proceedings* lists under the 10 January 1837 meeting the names and descriptions that were only given later by Gould at the 10 May meeting. Thus the published record, by transferring the events of 10 May back to 10 January and by deleting the earlier presentation, obscures the difficulties that Darwin's finches caused even such a celebrated ornithologist as John Gould.

17. For further details about Darwin's meeting with Gould, and evidence that they had not discussed the Galapagos specimens before this time, see Sulloway (1982*b*).

18. For further information see Sulloway, 1982*a*. Gould's 13 species are not identical, however, with the present 13 species of Galapagos finches. Contrary to the legend, Darwin collected only 9 of these 13 species. Four of Gould's species–*Geospiza strenua* (= *Geospiza magnirostris strenua* and *G. fortis*), *G. dentirostris* and *G. dubia* (= *G. fortis*), and *Cactornis assimilis* (= *G. scandens*)–have proved to be only slightly variant forms of 3 other species. Given the relative paucity of material with which he had to work, Gould's confusion is nevertheless understandable. The 4 species of Galapagos finches that Darwin did not collect are *Geospiza conirostris* (the Large Cactus Finch), *Camarhynchus pallidus* (the Woodpecker Finch), *C. heliobates* (the Mangrove Finch), and *C. pauper* (the Medium Tree Finch). These species were all procured by later expeditions between 1868 and 1899. The sole Cocos Island member of the Geospizinae (*Pinaroloxias inornata*) was collected in 1840 during the voyage of H.M.S. *Sulphur* and was described by Gould (1843).

19. It is often claimed that Darwin was impressed by the American character of his Galapagos finches (see, for example, Silverstein, 1974 : 505; and Ruse, 1979 : 164). But

Darwin's finches played no role in this aspect of his evolutionary insight. Rather it was the mockingbirds, the flycatchers, the dove, and numerous other typically American species that established this generalization about the Galapagos avifauna. The finches, in contrast, were placed with the Fringillidae in the nineteenth century, and this family of birds was then believed to be worldwide. It is only in this century that the Fringillidae and Emberizidae, under which Darwin's finches are now classified, have been distinguished as families of Old and New World finchlike species, respectively. Although Darwin's finches have no close ancestor on the American continent today, some ornithologists believe they arose from a form related to the emberizine genus *Volatinia* (and several similar genera). These species are all seed-eating ground birds that range from southern United States to northern Chile and Argentina (Paynter & Storer, 1970 : vii). Relying on osteological and other evidence, Steadman (in press) has argued that the Geospizinae evolved from *Volatinia jacarina,* the Blue-black Grassquit. He also contends that the Cocos Island Finch and the Galapagos finches were established by two independent invasions of this species from Central and South America, respectively.

20. For the date of FitzRoy's presentation of specimens, which included 187 skins, see the manuscript catalogue 'Zoological Accessions Aves, 1837–1851–3', pp. 7–15; British Museum (Natural History), Sub-department of Ornithology, Tring. FitzRoy presented one further specimen on 15 March 1837, an egg of *Rhea darwinii.* FitzRoy's Galapagos portion of the collection included 50 skins, 21 of them finches, all with an island locality. Some of these Galapagos specimens belonged to another shipmate, however; and only 24 Galapagos skins, 13 of them finches, actually went to the British Museum.

21. See DAR 29.3 : 26, 28–30. Ironically, that other shipmates on the *Beagle,* but not Darwin, recorded island localities for their birds marks Darwin as the only real scientist aboard that ship. For Darwin collected with a theory, however mistaken, in mind. The other shipmates were mere collectors, and their labelling practices reflect that fact.

22. That Darwin's manuscript notes on this question were initially compiled in connection with the writing of his *Journal* is reinforced by another consideration. On the list of Covington's and Fuller's birds, which occupies one of the four sheets, Darwin mistakenly referred *Camarhynchus psittacula* to the genus *Geospiza* (see Fig. 6). He also misspelled *psittacula* as *spittacula.* This same species name is misspelled and assigned to the genus *Geospiza* in a list of Galapagos species that Darwin compiled in the spring of 1837 during a meeting with John Gould (Sulloway, 1982*b*). Darwin was not, therefore, entirely familiar in the spring of 1837 with the generic or specific names that Gould had just given these species. The use of erroneous generic and specific names on the locality list for Covington's and Fuller's birds suggests that these notes too were compiled about this time. The name *psittacula* was altered to *psittaculus* in the *Zoology* (1841 : 103), so these notes on Covington's and Fuller's specimens clearly predate that change. I would assign Darwin's two other sheets of notes on his Galapagos finch localities to late 1840, when he was working on the final instalment of the ornithological portion of the *Zoology.* One sheet, which records all thirteen of FitzRoy's finch localities, may be dated by the use of the specific name *Camar[h]y[nchus] psittaculus.* The other, although it bears the name *psittacula,* is probably of the same date, since it contains a collated list of localities for all the *Beagle* collections as published in the *Zoology* (1841 : 100–106).

23. See pp. 64, 66, 71, and 73.

24. See 'Printed Numbers 3345[–3907]', Down House, under specimen nos. 3312–19. The catalogue is written in ink. The line under the first eight specimens and the comment '?Chatham Is^{d}??' were added later in pencil, almost certainly after Darwin's return to England.

25. Of those specimens for which island localities are listed (eighteen) or were later published by Darwin (two), or for which localities can be reconstructed on the basis of other evidence (nine), the sequence runs: James (3299); James (3303); James (3304); Charles (3306); Chatham (3307); Chatham (3308); Charles or James (3309); James (3310); the eight specimens of finch that Darwin later assigned to Chatham with three question marks

(3312–19); James (3330–32); James (3340); Charles or James (3342–44); Chatham (3345); Albemarle (3349); James (3350); James (3356); James (3362); and James (3374). I have deduced seven of these twenty-nine localities from information unknown to Darwin. *Certhidea olivacea* exhibits distinctive characteristics by island, and Darwin's specimens (3310 and 3340) definitely belong to the James Island form of this species. *Pyrocephalus dubius* (3345) is confined to Chatham Island, and hence Darwin's specimens of *P. nanus* (3309, 3342–44), a form that replaces *dubius* elsewhere in the archipelago, must have come from either Charles or James Island. The localities of two other specimens (3299 and 3362) can be deduced from Darwin's statement that they came from a salt lagoon, which he visited on James Island. Darwin also visited a salt lagoon on Albemarle Island, but he does not appear to have collected at this site.

26. In his manuscript notes on the collections of FitzRoy, Fuller, and Covington, Darwin listed this locality correctly as 'Charles [and] James Is^{d}.' see DAR 29.3.28. Nevertheless, because John Gould mistook one Chatham Island specimen of *G. fortis* for *G.* [*magnirostris*] *strenua,* the actual locality for the *Beagle* collections of *G. fortis* should have been Chatham, Charles, and James islands. Similarly, *G.* [*magnirostris*] *strenua,* reported as coming from Chatham and James islands in the *Zoology* (1841 : 101), was in fact collected only on James Island.

27. It is ironic, and Darwin (1839 : 629) was the first to admit it, that his Galapagos plants proved so valuable precisely because he was least accomplished in that field of natural history. For this reason he collected 'blindly' from each island he visited, mistaking representative species for duplicate specimens. That he fortunately recorded the island localities of his plant specimens reflects the way in which they were collected. Plants must be placed in a plant press soon after collection, and the plants from a given island would all tend to be pressed together rather than intermixed with plants from a separate island. Similarly, Darwin recorded separate island localities for his saltwater fish because they had to be numbered and preserved in spirits of wine soon after being caught.

28. The following specimens at the British Museum (Natural History), Sub-department of Ornithology, Tring, appear to have acquired localities—either on the labels or in the published type specimen catalogues—by reference to the *Zoology*: *Camarhynchus psittacula* (reg. no. 1855.12.19.22); two specimens of *Cactornis scandens* (nos. 1855.12.19.20 and 1855.12.19.125); two specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194); *Otus galapagoensis* = *Asio flammeus* (no. 1855.12.19.153); *Larus fuliginosa* (no. 1855.12.19.218); *Hirundo concolor* = *Progne modesta* (no. 1860.1.16.54); and *Dolichonyx oryzivorus* (no. 1881.5.1.2394). See Warren, 1966 : 104, 108; Warren & Harrison, 1971 : 127, 420, 448, 494; and Peters, 1960 : 87.

29. Darwin's specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194) do not necessarily come from James Island, as the labels and Warren & Harrison (1971 : 420) have claimed, although measurements appear to support this locality designation (see page 65). According to Lack (1945 : 14–15), one of Darwin's two specimens of *Cactornis scandens* (no. 1855.12.19.20), which are both labelled as coming from James Island, is actually a specimen of *G. difficilis* (now *nebulosa*) and belongs to the extinct Charles Island form of this species. Darwin was unable to supply an island locality for *C. assimilis,* which he probably did not distinguish from *C. scandens,* so it is unlikely that he was certain about the localities of any of his *scandens* specimens. Once again, see Warren & Harrison (1971 : 494) for the circular derivation of these *C. scandens* localities.

30. Both the reassignment of this specimen to *Camarhynchus crassirostris* and the change in its island locality were apparently done prior to Sharpe's (1888 : 16) catalogue of specimens at the British Museum.

31. The source of the first of these two errors began with Salvin's (1876 : 482) reassignment of the species *Geospiza nebulosa* to *G. fortis.* Since Darwin's specimens of *G. fortis* were supposed to have come from Chatham and Charles islands, and since the only extant specimen of *G. fortis* in the British Museum bears a Charles Island locality, subsequent ornithologists apparently assumed the FitzRoy specimen had come from the other published locality (e.g., Sharpe, 1888 : 11). Later, the erroneous Chatham Island locality was crossed out and the Charles locality reinstated, possibly by Kinnear (see note 32), but the presence of two island localities on this specimen has proved confusing for subsequent ornithologists (e.g., Lack, 1945 : 14–15).

The second incorrectly labelled FitzRoy specimen is the type of the Galapagos Rail (*Zapornia spilonota* Gould = *Laterallus spilonotus,* British Museum reg. no. 1837.2.21.404). Rothschild & Hartert (1899 : 184–85), noting that Darwin (1839 : 459) had described seeing water rails on James Island, erroneously concluded that the bird was collected by him on that island. FitzRoy, however, collected his specimen on Charles Island. In the *Zoology* (1841 : 132), Darwin gave only 'Galapagos Archipelago' as the locality for this species. Swarth (1931 : 53) and Warren (1966 : 279), following Rothschild & Hartert, have perpetuated the erroneous James Island locality for FitzRoy's specimen.

32. Swarth's erroneous conclusion was reinforced by the fact that some of FitzRoy's specimens do not have their localities recorded on the specimen tags but only in the museum's 'Zoological Accessions Aves, 1837–1851–3' register. Norman B. Kinnear, who worked in the Bird Room of the British Museum (Natural History), nevertheless understood that the localities of FitzRoy's specimens had been recorded in his old register. Using this information, he inserted a number of footnotes into Swarth's (1931) monograph indicating the localities of various unlabelled FitzRoy specimens. Swarth, however, chose to disregard this information, arguing that 'there have been so many chances for dissociation of specimens and data that my every instinct impels me to rely upon the evidence supplied by the specific or subspecific characters of the specimens rather than on what has been written about them' (1931 : 146 n.). Unfortunately, Swarth's ornithological intuitions were not as accurate as FitzRoy's recorded localities.

33. See 'Zoological Accessions Aves, 1854–1873', pp. 34–35, 64: registry nos. 1856.3.15.4, 1857.11.28.247, and 1857.11.28.248; British Museum (Natural History), Sub-department of Ornithology, Tring.

34. On the propriety of formally recognizing trinomials for *Geospiza magnirostris magnirostris* and *G. magnirostris strenua,* see note 53.

35. See 'Printed Numbers 3345[–3907]', Down House, under specimen nos. 3312–19.

36. Darwin's specimen of *Mimus parvulus* (= *Nesomimus parvulus,* no. 1855.12.19.92) exemplifies the process of relabelling based on whatever was written on the Zoological Society stands. One tag reads 'Mimus parvulus Loc. Galapagos Ex Coll. Darwin/Marked on old stand Albermarle Island Galapagos'. The second (and newer) tag merely gives 'Albermarle Island' as the locality.

37. The measurements for Gould's female type specimen of *Geospiza strenua* (no. 1855.12.19.83) are as follows: culmen from nostril, 14·0 mm; depth of bill, 14·8 mm; and wing, 74 mm – all within the range of *G. fortis,* although the Chatham Island form now has a maximum culmen of 13·8 mm. The smallest known race of *G. magnirostris* has a bill depth of 15·3 mm, 0·5 mm greater than this '*G. strenua*' specimen. Moreover, the extinct Chatham race of *G. magnirostris,* with its very large bill, probably had a minimum bill depth in females close to 17·5 mm. (See Lack, 1945 : 142–43.)

38. The measurements for this specimen are: culmen from nostril, 9·6 mm; depth of bill, 8·6 mm; and wing, 66·5 mm. Only one species, *Geospiza nebulosa* (formerly *difficilis*) exhibits characters in this range; and Darwin's specimen, given the islands he visited, accords with only one possible island form (*debilirostris*). See further Lack, 1947 : 174–76.

39. Characters such as culmen length, bill depth, and wing length follow normal distributions in birds, with the exception that character displacement among certain species of Darwin's finches, including *Geospiza magnirostris* and *G. fortis,* tends to limit variation at the extremes of the distribution. Thus the levels of significance cited here for Darwin's two small specimens of *G. magnirostris* are conservative estimates of their anomalous nature.

40. See Gould, 1837*a* : 5; & 1841 : 101. Eyton (1856 : 248) lists this specimen, along with the three other Galapagos finches, as part of his private collection. But Eyton's collection was so vast, amounting to four thousand specimens, that he may not have been aware that this specimen had been borrowed and never returned. Moreover, he probably drew up his published catalogue from a register rather than from a bird-by-bird inventory of his specimens. Eyton frequently loaned out specimens to fellow ornithologists, which was, in fact, his main purpose in publishing a catalogue.

41. The source for the erroneous Chatham Island locality may have been Sharpe (1888), who is known to have given incorrect localities as well for FitzRoy's specimen of *Geospiza nebulosa* and for Darwin's specimen of *Progne modesta.*

42. Gould (1837*a* : 7) was also uncertain about the sex of this bird, which he designated as 'young male?'.

43. The measurements for Darwin's specimen of *Cactornis assimilis* are: culmen from nostril, 14·4 mm; depth of bill, 10·1 mm; and wing, 71·5 mm. The measurements for FitzRoy's specimen are: culmen from nostril, 14·1 mm; depth of bill, 10·2 mm; and wing, 70·5 mm. There is no overlap between these two specimens and the limits for this species on James Island, which are: culmen from nostril, 11·7–13·8 mm; depth of bill, 7·8–9·5 mm; and wing, 65–72 mm. On Bindloe Island, where the measurements do overlap, the limits are: culmen from nostril, 13·6–15·8 mm; depth of bill, 9·5–11·9 mm; and wing, 68–75 mm. Darwin's specimen is also just within the limits for males of *Geospiza scandens* on Charles Island (Lack 1945 : 146; 1947 : 176), so the possibility cannot be ruled out that it came from that island.

44. In the case of the first two specimens, measurements confirm Swarth's opinion that they came from James Island rather than Chatham, since the wing length of both specimens exceeds the Chatham Island maximum for *Certhidea olivacea luteola.*

45. See Darwin 1963[1836] : 262–64. Nora Barlow, the editor of Darwin's *Ornithological Notes,* did not transcribe Darwin's comment about the loss of specimens of *Certhidea olivacea* at the Zoological Society. See further DAR 29.2 : MS p. 74v.

46. See 'Zoological Accessions Aves, 1854–1873', pp. 27, 64; British Museum (Natural History), Sub-department of Ornithology, Tring.

47. Hellyer drowned in March 1833 when he attempted to retrieve, from the water, a duck he had shot in the Falkland Islands. He apparently became entangled in a thick kelp bed. FitzRoy later lamented in this connection that 'the motive which urged him to strip and swim after the bird he had shot, was probably a desire to get it for my collection' (1839 : 272–73).

48. DAR 29.3 : 39–40. Darwin apparently had this catalogue copied after the voyage, using it in part to reconstruct the localities of FitzRoy's Galapagos specimens.

49. See 'Zoological Accessions Aves, 1837–1851–3', pp. 7–15: nos. 1837.2.21.231–417; British Museum (Natural History), Sub-department of Ornithology, Tring. The island localities in this new series of numbers are as follows: 1837.2.21.244 (James Island), 1837.2.21.263 (James Island), 1837.2.21.396–97 (Chatham Island), 1837.2.21.398–404 (Charles Island), and 1837.2.21.405–17 (James Island), for a total of twenty-four specimens. In the accessions catalogue and on the labels, these specimens are recorded as having been presented by Sir William Burnett and Captain Robert FitzRoy. In 1837 Sir William Burnett was Physician-General of the Navy and the person in charge of the Navy's official collections.

50. FitzRoy's specimen catalogue lists 26 birds taken on James Island. Fuller appears to have shot 12 of these specimens, all but one of which (*Strix punctatissima*) were retained by him (or by FitzRoy himself) and were mostly later acquired by the Haslar Museum. Bynoe therefore appears to have shot 14 birds on James Island. For further information, see notes 52 and 62, and Darwin (1963[1836]: 262–65).

51. To Darwin, FitzRoy wrote in a letter of 16 November 1837: 'I was . . . astonished at the total omission [in your acknowledgments] of any notice of the officers—either particular—or general.—My memory is rather tenacious respecting a variety of transactions in which you were concerned with them; and others in the Beagle. Perhaps you are not aware that the ship which carried us safely was the first employed in exploring and surveying whose Officers were not ordered to collect—and were therefore at liberty to keep the best of all—nay, all their specimens for themselves. To their honour—they gave you the preference.' See DAR 164.

52. Fuller, for example, collected the only specimen of *Strix punctatissima* Gould (= *Tyto alba*), a scarce Galapagos species of Barn Owl (Darwin, 1963[1836] : 262). To his credit he allowed FitzRoy to keep this specimen, which was presented to the British Museum (reg. no. 1837.2.21.244). Fuller also collected the only Galapagos specimen of the American Bobolink (*Dolichonyx oryzivorus*) and gave it to Darwin (reg. no. 1881.5.1.2394). In addition, Fuller evidently collected and retained after the voyage a specimen of flamingo from the Galapagos (*Phoenicopterus ruber* = FitzRoy no. 438). This bird was not considered to be a new species by John Gould.

53. Covington, whose collection is noticed separately, also procured specimens of this large-billed form of *magnirostris* on Charles Island, where the species has recently been found in a fossil state (Steadman, 1981). Fuller collected an additional specimen on Chatham Island, so the type locality for this subspecies is Chatham and Charles islands, as Darwin later reported in the *Zoology* (1841 : 100). Altogether, *Geospiza magnirostris magnirostris* is known from eight *Beagle* specimens, five from Charles Island and three, including two Darwin specimens of less than certain attribution, from Chatham Island. The use of a trinomial, provisionally recognized by Lack (1969 : 261) and by Paynter (1970 : 161 n.), therefore becomes necessary to distinguish this subspecies from *G. magnirostris strenua,* which is represented by at least one (and probably three) *Beagle* specimens collected by Fuller and Darwin on James Island. *G. magnirostris magnirostris* is distinguishable from at least 90 per cent of all specimens of *G. magnirostris strenua,* thus more than satisfying Lack's (1947 : 17) criterion of subspecific status.

54. The *Albatross* expedition (1888) procured a juvenile specimen of *Geospiza magnirostris* on Charles Island that Rothschild & Hartert (1899 : 154) believed might have overlapped, when full grown, with the dimensions of the large-billed *Beagle* specimens. The California Academy of Sciences (1905–6) also procured on Charles Island a specimen whose measurements overlapped with the smaller-billed form of *G. magnirostris.* Lack (1947 : 22) thought this bird must have been a straggler.

55. The measurements of this specimen are as follows: culmen from nostril, 14·3 mm; depth of bill, 16·0 mm; and wing, 81·5 mm. The ranges on Chatham Island for *Geospiza fortis* are: culmen from nostril, 9·9–13·8 mm; depth of bill, 10·5–16·4 mm; and wing, 65–78 mm. On Charles Island, which presently has the largest form of *G. fortis,* the maximums are 14·2 mm for culmen, 16·6 mm for depth of bill, and 80 mm for wing (Lack, 1945 : 143). In *G. magnirostris* the average minimums for culmen, bill depth, and wing are 14·4 mm, 17·3 mm, and 81 mm, respectively.

56. This specimen of '*Geospiza strenua*' departs from the mean measure of culmen, bill depth, and wing length in *G. magnirostris magnirostris* and *G. fortis* on Chatham Island by an average 3·6 and 3·3 standard deviations, respectively. The chances are less than one in a thousand that this specimen belongs to either of these two forms, unless it is of hybrid origin.

57. DAR 29.3 : 29. When I saw specimen no. 1837.2.21.411 in 1970, it possessed an old tag bearing the designation '*Geospiza parvula*' and indicating that it was FitzRoy's specimen no. 421 collected on James Island. This tag is now missing.

58. The measurements of FitzRoy's specimen are: culmen from nostril, 10·8 mm; depth of bill, 10·2 mm; and wing, 72 mm. The measurements for Darwin's specimen are: culmen from nostril, 11·0 mm; depth of bill, 10·4 mm; and wing, 72 mm. The culmen and wing measurements for these two specimens are within the limits of *Geospiza difficilis* on three of the six islands where it is found today, but the present maximum for bill depth in this species is 10·0 mm (in the James Island form–*debilirostris*). It should be noted that although the two *Beagle* specimens lack chestnut on the wing bar and undertail coverts, these characteristics are present in only about 70 per cent of the individuals in one of the three races of *G. difficilis* and are almost completely absent in another race.

59. According to Sundevall (1871), specimens of *Geospiza nebulosa* were collected on Chatham and Charles islands in 1852 by Dr Kinberg, surgeon and zoologist on the Swedish frigate *Eugenie*. See also Skogman (1854–55, **1:** 172–74). The catalogue of the Stockholm Naturhistoriska Riksmuseet lists only one specimen of *G. nebulosa*, a black male from Charles Island. The culmen length of this specimen is 10·5 mm, the bill depth 9·8 mm, and the wing length 72 mm, in extremely close agreement with the two *Beagle* specimens of this form. Sharpe (1888 : 12), who created the name *difficilis,* himself recognized under this name two specimens collected on Charles Island by Commander A. H. Markham in 1880. Measurements, however, establish that Markham's specimens (nos. 1885.12.14.296 and 1885.12.14.298) are examples of *G. fuliginosa* and *Camarhynchus parvulus.*

Peter Grant (personal communication) has suggested that the three extant specimens of *G. nebulosa*, which he has examined, might be hybrids between *G. fortis* and *G. scandens.* Hybridization between these two species is indeed known to occur on an occasional basis. Nevertheless, such an origin seems unlikely in the case of the three specimens of *G. nebulosa* for the following reasons. Lack (1945, 1947) examined and measured nearly every museum specimen of *G. fortis* and *G. scandens* collected since 1835. Out of 1827 specimens of these two species, Lack considered only 4 to be of possible hybrid origin, given their peculiarly intermediate character (1945 : 113). With an apparent hybridity rate of about one specimen in five hundred, the probability that two such hybrids would have been procured in only fifteen *Beagle* examples of these two species is extremely unlikely ($\chi^2 = 78{\cdot}81$, $P \ll 0{\cdot}0001$). Even with a hybridity rate as much as ten or twenty times greater, the chances of two hybrid specimens being taken in a group of only fifteen specimens is still very small. That a third specimen would have been taken by Kinberg, who collected only fifteen Geospizinae on Charles Island, is similarly improbable. Hybrids, moreover, tend to be intermediate in their basic characters, albeit with a certain amount of variation in the direction of the two parents. In contrast to Lack's four 'hybrid' specimens, none of the three *G. nebulosa* specimens conform to the expected character dimensions of a *G. fortis* × *G. scandens* hybrid. In particular, culmen length in *G. nebulosa* is an average of 2·4 standard deviations smaller than the expected hybrid size, and wing length is an average of 1·2 standard deviations too large (an anomalous discrepancy, since culmen and wing length are positively correlated in Darwin's finches). Based on culmen length, the probability that any one of these three specimens is of hybrid origin is very small (about one in a hundred). The probability that all three specimens are hybrids becomes even smaller (mathematically, about one in a million). Moreover, the distinctive culmen-to-wing ratio of *G. nebulosa* (0·150), which differs considerably from that found in *G. fortis* (0·164), *G. scandens* (0·198), and presumed *G. fortis* × *G. scandens* hybrids (0·184), is virtually identical to the ratio observed in *G. difficilis* (0·149). In short, the three extant specimens of *G. nebulosa* are simultaneously too uniform among themselves, and too deviant from other presumed or expected hybrids of *G. fortis* and *G. scandens,* to be of plausible hybrid origin. Additionally, the apparent hybridity rate between these two species is far too low to justify the belief that three hybrid specimens would have been taken among the small numbers of Geospizinae acquired by the *Beagle* and *Eugenie* collectors.

After a preliminary analysis of several hundred avian fossils from Charles Island, Steadman (personal communication) reports that at least two maxillas and one mandible appear to belong to *G. nebulosa nebulosa.* The apparent infrequency of these fossils in lowlands deposits, where they account for only about one per cent of the Geospizinae remains, is consistent with *G. nebulosa*'s preference for the humid zone on islands having such a zone. Even on islands with a humid zone, however, this species has occasionally been reported near the coast (Bowman, 1961 : 278–79).

60. The depth of bill of this specimen of *Camarhynchus psittacula* is larger than in any other known specimen. The specimen's measurements are: culmen from nostril, 10·4 mm; depth of bill, 12·5 mm; and wing, 78 mm. The limits for this species on James, where the depth of bill reaches its maximum in the archipelago, are: culmen from nostril, 9·1–10·4 mm; depth of bill, 9·4–11·9 mm; and wing, 72–77 mm (Lack, 1947 : 175). Although the bill measurements for this specimen overlap with those for *Platyspiza crassirostris,* the latter is a much larger species with a wing size of 85–91 mm on James Island.

61. On Fuller's appointment as FitzRoy's steward, see FitzRoy (1839 : 350). Fuller was apparently a good shot, as may be inferred from the twelve hundred pounds of fresh meat he supplied to the ship's company between 1832 and the middle of 1834 (FitzRoy, 1839, *Appendix* : 299).

62. Darwin identified these specimens in his manuscript notes as birds 'collected by Fuller in Capt. F. R.['s] possession'. The species names, catalogue numbers, and island localities are recorded in these notes. (See p. 58) and Fig. 6; and DAR 29.3 : 30.) Fuller may have collected other Galapagos birds; and, if so, this would help to explain the absence of some of the 18 Galapagos specimens that are listed in FitzRoy's catalogue but that were not presented to the British Museum in 1837.

63. See Darwin, 1967 : 89. I am grateful to David Stanbury for information regarding the history of the Haslar Museum and Dr Armstrong's association with that institution.

64. It is possible that FitzRoy himself withheld Fuller's specimens from the British Museum on the grounds that Fuller was his privately paid servant, and was not therefore collecting at the Royal Navy's expense. In any event, my categorization of Fuller's specimens as 'Fuller's collection' seems heuristically justified given the segregation and differing history of these birds.

65. See 'Book of Presents, 1854–1861', 12 January 1856; British Museum, Bloomsbury, London.

66. The measurements of the Cambridge specimen of *Geospiza magnirostris magnirostris* are: culmen from nostril, 18·2 mm; depth of bill, 23·8 mm; and wing, 92 mm (see also Benson, 1972 : 68). The ranges for the other seven *Beagle* specimens of the large-billed *magnirostris* are: culmen from nostril, 17·1–18·9 mm; depth of bill, 21·7–22·5 mm; and wing, 84–93 mm. The means for all eight specimens are: culmen from nostril, 18·0 mm; depth of bill, 22·3 mm; and wing, 88·8 mm. The average bill size for the three Chatham specimens is virtually identical with the average bill size for the five Charles Island specimens (17·9 mm vs. 18·0 mm for culmen from nostril, and 22·4 mm vs. 22·2 mm for bill depth). There can be no doubt about the locality of Fuller's specimen. According to FitzRoy's manuscript catalogue (see note 48), this specimen was collected on 18 September 1835, during the second day of the *Beagle*'s six-day visit to Chatham Island.

67. The measurements of this specimen of *Geospiza magnirostris strenua* are: culmen from nostril, 14·7 mm; depth of bill, 18·5 mm; and wing, 84 mm (see also Benson, 1972 : 68). The limits for this species on James are: culmen from nostril, 13·0–17·4 mm; depth of bill, 16·1–22·1 mm; and wing, 75–88 mm (Lack, 1945 : 142).

68. See DAR 29.3 : 30.

69. See Nora Barlow's Introduction to Darwin, 1963[1836] : 207–8.

70. If the 5 Geospizinae that I have attributed with some confidence to Darwin at the Leiden Rijksmuseum were indeed collected by him, then at least 29 and possibly all 31 of his voyage specimens are accounted for (see page 76). Had Darwin included Covington's 4 specimens in his voyage catalogue, then at least 33 finch specimens, 2 more than are recorded, ought to appear on that list. See also note 72. Even if the Leiden finch specimens are not Darwin's, it is highly unlikely that Covington's specimens were catalogued by Darwin. For if Covington had handed these specimens over to Darwin for tagging and cataloguing, neither person would later have been able to distinguish these four specimens (and their island localities) from the many other similar specimens in Darwin's collection.

71. Norman B. Kinnear, in a footnote inserted into Swarth (1931 : 169), erroneously states that Eyton purchased these birds in 1855 at the Zoological Society's sale. Eyton (1856 : 208, 248, 296) lists these six birds as part of his private collection.

72. See 'Zoological Accessions Aves, 1880–1884', p. 49; British Museum (Natural History), Sub-department of Ornithology, Tring. The British Museum registry nos. for Eyton's Galapagos mockingbird (*Mimus parvulus = Nesomimus melanotis,* Chatham Island) and dove (*Zenaida galapagoensis*) are 1881.2.18.80 and 1881.2.18.84, respectively. For the specific identity of the mockingbird, which was misclassified in 1881, see Swarth, 1931 : 119. The measurements for the dove do not agree with Gould's measurements for Darwin's type specimen, of which there was only one (1963[1836] : 262). Additionally, all four of Darwin's specimens of *Nesomimus* are accounted for in the British Museum collection (nos. 1855.12.19.223–25 and 1855.12.19.228). Hence neither of the Eyton specimens acquired by the British Museum in 1881 is Darwin's.

73. See the 'Zoological Accessions Aves, 1885–1887', pp. 127–28; British Museum (Natural History), Sub-department of Ornithology, Tring.

74. *Geospiza fuliginosa* is one of the commonest species of Darwin's finches. Given the size of his collection, Darwin should have taken at least five specimens of this species. The British Museum (Natural History) possesses only two Darwin specimens of *G. fuliginosa,* suggesting that as many as three specimens–the same number as is present in Leiden–may be missing.

75. See Darwin's *Ornithological Notes* (1963[1836] : 263; specimen nos. 3320–23). The British Museum (Natural History) possesses three Darwin specimens of *Cactornis scandens*–a jet black male, a specimen of dubious sex (probably a juvenile male), and a supposed female (Swarth, 1931 : 190, 198). Given the sexes reported in Darwin's *Ornithological Notes,* a juvenile male specimen is therefore missing.

76. Personal communication, letter of 21 October 1980.

77. See, for example, Darwin's specimens of *Cactornis assimilis, Geospiza dentirostris,* and *Camarhynchus psittacula*; FitzRoy's specimens of *G. magnirostris* (no. 1837.2.21.403) and *C. assimilis*; and Fuller's specimen of *C. psittacula*—all of which have been incorrectly sexed.

78. There are two registered FitzRoy specimens missing from the collection at the British Museum (Natural History). Only one of these specimens coincides with those in Leiden. It is extremely unlikely, however, that the similar Leiden specimen is FitzRoy's, since the five Leiden specimens were all acquired the same year from the same source (dealer Gustav Adolph Frank).

79. See du Petit-Thouars (1840–64, **2** : 279–322; **7** : 94).

80. Although Prévost & des Murs (1855 : 208–9) describe specimens of *Geospiza fuliginosa* from the voyage of the *Vénus,* the measurements given clearly indicate that they must have been examples of *G. fortis.* See also Néboux (1840).

81. According to Salvin (1876 : 463, n. 1), Léclancher's specimen of *Camarhynchus,* which was named *Guiraca cinerea* by Lafresnaye (1843), corresponds to no known species of this genus. The form is similar, however, to the larger species of the tree finches (*Camarhynchus* and *Platyspiza*), but it is unfortunately figured too imprecisely to allow an accurate determination of the species.

82. See the catalogue of his collection (Verreaux, 1865 : 204, 210).

83. See 'Zoological Accessions Aves, 1854–1873', pp. 64, 122: reg. nos. 1857.11.28.247 and 1857.11.28.248 (both *Geospiza*), and reg. no. 1860.1.16.54 (*Hirundo concolor = Progne modesta*); British Museum (Natural History), Sub-department of Ornithology, Tring.

84. My estimated total of 27 (and possibly 31) Darwin specimens includes a minimum of 16 extant Darwin specimens at the British Museum, and 11 to 13 specimens that have been lost or destroyed. The uncertainty regarding the latter number of specimens depends upon whether the 2 registered '*Geospiza*' that have disappeared from the British Museum since 1855 correspond with other specimens known to be missing from Darwin's collections. If the 5 specimens at the Leiden Rijksmuseum are also Darwin's, then the number of extant specimens is increased to 21, and the number of lost or destroyed specimens is reduced to 8 to 10. For the purposes of these estimates, I have assumed that at least one specimen of *Geospiza fortis* and two specimens of *Certhidea olivacea* that are credited to Darwin at the British Museum may have been obtained by Darwin, after the *Beagle* voyage, from other collectors. If these 3 specimens are Darwin's, then there are 19 extant specimens at the British Museum that were indeed collected by Darwin.

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Miscellanea

Contents

A taxonomic revision of the genus *Platycola* (Ciliophora: Peritrichida)

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Introduction

Platycola Kent, 1882 is a loricated ciliate belonging to the order Peritrichida Stein, 1859. When the genus was erected it consisted of eight species, and in the past century seventeen new species have been added. However, in that time there has been only one review of the genus (Kahl, 1935), and one account of its general biology (Kralik, 1961). In view of this, it was considered that another review of the genus *Platycola* was long overdue.

Like Trueba (1978) in his revision of the genus *Pyxicola* (Ciliophora: Peritrichida), the present author has imitated Noland and Finley's (1931) revision of the genus *Vorticella*. In so doing, the original descriptions of all twenty five species of *Platycola* have been compared. As a result, only thirteen species are recognised as valid while the rest are either considered to be synonymies or removed from the genus altogether. Drawings and descriptions of the thirteen recognised species are included together with a key to their identification.

General morphology and biology

A relatively modern account of the biology of a representative species of *Platycola* is given in Kralik (1961) so it is sufficient here to give a short summary. Typically, *Platycola* consists of one, two or sometimes more zooids within a decumbent lorica which has an aperture in the anterior region. The exact chemical nature of the peritrich lorica is not known and is usually called 'chitin', 'pseudochitin' or 'tectin' although Sleigh (1973) considered it most likely to be either a proteinaceous or mucopolysaccharide secretion. It is usually colourless or pale yellow when first formed but becoming dark yellow or brown with age, probably due to the deposition of iron on the surface (Kralik, 1961).

The zooid is usually trumpet-shaped or cylindrical and, when relaxed, may extend far beyond the aperture. When stimulated, it contracts quickly back into the lorica. As with most peritrichs, the ciliation is reduced to the three rows of peristomail cilia one outer (the haplokinety) and two inner (the polykinety). It is the beating action of these cilia which creates the feeding currents to sweep bacteria and algae down into the buccal cavity and eventually these pass into the cytoplasm where they are digested in food vacuoles. Excess water taken in by this process is pumped out of the cell by a contractile vacuole(s).

In *Platycola* there is a single macronucleus, which is usually long and conspicuous, and one micronucleus, which is small and inconspicuous. Reproduction occurs both asexually, by means of a division that is topographically longitudinal, and sexually, by conjugation which involves the fusion of a mobile microgamete with a sessile macrogamete. Both instances result in the formation of a normal vegetative parent cell and a free swimming daughter cell, or telotroch, which has an extra row of cilia near the scopular region called the aboral ciliary wreath. This enables the telotroch to swim away and colonise a new environment.

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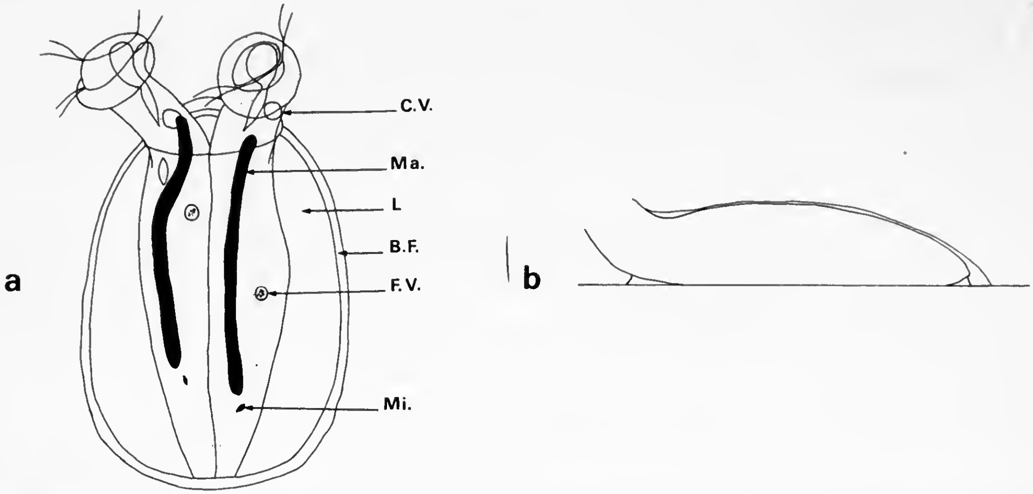

Fig. 1 *Platycola decumbens*, a. dorsal view showing two extended zooids; b. lateral view of lorica (after Kralik, 1961). B.F. = border fringe, C.V. = contractile vacuole, F.V. = food vacuole, L. = lorica, Ma. = macronucleus, Mi. = micronucleus.

The telotroch eventually settles on a substratum and immediately begins to secrete its lorica. The new lorica is slightly elastic at first and the zooid develops a conspicuous swelling near its basal region which gradually moves up towards the peristome, shaping the lorica wall as it goes. This swelling appears to be analagous to the 'growth cavity' described by Willis (1942) in the peritrich *Lagenophrys tattersalli*. When this process is complete, the swelling collapses and the zooid is reduced back to its normal size. The lorica wall now hardens and the zooid can begin to feed. Predators of *Platycola* include *Trachelophyllum chilense* (Ciliophora: Hapterida).

Taxonomic characters

There are few reliable characters on which the species of *Platycola* may be defined and ever since the genus was erected, the major reviews of Kent (1882), Kahl (1935) and Stiller (1971) have relied principally on the lorica, the substratum and, to a lesser extent, the zooid.

Lorica. In almost every species description, emphasis has been placed on the size, shape, colour, neck (length and direction) and, in one case, the striations of the lorica. However, Kralik (1961) showed that all these parameters are highly variable and concluded that the lorica alone could no longer be regarded as a reliable character on which to define a species.

Substratum. The substratum on which an individual is found is often cited as a significant part of the species description and this is especially true of the epibiotic forms. However, although there are a number of examples of species specificity among these symphoriont peritrichs (see Corliss, 1979 : 144), there is no evidence that this is true for *Platycola*. Until such evidence exists, a certain amount of reservation must be placed on the substratum as being a reliable character.

Zooid. Among the aloricate peritrichs a number of characters relating to the zooid are used to define species, for example body size and shape, position and shape of the macronucleus, number and position of contractile vacuoles and the presence of striations, but these are often omitted from species descriptions of *Platycola*. Indeed, in some cases, the only descriptions available are as a result of studies made on fixed, contracted cells, so that any information obtained relating to the zooid is of limited value. Nevertheless, these characters may be the most important and when available, are applied as such in this review.

Silver impregnations, biometric analysis and ultrastructural studies are now increasingly used in the taxonomy of both ciliates in general (Corliss, 1979) and the peritrichs in particular (Reid, 1967; Davidson & Finley, 1972; Foissner & Schiffmann, 1974, 1975, 1979; Foissner, 1978, 1979, 1981). However, the literature contains no record of any of these having been applied to *Platycola* spp. Until such information is available, we must rely on a combination of as many of the reliable characters listed above as possible, and reflect the hope of Finley and Bacon (1965) that 'perhaps there will come a time when every description of a new species of ciliate will include valid observations of such pertinent details'.

Taxonomic position and genus description

From its erection, *Platycola* Kent, 1882 has been included within the family Vaginicolidae de Fromentel, 1874 (which Kent considered to be a sub-family called Vaginicolina) and it has never been removed from that group. According to Corliss (1979), Vaginicolidae contains nine genera all of which are loricate, solitary and either with or without a stalk (generally very short when present); division is isotomic or anisotomic and some species may have a true operculum (e.g. *Pyxicola*). The genus *Platycola* has been defined by Curds *et al* (in press) as: 'body trumpet-shaped lying within a horizontal, pseudochitinous lorica to which it is attached at the posterior end. The lorica adheres along the length of one side to algae and other submerged objects by a dark, sticky substance. It has a simple aperture without valves and is turned up diagonally so that the extended animal may protrude upwards. The genus may be most easily confused with *Lagenophrys* which also has a lorica lying horizontally. However, in the latter genus, there is a complicated valve system to close the aperture and the animal is anchored laterally to the lorica'.

Key to the species of Platycola

1	Marine	2
–	Freshwater	3
2	Viewed dorsally, the lorica is circular or nearly so and, when present, the neck is short. The aperture is circular	***P. circularis*** (Fig. 5)
–	Viewed dorsally the lorica is oval and, when present, the neck is elongated. The aperture is oval	***P. hydrobiae*** (Fig. 10)
3	Zooid has one contractile vacuole	4
–	Zooid has two contractile vacuoles	***P. dilatata*** (Fig. 8)
4	Specifically epibiotic on the cave-dwelling *Microlistra spinossisima* (Crustacea: Isopoda)	5
–	When epibiotic, not found on *Microlistra spinossisima*	6
5	Macronucleus has a double loop to form an E-shape	***P. callistoma*** (Fig. 4)
–	Macronucleus ribbon-like, irregular but not E-shaped	***P. lageniformis*** (Fig. 11)
6	Not epibiotic, ventral wall follows the contour of substratum	7
–	Epibiotic, and the ventral wall depresses itself into the host substratum	***P. pala*** (Fig. 13)
7	Neck of lorica has no lateral cleft	8
–	Neck of lorica has a cleft and is 'U'-shaped when viewed laterally	***P. coelochila*** (Fig. 6)
8	Contractile vacuole situated in the upper 1/3 of the zooid, usually near the peristome lip	9
–	Contractile vacuole situated at or near the centre of the zooid	***P. baikalika*** (Fig. 2)
9	When fully extended the zooid(s) reaches well beyond the aperture	10
–	When fully extended the zooid(s) only reaches as far as or just beyond the aperture	11
10	Dorsal surface of lorica convex with no distinctive longitudinal ridge	***P. decumbens*** (Fig. 7)
–	Dorsal surface of lorica raised in a high, distinctive ridge which runs longitudinally down its centre	***P. steineri*** (Fig. 14)
11	Zooid(s) does not contain endosymbiotic zoochlorellae	12
–	Zooid(s) contains endosymbiotic zoochlorellae	***P. butschlii*** (Fig. 3)

12 Viewed dorsally, the lorica shape is irregular and asymmetrical with one side wall distinctly constricted, and the other straight . . . . **P. mollis** (Fig. 12)

– Viewed dorsally the lorica shape is elliptical or nearly so, being symmetrical about its centre axis . . . . **P. gracilis** (Fig. 9)

Descriptions of valid species

Thirteen of the 25 described species are recognised here to be valid. Of the remaining 12, 10 are listed below as synonyms of *Platycola* while two are transfered to other genera. *P. cylindrica* Vuxanovici, 1963 is transfered to the genus *Vaginicola* and *P. nigra* Wailes, 1928 has already been removed from the genus by Dons (1940) who considered it to be a folliculinid. In all Figs, scale: 100 μm.

Platycola baikalica Swarczewsky, 1930

Vaginicola baikalica Swarczewsky, 1930.

Diagnosis (Fig. 2). The lorica is pale yellow and usually oval or circular when viewed from above. The neck is directed forwards and upwards at an angle. The dorsal wall is distinctly arched and may reach a height of up to 40 μm. Each zooid has one contractile vacuole near its centre. The ribbon-like macronucleus is long, thin and longitudinally orientated within the zooid.

Lorica 90 μm long × 67–70 μm wide. Neck 5–6 μm long × 60–65 μm wide. The neck is raised 28–30 μm above the substratum.

Substratum. Epizooic on the gammarids: *Brandtia lata* (Crustacea: Amphipoda), *Brandtia latissima* (Crustacea: Amphipoda), *Pallasea grubei* (Crustacea: Amphipoda) and *Echinogammarus fuscus* (Crustacea: Amphipoda).

Habitat. Freshwater in Lake Baikal.

Remarks. This species has been described once and no diagrams showing extended zooids are available.

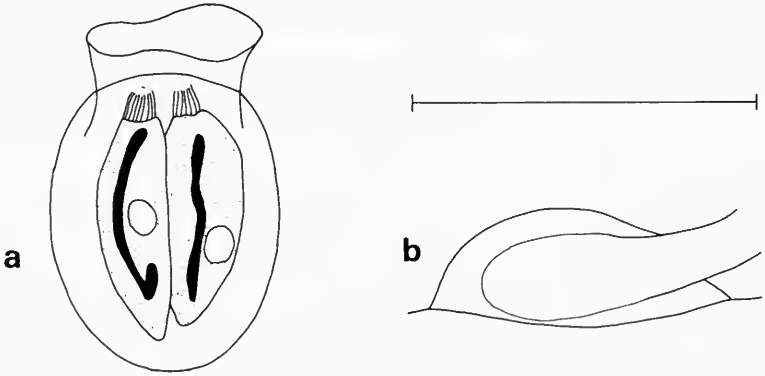

Fig. 2 *Platycola baikalica*, a. dorsal view; b. lateral view (after Swarczewsky, 1930).

Platycola butschlii Nüsslin, 1884

Vaginicola butschlii Nüsslin, 1884.

Diagnosis (Fig. 3). The lorica is variable in shape but usually wide and well rounded at the base. The neck is a simple extension of the lorica wall and is distinguished by a slight constriction at its base. The wavy aperture is wide and faces upwards. The adhesive cement can be seen only around the rear 1/3 of the lorica.

The zooid is squat and contains numerous endosymbiotic zoochlorellae. The macronucleus is long and thin with two or more distinct bends (Fig. 3b).

Lorica 80–100 μm long × 54–110 μm wide. Aperture 20–40 μm wide.

SUBSTRATUM. Submerged plants and mosses.

HABITAT. Freshwater in Lake Herrenwasser.

REMARKS. The only species of *Platycola* with endosymbiotic zoochlorellae.

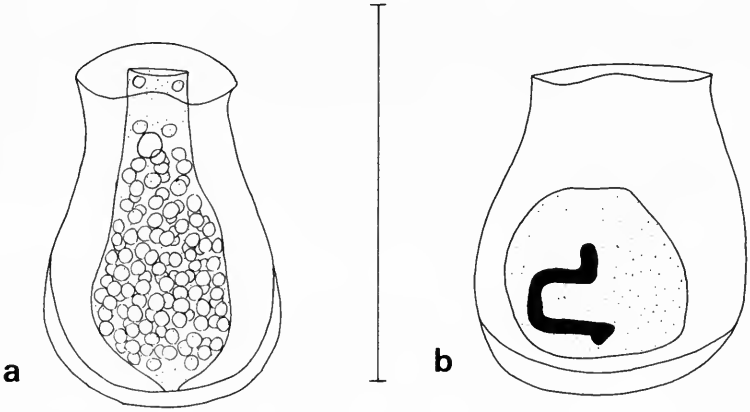

Fig. 3 *Platycola butschlii*, a. dorsal view of zooid with endosymbiotic zoochlorellae; b. dorsal view showing the macronucleus within a contracted zooid (after Nüsslin, 1884).

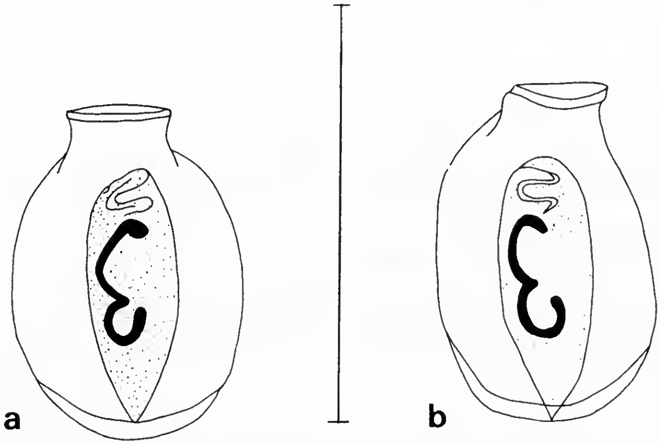

Fig. 4 *Platycola callistoma*, a. dorsal view; b. dorsal view showing variation of lorica neck (after Hadzi, 1940).

Platycola callistoma Hadzi, 1940

DIAGNOSIS (Fig. 4). The lorica is colourless and usually oval in shape when viewed dorsally. The neck is easily distinguished being slightly flattened in the dorso-ventral plane. The zooid appears to be unstriated. The macronucleus lies longitudinally in the body and has a distinctive double loop.

Lorica 73 μm long × 55 μm wide. Neck 30 μm wide at the aperture and 22 μm wide at the base. Zooid 60 μm long × 20 μm wide.

SUBSTRATUM. Epizooic on the cave-dwelling *Microlistra spinosissima* (Crustacea: Isopoda).

HABITAT. Freshwater in Yugoslavia.

REMARKS. From a single description of a contracted individual, the most distinctive characteristics of this species appear to be its substratum and macronuclear shape.

Platycola circularis Dons, 1940

DIAGNOSIS (Fig. 5). The lorica is colourless, smooth and relatively flat when viewed laterally. When viewed dorsally it is circular or nearly circular and usually without a neck. When present, the neck is very short. The macronucleus is short, sausage-shaped, slightly curved and usually situated obliquely, or at right angles to the longitudinal axis, across the centre of the zooid.

Lorica 40–65 μm in diameter. Aperture 13–16 μm wide. Neck, up to 5 μm long. Macronucleus, 30–40 μm long × 5–7 μm thick.

SUBSTRATUM. Epizooic on the uropods of *Limnoria* sp. (Crustacea: Isopoda).

HABITAT. Marine.

REMARKS. *P. circularis* has been described once and its most distinctive characteristics appear to be its circular lorica and its short, obliquely situated macronucleus. Only contracted forms were drawn and no diagrams of relaxed zooids are available.

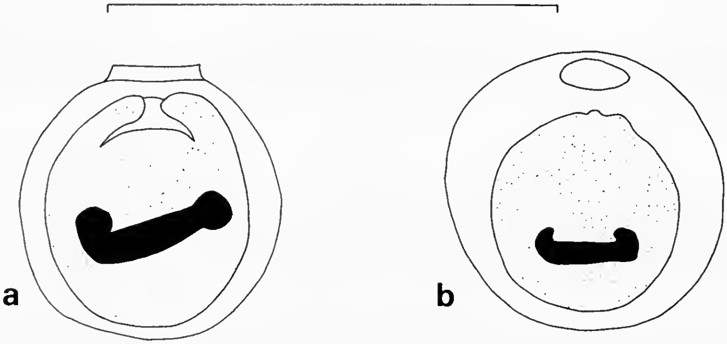

Fig. 5 *Platycola circularis*, a. dorsal view of lorica with neck; b. dorsal view of lorica without neck (after Dons, 1940).

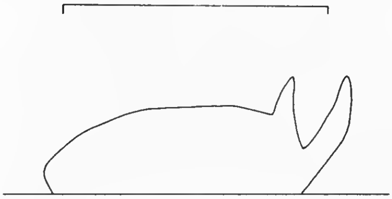

Fig. 6 *Platycola coelochila* lateral view of lorica (after Stokes, 1887).

Platycola coelochila Stokes, 1887

DIAGNOSIS (Fig. 6). Stokes (1887) described the lorica as being 'broadly ovate' from the dorsal aspect with its length less than three times the width. The posterior end is rounded and the dorsal surface convex. The short, vertical neck has a cleft, forming a 'U'-shape from the lateral view. The lorica is yellow, becoming brown with age. The zooid protrudes for a considerable distance beyond the aperture when fully extended.

Lorica 110 μm long.

SUBSTRATUM. On the roots of *Lemna* sp.

HABITAT. Freshwater from North America.

REMARKS. Stokes' (1887) diagram shows the lorica from a lateral view and without a zooid. However, until a more detailed description is available, it must remain a distinct species on the basis of the shape of its neck.

Platycola decumbens Ehrenberg, 1830

Vaginicola decumbens Ehrenberg, 1830.
Platycola ampulla de Fromentel, 1874.
Platycola regularis de Fromentel, 1874.
Platycola striata de Fromentel, 1874.
Platycola truncata de Fromentel, 1874.
Platycola longicollis Kent, 1882.
Platycola longicollis var. *intermedia* Kellicott, 1884. (=*P. intermedia* Kahl, 1935).
Platycola longicollis var. *reflexa* Mermod, 1914. (=*P. reflexa* Kahl, 1935).
Platycola amphora Swarczewsky, 1930.
Platycola amphoroides Sommer, 1951.

DIAGNOSIS (Fig. 7). The lorica varies considerably in shape (see Fig. 7) but from above, is usually oval, or rectangular with rounded corners. The colour varies from transparent or pale yellow (usually in young cells) to dark yellow or brown (usually in mature cells). Striations on the lorica are absent in most individuals though others may be either partly or completely striated. The neck length is highly variable but the aperture faces forwards and upwards. The neck is frequently colourless. There are usually two zooids in each lorica though this number may vary from one to four. One contractile vacuole is present, situated near the peristome lip. The macronucleus is long, straight and longitudinally orientated in the body. The pellicle is finely striated transversely. When relaxed the zooids extend well beyond the aperture and are usually held in a vertical position.

Lorica 65–145 μm long (average 96 μm) $\times$ 44–110 μm wide (average 75 μm). Zooid 79–168 μm long (average 142 μm) $\times$ 12–26 μm wide (average 19 μm). Peristome 21–55 μm wide (average 30 μm). Micronucleus 1·6–10·2 μm (average 3·5 μm) $\times$ 1·0–4·0 μm wide (average 1·3 μm).

SUBSTRATUM. A wide variety of plants (*Lemna* spp. *Ceratophylum* sp., various algae), animals (mollusc shells) and abiotic substrata.

HABITAT. Freshwater, widely distributed in both flowing and standing water in North America and Europe.

REMARKS. Kralik (1961) redescribed a freshwater species of *Platycola* in considerable detail which he identified as *P. truncata* de Fromentel, 1874, and among the species which he found to be synonymous with this was *P. decumbens* Ehrenberg, 1830. However, the name *P. decumbens* clearly predates that of *P. truncata*. So, in accordance with the Rules of Zoological Nomenclature (1964), *P. decumbens* should be considered the correct name and *P. truncata* a junior synonym. Of the species listed in the synonyms above, *P. reflexa* and *P. intermedia* have been synonymised here for the first time. Both were thought to be distinct on the basis of their loricae (Kahl, 1935). However, Kralik (1961) has shown the lorica of *P. truncata* (=*P. decumbens*) to be highly variable and, in the opinion of the present author, sufficiently so to encompass both of these species. Of the remainder, *P. amphora*, *P. amphoroides*, *P. longicollis*, *P. regularis* and *P. striata* were synonymised by Kralik (1961) and *P. ampulla* by Dons (1922).

Platycola dilatata de Fromentel, 1874

Vaginicola dilatata de Fromentel, 1874.
Platycola donsi Kahl, 1935.
Platycola tincta de Fromentel, 1874.

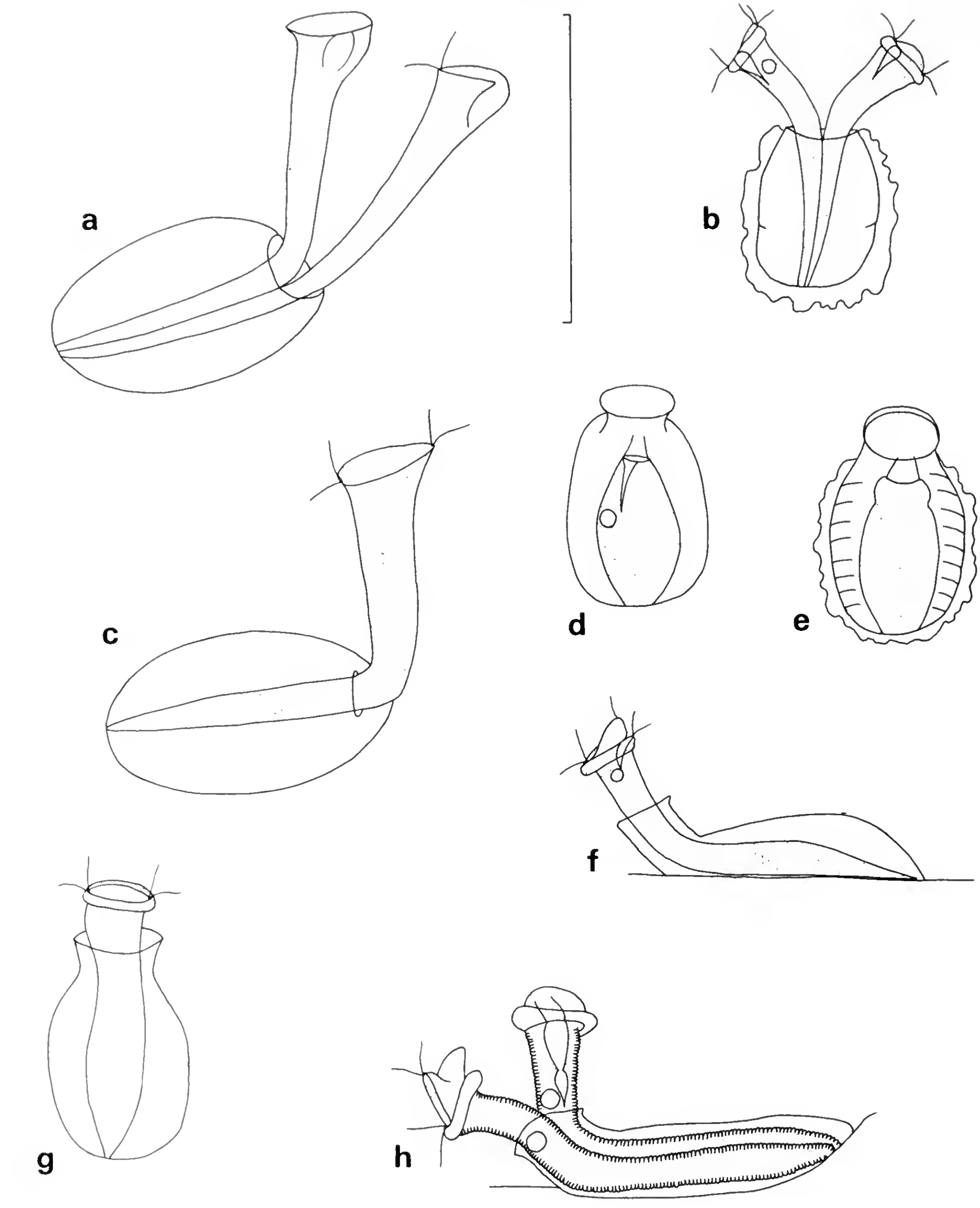

Fig. 7 *Platycola decumbens*, a. dorsal view (after Ehrenberg, 1930); b. (=*P. truncata*) dorsal view (after de Fromentel, 1874); c. dorsal view (after Ehrenberg, 1830); d. (=*P. regularis*) dorsal view (after de Fromentel, 1874); e. (=*P. striata*) dorsal view (after de Fromentel, 1874); f. (=*P. longicollis*) lateral view (after Kent, 1882); g. (=*P. ampulla*) dorsal view (after de Fromentel, 1874); h. (=*P. amphoroides*) lateral view (after Sommer, 1952).

Diagnosis (Fig. 8). The lorica is oval or nearly oval when viewed dorsally and there is a wide border fringe of adhesive cement. The lorica is pale yellow in young cells, becoming brown with age. The neck is short, colourless and slightly constricted at the base. The zooid is large and almost cylindrical though slightly widened at the peristome. When relaxed, it extends well beyond the aperture. The cytoplasm is finely granular but otherwise transparent, there are two contractile vacuoles and the pellicle is finely striated transversely.

Lorica 75 μm long × 50 μm wide. Neck 10 μm long, aperture 30 μm wide.

Substratum. Submerged plants and algae.

Habitat. Freshwater.

Remarks. The most distinctive feature of *P. dilatata* is the fact that it has two contractile vacuoles per zooid, a characteristic shared by only one other previously described species, *P. tincta* de Fromentel, 1874. Dons (1922) considered the two to be identical and designated *P. dilatata* the senior synonym. However, Kahl (1935) was of the opinion that Dons (1922) had seen a new species and named it *P. donsi*, but Dons (1940) himself later reversed this decision. Kralik (1961), mainly on the basis of the lorica, regarded *P. dilatata* as synonymous with *P. truncata*. However this is clearly erroneous as *P. truncata* (= *P. decumbens*) has only one contractile vacuole.

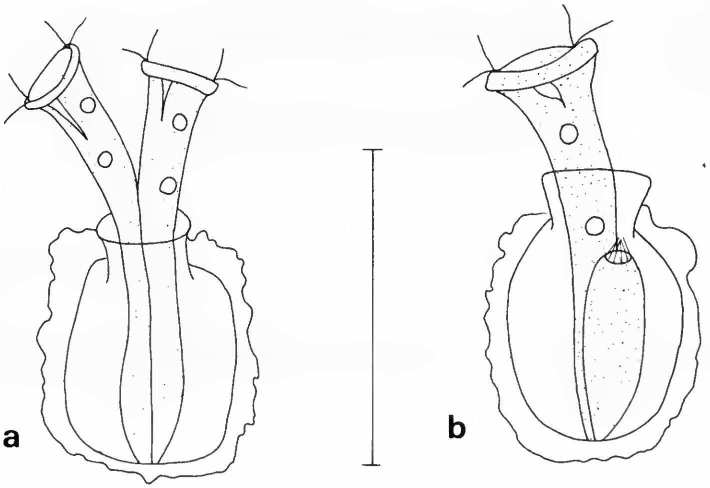

Fig. 8 *Platycola dilatata*, a. dorsal view; b. (= *P. tincta*) dorsal view (after de Fromentel, 1874).

Platycola gracilis de Fromentel, 1874

Vaginicola gracilis de Fromentel, 1874.

Diagnosis (Fig. 9). From the dorsal view, the lorica is somewhat elongated, almost cylindrical, but rounded at the base. The neck is short and also attached to the substratum along its length. The aperture faces upwards slightly. The zooid is broad but fairly short and may reach just beyond the aperture when fully extended. The peristome is wide and the disc is flat and slightly elevated. There is one contractile vacuole just below the peristome and the macronucleus is short, slightly curved and situated longitudinally in the upper 1/3 of the body.

Lorica 60 μm long × 37 μm wide. Aperture 30 μm wide.

Substratum. Submerged plants and algae.

Habitat. Freshwater in France.

Remarks. The most distinctive features of this species are its elongated lorica, the wide peristome and the very conspicuous ciliary wreath.

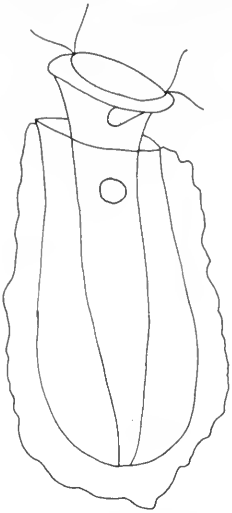

Fig. 9 *Platycola gracilis* dorsal view (after de Fromentel, 1874).

Platycola hydrobiae Hofker, 1940

Vaginicola hydrobiae Hofker, 1940.

DIAGNOSIS (Fig. 10). Viewed dorsally, the yellow lorica is shaped like an elongated ellipse, truncated at the anterior end by the presence of a broad, slit-like aperture. When present, the neck is a simple extension of the lorica and is attached to the substratum. The macronucleus is very short and thick and situated in the upper half of the zoid.

Lorica 85 μm long × 55 μm wide. Aperture 35 μm wide.

SUBSTRATUM. On *Hydrobia* (Mollusca: Gastropoda).

HABITAT. Marine, found in the North Sea.

REMARKS. *P. hydrobiae* has only been described once and no diagrams showing extended zooids are available. The lorica shape is variable. The most distinctive characters appear to be the aperture, which faces forwards and is not raised off the substratum, and the shape of the macronucleus.

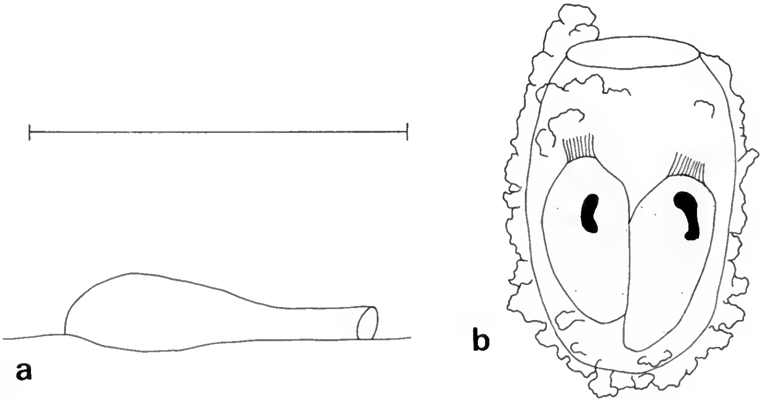

Fig. 10 *Platycola hydrobiae*, a. lateral view; b. dorsal view (after Hofker, 1930).

Platycola lageniformis Hadzi, 1940

Diagnosis (Fig. 11). The lorica is slim and elliptical in shape when viewed dorsally, but slightly rounded at the base. The neck is fairly long and faces upwards, almost at right angles to the substratum, and is slightly constricted at its base. There are usually one or two zooids in each lorica, each with a single contractile vacuole and a long ribbon-like macronucleus.

Lorica 120 μm long × 50 μm wide. Aperture 20 μm wide.

Substratum. Epizooic on the cave-dwelling *Microlistra spinosissima* (Crustacea: Isopoda).

Habitat. Freshwater in Yugoslavia.

Remarks. This species was described from a single study made on fixed, contracted specimens. Any judgement on the validity of its rank as a separate species cannot be made until fresh, unfixed specimens have been described.

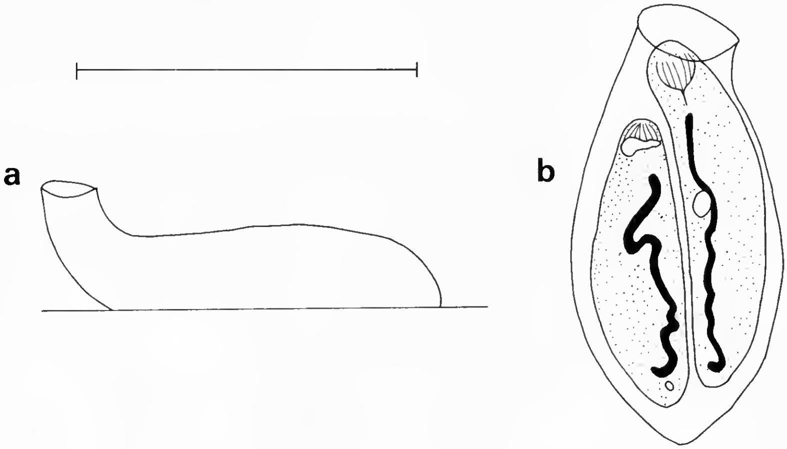

Fig. 11 *Platycola lageniformis*, a. lateral view; b. dorsal view (after Hadzi, 1940).

Platycola mollis de Fromentel, 1874

Vaginicola mollis de Fromentel, 1874.

Diagnosis (Fig. 12). The lorica is colourless to pale yellow, of irregular shape, and about three times longer than it is wide. On one side the neck is a straight continuation of the lorica wall while on the other side, it is sharply constricted. The neck is truncated obliquely by the aperture which faces slightly upwards. The adhesive cement is visible around the lower part of the lorica only. The zooid is short, reaching only as far as the aperture when fully extended. The peristome is wide, with a conspicuous ciliary wreath. The cytoplasm is granular and has one contractile vacuole. In his original description, de Fromentel (1874) describes the pellicle as being 'finely punctate'.

Lorica 100 μm long × 32 μm wide. Aperture 27 μm wide.

Substratum. Submerged plants and algae.

Habitat. Freshwater in Europe.

Remarks. This species is characterised by its short zooid and irregular, though distinctive, shape of its lorica.

Platycola pala Swarczwesky, 1930

Vaginicola pala Swarczewsky, 1930.

Diagnosis (Fig. 13). The lorica is colourless and, when viewed dorsally, oval or nearly oval

Fig. 12 *Platycola mollis* dorsal view, zooid partly contracted (after de Fromentel, 1874).

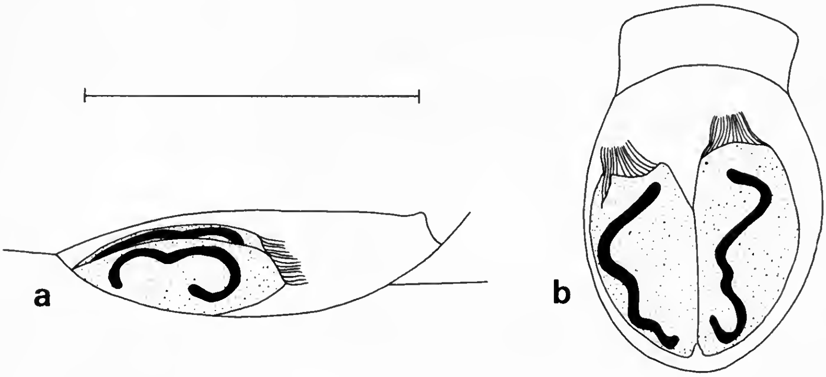

Fig. 13 *Platycola pala*, a. lateral view; b. dorsal view (after Swarczewsky, 1930).

in shape. From the lateral aspect, the convex dorsal wall has a low elevation while the ventral wall lies depressed into its substratum. The neck is a simple continuation of the ventral wall which extends forwards and upwards beyond the dorsal wall to form a platform (Fig. 13a). The macronucleus is long, thin and coiled with its ends turned back.

Lorica 87–97 μm long × 30–70 μm wide. Neck 16 μm long × 50 μm wide at the aperture.

Substratum. Epizooic on *Parapallesa pazill* (Crustacea: Amphipoda).

Habitat. Freshwater in Lake Baikal.

Remarks. This species has been described on a single occasion and no diagram of extended zooids are available. Its most distinctive characters are that it lies depressed in its substrate, and that the neck is formed by the lower wall only.

Platycola steineri Penard, 1914

Vaginicola steineri Penard, 1914.

Diagnosis (Fig. 14). When observed from above, the lorica is slim, elliptical, and slightly rounded at its base. A lateral view shows that the rear half of the lorica is raised and has a trough-like depression running longitudinally down its centre (see Fig. 14a). The neck is short and raised with a well defined aperture, which is elliptical or reniform, and faces upwards. The zooid extends well beyond the aperture when relaxed. The disc is wide, flat and protrudes obliquely above the peristome. The pellicle is finely striated transversely. There is one contractile vacuole situated just below the peristome lip, the macronucleus is straight and lies longitudinally in the zooid.

Lorica 78–88 μm long × 40 μm wide. Zooid 100–118 μm long. Macronucleus 25–29 μm long.

SUBSTRATUM. Moss.

HABITAT. Freshwater in Switzerland.

REMARKS. This species may be most easily identified by its distinctive lorica profile, striated zooid and long, straight macronucleus.

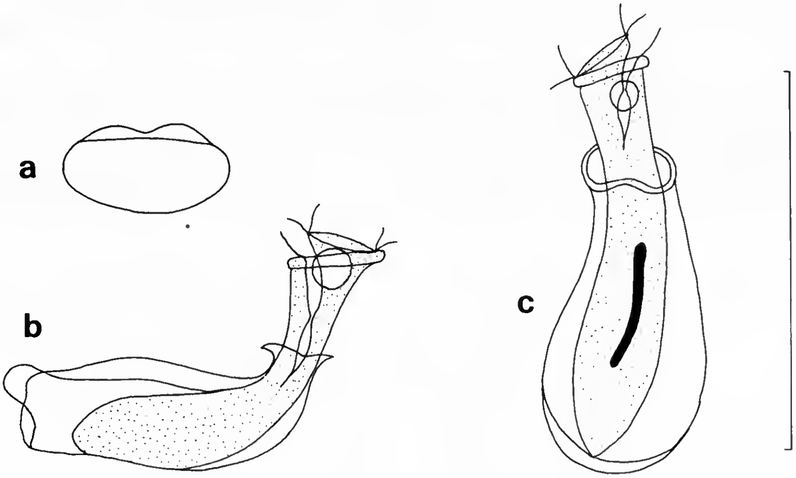

Fig. 14 *Platycola steineri*, a. posterior view of lorica; b. lateral view; c. dorsal view (after Penard, 1914).

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The taxonomy and zoogeography of the genus *Ophiocten* (Echinodermata: Ophiuroidea) in the North Atlantic Ocean

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Introduction

Since the late nineteenth century a large number of samples containing species of the genus *Ophiocten* have been recovered by many expeditions to the North Atlantic Ocean. These were described by various authors under several names. Mortensen (1927), attempting the first revision of the North Atlantic *Ophiocten* species, recognised four species in British waters: *O. sericeum* (Forbes), *O. scutatum* Koehler, *O. latens* Koehler and *O. hastatum* Lyman. Subsequently Mortensen (1933*a*) tried to clarify the confusion surrounding *Ophiocten sericeum* by referring *Ophioglypha signata* Verrill, 1882, *Ophioglypha gracilis* G. O. Sars, 1871, *Ophiocten le danteci* Koehler, 1897, *Ophiocten amitinum* var. *boreale* Hertz, 1927, and *Ophiocten abyssicolum* (Forbes, 1843), to the synonymy of *O. sericeum.* He recognised two varieties of *O. sericeum*, one in the 'warm water' area and one in the 'cold water' area of the North Atlantic Ocean. Semenova, Mileikovsky and Nesis (1964) treated these varieties as subspecies; *Ophiocten sericeum gracilis* (G. O. Sars) from the warm water region and *O. sericeum sericeum* (Forbes), the cold water subspecies.

The Scottish Marine Biological Association's deep sea sampling programme has collected many specimens of *Ophiocten* from bathyal depths on the Wyville Thomson Ridge, within the Rockall Trough and along the continental slope to the south west of Ireland. Close examination of these samples has thrown light on the controversy surrounding the taxonomy of *Ophiocten sericeum.* The present study also examines the affinities between the abyssal *Ophiocten hastatum* Lyman and the other deep water species outside the Atlantic Ocean, and a new abyssal species from the Bay of Biscay is described.

Systematic description

Genus *OPHIOCTEN* Lütken, 1855

Ophiocten: Lütken, 1855 : 97; 1858 : 51–52; Lyman, 1865 : 53; Ljungman, 1865 : 360; 1867 : 307; Lyman, 1882 : 78; Bell, 1892 : 113; Clark, 1915 : 328; Matsumoto, 1915.
Ophiura (pt): Guille, in press.

TYPE SPECIES. *Ophiocten kröyeri* Lütken, 1855, by monotypy, later considered by Ljungman (1865) to be conspecific with *Ophiura sericea* Forbes, 1852 which he referred to *Ophiocten.*

A genus of the subfamily Ophiurinae, family Ophiuridae, with a flat disk covered with small plates amongst which the primary plates are usually distinct; margin of the disk generally

Bull. Br. Mus. nat. Hist. (Zool.) **43** (3) : 109–128 Issued 30 September 1982

sharp; the disk not, or only weakly, indented above the arms; arm combs often continuous over the base of the arms; the jaw with a spiniform or angular apical papilla flanked by oral papillae of which the distalmost ones become blocklike; the adoral plates narrow; the oral shield ranges from being distinctly broader than long to longer than broad, depending on the species; the second oral tentacle pore emerging superficially outside the mouth slit; the genital slits distinct and in some species lined with papillae; lateral arm plates often striated, usually bearing three arm spines; the ventral arm plates separated distally, the distal edge usually convex and the proximal edge flat or angular, being either very obtuse or extended to form a more acute angle; the proximal tentacle pores large and open distally with one or two small tentacle scales on the proximal edge of the pore. This genus is cosmopolitan with species in all oceans.

REMARKS. *Ophiocten* is closely related to the genus *Ophiura* with *Ophiura affinis* occupying an isolated intermediate position between the two genera as shown in Table 1. Certain characteristics of *O. affinis*, such as a well developed arm comb, suggest an affinity with *Ophiura* while others, such as the emergence of the second oral tentacle pore outside the mouth slit, the shape of the tentacle pores and ventral arm plates, suggest affinities with *Ophiocten*.

This intermediate position was first noted by Mortensen (1927, 1933*b*, 1936) who questioned the validity of *Ophiocten*. Clark and Courtman-Stock (1976) also commented on the lack of distinction between these two genera and Guille (in press) considers that the evidence provided by *Ophiura affinis* and *Ophiura affinis simulans* is sufficient to warrant merging *Ophiocten* with *Ophiura*.

Certainly *O. affinis* has features common to both genera, but it appears to be the only such species. No gradation is evident from the literature between species of *Ophiura* such as the type species, *Ophiura ophiura* Linnaeus (formerly *O. texturata* Lamarck) and *Ophiura ljungmani* (Lyman) through *Ophiura affinis* to *Ophiocten*. Rather the two genera appear to be easily distinguished, with *Ophiocten* being well defined. *Ophiura* and *Ophiocten* are compared together with *Ophiura affinis* in Table 1.

Despite the apparently intermediate position of *Ophiura affinis* we consider the characters exhibited by *Ophiocten* justify the generic separation. Table 1 shows that the only characters which relate *Ophiura affinis* to *Ophiura* are the form of the arm combs and the indented

Table 1 Comparison of *Ophiocten*, *Ophiura affinis* and *Ophiura* (characters arranged in decreasing order of importance)

Characters	*Ophiocten*	*Ophiura affinis*	*Ophiura*
Emergence of second oral tentacle pore	Away from mouth slit (fig. 1d)	Away from mouth slit (fig. 1d)	Via a furrow into mouth slit (fig. 1e)
Arm combs	Simple (fig. 1a)	Intermediate (fig. 1b)	Well developed (fig. 1c)
Disk margin above arm bases	Without a notch	With well developed notch	With well developed notch
Shape of the ventral arm plates	Proximal side produced distal side rounded (fig. 1h, i)	Proximal side produced distal side rounded (fig. 1h, i)	Scallop-shaped, irregularly hexagonal but not as *Ophiocten* (fig. 1j, k)
Tentacle pore and scales of the proximal arm segments	Large with only a small tentacle scale (fig. 1f)	Large with only small tentacle scale (fig. 1f)	Large with many, often large, tentacle scales (fig. 1g)

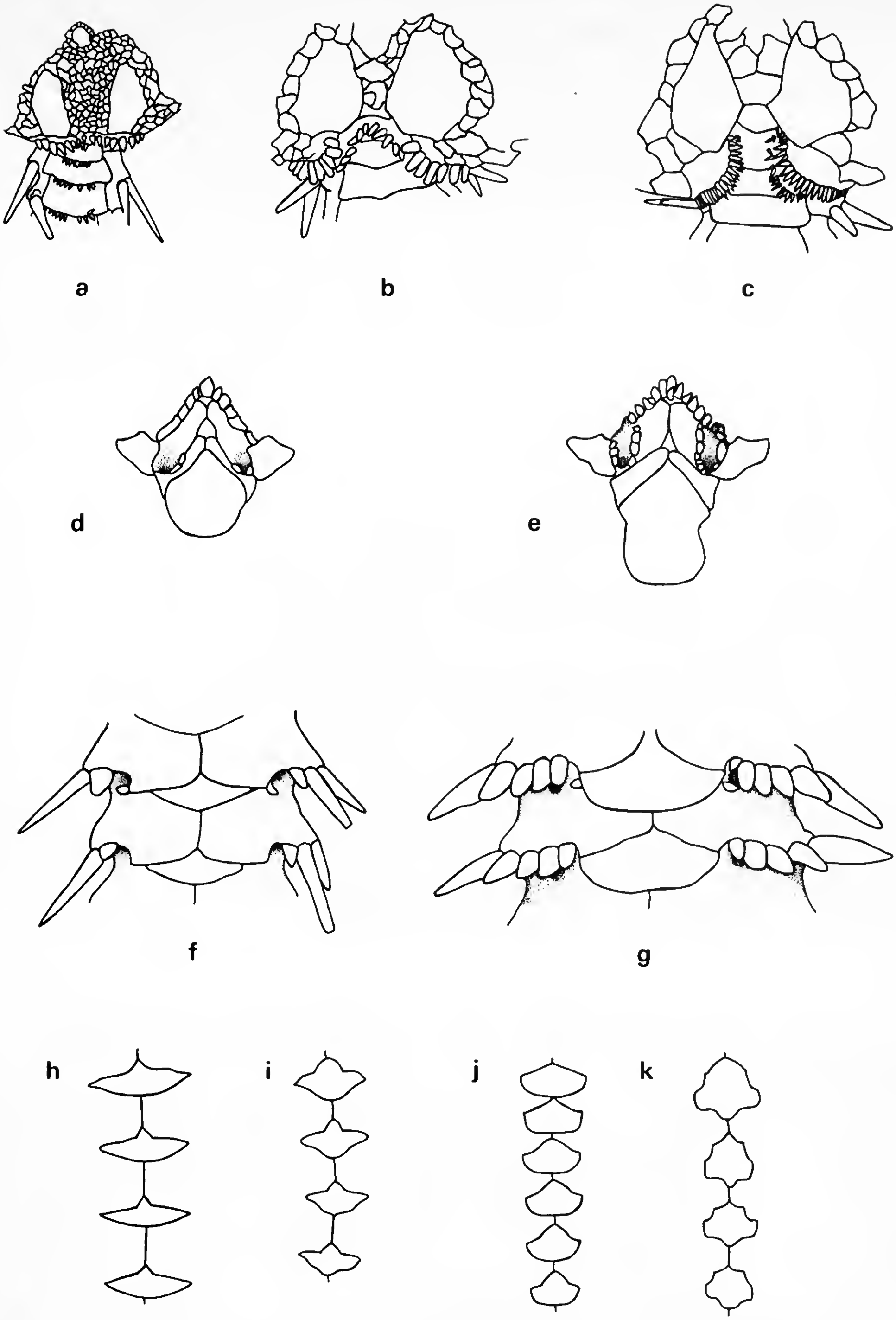


Fig. 1 Diagrams of characters referred to in Table 1. The arm comb of, (a) *Ophiocten sericeum*; (b) *Ophiura affinis*; (c) *Ophiura ophiura*; (d) the jaw shape characteristic of *Ophiocten* and *Ophiura affinis*; (e) the jaw shape characteristic of *Ophiura*; (f) the ventral side of the arm, characteristic of *Ophiocten* and *Ophiura affinis*; (g) the ventral side of the arm characteristic of many *Ophiura* species; (h)–(k) the ventral arm plate arrangement of, (h) *Ophiocten sericeum*; (i) *Ophiocten gracilis*; (j) *Ophiura ophiura*; and (k) *Ophiura ljungmani*. Figures are not drawn to the same scale.

disk, while the other characters indicate a closer affinity with *Ophiocten*. Indeed, Koehler (1897) described some small *Ophiura affinis* as a new species of *Ophiocten*, *O. scutatum*. Possibly *O. affinis* should be referred to a separate genus but this is inadvisable until *Ophiura* itself is revised.

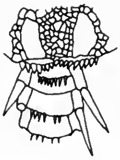
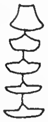
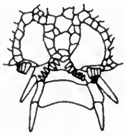
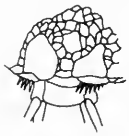
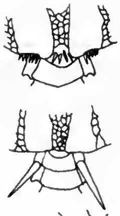
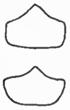
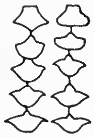
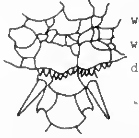
Characters of taxonomic value

a *The oral shield*: the main features of this plate considered are: 1 its overall shape; 2 the length to breadth ratio; 3 the extent of the proximal inner angle. Mortensen (1927) considered the shape of the oral shield to be of great taxonomic value. The identities of *Ophiocten sericeum* and *O. gracilis* (Sars, 1871) were confused by many authors who failed to notice the different shape of this plate in these species.

b *The second and subsequent ventral arm plates*: the important features are: 1 the shape of the plates; 2 whether the proximal angle is obtuse, as in *O. sericeum*, or produced into a point as in *O. gracilis* and *O. abyssicolum* (Forbes, 1843); 3 the distal edge, whether round as in *O. sericeum*, indented as in *O. gracilis* or angular as in *O. abyssicolum*.

c *Occurrence of genital papillae*: the present study indicates that the extent of these spinelets along the genital plates is a useful taxonomic character which was previously unconsidered.

Table 2 Comparison of the five species of *Ophiocten* occurring in the North Atlantic

SPECIES	CHARACTERS				
	Arm comb	Dorsal arm plate	Oral shield	Genital papillae	Ventral arm plate
sericeum		weakly arched slightly convex distal edge		line full length of genital slit	
abyssicolum		strongly arched almost straight distal edge		extend only half way down genital slit	
gracilis		strongly arched slightly convex distal edge		extend only half way down genital slit	
hastatum		may be ridged with convex distal edge		confined to edge of disk or absent	
centobi		weakly arched with convex distal edge		line full length of genital slit	

d *Arm combs*: several features of the arm comb should be considered: 1 whether its spinelets are confined to the disk edge on either side of the arm base or more usually form a continuous fringe over the arms; 2 whether supplementary spinelets are found on the dorsal arm plates; 3 the arm comb spinelets themselves may be characteristic and either thin and needlelike as in *O. gracilis*, or have slightly blunt tips as in *O. abyssicolum*, or they may be short, rounded triangular and toothlike as in *O. sericeum*. In some cases the spinelets may be rubbed off in preservation but their bases can usually be seen. Mortensen (1933a) did not consider arm-comb characters to be of value, particularly in the case of *O. latens* (now *O. hastatum*) where arm-comb spinelets (and also genital papillae) are often absent. However, we consider that these characters have proved useful for separating the individual species.

e *Dorsal arm plates*: in some species these plates may be arched giving the arm a carinate appearance. However, in some specimens this feature is less obvious.

Key to the species of *Ophiocten* (see also Table 2)

1 Oral shield broader than long or square with obtuse proximal angle 2
– Oral shields longer than broad 4

2 Genital papillae absent. Dorsal arm spine very long, up to 2 arm segments long **Ophiocten hastatum** Lyman, 1878 p. 117
– Genital papillae present 3

3 Genital papillae extending along the distal half of the genital slit. Radial shields separated and longer than broad . . . . **Ophiocten gracilis** (G. O. Sars, 1871) p. 115
– Genital papillae extending the full length of the genital slit. Radial shields contiguous and broader than long . . . . **Ophiocten centobi** sp. nov. p. 119

4 Genital papillae extending along the distal half of the genital slit. Ventral arm plates wider than long with a distinctly convex outer edge **Ophiocten abyssicolum** (Forbes, 1843) p. 114
– Genital papillae extending along the entire length of the genital slit. Ventral arm plates much wider than long and widely separated . . . **Ophiocten sericeum** (Forbes, 1852) p. 113

Ophiocten sericeum (Forbes, 1852)
(Fig. 2)

Ophiura sericea Forbes, 1852 : 215.
Ophiocten sericeum: Ljungman, 1867 : 307; Duncan & Sladen, 1881 : 65–66; Bell, 1892 : 113–114 (part); Grieg, 1893 : 9–10 (part); 1900 : 246; 1903 : 26 (part); Michailovskij, 1903 : 492, 531; 1904 : 173; Koehler, 1909 : 166; Mortensen, 1927 : 247 (part); 1932 : 34; 1933 : 96–98 (part); Thorson, 1934 : 4; Djakanov, 1954 : 92; Grainger, 1955 : 910; Semenova, Mileikovsky, Nesis, 1964 (part).
Ophiocten kröyeri Lütken, 1855 : 102; 1858 : 52; 1859 : 28, 52–53; Lyman, 1865 : 53.

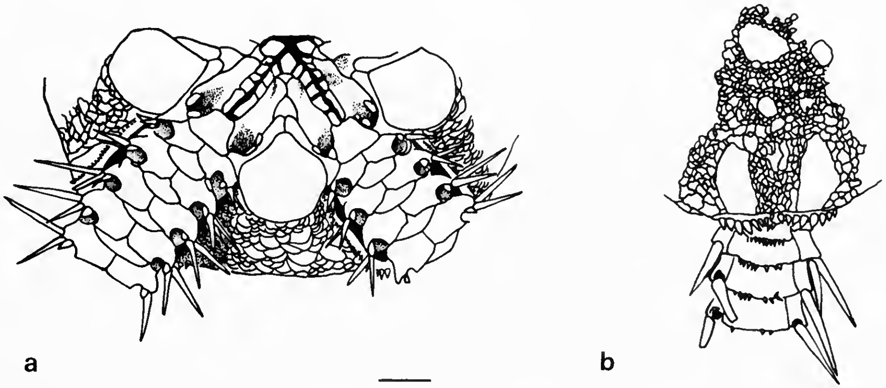


Fig. 2 *Ophiocten sericeum* (Forbes), (a) Ventral; and (b) dorsal views of part of the disk. Bar scale = 1 mm.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 18 mm; dorsal surface of disk with distinct primary plates showing radiating structure; radial shields longer than broad, approximately equal in length to half disk radius, only part of the distal edge reaching the disk edge; arm combs consisting of well developed spines and some massive papillae, extending across the base of the arm.

Dorsal arm plates not strongly arched with only a slightly convex distal edge; up to eight of the proximal dorsal arm plates with their distal edges fringed with papillae (this can be seen in specimens with disk diameter greater than 4 mm); second ventral arm plate flat or with a very slightly convex distal edge; other ventral arm plates much wider than long, separated, with the distal edge gently curved; three arm spines of approximately similar size, although the dorsalmost spine may be longer than the other two; the longest spine is about one arm segment long.

Oral shields always longer than broad, with an acute proximal angle and an almost semicircular distal edge; the apical papilla stout and spinelike or sometimes angular; three or four oral papillae; the proximal ones spinelike the distal becoming blocklike; genital papillae fringing the whole length of the genital slit.

RANGE. This species has its centre of distribution in the shallow high Arctic Ocean but may penetrate the deeper waters of the Norwegian Basin to a depth of about 2000 m. It has been recorded from the Kara Sea, Barents Sea, Spitzbergen, northern Greenland, Davis Strait and Baffin Bay.

REMARKS. Development is planktotrophic (Thorson, 1934). *O. sericeum* is a distinctive species easily recognised by the shape of the oral shield, the extent of the genital papillae, the presence of papillae on the proximal dorsal arm plates and the shape of the arm comb spinelets. This is the cold water form of Grieg (1903), Mortensen (1933a) and Semenova, Mileikovsky and Nesis (1964).

Ophiocten abyssicolum (Forbes, 1843)
(Fig. 3a–c)

Ophiura abyssicola Forbes, 1843 : 146.
Ophiocten abyssicolum: Marenzeller, 1895 : 190; Koehler, 1907 : 269; Cherbonnier, 1958 : 37; Cherbonnier & Guille, 1967 : 322.
Ophiura signata: Kemp, 1905 : 193 (part); Farran, 1913 : 30 (part); Mortensen, 1927 : 245 (part).
Ophiocten sericeum: Mortensen, 1927 : 247 (part); Nobre, 1931 : 92–93.
Ophiocten sericeum: Cherbonnier, 1970 : 344; 1267 (*non O. sericeum* Forbes, 1852).

MATERIAL EXAMINED. See Appendix.

DIAGNOSIS. Disk diameter up to 8 mm; dorsal surface matt when dried with large obvious primary plates each encircled by a ring of small contiguous plates; radial shields small, less than one third disk radius, separated radially by a line of overlapping small plates; the distal edge of the radial shields extending to the disk edge; four or five comb papillae arise at the interradial edge of each radial shield but not forming a continuous comb across the base of the arm, a few small papillae arising on the first or second arm plate giving the impression of an inner arm comb, however, this is not as extensive or well developed as the secondary arm combs found in *Ophiura* species (see Fig. 1).

Dorsal arm plates strongly arched; only the first dorsal arm plate with any spinelets; the ventral arm plates widely separated, the proximal edge with an acute peak in the middle and an angular distal edge (Fig. 3a); the tentacle scale large and triangular; arm spines stubby in appearance and of equal size, just shorter than the corresponding arm segment.

Oral shield longer than broad, equal in length to half disk radius, the proximal angle acute, with parallel sides and a semi-circular distal end; the apical papilla conelike and flanked by three mouth papillae each side, spine-like proximally, broad and block-like distally; genital papillae limited to the distal half of the genital slit.

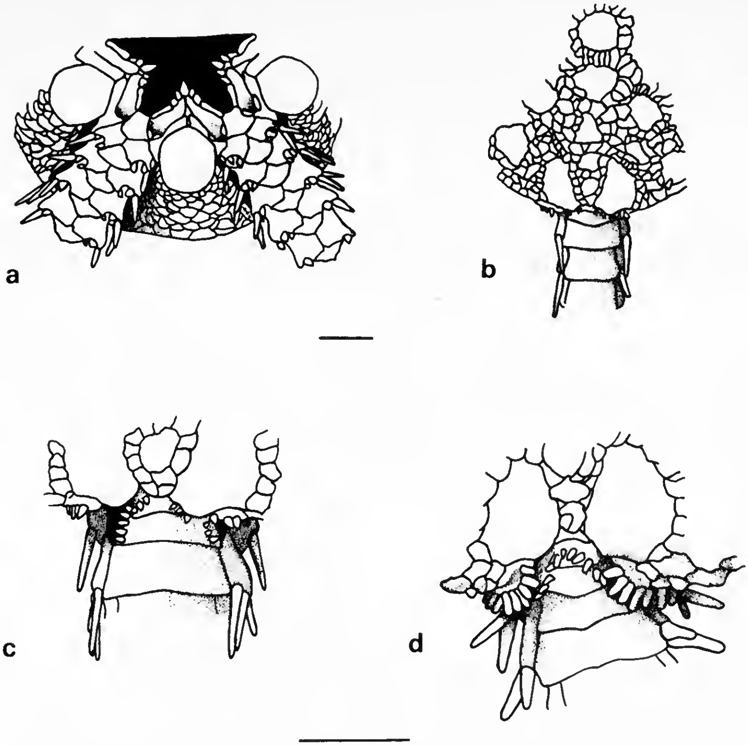


Fig. 3 (a)–(c) *Ophiocten abyssicolum* (Forbes), (a) ventral and (b) dorsal views of part of the disk; (c) an arm base showing the arrangement of the arm comb. The black areas are covered by skin in the specimen (d) *Ophiura affinis*, the arrangement of the arm comb. Bar scales = 1 mm.

RANGE. This species is found from the Mediterranean as far north as S.W. Ireland. It is found at depths below 100 m in the Mediterranean, 300–500 m in the Bay of Biscay and between 300–1000 m off S.W. Ireland.

REMARKS. The form of the papillae on the dorsal arm plates may suggest an affinity with *Ophiura affinis* but there are a number of differences. Firstly the form of the genital plate is different, being well developed and widest in the dorso-ventral plane on each side of the arm in *Ophiura affinis*, while in *Ophiocten abyssicolum* (and *Ophiocten* in general) it is thin and compressed laterally, being widest at the edge of the disk. Secondly, there is a distinct notch in *Ophiura affinis* which is absent in *Ophiocten abyssicolum.*

Kemp (1905) confused this species and *Ophiocten gracilis* and considered both as variations of one species which he thought was Verrill's *Ophiura signata.* The specimens from the *Helga* (Kemp, 1905, Plate 35, Fig. 6) are in fact *O. abyssicolum.*

Ophiocten gracilis (G. O. Sars, 1871)
(Fig. 4)

Ophioglypha gracilis G. O. Sars, 1871 : 18.
Ophioglypha signata Verrill, 1882 : 220; Hoyle, 1884 : 718.
Ophiocten pattersoni Lyman, 1883 : 244.
Ophiocten sericeum: Hoyle, 1884 : 718 (part); Bell, 1892 : 113–114 (part); Grieg, 1893 : 9–10; 1903 : 26 (part); Mortensen, 1927 : 247 (part).
Ophiocten le danteci Koehler, 1896 : 72.
Ophiura signata: Kemp, 1905 : 193 (part); Farran, 1913 : 30 (part).
Ophiocten hastatum: Koehler, 1914 : 37; Schoener, 1971 : 153–160; (*non O. hastatum* Lyman, 1878).
Ophiocten amitinum var. *boreale* Hertz, 1927*a* : 64.

Ophiocten sericeum var. *gracilis* Mortensen, 1933*a* : 98.
Ophiocten sericeum gracilis Semenova, Mileikovsky & Nesis, 1964.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 12 mm; dorsal surface matt when dried with obvious primary plates; radial shields less than half disk radius, extending to the edge of the disk; arm comb moderately well developed but spinelets more slender than in *O. sericeum* (Fig. 4b, d); first dorsal arm plate with spinelets, other proximal plates rarely if ever with spinelets on the distal edge.

Dorsal arm plates usually strongly ridged; second ventral arm plate longer than broad with an acute proximal angle and a very convex distal edge; distal arm plates with a convex distal edge and lateral indentations; arm spines of similar length, nearly one arm segment long proximally, in some cases the dorsal spine is longer than the other two.

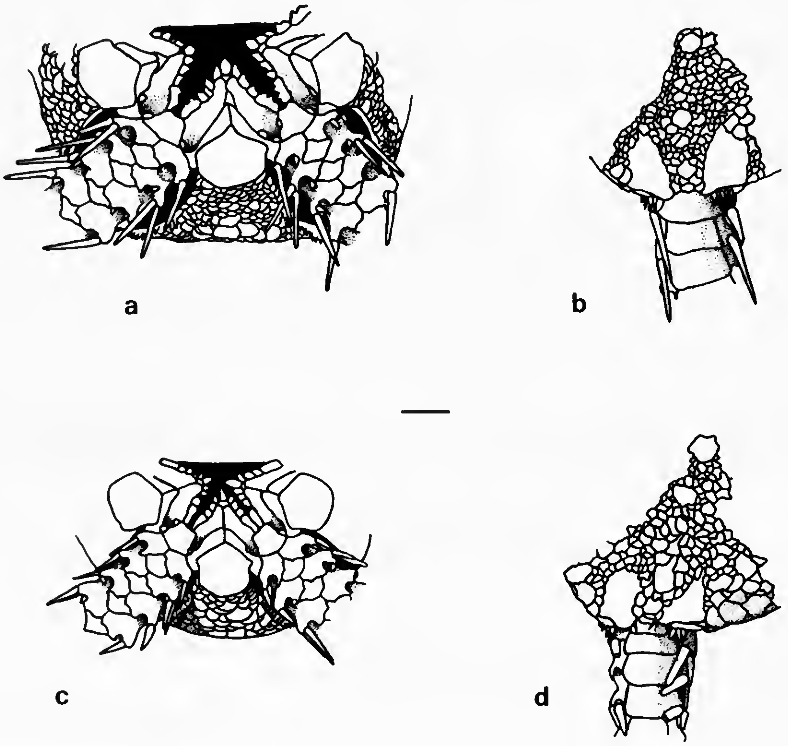


Fig. 4 *Ophiocten gracilis* (G. O. Sars), (a) ventral and (b) dorsal views of part of the disk of a specimen from the Rockall Trough; (c) ventral and (d) dorsal views of part of the disk of a specimen from *Albatross* Stn. 2582, off Rhode I. Bar scale = 1 mm.

Oral shields broader than long or almost square, the proximal angle being very obtuse, often with lateral projections giving the shield a squat, arrow-shape, the distal edge gently convex; the apical papilla stout with three to four oral papillae each side, which become blocklike distally; often the distal papillae with secondary points; genital papillae only extend along the distal half (i.e. from the arm combs towards the oral shield) of the genital slit.

RANGE. This is an upper bathyal species with a vertical distribution of 600–1200 m, found within the Rockall Trough from the southern slope of the Wyville Thomson Ridge and as far south as western Ireland, and off the eastern seaboard of North America. *O. gracilis* has also been recorded by the *Ingolf* (see Appendix) from the Norwegian Sea north of Iceland from depths of 106–1909 m. Whether its occurrence in these waters represents part of its range, or is a result of settlement of larvae accidentally brought into the Norwegian Sea by surface currents from neighbouring populations, has yet to be determined. It is highly probable that *Ophiopluteus ramosus* Mortensen, 1898 is the larva of this species (Semenova, Mileikovsky & Nesis, 1964). Postlarvae of this species have been identified in samples taken in the summer months at depths to 2925 m in the Rockall Trough. They do not appear to survive into the following winter at these depths (Gage & Tyler, 1981).

REMARKS. The true identity of this species has been subject to considerable confusion. G. O. Sars (1871) described it as an *Ophioglypha*, a synonym of *Ophiura*, but subsequently Lyman (1878) and then Grieg (1893), assigned it to *Ophiocten*. However Grieg synonymized *O. gracilis* with *Ophiocten sericeum*, since he doubted the importance of the arm combs as specific characters. In taking this action, he overlooked the different shape of the oral shield. Later Grieg (1903) recognised two forms of *Ophiocten sericeum*, a warm water form, the *Ophiocten gracilis* of this study, and a more robust cold water form, *O. sericeum*, but he did not name them. Mortensen (1933*a*) also recognised these two varieties and Semenova, Mileikovsky & Nesis (1964) proposed that they should be considered as subspecies.

On the Atlantic seaboard of North America the situation was equally confused. Verrill (1882) described *Ophioglypha signata* and Lyman (1883) *Ophiocten pattersoni* both from specimens now considered to be conspecific with *Ophiocten gracilis* (Sars). Koehler (1914) perhaps not realising the existence of these previous names, erroneously identified his specimens as *Ophiocten hastatum*. In fact, there are no published records of *Ophiocten hastatum* Lyman (sensu stricto) occurring in the western basin of the Atlantic.

Several authors, including Hoyle (1884), Kemp (1905) and Farran (1913), studying specimens from S.W. Ireland, overlooked the existence and priority of *O. gracilis* and named their specimens *Ophiura signata* using Verrill's name.

Mortensen (1927, 1933*a*) synonymized all of these names with *Ophiocten sericeum* although as stated previously he recognised two varieties of *O. sericeum*.

Ophiocten gracilis differs from *O. sericeum* in the shape and dimensions of the oral shield, the extent of the genital papillae lining the genital slit and the form of the arm comb spinelets.

Ophiocten hastatum Lyman, 1878

(Fig. 5)

Ophiocten hastatum Lyman, 1878 : 103; 1882 : 82; Koehler, 1898 : 42–44; 1909 : 165.
Ophiocten longispinum Koehler, 1896*a* : 204–205; 1896*b* : 243.
Ophiocten sericeum: Hoyle, 1884 : 718 (part); Bell, 1892 : 113–114 (part) (*non O. sericeum* (Forbes, 1852)).
Ophiocten pacificum Lütken & Mortensen, 1899 : 131; H. L. Clark, 1911 : 96–97; H. L. Clark, 1923 : 364; Hertz, 1927*b* : 11–12; Jumars, 1976 : 244.
Ophiocten latens Koehler, 1906 : 13; 1907 : 267; 1921 : 5; Grieg, 1921 : 33; 1932 : 33; Mortensen, 1927 : 246; 1932 : 35; 1933*a* : 98–99; 1933*b* : 392–393; Cherbonnier & Sibuet, 1972 : 1384; A. M. Clark & Courtman-Stock, 1976 : 189.
Ophiura hastata Guille, in press.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 12 mm; dorsal surface matt when dried with indistinct primary plates showing a 'mottled' centre and radiating striations; secondary plates small and overlapping; radial shields approximately half disk radius with their distal edges reaching the disk edge, the two shields of each pair separated radially by at least three secondary plates; arm combs reduced, sometimes absent altogether.

Dorsal arm plates sometimes strongly arched with convex distal edge, distal edge not lined by papillae; second ventral arm plate broader than long, in some specimens contiguous with

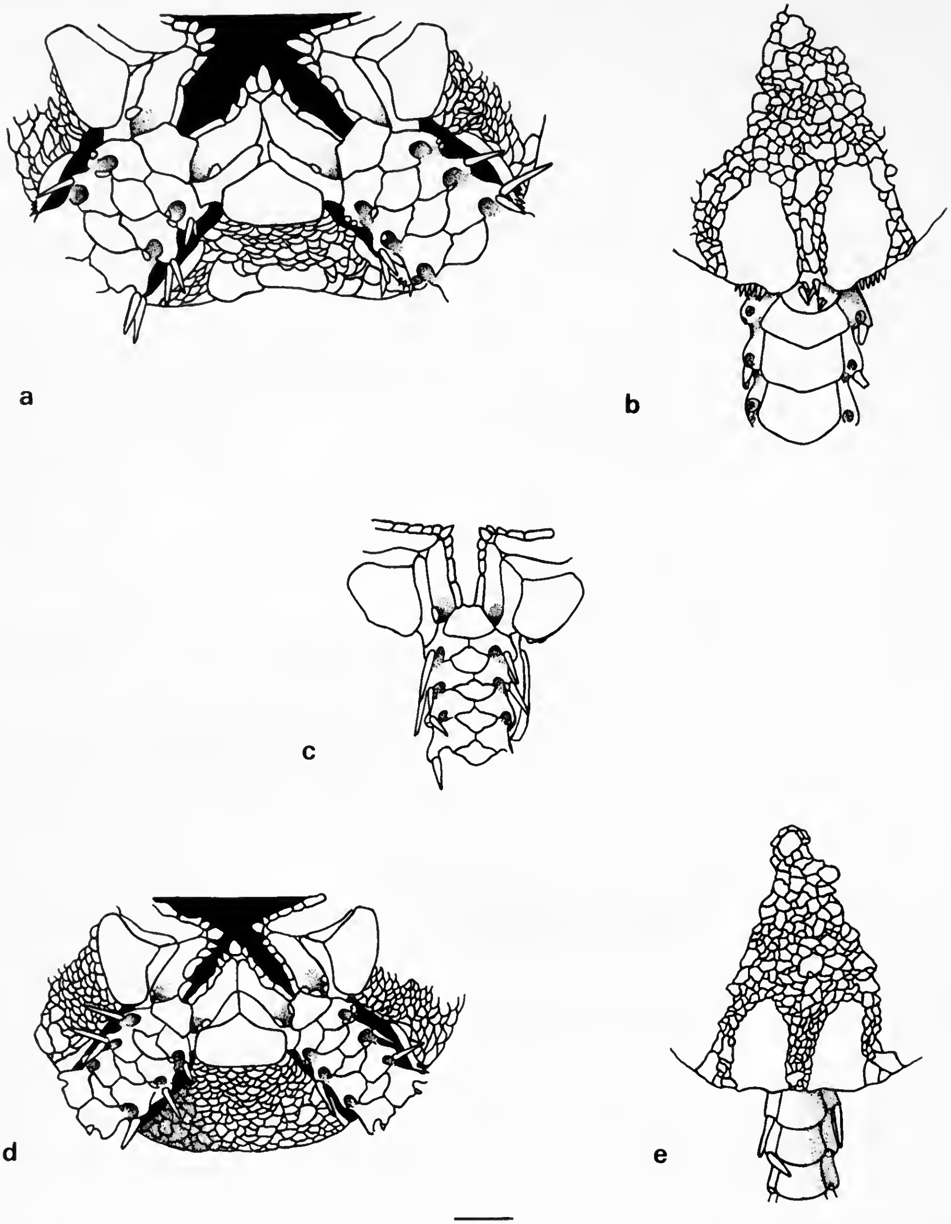


Fig. 5 *Ophiocten hastatum* Lyman, (a) ventral and (b) dorsal views of part of the disk of one of the paratypes; (c) ventral view of part of the disk of the syntype of *Ophiocten pacificum* Lütken & Mtsn.; (d) ventral and (e) dorsal view of part of the disk of a specimen from the Bay of Biscay. Bar scale = 1 mm.

the third ventral armplate; subsequent ventral armplates separated, with an obtuse proximal angle and a rounded distal edge; three arm spines, the dorsal spine twice the length of the lower spine and up to 1–1·5 arm segments long.

Oral shields considerably broader than long with a flat or slightly convex distal edge, sometimes with small lateral projections as in *O. gracilis* giving a squat arrow-shaped appearance; apical papilla stout with two pointed and distally two blocklike oral papillae on each side;

genital papillae absent (except in a few cases when they are confined to the distal edge of the genital plate).

RANGE. This species is found between 1130–4700 m. It appears to be cosmopolitan, being recorded from the Eastern Atlantic, off southern Africa, Kerguelen and Prince Edward Island in the Southern Ocean, in the east Pacific off southern California and Panama and in the west Pacific off Japan.

REMARKS. A comparison of the type specimens of *Ophiocten hastatum* and *O. latens* using the characters mentioned above has not revealed any significant specific differences between them and we conclude that they are conspecific. The differences that do exist, such as the extent of the arm comb and the length of the arm spines, once thought to separate them, are now considered to be intraspecific variations.

Although Mortensen (1933*b*) refuted H. L. Clark's (1923) suggestion that *O. pacificum* was present off southern Africa, an examination of one of the syntypes (Albatross Stn. 3393, 1836 m E. Pacific) together with the description given by Lütken and Mortensen (1899) confirms that *O. pacificum* is conspecific with *O. hastatum*. The disk of the syntype of *O. pacificum* in the BM(NH) is badly damaged but the other features are consistent with those of *O. hastatum*.

Ophiocten australis Baker, 1979, from off southern Tasmania, 800–1772 m, may also be conspecific with *O. hastatum*. Certainly the figures and description resemble Atlantic specimens of *O. hastatum*.

Ophiocten centobi sp. nov.
(Figs. 6, 7)

The holotype has a disk diameter of 4·5 mm, the two paratypes 4 mm and 3·5 mm respectively. The disk is round with very large, conspicuous centrodorsal and primary plates which are nearly contiguous but are separated from one another by a ring of much smaller plates. The radial shields are small, nearly twice as broad as long and contiguous for most of their length. The arm comb forms a continuous fringe over the arm base and is comprised of stout, pointed papillae. The ventral interradial areas are covered with large plates.

The dorsal arm plates are not strongly arched. They are contiguous, fan shaped with a convex distal edge. None of the dorsal arm plates carry spinelets on their distal edge. The ventral arm plates are widely separated. The distal edge of the plate is rounded while the proximal angle is acute. The tentacle pores are of the typical *Ophiocten* kind (see Fig. 1f). The proximal pores have two, sometimes three tentacle scales, the distal ones, two then one tentacle scale. There are 3 long pointed arm spines of which the dorsalmost is usually the longest.

There is one pointed apical papilla at the apex of the jaw flanked on either side by 3 to 4 oral papillae. The proximal oral papillae are pointed but the distalmost one is blocklike. The adoral shields are long and thin. The oral shield is as broad as or broader than long with an acute proximal angle and a convex distal edge. In some cases the oral shield may be quite rounded while in others there is a suggestion of small lateral projections. The genital slits are conspicuous and are lined along their entire length by stout, pointed papillae.

DERIVATION OF NAME. The specific name is derived from the initials of the Centre National de Tri d'Oceanographie Biologique (CENTOB).

TYPE LOCALITY. *Cymor* drague 15 : 47°44′ N : 8°21′ W. Bay of Biscay. 2420 m.

The holotype is deposited in the Museum National d'Histoire Naturelle, Paris, one paratype is deposited in the British Museum (Natural History), London, the other in the Centre Oceanologique de Bretagne at Brest.

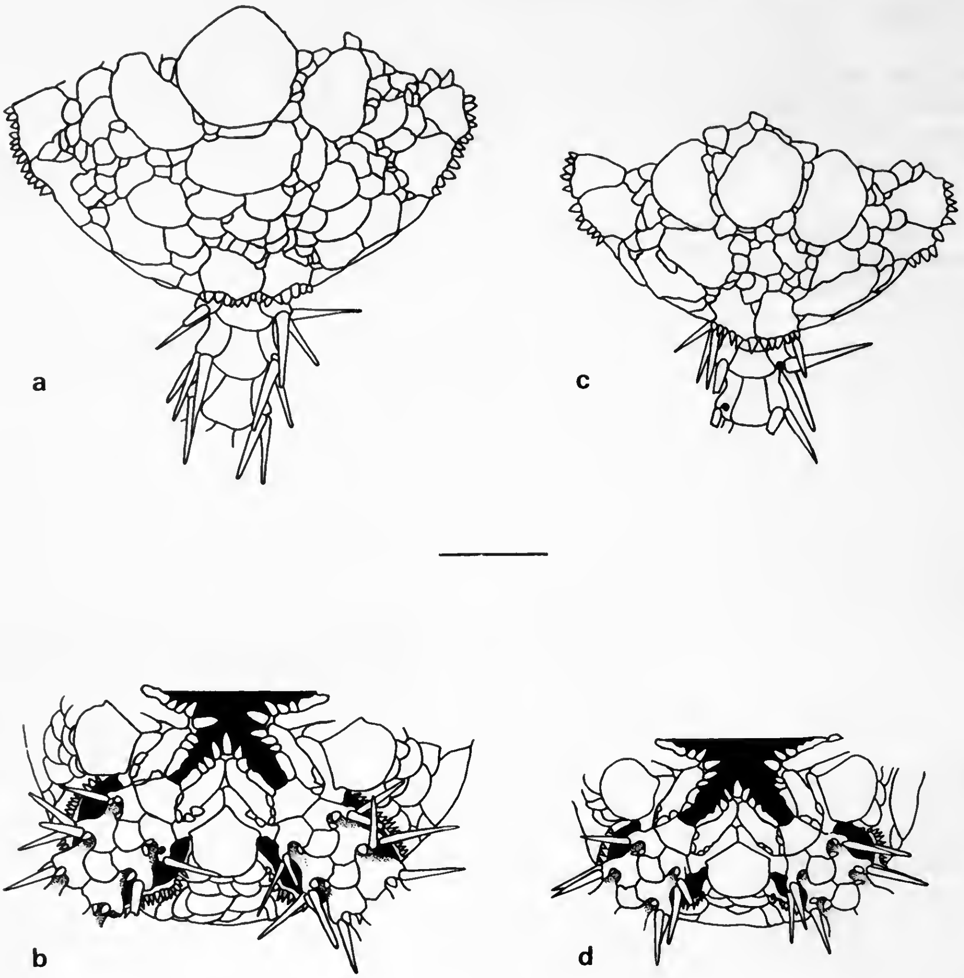


Fig. 6 *Ophiocten centobi* sp. nov., (a) dorsal and (b) ventral view of part of the disk of the holotype; (c) dorsal and (d) ventral view of part of the disk of a paratype. Bar scale = 1 mm.

REMARKS. As shown in Table 2, the scaling of the disk, the form of the arm combs, the contiguous radial shields and the extent and composition of the genital papillae differentiate *Ophiocten centobi* from the other N. Atlantic species. A large conspicuous primary rosette is also found in the Antarctic species *Ophiocten ultimum* Hertz, 1927, *O. carinatum* Hertz, 1927, *Ophiocten megaloplax* Koehler, 1901 and *Ophiocten banzarei* Madsen, 1967. *O. centobi* differs from the first two in the form of the radial shields which are broader than long while in *O. ultimum* and *O. carinatum* they are larger and longer than broad. *O. megaloplax*, and also *O. carinatum*, differ mainly because they lack genital papillae on the genital slit. The lack of an arm comb and the presence of four arm spines differentiates *O. banzarei* from *O. centobi*.

None of the characters, particularly the large primary rosette, are merely due to the small size of the specimens. Similar sized specimens of *O. gracilis*, *O. abyssicolum* and *O. hastatum* all show recognisable adult features and the primary rosette is very much smaller.

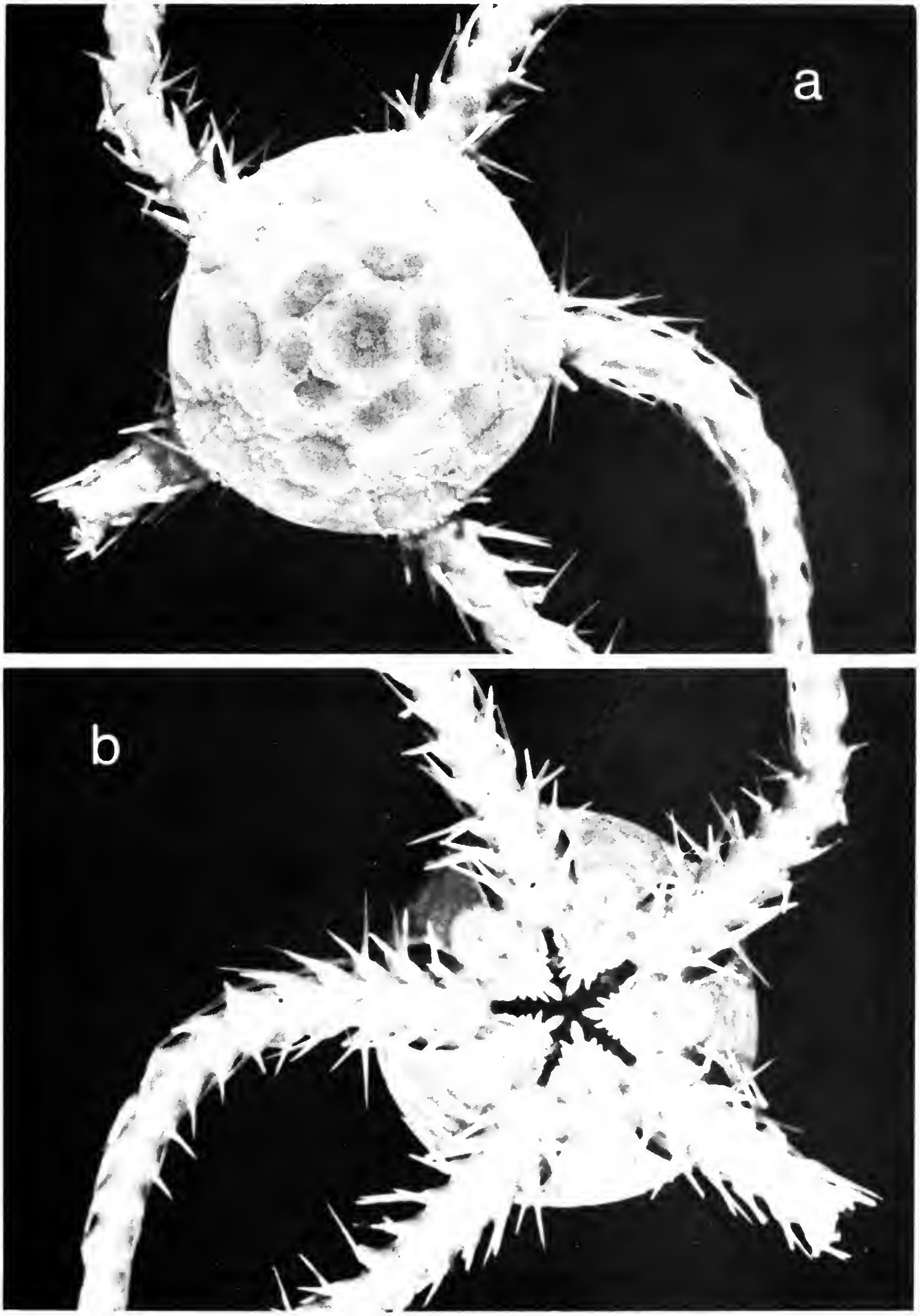


Fig. 7 *Ophiocten centobi* sp. nov., (a) dorsal and (b) ventral view of the holotype.

Discussion

To summarise our taxonomic conclusions, five species are recognised: *Ophiocten sericeum* (Forbes), which is restricted to Arctic Seas; *O. gracilis* (Sars), a boreal species found off Ireland, the Rockall Trough, S. Iceland, south Greenland and off eastern N. America (previously described under a variety of names and often confused with *O. sericeum*, see page 117); *O. abyssicolum* (Forbes), recorded from the Mediterranean as far north as south west Ireland; *O. hastatum* Lyman, an abyssal species (which we consider to be conspecific with *O. latens* Koehler and *O. pacificum* Lütken and Mortensen); and *O. centobi*, a new abyssal species from the Bay of Biscay. *O. scutatum* Koehler, 1896, is considered conspecific with *Ophiura affinis*.

The type species of *Ophiocten*, *O. sericeum* is a shallow or bathyal Arctic species found to a depth of 2000 m. This species was originally thought to occur commonly to the south of the Wyville Thomson Ridge in progressively deeper water and also in the Mediterranean (Mortensen, 1933*a*). Though the pelagic larvae of *O. sericeum* could be carried south, Mileikovsky (1971) has shown that this is unlikely because the larvae of Arctic ophiuroids are not dispersed far from their breeding grounds. The supposed Mediterranean population has been shown by Cherbonnier (1958) to be *Ophiocten abyssicolum* (Forbes, 1843).

We believe that those specimens found at intermediate depths along the slope to the west of the British Isles, and originally described as *Ophiocten sericeum* or *Ophiura signata*, are *Ophiocten gracilis* and *Ophiocten abyssicolum*. These two species are distinguished by the shapes of the mouth shield, the ventral arm plates and the arm comb arrangement. *Ophiocten gracilis* has a wide distribution on the upper slope of the N. Atlantic from western Scotland round the Faroes, Iceland-Greenland Ridge down to the eastern United States. On the slope southwards from western Scotland *O. gracilis* is replaced by *Ophiocten abyssicolum* which extends along the western European slope to the Straits of Gibralter and the Mediterranean. The distribution of these two species clarifies the confusion over the identity of the *Ophiocten* species found on the slope to the west of the British Isles described by Kemp (1905). In water greater than 2000 m deep, the species found are: *Ophiocten hastatum* (recorded as *O. latens*), which is easily distinguishable from the other species by the very broad mouth shield, and the long upper arm spine, the reduced arm comb and extent of the genital papillae, and *Ophiocten centobi*.

The distribution of the five species within the North Atlantic is closely related to the hydrography of the main water masses.

The water masses of the N.E. Atlantic have been described by Cooper (1952) and Ellett and Martin (1973), and the northward modification of the intermediate water originating from the Mediterranean outflow has been discussed in detail by Pingree & Morrison (1973) and Reid (1979). We believe that *O. sericeum* is indicative of cold Norwegian Sea Deep Water and, as this species has a pelagic larva, it may occasionally cross the Scotland-Greenland ridges in the Norwegian Sea overflow to live as a 'guest' population (*sensu* Madsen, 1961) around the northern fringes of the North Atlantic where the incoming water is least modified. *O. abyssicolum* is found as far north as S.W. Ireland on the eastern Atlantic slopes in association with the salinity maximum due to Gibralter water (Cooper, 1952; Cooper, Jones & Lee, 1962). Further north, off western Scotland, where the intermediate salinity maximum is not evident and Gibraltar influence can only be traced by lower oxygen content (Ellett & Martin, 1973), *O. gracilis* is found. Finally, *O. hastatum* and *O. centobi* are found in the colder deep waters (Labrador Sea water and Northeast Atlantic Deep water in the European Basin; Ellett & Martin, 1973) beneath the Gibralter water layers.

These conclusions on the taxonomy and zoogeography of the different North Atlantic species of *Ophiocten*, especially in relation to the water mass distribution, help to clarify the confusion found in previous accounts.

Acknowledgements

A study of this type is not possible without the help of many colleagues and we would like to thank especially: Miss A. M. Clark, B.M.(N.H.) for helpful suggestions and critically reading this manuscript; Professeur A. Guille, (MNHN, Paris) for loaning us material and for giving us a copy of his forthcoming paper; Miss M. E. Downey (USNM), Mr J. M. C. Holmes (Dublin Museum), Dr F. J. Madsen (Zoologisk Museum, Copenhagen); Dr A. L. Rice (IOS); Monsieur M. Segonzac and Dr M. Sibuet, Biogas specimens, Dr L. Pastouret, *Cymor* specimens, (CENTOB); Professor E. Tortonese, Genoa; The Director (The Zoology Museum, Bergen) and Professor R. M. Woolacott (MCZ) for providing material from their collections. Mr D. Ellett (SMBA) kindly provided stimulating discussion on the hydrography of the N.E. Atlantic.

We also wish to thank Professor F. T. Banner for facilities in the Department of Ocenaography and the Master, Officers and Crew of R.R.S. *Challenger* for their co-operation and friendly interest at sea. This study was completed during the tenure of NERC Grant GR3/4131 to P.A.T., which is gratefully acknowledged.

Appendix

Samples examined:

(i) *Ingolf* specimens from the Zoologisk Museum, Copenhagen identified by Mortensen (1933*a*) as *Ophiocten sericeum.*

	Locality		*Depth*	*Our identification*
Stn 100	66° 23′ N	14° 12′ W	111 m	*Ophiocten gracilis*
Stn 124	67° 40′ N	15° 40′ W	932 m	*Ophiocten gracilis*
Stn 104	66° 23′ N	7° 25′ W	1802 m	*Ophiocten gracilis*
Stn 118	68° 27′ N	8° 20′ W	1996 m	*Ophiocten gracilis*
Stn 138	63° 26′ N	7° 56′ W	887 m	*Ophiocten gracilis*
Stn 103	66° 23′ N	8° 52′ W	1090 m	*Ophiocten gracilis*
Stn 27	64° 51′ N	55° 10′ W	740 m	*Ophiocten gracilis*
Stn 120	67° 29′ N	11° 32′ W	1666 m	*Ophiocten gracilis*
Stn 5	64° 40′ N	12° 09′ W	279 m	*Ophiocten gracilis*
Stn 4	64° 07′ N	11° 12′ W	446 m	*Ophiocten gracilis*

(ii) *Albatross* specimens from the United States National Museum, Washington, cited by Koehler (1914) as *O. hastatum.*

Stn 2415	30° 44′ N	79° 26′ W	900 m	*O. gracilis*
Stn 2429	45° 55′ 30″ N	50° 51′ W	857 m	*O. gracilis*
Stn 2542	40° 00′ 15″ N	20° 42′ 20″ W	235 m	*O. gracilis*
Stn 2582–3	39° 50′ N	71° 43′ W	249 m	*O. gracilis*

(iii) *Blake* specimen from the Museum of Comparative Zoology, Harvard, identified by Lyman 1883 as *Ophiocten pattersoni.*

Stn 344	40° 1′ N	70° 58′ W	HOLOTYPE	*O. gracilis*

(iv) Specimens from the Museum National d'Histoire Naturelle, Paris

(a) identified as *Ophiocten latens*

Travailleur et *Talisman* 1883

Stn 134	42° 19′ N	23° 26′ W	4060 m	SYNTYPES	*O. hastatum*

(b) identified as *Ophiocten hastatum*

Marion Island (Antarctique)	Southern Ocean	*O. hastatum*

(v) Specimens from the 'Biogas' and 'Polygas' Investigations (Centre Oceanologique de Bretagne, Brest) in the Bay of Biscay.

ES = epibenthic sledge samples, T = Trawl samples

Stn 1 ES 47° 30′ – 47° 39′ N : 8° 30′ – 8° 46′ W
2100 m (average) ES 340 specimens *O. hastatum*

Stn 2	ES 47° 25′ – 47° 36′ N : 9° 00′ – 9°15′ W		
	3000 m (average)	ES 124 specimens	*O. hastatum*
	ES 47° 25′ – 47° 36′ N : 9°00′ – 9° 15′ W		
	3000 m (average)	T 57 specimens	*O. hastatum*
Stn 3	47° 30′ – 47° 40′ N : 9° 28′ – 9° 44′ N		
	4200 (average)	ES 37 specimens	*O. hastatum*
Stn 5	44° 20′ – 44° 32′ N : 4° 45′ – 4° 56′ W		
	4500 m (average)	ES 578 specimens T 295 specimens	*O. hastatum*
Stn 6	44° 03′ – 44° 12′ N : 4° 10′ – 4° 23′ N		
	2000 m (average)	ES 16 specimens T 53 specimens	*O. hastatum*

(vi) Specimens from *Discovery* Investigations, Institute of Oceanographic Sciences.

Stn 8511	1	41° 55′ N : 11° 15′ W	2399–2384 m	*O. hastatum*
8512	4	42° 15′ N : 11° 36′ W	2281–2465 m	*O. hastatum*

(vii) Specimens from the British Museum (Natural History).

(a) *Challenger* specimens identified as *Ophiocten hastatum* by Lyman (1878–1882).

Stn 146	40° 46′ S : 45° 31′ E	2515 m	
	Holotype and Paratypes		1882.12.23.352
Stn 146	40° 46′ S : 45° 31′ E	2515 m	
	7 specimens		1956.10.2.21.24
Stn 78	37° 34′ N : 25° 13′ W	1829 m	
	1 specimen		1882.12.23.351
Stn 168	40° 28′ S : 177° 43′ E	2012 m	
	3 specimens		1882.12.23.220
Stn 168	40° 28′ S : 177° 43′ E	2012 m	
	3 specimens		1956.10.2.16–17

(b) Specimens originally identified as *Ophiura signata.*

Oxford University Expedition. Spitzbergen.			
	4 specimens	1923.7.6.12–14	*O. sericeum*
J. M. Wordie. Baffin Island, Eglington Fjord.			
	2 specimens	1935.10.19.1	*O. sericeum*
Oxford University Ellesmere I. Expedition. Faylte Fjord, Greenland			
	5–21 specimens	1936.5.26.4	*O. sericeum*
Rosaura. Stn 1 65° 35′ N : 37° 20′ W 25–50 m			
	6 specimens	1949.1.19.80	*O. sericeum*
William E. Ripley. 71° 34′ N : 150° 22′ W			
		1955.6.23.14	*O. sericeum*
Ernest Holt. 70° 20′ N : 33° 32′ E 165 m			
	20 specimens	1969.6.12.246–255	*O. sericeum*
Spitzbergen. 60–64 m			
	1 specimen	1969.8.25.33	*O. sericeum*
Porcupine. Stn. 47 59° 34′ N ; 7° 18′ W 975·6 m			
		1908.2.19.28–34	*O. gracilis*
Procupine. Stn 88. 59° 26′ N : 8° 23′ W 1057 m			
		1890.2.19.147.160	*O. gracilis*
Porcupine. Stn 77. 60° 34′ N : 4° 40′ W 1124 m			
	12 specimens	1890.2.19.191–195	*O. gracilis*
Thomson Collection. Lofoten Island 18–30 m			
	2 specimens	1890.2.20.202	*O. gracilis*
Triton. Wyville Thomson Ridge 829 m			
	15 specimens	1925.10.30.21.31	*O. gracilis*
Triton. West of Wyville Thomson Ridge 513–779 m			
	16 specimens	1925.10.30.52–59	*O. gracilis*
Porcupine. Stn 23a 56° 13′ N : 14° 18′ W 768 m			
	2 specimens	1890.2.19.25	*O. gracilis*

Knight Errant. N. of N. Rona 972 m
6 specimens 1925.10.30.177–179 *O. gracilis*
Manahine. Stn 5 S.W. Ireland 720–819 m
20 specimens 1950.8.14.20.26 *O. gracilis*
Irish Fisheries. Stn SR 1173 m
5 specimens 1914.1.30.62–63 *O. gracilis*
Norman Collection. Off Martha's Vineyard N.E. America 140 m
2 specimens 1910.2.1.197–198 *O. gracilis*
Norman Collection. Faeroe Channel 838 m
8 specimens 1910.2.1.214–217 *O. gracilis*
Norman Collection. Off Cleggin Head, Ireland
5 specimens 1910.2.1.2.18 *O. abyssicolum*
Irish Dept. Agriculture. Off Kerry 606 m
10 specimens 1904.1.2.4.2–6 *O. abyssicolum*
E. W. L. Holb. 52° 2′ N : 12° 8′ W 817 m
7 specimens 1914.6.12.11.14 *O. abyssicolum*

(c) Other material examined

Greenland. 1 specimen 1858.9.10.18 *O. sericeum*
Spitzbergen. 90 m
2 specimens 1868.6.19.25 *O. sericeum*
Arctic Expedition 1875. Winter Quarters 20 m
1 specimen 1880.10.1.27 *O. sericeum*
Franz Joseph Land.
1 specimen 1880.11.2.17 *O. sericeum*
Kara Sera (Kara Haven).
1 specimen 1890.1.9.6–9 *O. sericeum*
Norman Collection. Greenland.
2 specimens 1914.6.12.19–22 *O. sericeum*
Porcupine. Stn 37 48° 38′ N : 12° 8 W 4563 m
4 specimens 1890.2.19.92 *O. hastatum*
Albatross. Stn 3393 1836 m
Syntype of *O. pacificum* 1901.4.9.48 *O. hastatum*
Discovery. Investigations Stn 7711/57 54° 48′ N : 20° 03′ W
2658–2656 m. 1976.7.30.122–130 *O. hastatum*

(viii) Specimens from sampling undertaken by the Scottish Marine Biological Association, mainly from R.R.S. *Challenger.*

ES = Epibenthic sledge; SBC = spade box corer; AT = Agassiz Trawl.

ES 10	56° 37′ N : 11° 04′ W	2540 m	43 486 specimens	*O. gracilis*
ES 18	56° 44′ N : 09° 20′ W	1392 m	4441 specimens	*O. gracilis*
ES 20	56° 46′ N : 09° 17′ W	1271 m	7465 specimens	*O. gracilis*
ES 22	56° 41′ N : 09° 22′ W	1028 m	6761 specimens	*O. gracilis*
ES 23	56° 37′ N : 09° 10′ W	704 m	5665 specimens	*O. gracilis*
ES 27	54° 40′ N : 12° 16′ W	2880 m	3 specimens	*O. gracilis*
ES 54	54° 40′ N : 12° 16′ W	2878 m	1 specimen	*O. gracilis*
ES 59	54° 40′ N : 12° 20′ W	2900 m	2281 specimens	*O. gracilis*
ES 69	53° 39′ N : 07° 12′ W	1050 m	48 specimens	*O. gracilis*
ES 90	60° 05′ N : 05° 55′ W	1040 m	10 specimens	*O. gracilis*
ES 99	60° 00′ N : 10° 35′ W	1160 m	2 specimens	*O. gracilis*
ES 115	56° 29′ N : 10° 22′ W	1000 m	113 specimens	*O. gracilis*
ES 129	54° 39′ N : 12° 17′ W	2900 m	5 specimens	*O. gracilis*
ES 135	54° 39′ N : 12° 16′ W	2900 m	15 561 specimens	*O. gracilis*
ES 137	54° 34′ N : 12° 19′ W	2900 m	35 specimens	*O. gracilis*
ES 147	54° 36′ N : 12° 19′ W	2921 m	10 263 specimens	*O. gracilis*
ES 164	54° 37′ N : 12° 24′ W	2925 m	417 specimens	*O. gracilis*
ES 172	54° 39′ N : 12° 17′ W	2910 m	1650 specimens	*O. gracilis*
ES 176	57° 15′ N : 10° 26′ W	2200 m	10 380 specimens	*O. gracilis*
ES 178	56° 33′ N : 09° 17′ W	997 m	147 specimens	*O. gracilis*
ES 180	54° 42′ N : 12° 11·5′ W	2886 m	8 specimens	*O. gracilis*

ES 184	57° 14′ N : 10° 24′ W	2260 m	650 specimens	*O. gracilis*
SBC 65	56° 39′ N : 09° 40′ W	1600 m	21 specimens	*O. gracilis*
SBC 66	56° 39′ N : 09° 23′ W	1200 m	57 specimens	*O. gracilis*
SBC 67	56° 39′ N : 09° 13′ W	1000 m	26 specimens	*O. gracilis*
AT 90a	60° 05′ N : 05° 57′ W	1040 m	1 specimen	*O. gracilis*
AT 1		750 m	77 specimens	*O. gracilis*
AT 141	54° 44′ N : 12° 14′ W	2909 m	2 specimens	*O. gracilis*
ES 6	55° 03′ N : 12° 29′ W	2900 m	9 specimens	*O. hastatum*
ES 27	54° 40′ N : 12° 16′ W	2880 m	1 specimen	*O. hastatum*
ES 52	54° 40′ N : 12° 16′ W	2886 m	2 specimens	*O. hastatum*
ES 55	54° 40′ N : 12° 16′ W	2886 m	1 specimen	*O. hastatum*
ES 111	54° 40′ N : 12° 16′ W	2886 m	1 specimen	*O. hastatum*
ES 129	54° 39′ N : 12° 17′ W	2960 m	1 specimen	*O. hastatum*
ES 137	54° 34′ N : 12° 19′ W	2900 m	2 specimens	*O. hastatum*
ES 140	54° 40′ N : 12° 16′ W	2912 m	7 specimens	*O. hastatum*
ES 147	54° 36′ N : 12° 19′ W	2921 m	7 specimens	*O. hastatum*
AT 107a	57° 07′ N : 12° 06′ W	2000 m	10 specimens	*O. hastatum*
AT 119	54° 40′ N : 12° 14′ W	2908 m	1 specimen	*O. hastatum*
AT 121	54° 37′ N : 12° 09′ W	2910 m	187 specimens	*O. hastatum*

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Developmental stages of *Oncaea media* Giesbrecht, 1891 and *Oncaea subtilis* Giesbrecht, 1892

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Introduction

Few studies have been made of the life-cycles of copepod species belonging to the cyclopoid family Oncaeidae although they are common in the plankton. Björnberg (1972) described some of the developmental stages of *Oncaea venusta* Philippi, 1843 and *O. media* Giesbrecht, 1891 using material from the coastal waters of Brazil and Curaçao, and from rearing experiments, but could not assign the wild copepodids to a species. Digby (1950) encountered a similar problem in which *O. venusta* and *Corycaeus* in the Plymouth plankton were '. . . accompanied by large numbers of nauplii which were counted *in toto*: they probably comprised nauplii of these two species together with possibly *Euterpina* and other harpacticoids'. Since the larval stages could not be identified Digby was unable to estimate the local population of *O. venusta*. Hanaoka (1952) described the third, fourth and fifth nauplii of *O. mediterranea* Claus, 1863.

There have been many studies of development in the Oithonidae (Oberg, 1906; Murphy, 1923; Gibbons & Ogilvie, 1933; Krishnaswamy, 1950; Rao, 1958; Sazhina, 1960; Haq, 1965; Faber, 1966; Björnberg, 1968, 1972; Goswami, 1975; Fanta, 1976; Fonseca, 1976; Fonseca & Prado, 1979; Uchima, 1979), but few for the Corycaeidae (Hanaoka, 1952; Johnson, 1969; Björnberg, 1972; Gibson & Grice, 1978) and only those mentioned above for the Oncaeidae. Members of all three families exhibit the same sequence of developmental stages, six nauplius and five copepodid. The lack of data for *Oncaea* can be attributed to the small size of the nauplii and the difficulties of rearing them in the laboratory.

Materials and methods

Copepodids and adults of both species were collected in September 1979 at the mouth of the English Channel (48°N 7°30′W, 48°30′N 7°W and 49°N 6°30′W) during a cruise of the R.V. 'Sarsia', and donated to the British Museum (Natural History) by the Marine Biological Association, Plymouth. The material was taken using a pump system with 80 μm and 200 μm mesh filters. Adults were also collected in September 1979 and August to October 1980 in Plymouth Sound using 170 μm and 343 μm nets fished at the surface and at 30 m depth. All this material was preserved in 10% sea-water formalin. Further nauplii and copepodids of *O. media* and nauplii of *O. subtilis* were reared from ovigerous females in the laboratory. Single ovigerous females were placed in phials containing approximately 20 ml of filtered sea water containing dense cultures of one species or a combination of two or more species of the following unicellular algae: *Peridinium trochoideum* (Stein) Lemmermann, *Thalassiosira rotula* Meunier and *Isochrysis galbana* Parke. The phials were maintained at 12, 15, 18 and 20°C on a 12 : 12 hour light : dark cycle. The larvae were harvested periodically and preserved in 10% sea-water formalin. Adults and copepodids were measured and dissected in lactophenol; all material was stained with chlorazol black and mounted in polyvinyl lactophenol. Drawings were either made with the aid of a *camera lucida* or traced from SEM micrographs. Specimens were measured using an eyepiece

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micrometer, total copepodid body length being the distance from the tip of the rostrum to the apex of the caudal rami. Specimens were prepared for scanning electron microscopy by critical-point drying, coated with gold-palladium, and examined using an ISI 60A Stereoscan microscope.

Descriptions of developmental stages

The formulae used to describe the armature of nauplius mouthparts are derived as follows. Setae are given in arabic and spines in roman numerals. The armature of each segment is written between colons and each limb is given a separate grouping; thus 1+I: 0: 3+3 terminal, describes a limb whose first segment bears a seta and a spine, whose second segment is unarmed and whose terminal segment bears two groups of three setae, of which one group is terminal. A question mark indicates that an armature formula is uncertain and is used when a segment bears fewer elements than the previous stage, or if the limb of a specimen is obscured. Each formula is derived from the study of several individuals, where possible, and may not tally precisely with the figured specimen. Some of the segmentation is poorly defined, especially in early developmental stages and may apparently differ in the figures between left and right sides of the same individual.

Oncaea media Giesbrecht, 1891

NAUPLIUS STAGES. *Nauplius 1* (Fig. 1a). Length 0·06 to 0·07 mm (7 reared specimens). Oval body. First antenna, 1: 1: 3. Second antenna: coxopodite, 1; basipodite, 1; endopodite, 2 terminal; exopodite 5-segmented, 1: 1: 1: 1: 3. Mandible: coxopodite, 0; basipodite, 0; endopodite, 5; exopodite 2-segmented, 1?: 2 terminal. Caudal armature, a pair of fine setae.
Nauplius 2 (Fig. 1b). Length 0·07 to 0·09 mm (8 reared specimens). Oval body. First antenna, 1: 1: 2? Second antenna: coxopodite, I; basipodite, 2; endopodite, 2; exopodite, 1: 1: 1: 1: 3. Mandible (Fig. 1c): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3, external lobe, 3; exopodite, 2 terminal. Caudal armature, a pair of long setae.
Nauplius 3 (Fig. 1d). Length 0·08 to 0·1 mm (4 reared specimens). Rounded oblong body. First antenna, 1: 1: 4. Second antenna: coxopodite, I+1; basipodite, 3; endopodite 2-segmented, 2: 3; exopodite, 2: 1: 1: 1: 3. Mandible (Fig. 1e): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3, external lobe, 4; exopodite, 2 terminal. Caudal armature, 2 pairs of long setae.
Nauplius 4 (Fig. 1f). Length 0·09 to 0·13 mm (28 reared specimens). Long oblong, or oval body; internal body division visible. First antenna, 1: 2: 2+4 terminal. Second antenna: coxopodite, I+1; basipodite, 3; endopodite, 2: 3; exopodite, 2: 1: 1: 1: 3. Mandible: coxopodite, 1; basipodite, 1; endopodite, internal lobe 4, external lobe, 4; exopodite (obscured Fig. 1f), 2 terminal. First maxilla represented by a ventral spine. Caudal armature, 2 or 3 pairs of long setae.
Nauplius 5 (Fig. 1g). Length 0·09 to 0·15 mm (17 reared specimens). Long oblong, or oval body; internal body divisions visible. First antenna, 1: 3: 2+3? terminal. Second antenna: coxopodite, I long +1; basipodite, 3; endopodite, 3+3 terminal; exopodite, 2: 1: 1: 1: 4. Mandible (Fig. 1h): coxopodite, 1; basipodite, 1; endopodite, internal lobe, 3? (2 bearing paired spinules), external lobe, 5; exopodite, 1+2 terminal. First maxilla, single lobe bearing a long and a short seta. Caudal armature, 2 or 3 pairs of long setae and a pair of medial spinules.
Nauplius 6 (Fig. 1i). Length 0·11 to 0·14 mm (5 reared specimens, smallest measured from critical point dried specimen). Rectangular, segmented body. Posterior labral margin bearing row of setules. First antenna, I: 1?: 2+3? terminal. Second antenna: coxopodite, I+1, both pinnate; basipodite, 2?; postero-ventral surfaces of coxopodite and basipodite covered with clusters of spinules; endopodite, 4+4 terminal; exopodite 2: 1: 1: 1: 4. Mandible: coxopodite, I pinnate; basipodite, II pinnate; endopodite, internal lobe, 4 (3 bearing paired

spinules), external lobe, 4; exopodite, 5 (1 pinnate). First maxilla 2-segmented, terminal segment bilobed, inner lobe, II, outer lobe, a very long terminal seta (broken in Fig. 1i)+2 terminal. Pair of small spines situated postero-laterally to first maxillae. Caudal armature, 2 pairs of robust setae (1 pair setose) and a pair of medial spinules; postero-ventral surface bearing 2 subterminal rows of setules.

COPEPODID STAGES. *Copepodid 1* (Fig. 2a). Length 0·22 mm (1 reared specimen). Prosome 5-segmented, urosome single-segmented. First antenna 3-segmented; appendage damaged in dissection, therefore armature uncertain. Second antenna 3-segmented (Fig. 3a); first segment bearing a long distal seta; second segment unarmed; terminal segment bearing 3 proximal setae and a proximal spine and 5 distal setae. Mandible, first and second maxillae and maxilliped lost in dissection. Armature of natatory legs (Fig. 4a–d) given in table 1; first natatory legs damaged in dissection; endopodite of second natatory leg bilaterally setose, seta on internal margin pinnate; seta on internal margin of exopodite pinnate; external spines of exopodite bilaterally serrate.

Copepodid 2 (Fig. 2b). Length 0·25 to 0·32 mm (1 reared specimen and 2 from pump samples). Urosome 2-segmented. Caudal rami bearing 3 distal setae (2 longest pinnate), a distal spine and a dorsal seta. First antenna 3-segmented (Fig. 3b); armature, 0: 4: 8. Armature of second antenna similar to copepodid 1. Mandible, first and second maxillae lost in dissection. Maxilliped 3-segmented (Fig. 3c); first segment unarmed; internal surface of second segment bearing 2 spines and 3 setae; terminal segment produced as a curved claw. Armature of natatory legs (Fig. 4e–g) given in table 1; second natatory legs lost in dissection; terminal spines of exopodites unilaterally serrate, those of endopodites bilaterally serrate; external spines of exopodites bilaterally serrate; all setae pinnate.

Copepodid 3 (Fig. 2c). Length 0·36 to 0·42 mm (4 specimens from pump samples). Urosome 3-segmented (Fig. 3d). Caudal rami bearing 3 distal setae (2 longest pinnate), a distal setose spine and a dorsal seta. First antenna 5-segmented (Fig. 3e); armature, 2: 4: 3: 3: 7+1 esthete. Armature of second antenna similar to copepodid 1 (Fig. 3f). Mandible single-segmented (Fig. 3g), bearing 2 broad, dentate blades and a spine. First maxilla also single-segmented (Fig. 3h), bearing 4 stout, terminal setae. Second maxilla 2-segmented (Fig. 3i); first segment unarmed; second segment produced distally as a unilaterally spinulose claw, also having an external seta and an internal bilaterally spinulose element. Maxilliped 4-segmented (Fig. 3j); first and third segments unarmed; internal surface of second segment bearing 2 spines, proximal smooth, distal setose; fourth segment produced as a curved claw. Armature of natatory legs (Fig. 4h–k) given in table 1; external margins of endopodites setulose; terminal spines of exopodites unilaterally serrate, those of first, second and third endopodites bilaterally serrate; external spines of exopodites bilaterally serrate; all setae pinnate except those on basipodites; first, second and third endopodites terminating in conical projections. Fifth leg represented by a single seta on first urosome segment (Fig. 3d).

Copepodid 4 (Fig. 2d). Length 0·33 to 0·49 mm (1 reared specimen and 9 from pump samples). Urosome 4-segmented (Fig. 3k). Caudal rami bearing lateral setose spine in addition to dorsal and distal armature mentioned above. First antenna 6-segmented (Fig. 3l); armature, 1: 1: 3: 2: 0: 5 (some elements may be missing). Proximal armature of second antenna similar to copepodid 1, distal armature of terminal segment comprising 6 setae (Fig. 3m). Mandible and second maxilla lost in dissection. First maxilla single-segmented (Fig. 3n), bearing 2 stout setae plus a long seta and a shorter pinnate seta. Armature of maxilliped similar to copepodid 3. Armature of natatory legs (Fig. 4l–o) given in table 1; exopodites and endopodites 2-segmented; all setae pinnate except those on basipodites. Armature of fifth leg similar to copepodid 3.

Copepodid 5: *Female* (Fig. 2e and f). Length 0·5 to 0·59 mm (1 reared specimen, 1 netted specimen and 3 from pump samples). Urosome 4-segmented (Fig. 3o); genital setules situated laterally on second segment, anterior to midpoint; genital segment approximately uniform in width. Armature of caudal rami similar to copepodid 3; all distal setae pinnate. First antenna 6-segmented (Fig. 3p); armature, 3: 6: 4: 2: 2: 6 (some elements may be

Table 1 Armature of legs 1 to 4 in the copepodid stages and adults of *Oncaea media* (i = internal; e = external; t = terminal)

Copepodid stage:	I	II	III	IV	V	ADULT (VI)
Leg 1						
coxopodite	0	0	0	0	0	0
basipodite	0	?	Ii,1e	Ii,1e	Ii,1e	Ii,1e
endopodite						
segment 1	–	–	–	–	1i	1i
segment 2	–	0	1i	1i	1i	1i
segment 3	1i,Ie,1t	2 + Ii,2e,It	6i,It	5i,It	5i,It	5i,It
exopodite						
segment 1	–	–	–	–	Ie	Ie
segment 2	–	Ie	Ie	Ie	1i,Ie	1i,Ie
segment 3	?	4i,IIe,It	4i,IIIe,It	4i,IIIe,It	4i,IIIe,It	4i,IIIe,It
Leg 2						
coxopodite	0		0	0	0	0
basipodite	0	LOST	1e	1e	1e	1e
endopodite						
segment 1	–		–	–	1i	1i
segment 2	–		1i	1i	2i	2i
segment 3	1i,1e,2t		4i,IIe,It	5i,IIe,It	3i,IIe,It	3i,IIe,It
exopodite						
segment 1	–		–	–	Ie	Ie
segment 2	–		Ie	Ie	1i,Ie	1i,Ie
segment 3	3i,IIIe,It		5i,IIIe,It	5i,IIIe,It	5i,IIIe,It	5i,IIIe,It
Leg 3						
coxopodite	single lobe bearing 2 setae 1 spine	0	0	0	0	0
basipodite		0	1e	1e	1e	1e
endopodite						
segment 1		–	–	–	1i	1i
segment 2		1i	1i	1i	2i	2i
segment 3		1i,Ie,It	2i,IIe,It	3i,IIe,It	2i,IIe,It	2i,IIe,It
exopodite						
segment 1		–	–	–	Ie	Ie
segment 2		Ie	Ie	Ie	1i,Ie	1i,Ie
segment 3		4i,IIe,It	4i,IIe,It	5i,IIIe,It	5i,IIe,It	5i,IIe,It
Leg 4						
coxopodite	single lobe bearing 3 setae 1 spine	single lobe bearing 1? seta 1 spine	0	0	0	0
basipodite			0	0	1e	1e
endopodite						
segment 1			–	–	1i	1i
segment 2			–	1i	2i	2i
segment 3			2i,1e,It	2i,IIe,It	1i,IIe,It	1i,IIe,It
exopodite						
segment 1			–	–	Ie	ie
segment 2			–	Ie	1i,Ie	1i,Ie
segment 3			3i,IIIe,It	5i,IIIe,It	5i,IIe,It	5i,IIe,It

missing). Internal surface of second segment of second antenna armed with a distal row of setules (Fig. 3q). Armature of mandible similar to copepodid 3 (Fig. 3r). Internal margin of first maxilla bearing 5 terminal elements and a seta (Fig. 3s). Armature of second maxilla similar to copepodid 3 (Fig. 3t). Internal surface of second maxilliped segment setulose (Fig. 3u), also bearing 2 setose spines; terminal claw bearing row of spinules on concave margin, a stout spine on internal base and a small seta on external base. Armature of natatory legs (Fig. 5a–d) given in table 1; exopodites and endopodites 3-segmented; all setae pinnate except those on basipodites. Fifth leg consisting of a small cylindrical segment bearing 2 terminal setae and a seta on dorsal surface of first urosome segment (Fig. 3o).

Male. Length 0·55 mm (1 specimen from pump samples). Armature of mouthparts and natatory legs similar to female copepodid 5. Urosome 5-segmented (Fig. 3v). Armature of fifth leg and caudal rami similar to female copepodid 5, except that cylindrical segment of female leg 5 is replaced in male by protuberance fused to first urosome segment.

ADULT. *Female* (Fig. 2g and h). Length 0·49 to 0·76 mm, mean 0·62 mm (500 specimens from pump and net samples). Ratio of prosome and urosome lengths 1·6: 1. Third prosome segment without a dorsal projection. Head (first prosome division) equal in length to width. Proportional lengths of urosome segments and caudal rami 13: 42: 8: 7: 12: 18 (Fig. 3v′); genital apparatus situated anterior to midpoint on dorsal surface of genital segment, each aperture armed with a setule; length to width ratio of genital segment 1·6: 1; maximum width anterior to genital apparatus. Caudal rami 2·5 to 3 times as long as wide; armature similar to female copepodid 5. First antenna 6-segmented (Fig. 3w); armature, 3: 6: 4 + I; 3: 2: 6; ratio of segment lengths 12: 18: 32: 9: 5: 7. Armature of second antenna similar to female copepodid 5 (Fig. 3w′), distal seta on first segment setose; terminal segment shorter than second segment. Armature of mandible similar to female copepodid 5 (Fig. 3x). First maxilla bearing 6 terminal elements and an internal seta (Fig. 3x′). Armature of second maxilla (Fig. 3y) and maxilliped (Fig. 3y′) similar to female copepodid 5. Armature of natatory legs (Fig. 5e–h) given in table 1. Armature of fifth leg similar to female copepodid 5.

Male (Fig. 2i and j). Length 0·37 to 0·58 mm, mean 0·48 mm (100 specimens from pump and net samples). Ratio of prosome and urosome lengths 2: 1. Head equal in length to width. Proportional lengths of urosome segments and caudal rami 14: 50: 3: 2: 2: 7: 9 (Fig. 3z); genital lappets produced as small postero-ventral processes; length to width ratio of genital segment 1·2: 1. Caudal rami 1·5 to 2 times as long as wide; armature similar to female. Armature of mouthparts similar to female, except first antenna and maxilliped. First antenna 4-segmented (segments corresponding to 3 terminal segments of female first antenna fused in male). Maxilliped 3-segmented (Fig. 3z′); second segment bearing 2 rows of stout setules on internal surfaces; terminal claw bearing a setose spine on internal base. Armature of natatory legs similar to female adult. Armature of fifth leg similar to male copepodid 5.

MATERIAL EXAMINED. 79 nauplii reared from adults caught in Plymouth Sound, 1981 : 221. 4 Reared copepodids, 1981 : 222 and 1981 : 223. 19 copepodids, 5♀♀ adults and 113♂♂ adults from samples F150, F152–155 and F165–173, 90–10 m, 48°N 7°30′W and 48°30′N 7°W, 1981 : 224 and 1981 : 225. 1 Copepodid, 493♀♀ adults and 103♂♂ adults from Plymouth Sound, 0–30 m, 1981 : 226–232.

REMARKS. Sexual dimorphism in the length of the second urosome segment of *Oncaea* sp. has been reported at copepodid stage 4 by Björnberg (1972), but she does not assign the morphs to sexes. However, the small postero-lateral processes of the shorter segmented morph, shown in figure 600 (Björnberg, 1972) may be precursors of the male genital lappets. Only one copepodid 4 morph was found in the present material. Dimorphism at copepodid stage 5 is also restricted to the posterior body segments; the well-documented sexual dimorphism in the first antenna and the maxilliped does not emerge until the adult stages.

Sewell (1947) reports two forms of female adult *O. media*: *O. media minor* and *O. media major*, and separates them by body length and structure of the caudal rami. According to these criteria the present material is *O. media minor*.

Oncaea subtilis Giesbrecht, 1892

NAUPLIUS STAGES. *Nauplius 1* (Fig. 6a). Length 0·07 mm (3 reared specimens). Oval body. First antenna, 0: 1: 3/4. Second antenna: coxopodite, 1; basipodite, 2; endopodite single-segmented, 1+2 terminal; exopodite 5-segmented, 1: 1: 1: 1: 3. Mandible: coxopodite, 0; basipodite, 0; endopodite, 2+4; exopodite 2-segmented, 0: 2. Caudal armature, a pair of setae. Segmentation of appendages more pronounced than nauplius 1 of *O. media.*

Nauplius 2 (Fig. 6b). Length 0·07 and 0·08 mm (2 reared specimens). Oval body. First antenna, 0: 2: 5. Second antenna: coxopodite, 0?; basipodite, 2; endopodite, 1: 0: 3; exopodite 4?-segmented, 1: 1: 1: 4. Mandible: coxopodite, 0; basipodite, 0; endopodite, internal lobe, 3, external lobe, 3; exopodite 2-segmented, 2 terminal. Caudal armature, a pair of long setae. Segmentation of appendages more pronounced than nauplius 2 of *O. media.*

Nauplius 3 (Fig. 6c). Length 0·08 mm (1 reared specimen). Rounded oblong body. First antenna, 1: 2: 2+4 terminal. Second antenna: coxopodite, I+1 (seta bearing paired spinules); basipodite, 3; endopodite, 2+2 terminal; exopodite 5-segmented, 0?: 0?: 1: 2: 4. Mandible: coxopodite, 0; basipodite, 1; endopodite, internal lobe, 3 (1 bearing paired spinules), external lobe, 2?; exopodite, 2 terminal. Caudal armature, 2 pairs of setae.

Nauplius 4 (Fig. 6d). Length 0·12 mm (1 reared specimen). Long oblong body. First antenna, 1: 3: 3? Second antenna: Coxopodite, I+1; basipodite, 3; endopodite single segmented, 2+2 terminal; exopodite, 0?: 0?: 1: 0?: 3? Mandible: coxopodite, 0; basipodite, 0?; endopodite, internal lobe, 3 (bearing paired spinules), external lobe, 3 (2 bearing paired spinules); exopodite 3-segmented, 0: 1: 3. Caudal armature, 2 pairs of setae.

Nauplius 5 (Fig. 6e). Length 0·14 mm (1 reared specimen). Rotund body. First antenna, 1: 1?: 2+4. Second antenna: coxopodite, 0?, basipodite, I+2, endopodite, 4 terminal; exopodite, 2: 1: 1: 1: 3? Mandible: coxopodite, 0; basipodite, 0?, endopodite, internal lobe, 3 (2 bearing paired spinules), external lobe, 1?; exopodite 3-segmented, 0: 1: 3. First maxilla single-segmented, bearing a lateral and 2 terminal setae (1 very long). Caudal armature, 2 pairs of setae.

Nauplius 6 (Fig. 6f and g). Length 0·11 to 0·14 mm (4 reared specimens). Rotund body. First antenna, 2: 1?: 2+4 terminal. Second antenna: coxopodite, 0?; basipodite, 1?; endopodite, 2+4; exopodite, 2: 1: 1: 1: 5. Mandible: coxopodite, 0; basipodite, 1; endopodite, internal lobe, 3 (bearing paired spinules), external lobe, 4; exopodite 3-segmented, 0: 1: 3. First maxilla 2-segmented, basal segment bearing 1 long and 2 short terminal setae; terminal segment bearing a long and a short seta. Pair of setose spines situated postero-laterally to first maxillae. Caudal armature, 2 pairs of setae.

COPEPODID STAGES. *Copepodid 2* (Fig. 7a). Earliest copepodid found in the plankton. Length 0·28 mm (1 specimen from pump samples). Prosome 5-segmented, urosome 2-segmented, (Fig. 8a). Caudal rami bearing 3 distal setae, a distal and a lateral spine, and a dorsal seta. First antenna 6-segmented (Fig. 8b); armature, 1: 1: 5: 1: 2: 7. Second antenna 3-segmented (Fig. 8c); first segment bearing a long distal seta; second segment unarmed; terminal segment bearing 3 proximal setae, a proximal curved, pinnate spine and 4 distal curved setae. Mandible single-segmented (Fig. 8d), bearing 2 broad blades and 2 spines. First maxilla lost in dissection. Second maxilla 2-segmented (Fig. 8e); first segment unarmed; second segment produced distally as a unilaterally setose claw, also having an external spinulose seta, an internal pinnate element and a thin seta. Maxilliped 4-segmented (Fig. 8f); first and third segments unarmed; internal surface of second segment bearing 2 spinulose spines and a row of spinules; fourth segment produced as a curved claw, bearing a row of spinules on concave surface. Armature of natatory legs (Fig. 9a–d) given in table 2; terminal spines of first and second exopodites and second endopodite unilaterally serrate; external spines of first and second exopodites bilaterally serrate; terminal spine of first endopodite bilaterally serrate; all setae pinnate except those on basipodites.

Copepodid 3 (Fig. 7b). Length 0·28 to 0·34 mm (5 specimens from pump samples). Urosome 3-segmented (Fig. 8g). Caudal rami bearing 3 distal setae (2 longest setose), a distal and a lateral spine, and a dorsal seta. First antenna 6-segmented (Fig. 8h); armature, 1: 4: 2: 1: 1:

Table 2 Armature of legs 1 to 4 in the copepodid stages 2 to 5 and adults of *Oncaea subtilis*, (notation as for Table 1)

Copepodid stage:	II	III	IV	V	ADULT (VI)
Leg 1					
coxopodite	0	0	0	0	0
basipodite	Ii,1e	Ii,1e	Ii,1e	Ii,1e	Ii,1e
endopodite					
segment 1	–	–	–	0	0
segment 2	1i	1i	1i	1i	1i
segment 3	5i,It	5i,It	5i,It	5i,It	5i,It
exopodite					
segment 1	–	–	–	Ie	Ie
segment 2	Ie	Ie	Ie	Ie	1i,Ie
segment 3	4i,IIIe,It	4i,IIIe,It	5i,IIIe,It	4i,IIIe,It	4i,IIIe,It
Leg 2					
coxopodite	0	0	0	0	0
basipodite	1e	1e	1e	1e	1e
endopodite					
segment 1	–	–	–	1i	1i
segment 2	1i	1i	1i	2i	2i
segment 3	4i,Ie,It	4i,Ie,It	4i,Ie,It	3i,Ie,It	3i,Ie,It
exopodite					
segment 1	–	–	–	Ie	Ie
segment 2	Ie	Ie	Ie	1i,Ie	1i,Ie
segment 3	4i,IIIe,It	5i,IIIe,It	5i,IIIe,It	5i,IIIe,It	5i,IIIe,It
Leg 3					
coxopodite	0	0	0	0	0
basipodite	1e	1e	1e	1e	1e
endopodite					
segment 1	–	–	–	1i	1i
segment 2	–	1i	1i	2i	2i
segment 3	2i,Ie,It	2i,Ie,It	3i,Ie,It	2i,Ie,It	2i,Ie,It
exopodite					
segment 1	–	–	–	Ie	Ie
segment 2	–	Ie	Ie	1i,Ie	1i,Ie
segment 3	3i,IIIe,It	4i,IIe,It	5i,IIIe,It	5i,IIe,It	5i,IIe,It
Leg 4					
coxopodite	single lobe bearing 1 seta 2 spines	0	0	0	0
basipodite		1e	1e	1e	1e
endopodite					
segment 1		–	–	1i	1i
segment 2		–	1i	2i	2i
segment 3		2i,It	3i,It	1i,Ie,It	1i,Ie,It
exopodite					
segment 1		–	–	Ie	Ie
segment 2		–	–	1i,Ie	1i,Ie
segment 3		3i,IIIe,It	5i,IVe,It	5i,IIe,It	5i,IIe,It

Table 3 Size in microns of *Oncaea* nauplii, data from Hanaoka (1952), Björnberg (1972) and present study

	Oncaea media (present account)	*Oncaea subtilis* (present account)	*Oncaea mediterranea* (Hanaoka)	*Oncaea media* (Björnberg)	*Oncaea venusta* (Björnberg)
Nauplius 1	60–70	70	–	50–60	90
Nauplius 2	70–90	70–80	–	80	90
Nauplius 3	80–100	80	125*	90	–
Nauplius 4	90–130	120	150*	100	–
Nauplius 5	90–150	140	185*	130–150	–
Nauplius 6	110–140	110–140	–	150–180	–

*These are probably stages 4 to 6.

6 + 1 esthete (some elements may be missing). Second antenna 3-segmented (Fig. 8i); first segment bearing a long distal pinnate seta; second segment unarmed; proximal armature of terminal segment similar to copepodid 2; distal armature comprising 3 long curved, pinnate setae and a short seta. Armature of mandible similar to copepodid 2 (Fig. 8j), both spines setose. First maxilla single-segmented (Fig. 8k), bearing 6 terminal setae (1 setose). Second maxilla 2-segmented (Fig. 8l); first segment unarmed; second segment produced distally as a unilaterally setose claw, additional armature similar to copepodid 2. Armature of maxilliped similar to copepodid 2 (Fig. 8m), internal surface of second segment bearing 2 rows of setules and 2 pinnate setae. Armature of natatory legs (Fig. 9e–h) given in table 2; terminal exopodite spines unilaterally serrate; external spines of first, second and third exopodites bilaterally serrate; terminal spines of first, second and third endopodites bilaterally serrate; all setae pinnate except those on bases. Fifth leg represented by a single seta on first urosome segment (Fig. 8g).

Copepodid 4 (Fig. 7c and d). Length 0·32 to 0·36 mm (13 specimens from pump samples). Urosome 4-segmented. Armature of caudal rami similar to copepodid 3. First antenna 6-segmented (Fig. 8n); armature 2: 4: 2: 3: 2: 5 + 1 esthete. Armature of second antenna similar to copepodid 3. Mandible and first maxilla lost in dissection. Armature of second maxilla (Fig. 8o) and maxilliped similar to copepodids 2 and 3. Armature of natatory legs (Fig. 9i–l) given in table 2; terminal exopodite spines unilaterally serrate; external exopodite spines bilaterally serrate; terminal endopodite spines bilaterally serrate; all setae pinnate except those on basipodites. Fifth leg represented by 2 setae on first urosome segment.

Copepodid 5: *Female* (Fig. 7e). Length 0·36 to 0·48 mm (12 specimens from pump samples). Urosome 4-segmented (Fig. 8p); genital setules situated laterally on second segment. Armature of caudal rami similar to copepodid 3. First antenna 6-segmented (Fig. 8q); armature, 2: 6: 4: 2: 2: 5 + 1 esthete. Second antenna 3-segmented (Fig. 8r); first segment bearing a long distal setose seta and a row of denticles on external margin, external margin of second segment bearing a row of spinules; proximal armature of terminal segment similar to copepodid 4; distal armature comprising 5 curved, pinnate setae and a spine. Armature of mandible similar to copepodid 2 (Fig. 8s), and of first and second maxilla similar to copepodid 3. Internal surface of second segment of maxilliped bearing row of setules (Fig. 8t); terminal claw having a stout, setose spine on internal base and a small seta on external base. Armature of natatory legs (Fig. 9m–p) given in table 2. Fifth leg consisting of a pair of setae on postero-lateral margin of first urosome segment and a single seta on the dorsal surface (Fig. 8p).

Male (Fig. 7f and g). Length 0·34 to 0·4 mm (7 specimens from pump samples). Armature of mouthparts and natatory legs similar to female copepodid 5. Urosome 5-segmented (Fig. 8u). Armature of caudal rami similar to female copepodid 5. Fifth leg consisting of 2 setae on a tubercle.

ADULT. *Female* (Fig. 7h). Length 0·46 to 0·69 mm, mean 0·5 mm (75 specimens from pump and net samples). Ratio of prosome and urosome lengths 3: 2. Third prosome segment without a dorsal projection. Head 1·1 times longer than wide. Proportional lengths of urosome segments and caudal rami 5: 23: 10: 9: 8: 8 (Fig. 8v); genital apparatus situated anterior to midpoint of dorsal surface of genital segment; each aperture armed with a setule; 1 specimen bearing spermatophores (Fig. 7i); length to width ratio of genital segment 1·2: 1; maximum width at level of genital apparatus. Caudal rami twice as long as wide; armature similar to copepodid 3. First antenna 6-segmented (Fig. 8w); armature, 3: 8: 4: 3: 1: 5+1 esthete; ratio of segment lengths 9: 11: 31: 6: 4: 5. Armature of second antenna (Fig. 8w′) and mandible (Fig. 8x) similar to copepodid 5. Terminal segment of second antenna longer than second segment. First maxilla bilobed (Fig. 8x′), bearing 3 setae on internal lobe (1 setose), 4 setae on external lobe (1 setose), and a seta on internal margin. Second maxilla 2-segmented (Fig. 8y); second segment produced distally as a unilaterally spinulose claw, also having an external pinnate seta and an internal bilaterally spinulose element. Maxilliped 4-segmented (Fig. 8y′); armature similar to female copepodid 5. Armature of natatory legs (Fig. 7j–m) given in table 2. Armature of fifth leg similar to female copepodid 5.

Male (Fig. 7n). Length 0·38 to 0·44 mm, mean 0·41 mm (32 specimens from pump and net samples). Ratio of prosome and urosome lengths 1·8: 1. Proportional lengths of urosome segments and caudal rami 8: 51: 2: 2: 3: 13: 11 (Fig. 8z); genital lappets produced as small postero-ventral processes; length to width ratio of genital segment 1·9: 1. Caudal rami 2·5 times as long as wide; armature similar to copepodid 3. Armature of mouthparts similar to female adult, except first antenna and maxilliped. First antenna 4-segmented (segments corresponding to 3 terminal segments of female first antenna fused in male). Maxilliped 3-segmented (Fig. 8z′); second segment bearing a row of stout setules and 2 spines on internal surface; terminal claw having a spine on internal base. Armature of natatory legs similar to female adult. Armature of fifth leg similar to male copepodid 5, but with additional seta on dorsal surface of first urosome segment.

MATERIAL EXAMINED. 13 nauplii reared from adults caught in Plymouth Sound, 1981 : 234. 706 copepodids, 421♀♀ adults and 576♂♂ adults from samples F89–92, F125–129, F150–155 and F165–173, 48°N 7°30′W, 48°30′N 7°W and 49°N 6°30′W, 1981 : 235 and 1981 : 236. 88♀♀ adults and 1♂ adult from Plymouth Sound 0–30 m, 1981 : 237–241.

REMARKS. All but the largest specimens of the earlier stages would have passed through the filtering mesh of the pump system, thus few of the specimens examined were stage 2, and none were stage 1. Also the quoted size ranges for copepodids 2 and 3 may be biased by this sampling method, towards the largest individuals. Few stage 4 individuals were caught, but this stage may be relatively brief and therefore infrequently caught in the plankton. All of the stage 4 copepodids examined bear small postero-lateral processes on the second urosome segment. It is assumed that this is the male morph. Sexual dimorphism at copepodid 5 is restricted to the posterior body segments; dimorphism of the first antenna and maxilliped does not emerge until the adult stages. All the present material has orange colouration; the caudal setae are especially brightly pigmented.

Comparison with other Oncaeid larvae

The nauplii of *O. media*, *O. subtilis* and early *O. venusta* are similar in size (Table 3), but according to Hanaoka (1952), those of *O. mediterranea* are larger. Adults of these species differ greatly in size and present data indicate that such divergence is not initiated until copepodid 3 in *O. media* and *O. subtilis*. Inter- and intra-specific morphological differences between nauplii of *Oncaea* are mainly confined to variations in the armature and segmentation of the appendages (Table 4). Björnberg (1972) noted several minor variations among *O. media* nauplii.

Table 4 Armature of appendages and caudal rami of *Oncaea* nauplii, data from Hanaoka (1952), Björnberg (1972) and present study

Nauplius	*Oncaea media* (present data)						*Oncaea subtilis* (present data)					
stage:	1	2	3	4	5	6	1	2	3	4	5	6
First antenna	1:1:3	1:1:2?	1:1:4	1:2:2+4	1:3:2+3?	I:1?:2+3?	0:1:3/4	0:2:5	1:2:2+4	1:3:3?	1:1?:2+4	2:1?:2+4
Second antenna												
coxopodite	1	I	1+1	I+1	I+1	I+1	1	0?	I+1	I+1	0?	0?
basipodite	1	2	3	3	3	2?	2	2	3	3	I+2	1?
endopodite	2	2	2:3	2:3	3+3	4+4	1+2	1:0:3	2+2	2+2	4	2+4
exopodite	1:1:1:1:3	1:1:1:1:3	2:1:1:1:3	2:1:1:1:3	2:1:1:1:4	2:1:1:1:4	1:1:1:1:3	1:1:1:4	0?:0?:1: 2:4	0?:0?:1: 0?:3?	2:1:1;1:3?	2:1:1:1:5
Mandible												
coxopodite	0	1	1	1	1	I	0	0	0	0	0	0
basipodite	0	1	1	1	1	Il	0	0	1	0?	0?	1
endopodite	5	3:3	3:4	4:4	3?:5	4:4	2 + 4	3:3	3:2?	3:3	3:1?	3:4
exopodite	1?:2	2	2	2	1+2	5	0:2	0:2	0:2	0:1:3	0:1;3	0:1:3
First maxilla	–	–	–	1	2	Il:1+2	–	–	–	–	1+2	3:2
Caudal rami	1pr	1pr	2pr	2/3pr	2/3pr+Ipr	2pr+Ipr	1pr	1pr	2pr	2pr	2pr	2pr

Table 4 (continued)

Nauplius	*Oncaea mediterranea* (Hanaoka*)			*Oncaea media* (Björnberg)						*Oncaea venusta* (Björnberg)	
stage:	3	4	5	1	2	3	4	5	6	1	2
First antenna	0:0:1:3	0:I:1:4	0:I:I + 1:4	1:1:3/4	1:1:3?	1:1:3	1:2:3	1:2:5	1:2:6/7	DATA NOT AVAILABLE	1:1:4
Second antenna											
coxopodite	II	II	II	1 + 1	I	I + 1	I + 1	I + 1	0:II		II
basipodite	I	I	II	2	II	I + 1	1 + 2/I	2 + 1/0	I + 1		2
endopodite	II + 2	2 + 2	2:2	2/3	1/2 + 3/2	2:3	3 + 1 + 1	2 + 4	2/3 + 3/4		2 + 3
exopodite	1:1:1:1:2	1:1:1:1:2	I + 1:2:0 :1:1:2	1:1:1:1:3	4 segm. 7/8	5 segm. 5	5 segm. 6	5 segm. 6/8	6 segm. 8		4 segm. 6/7
Mandible											
coxopodite	0	0	I	1/2	1	1	1	1	I		1
basipodite	2	2	2	2	1/2	1	2	2	2		2
endopodite	3:3	3:3	3:4	II:4	3:4	3:4	3:4	3:4	3:4/5		3:4
exopodite	1:1:1:1	1:1:1:2	1:1:1:2	1:1:1	3	4 segm. 4	4 segm. 4	4 segm. 4	5 segm. 5/6		4 segm. 5
First maxilla	1	2	bas. 2 end. 3 ex. 0:0:1	–	–	I	I	2	bas. 1 end. II ex. 2		I
Caudal rami	2pr	2pr	2pr + IIpr	1pr	1pr	2pr	2pr	2pr	2pr + Ipr	1pr	1pr

---

*These are probably stages 4 to 6, armatures taken from 1952: Figures 2–6.

Early *O. mediterranea* and *O. venusta* nauplii are more advanced than those of other species, the first maxilla and the labral row of setae appearing simultaneously in *O. venusta* at nauplius 2 and sequentially in *O. mediterranea* at nauplii 3 and 4. In contrast to this, the labral setae first appear in *O. media* at nauplius 6, but do not appear at all in *O. subtilis*. The first maxilla appears at nauplius 5 in *O. media* and *O. subtilis* (the precursor at nauplius 4 is a ventral spine), developing into a two-segmented structure in each case, whilst Hanaoka (1952) reports it to be multi-segmented in *O. mediterranea* nauplius 5. In my opinion Hanaoka assigns the nauplii wrongly, describing stage 4 as stage 3, stage 5 as stage 4 and stage 6 as stage 5. Björnberg reports maxillulary spines for *O. media* nauplius 3. Caudal spines first appear at *O. media* nauplius 5, but at nauplius 4 (*sensu* Hanaoka) of *O. mediterranea* and do not appear at all in *O. subtilis*. Variation in the caudal armature of *O. media* nauplii 4 and 5 is a newly reported phenomenon. A key to the stages of *O. media* and *O. subtilis* nauplii has been constructed from present data, but it is doubtful whether young nauplii from the plankton could be assigned to species purely on present knowledge of their morphology.

Several authors have described, but not identified stage 5 *Oncaea* copepodids (Vilela, 1968; Björnberg, 1972; Boxshall, 1977), but only Björnberg has described stages 2 to 4. She depicted the first antenna as being seven and latterly six-segmented. Early copepodids, 1 and 2, of *O. media* have a three-segmented first antenna, those of *O. subtilis* copepodids, 2 to 5, are all six-segmented. Similarly the armature of the second antenna is different in the second copepodids of these and Björnberg's species, becoming more alike in later stages. The maxilliped of *O. media* copepodid 2 is three-segmented, expanding to four segments at copepodid 3; both *Oncaea* sp. (Björnberg, 1972) and *O. subtilis* second copepodids have a four-segmented maxilliped. The armature of the other mouthparts of *Oncaea* sp. (Björnberg) is inadequately described for comparison with the other species. The armature of the first leg endopodite and the segmentation of the third leg endopodite of *O. media* copepodid 2 (Table 1) are very different to those of *O. subtilis* (Table 2) and *Oncaea* sp. (Björnberg); the figured specimen of *O. media* may be abnormal in these respects. Figured specimens of *Oncaea* sp. lack the basipodite seta common to all copepodids of *O. media* and *O. subtilis*. All other differences of the natatory legs are minor. There are no data on the early development of the fifth leg of *Oncaea* sp. Also Björnberg (1972: Figures 596–602) shows *Oncaea* sp. copepodids which lack the dorsal setae of the caudal rami. In contrast to the nauplii the copepodids are relatively easy to assign to species; those of *O. subtilis* being more slender and smaller than those of *O. media*. A key to the stages based on all available data is presented below. The descriptions of females of *Oncaea obscura* Farran, 1908, *O. neobscura*, Razouls, 1969 and *O. parobscura*, Shmeleva, 1979 are similar to those of stage 5 male copepodids. None of the authors mention or figure the external genital openings which are common to all female adults other than those of these three species, but their figures show postero-lateral processes on an almost parallel-sided genital segment; these processes are common to *O. media* and *O. subtilis* stage 5 males. Significantly only one male adult is described: that of *O. obscura*, but Farran notes morphological differences of the second antenna and fourth endopodite which suggest that it is the male of a different species. In my opinion the descriptions of females of *O. obscura*, *O. neobscura* and *O. parobscura* are descriptions of stage 5 males of unidentified species of the genus *Oncaea*.

Key to nauplius stages

1	One pair of caudal setae	2
	Two or more pairs of caudal setae	3
2	Mandibular endopodite single-lobed	**STAGE 1***
	Mandibular endopodite bilobed	**STAGE 2**
3	First maxilla absent, body rounded oblong or long oblong	4
	First maxilla present, body oval or rotund	5

4	Ventral spines absent	**STAGE 3**
	Ventral spines (precursor of first maxilla) present	**STAGE 4**
5	First maxilla single-lobed	**STAGE 5**
	First maxilla composed of more than one segment	**STAGE 6**

*Björnberg describes a stage 1 *O. media* nauplius which has bilobed mandibular endopodites.

Key to copepodid stages

1	Urosome one-segmented, two pairs of natatory legs	**STAGE 1**
	Urosome two- or more segmented, three or more pairs of natatory legs	2
2	Urosome two-segmented, three pairs of natatory legs	**STAGE 2**
	Urosome three- or more segmented, four pairs of natatory legs	3
3	Urosome three-segmented, fourth natatory endopodites single-segmented	**STAGE 3**
	Urosome four- or more segmented	4
4	Urosome four-segmented	5
	Urosome five- or more segmented, fourth natatory endopodites three-segmented	6
5	Second urosome segment parallel-sided, fourth natatory endopodites two-segmented	**STAGE 4**
	Second urosome segment usually convex-sided, bearing lateral setules fourth natatory endopodites three-segmented	**STAGE 5♀**
6	Urosome five-segmented	7
	Urosome six-segmented, second segment bearing genital lappets	**STAGE 6 (ADULT) ♂**
7	Second urosome segment bearing setules on dorsal surface over genital apertures	**STAGE 6 (ADULT)♀**
	No external openings on dorsal surface of second urosome segment, but having small postero-lateral processes	**STAGE 5♂**

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I wish to thank Dr R. P. Harris (M.B.A.) for his help and advice with the larval rearing programme, and for arranging for preserved material to be donated to the BM(NH); Dr P. Carey for his help with the preparation of specimens for electron microscopy; and Drs G. A. Boxshall and R. J. Lincoln for commenting upon the manuscript. This work was undertaken while the author was in receipt of a BM(NH) postgraduate studentship.

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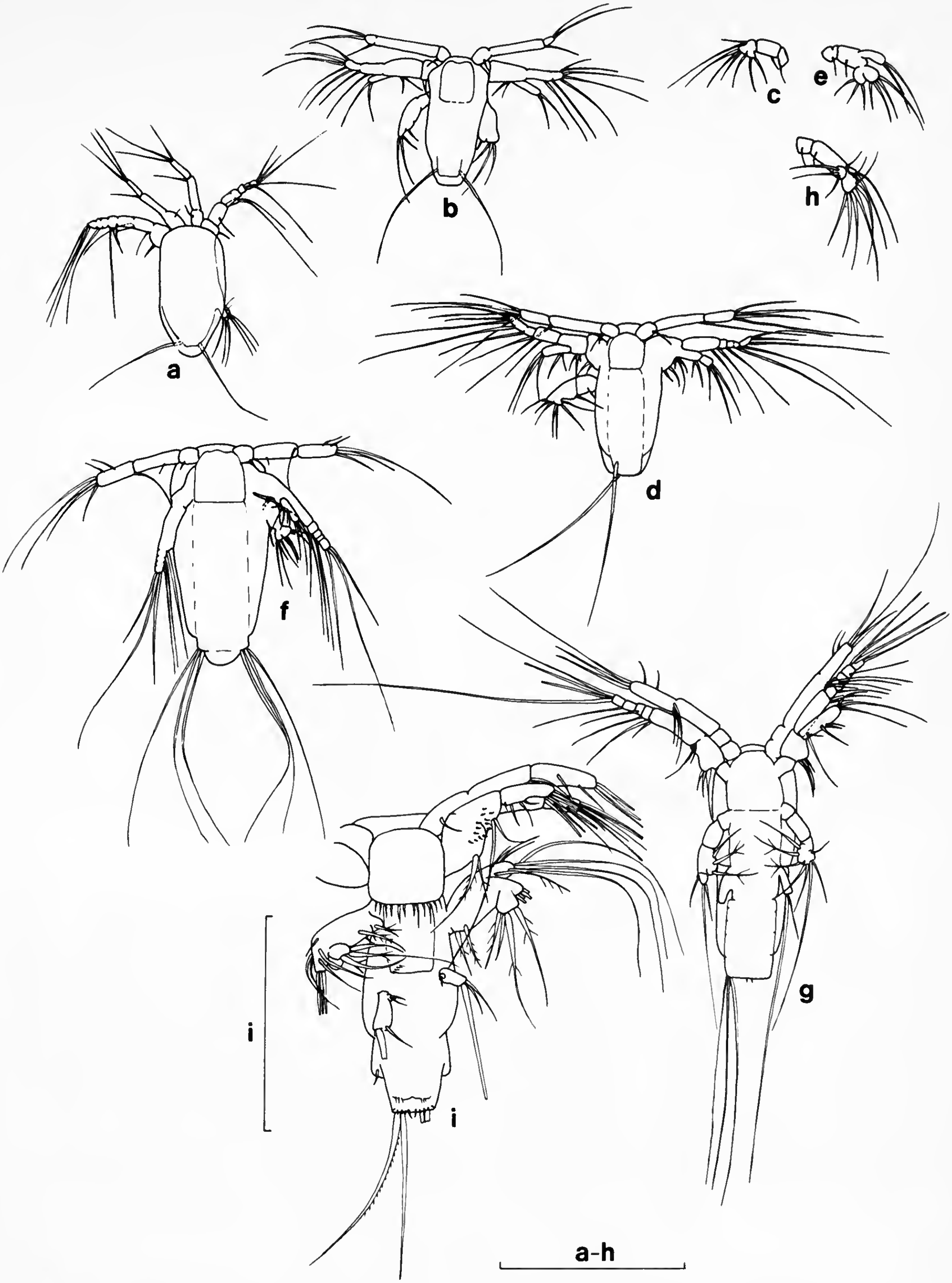


Fig. 1 *Oncaea media*. a. nauplius 1, dorsal (only right mandible shown); b. nauplius 2, dorsal; c. nauplius 2, mandible; d. nauplius 3, ventral (only right mandible shown); e. nauplius 3, mandible; f. nauplius 4, ventral (only left mandible shown); g. nauplius 5, ventral; h. nauplius 5, mandible; i. nauplius 6, ventral. Scales 100 microns, scale for nauplii 1 to 5 and mandibles at base of figure.

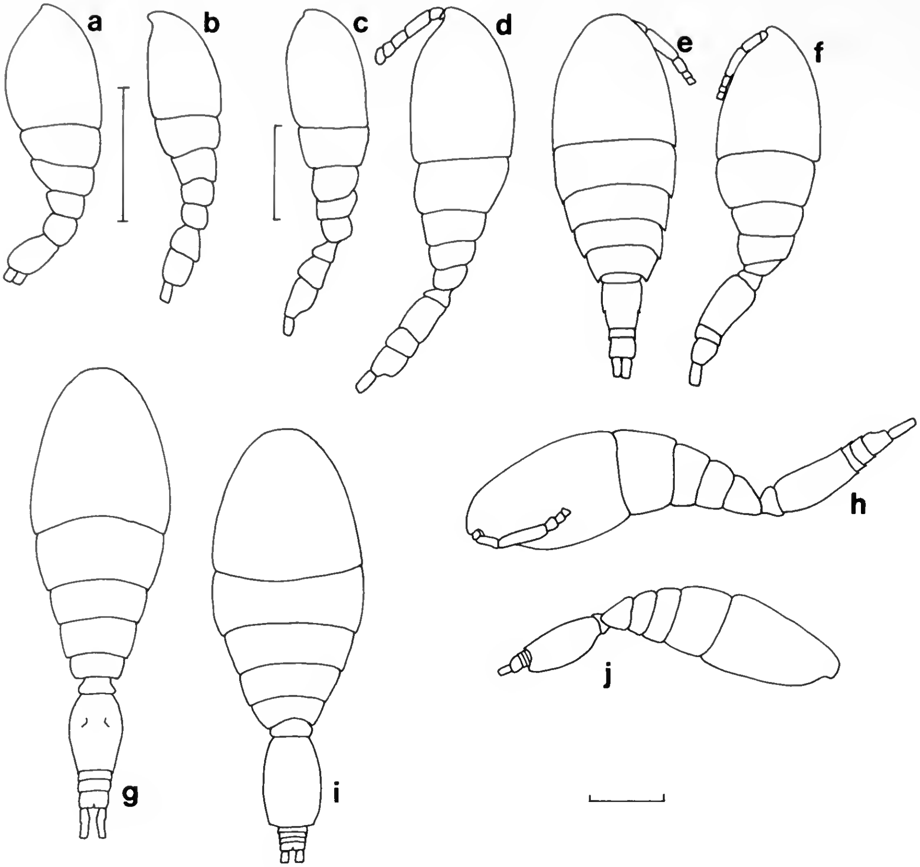
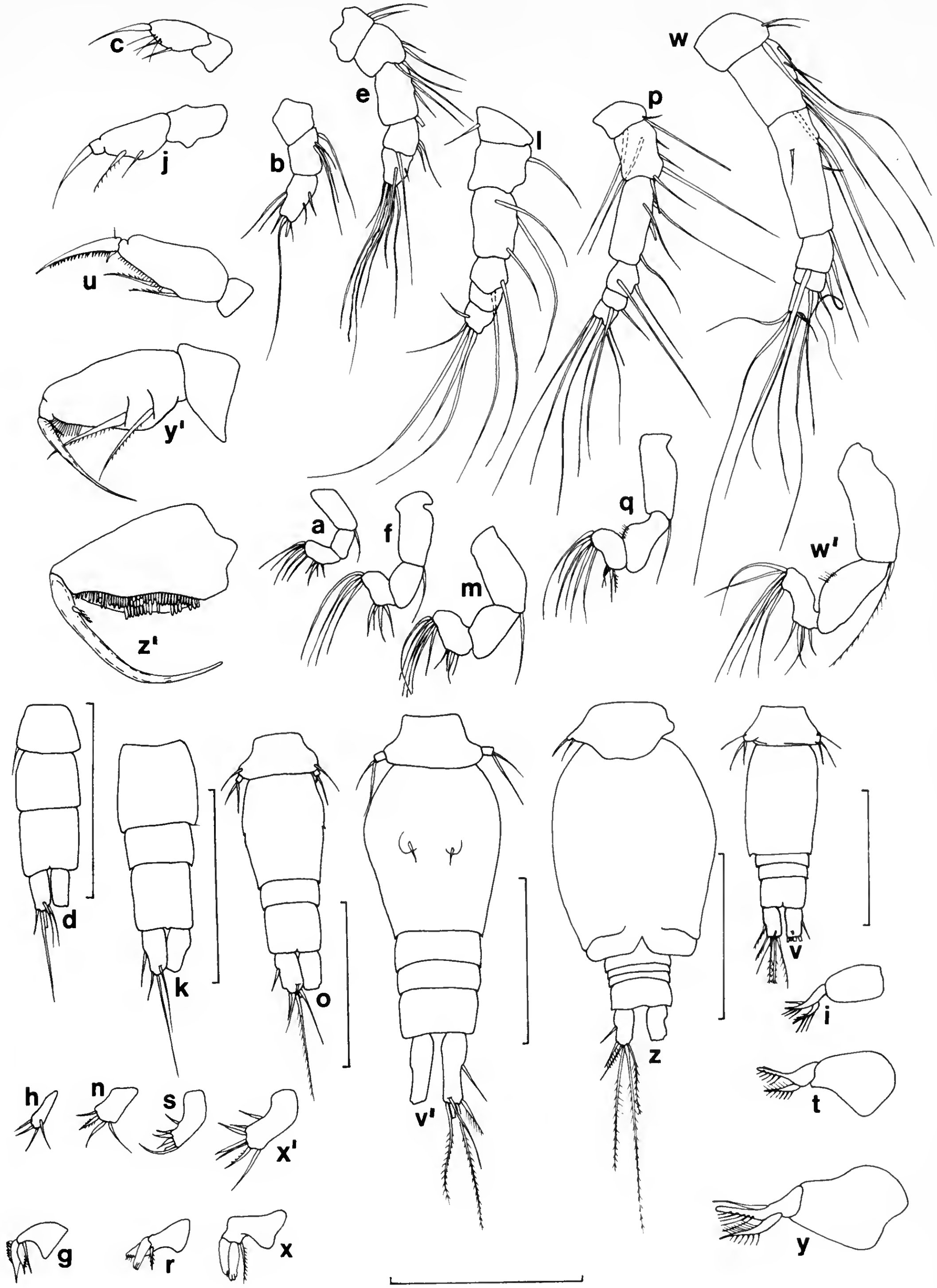


Fig. 2 *Oncaea media.* a. copepodid 1, lateral; b. copepodid 2, lateral; c. copepodid 3, lateral; d. copepodid 4, lateral; e. female copepodid 5, dorsal; f. female copepodid 5, lateral; g. female adult, dorsal; h. female adult, lateral; i. male adult, dorsal; j. male adult, lateral. Scales 100 microns, scale for copepodids 3 and 4 next to Fig. 2c, scale for copepodid 5 and adults at base of figure.

Fig. 3 *Oncaea media.* a. copepodid 1, second antenna; b. copepodid 2, first antenna; c. maxilliped; d. copepodid 3, urosome, dorsal; e. first antenna; f. second antenna; g. mandible; h. first maxilla; i. second maxilla; j. maxilliped; k. copepodid 4, urosome, dorsal (first urosome segment and some elements from caudal rami missing); l. first antenna; m. second antenna; n. first maxilla; o. female copepodid 5, urosome, dorsal; p. first antenna; q. second antenna; r. mandible; s. first maxilla; t. second maxilla; u. maxilliped; v. male copepodid 5, urosome, dorsal; v′. female adult, urosome, dorsal (dorsal seta of fifth leg missing); w. first antenna; w′. second antenna; x. mandible; x′. first maxilla; y. second maxilla; y′. maxilliped; z. male adult, urosome, ventral; z′. maxilliped. Scales 100 microns, scale for mouthparts at base of figure.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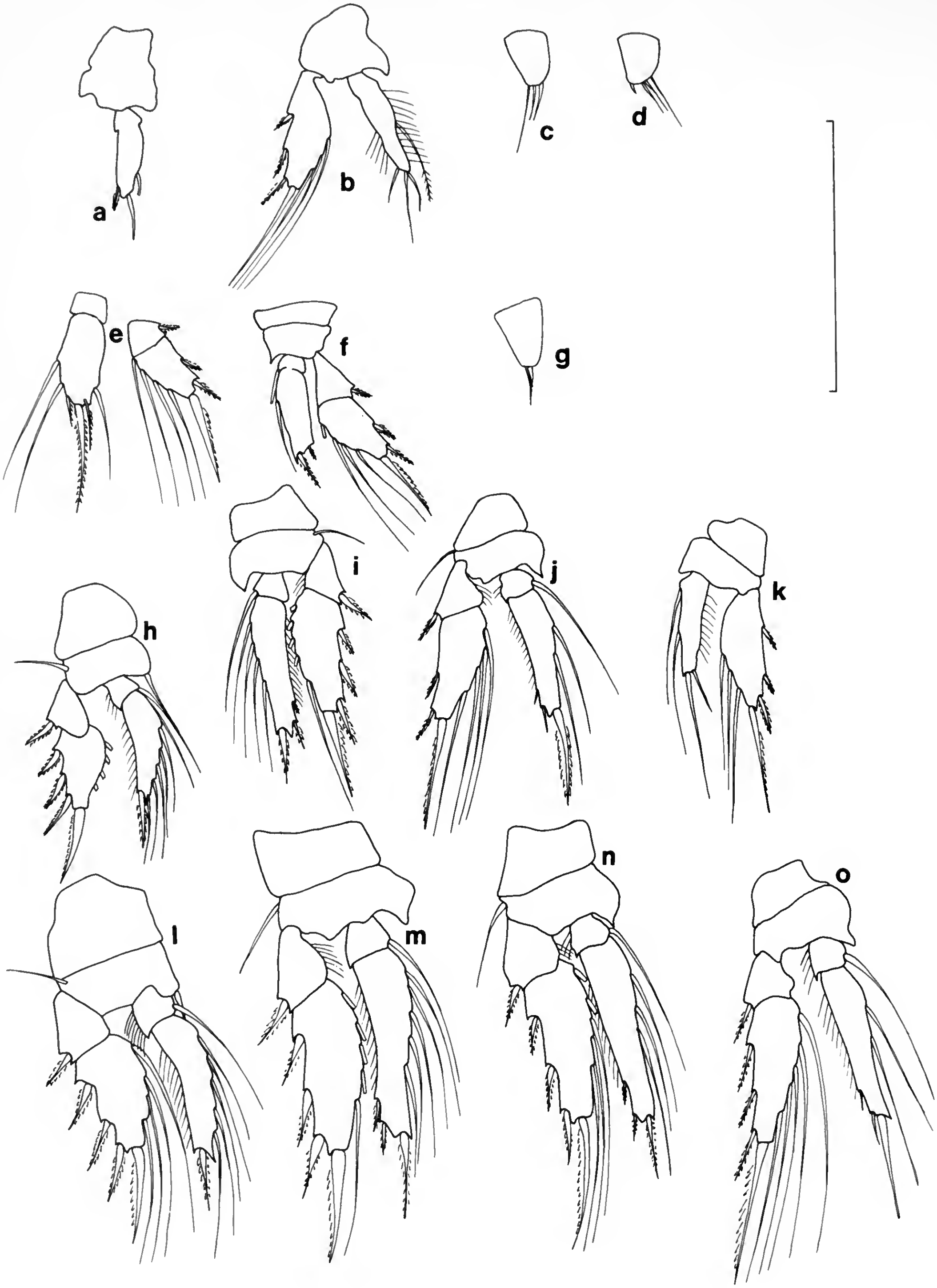

Fig. 4 *Oncaea media*. a. copepodid 1, leg 1 (damaged in dissection); b. leg 2; c. leg 3; d. leg 4; e. copepodid 2, leg 1 (coxapodite and basipodite missing); f. leg 3; g. leg 4; h. copepodid 3, leg 1; i. leg 2; j. leg 3; k. leg 4; l. copepodid 4, leg 1; m. leg 2; n. leg 3; o. leg 4. Scale 100 microns.

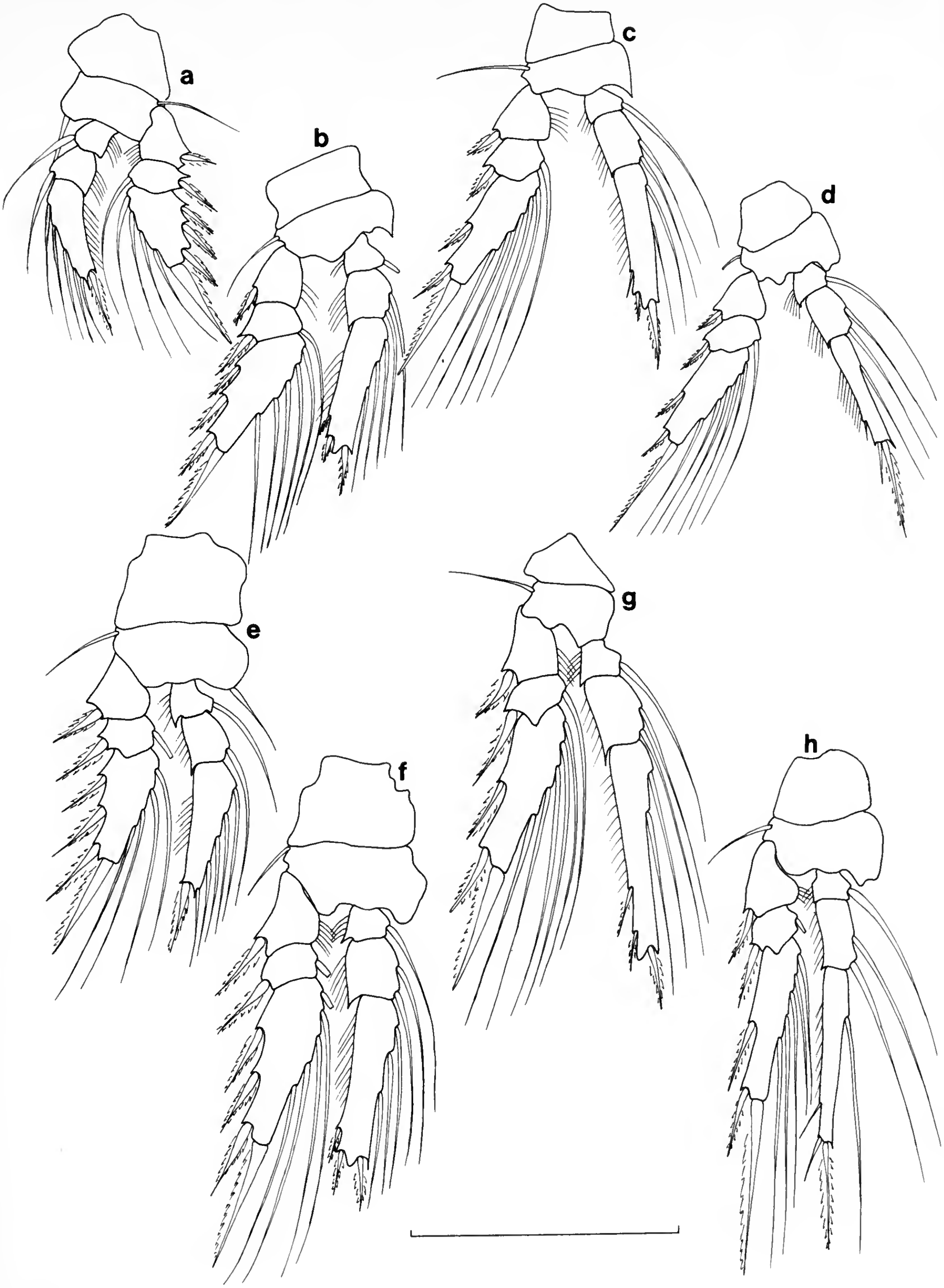

Fig. 5 *Oncaea media.* a. female copepodid 5, leg 1; b. leg 2; c. leg 3; d. leg 4; e. female adult, leg 1; f. leg 2; g. leg 3; h. leg 4. Scale 100 microns.

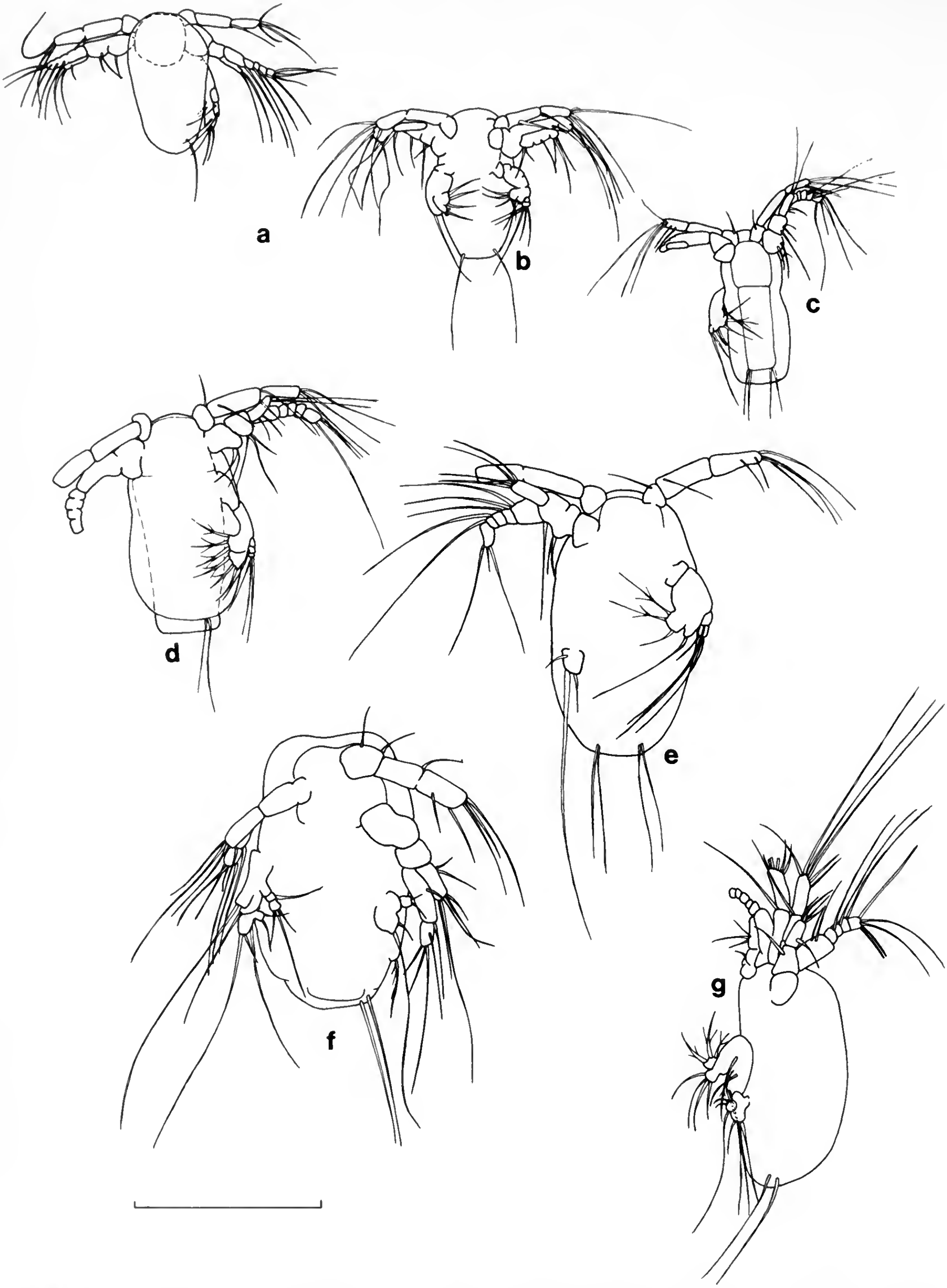

Fig. 6 *Oncaea subtilis*. a. nauplius 1, dorsal (only right mandible shown); b. nauplius 2, ventral; c. nauplius 3, ventral (only right mandible shown); d. nauplius 4, ventral (only left mandible shown); e. nauplius 5, ventral (right second antenna, left mandible and right first maxilla shown); f. nauplius 6, ventral (left first antenna, right mandible, left first maxilla and left second maxilla shown); g. nauplius 6, lateral. Scale 100 microns.

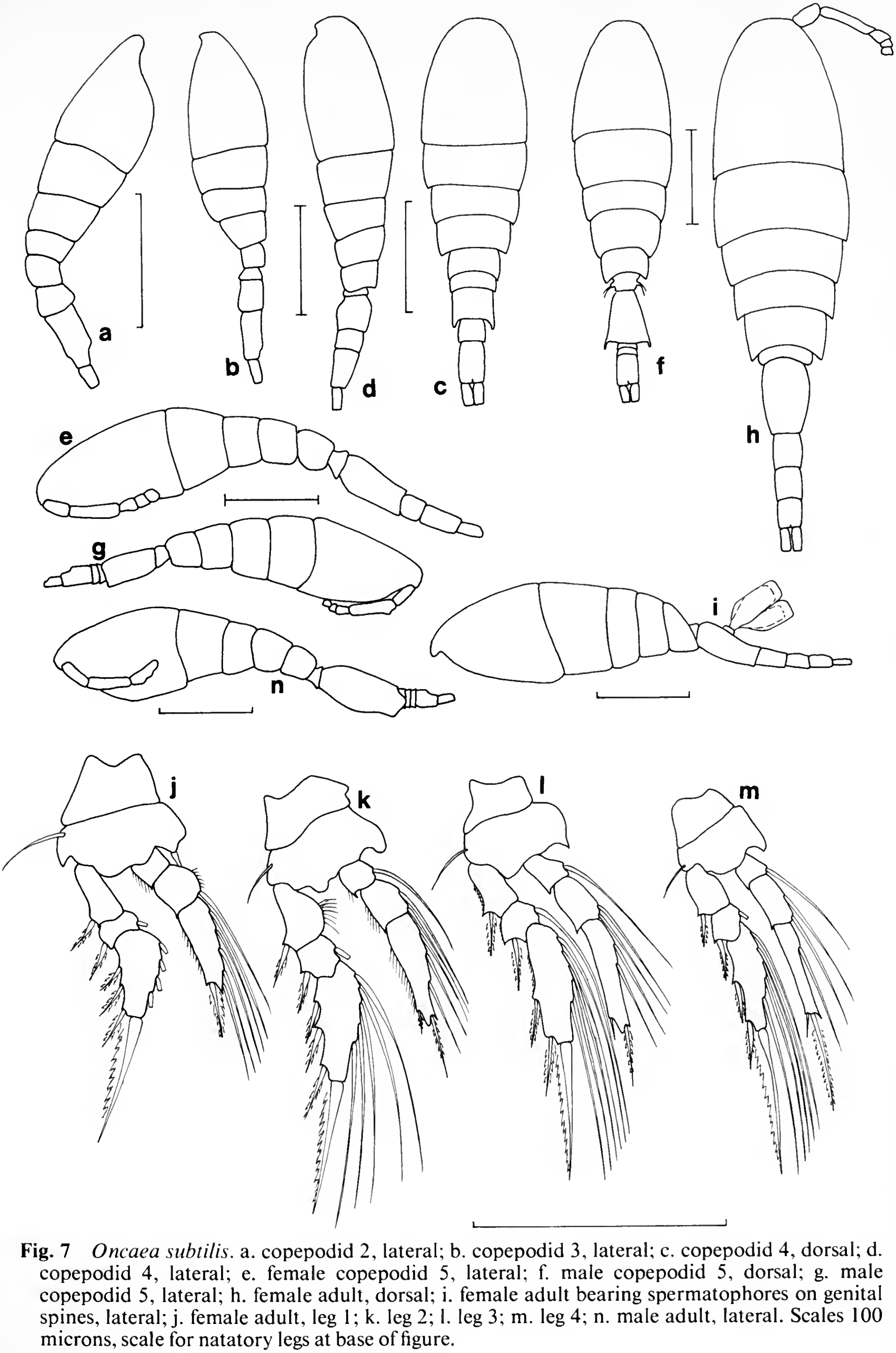

Fig. 7 *Oncaea subtilis*. a. copepodid 2, lateral; b. copepodid 3, lateral; c. copepodid 4, dorsal; d. copepodid 4, lateral; e. female copepodid 5, lateral; f. male copepodid 5, dorsal; g. male copepodid 5, lateral; h. female adult, dorsal; i. female adult bearing spermatophores on genital spines, lateral; j. female adult, leg 1; k. leg 2; l. leg 3; m. leg 4; n. male adult, lateral. Scales 100 microns, scale for natatory legs at base of figure.

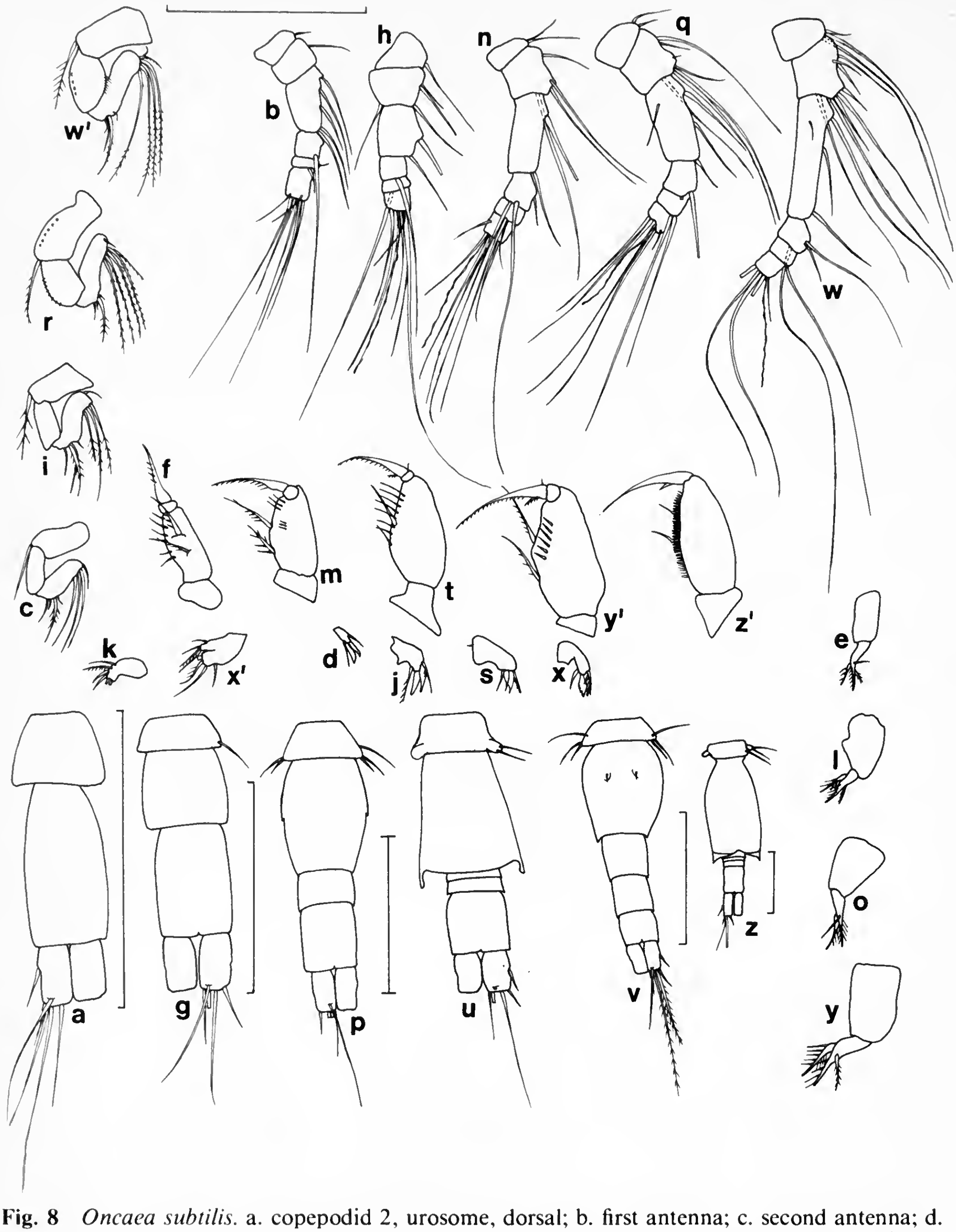

Fig. 8 *Oncaea subtilis.* a. copepodid 2, urosome, dorsal; b. first antenna; c. second antenna; d. mandible; e. second maxilla; f. maxilliped; g. copepodid 3, urosome, dorsal (lateral spine missing from caudal rami); h. first antenna; i. second antenna; j. mandible; k. first maxilla; l. second maxilla; m. maxilliped; n. copepodid 4, first antenna; o. second maxilla; p. female copepodid 5, urosome, dorsal (lateral spine missing from caudal rami); q. first antenna; r. second antenna; s. mandible; t. maxilliped; u. male copepodid 5, urosome, dorsal; v. female adult, urosome, dorsal; w. first antenna; w′. second antenna; x. mandible; x′. first maxilla; y. second maxilla; y . maxilliped; z. male adult, urosome, ventral; z′. maxilliped. Scales 100 microns, scale for mouthparts at top of figure.

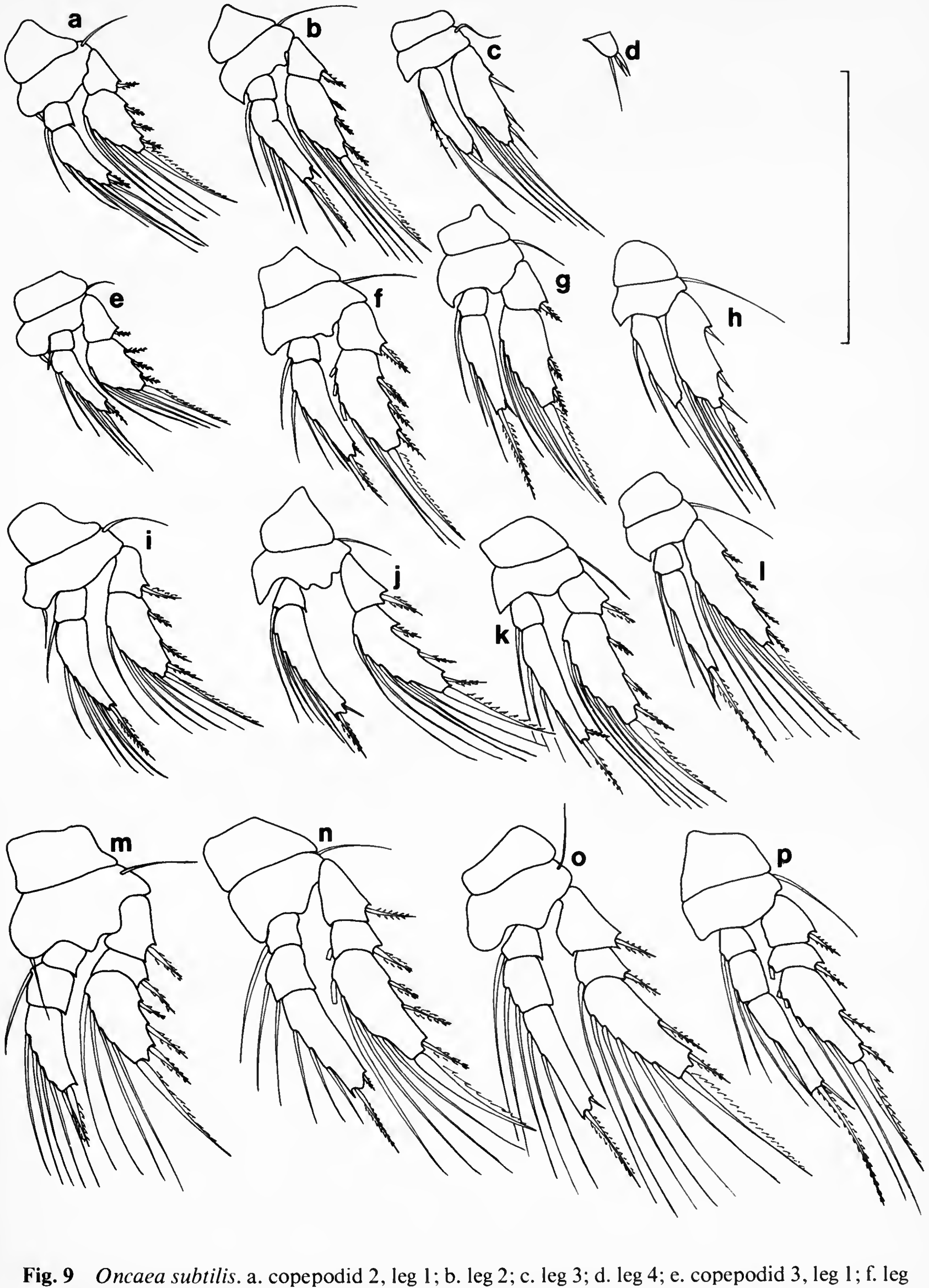

Fig. 9 *Oncaea subtilis*. a. copepodid 2, leg 1; b. leg 2; c. leg 3; d. leg 4; e. copepodid 3, leg 1; f. leg 2; g. leg 3; h. leg 4; i. copepodid 4, leg 1; j. leg 2; k. leg 3; l. leg 4; m. female copepodid 5, leg 1; n. leg 2; o. leg 3; p. leg 4. Scale 100 microns.

Generic characters in the Polynoinae (Annelida, Polychaeta), with notes on the higher classification of scale-worms (Aphroditacea)

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Introduction

A comparison of Fauvel, 1923 and Hartmann-Schröder, 1971, with Hartman, 1959, 1965 and Fauchald, 1977 shows that the limits of the genus *Harmothoe* and its sub-genera are confused. *Antinoella* Augener, 1928, *Austrolaenilla* Bergström, 1916, *Eucranta* Malmgren, 1865, *Eunoe* Malmgren, 1865 and *Harmothoe* Kinberg, 1855, are variously considered as genera or sub-genera of *Harmothoe sensu lato*. It was decided that this situation should be investigated preparatory to a study of the scale-worms of north-western Europe (George & Muir, in prep.).

The sub-family under consideration in this paper is often referred to as the Harmothoinae Willey, 1902. However, as the categories family and sub-family are co-ordinate according to the International Code of Zoological Nomenclature 1964 (articles 36 and 37), the correct name is Polynoinae Kinberg, 1855.

It should be borne in mind also that the word Polynoinae is often used to refer to that taxon herein called the family Polynoidae, when that family is thought of as a sub-family of the Aphroditidae (e.g. Fauvel, 1923; Day, 1967). The family Aphroditidae as used by these authors is equivalent to Fauchald's (1977) super-family Aphroditacea, i.e. it includes all scale-worms and excludes all others.

Materials and methods

Thirty-four of the genera or sub-genera, including the disputed five, of the Polynoinae were investigated. The type specimens of the type species of each genus were examined, where possible. The other type specimens appear to be either missing or not available on loan. For all except one of these remaining genera it was considered unsafe to rely on early, incomplete descriptions or possibly misidentified specimens from localities sometimes far distant from the type locality.

The exception was made for the important genus *Polynoe*, which provides the stem for the family-group names. *Polynoe scolopendrina*, the species usually cited as the type species (see Muir, 1979), has been described many times and there are many specimens in the collection of the BM(NH). A description was therefore compiled from Savigny, 1822; Fauvel, 1923; Day, 1967; Hartmann-Schröder, 1971 and ZK 1938.5.25.7, a specimen from East London, South Africa, which matches the description of Savigny, 1822. The type locality is 'côtes de l'océan', which refers to the Atlantic coast of France. As Savigny's polychaete type specimens are not in the Museum National d'Histoire Naturelle, Paris (Renaud-Mornant, *pers. comm.*), they have probably been destroyed (see Pallary, 1932).

The nominal genera studied are listed in Table 1, which also gives the Operational Taxonomic Unit (O.T.U.) numbers, i.e. *Bathylevensteinia* was the twenty-fifth taxon to have its details entered into the computer.

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Table 1 O.T.U. coding, with a list of material studied

O.T.U. number	Nominal genus	Type species	Material studied
01	Acanthicolepis McIntosh, 1900	Polynoe asperrima Sars, 1861	Oslo C 3154, syntypes
02	Adyte Saint-Joseph, 1899	Hermadion assimile McIntosh, 1876	BM(NH) ZK 1921.5.1.498–500, syntypes
03	Antinoe Kinberg, 1855	Antinoe microps Kinberg, 1855	Stockholm Typsaml. 407, holotype
04	Antinoella Augener, 1928	Antinoe sarsi Kinberg in Retzius, 1857	Stockholm 410, 413, syntypes
05	Arcteobia Annenkova, 1937	Eupolynoe anticostiensis McIntosh, 1874	BM(NH) ZK 1921.5.1.554–5, syntypes
06	Australaugeneria Pettibone, 1969*a*	Polynoe rutilans Grube, 1878	Pettibone, 1969*a* & pers. comm.
07	Austrolaenilla Bergström, 1916	Austrolaenilla antarctica Bergström, 1916	Stockholm Typsaml. 590, syntypes
08	Barrukia Bergström, 1916	Gattyana cristata Willey, 1902	BM(NH) ZK 1902.1.8.23–5, syntypes
25	Bathylevensteinia Pettibone, 1976	Macellicephala bicornis Levenstein, 1962	Pettibone, 1976 & pers. comm.
09	Enipo Malmgren, 1865	Enipo kinbergi Malmgren, 1865	Stockholm Typsaml. 2377, syntype
10	Eucranta Malmgren, 1865	Eucranta villosa Malmgren, 1865	Stockholm Typsaml. 2378, syntypes
11	Eunoe Malmgren, 1865	Eunoe oerstedi Malmgren, 1865	Stockholm Typsaml. 2390, 2391, 2395, syntypes
26	Gesiella Pettibone, 1976	Macellicephala jameensis Hartmann-Schröder, 1974	Hartmann-Schröder, 1974 & Pettibone, 1976
12	Gorekia Bergström, 1916	Malmgrenia crassicirris Willey, 1902	BM(NH) ZK 1902.1.8.67–74, syntypes
13	Harmothoe Kinberg, 1855	Harmothoe spinosa Kinberg, 1855	Stockholm Typsaml. 409, syntypes
14	Hartmania Pettibone, 1955	Hartmania moorei Pettibone, 1955	Pettibone, 1955 & pers. comm.
15	Herdmanella Darboux, 1899	Polynoe (?) ascidioides McIntosh, 1885	BM(NH) ZK 1855.12.1.92. holotype
27	Hermadion Kinberg, 1855	Hermadion magalhaensi Kinberg, 1855	Stockholm Typsaml. 532, holotype
16	Intoshella Darboux, 1899	Polynoe (Langerhansia) euplectellae McIntosh, 1885	BM(NH) ZK 1885.12.1.91, ZK 1921.5.1.548, syntypes
28	Kermadecella Darboux, 1899	Polynoe magnipalpa McIntosh, 1885	BM(NH) ZK 1885.12.1.98–98a, syntypes
17	Lagisca Malmgren, 1865	Polynoe rarispina Sars, 1861	Oslo C 3157, syntypes
18	Leucia Malmgren, 1867	Polynoe nivea Sars, 1863	Oslo C 3156, syntypes
19	Melaenis Malmgren, 1865	Melaenis loveni Malmgren, 1865	Stockholm Typsaml. 2383, syntype
20	Nemidia Malmgren, 1865	Nemidia torelli Malmgren, 1865	Stockholm Typsaml. 2379, syntypes
30	Neohololepidella Pettibone, 1969*b*	Neohololepidella murrayi Pettibone, 1969*b*	BM(NH) ZK 1937.9.2.29, holotype
21	Paradyte Pettibone, 1969*a*	Polynoe crinoidicola Potts, 1910	BM(NH) ZK 1924.3.1.85, syntypes
22	Phyllohartmania Pettibone, 1961	Phyllohartmania taylori Pettibone, 1961	Pettibone, 1961 & pers. comm.
23	Phyllosheila Pettibone, 1961	Phyllosheila wigleyi Pettibone, 1961	Pettibone, 1961 & pers. comm.
31	Polyeunoa McIntosh, 1885	Polyeunoa laevis McIntosh, 1885	BM(NH) ZK 1885.12.1.55, syntypes
29	Polynoe Savigny, 1818	Polynoe scolopendrina Savigny, 1822	See text
32	Polynoella McIntosh, 1885	Polynoella levisetosa McIntosh, 1885	BM(NH) ZK 1885.12.1.105, holotype
33	Robertianella McIntosh, 1885	Polynoe (Robertianella) synophthalma McIntosh, 1885	BM(NH) ZK 1885.12.1.101–2, syntypes
34	Scalisetosus McIntosh, 1885	Scalisetosus ceramensis McIntosh, 1885	BM(NH) ZK 1885.12.1.85, holotype
24	Tenonia Nichols, 1969	Tenonia kitsapensis Nichols, 1969	Nichols, 1969

Details of the external morphology of the worms were examined using a Wild M4A binocular microscope, at a magnification of ×60. Chaetae were examined, after removal of a parapodium and mounting in polyvinyl lactophenol, using a Wild M20 microscope, at a magnification of ×500.

Characters

The characters are discussed here in detail, because there is some confusion of terminology in the literature. Although internal characters have been used in some families (e.g. pharyngeal armature in Nereididae, nephridia in Terebellidae), only external characters have been examined in this study of type material. The character numbers and codings, as used in the data matrix, are listed after the discussion of the possible characters and their states.

Length, width and number of segments

Where possible, the length of the body (including head) and the greatest width (including parapodia, but not including chaetae) were measured. These measurements were then ranged from 0 to 100 (i.e. they were expressed as a percentage of the maximum length or width found). It will be seen from Fig. 1a that *Eunoe* (O.T.U. 11) is longer and wider than any other specimen measured. The other O.T.U.s, however, do not form a straight line between *Eunoe* and the origin. Length and width are therefore not perfectly correlated and must both be considered in the numerical part of this paper, even though width was measured more accurately than length in those cases where specimens were coiled or fragmented.

The relationship of length and width is easier to see in Fig. 1b, where a ranged value of length divided by width is plotted against a ranged value representing the number of segments. The number of segments for this purpose includes all the segments between the head and the pygidium, i.e. it includes the tentacular cirrus segment.

It will be seen that there are two groups along the L/W axis. Most of the O.T.U.s, including *Eunoe*, are grouped between 17 and 62 on this axis. The second group lies between 90 and 100 on the L/W axis and can be thought of as relatively long and thin, as opposed to the first group, which are more oval in shape and more obviously dorso-ventrally flattened.

Another interpretation of this scatter-diagram is that, apart from O.T.U.s 16 and 9, there is a correlation between shape and number of segments. If worm A has more segments than worm B it will probably be **relatively** longer and thinner, although not necessarily longer in **absolute** terms.

Grouping along the S axis is not so obvious as that along the L/W axis, with most of the O.T.U.s between 12 and 54, then *Polyeunoa* (O.T.U. 31) at 65, *Polynoe* (29) at 80 and *Neohololepidella* (30) at 100.

Head appendages

All members of the Polynoinae, when intact, have three antennae; one median antenna attached via a ceratophore to the anterior margin of the head and two lateral antennae attached via their ceratophores sub-distally and ventrally on the head. The lateral antennae appear always to be shorter than the median antenna, so this ratio was not used as a character.

Daly (1973*a*) has investigated the structure and function of the appendages of *Harmothoe imbricata* and describes the papillae on the surface of the antennae. It is likely that the antennae of all polynoid worms have a similar structure and function, although they are often described as smooth. The antennae, when present, were examined at a magnification of ×60 and described as either smooth or ornamented.

Daly (1973*a*) has described two different types of papillae on the surface of the palps, although these were not noted by Åkesson, 1963. The palps are described here as smooth or ornamented at ×60 and their length is compared with that of the median antenna when possible.

The head often carries eyes, usually four in number; a posterior pair and a pair wider apart, often at the sides of the head. I agree with Darboux (1899) that this is not an important characteristic. Not only does the pigment of the eyes fade after prolonged immersion in preserving fluids, so their presence is likely to be missed, but in some polychaetes the number and distribution of eyes is known to vary during the development of one individual, and also between individuals of one species.

Cirri

The various cirri have a similar structure and function to the antennae (Daly, 1973*a*). All polynoids possess two pairs of tentacular cirri. These structures, looking similar to the antennae, are attached via cirrophores directly to the sides of the first segment behind the head and are directed forward like the antennae. The dorsal pair are generally slightly longer than the ventral pair. The length of the longest tentacular cirrus is compared with that of the median antenna and they are described as smooth or ornamented.

The dorsal cirri are slightly more variable in shape than the antennae, not always having a sub-terminal swelling as the antennae do. They have been described as smooth or ornamented, and their length is compared with that of the parapodial lobes, i.e. if the tip of the cirrus extended further from the body than the lobes of the parapodium, it was described as longer.

Two types of ventral cirri occur in intact specimens. The most anterior pair are usually much longer than the others, and directed forwards, but were usually missing in the specimens studied. The normal ventral cirri are assessed for surface ornamentation, and length in comparison with that of the parapodia.

The anal cirri (sometimes called urites) were almost always missing in the specimens studied. They are usually similar to the dorsal cirri.

Parapodia

In the Polynoidae each segment except that bearing the tentacular cirri bears well-developed parapodia. In some cases the parapodia are distinctly elongated (i.e. the length of the parapodium from the side of the body to its distal extremity approaches the width of the body), so parapodial length was used as a character in the numerical analyses. The elongated state was present in eight of the thirty-four O.T.U.s investigated (23·5%), but is also found in some genera of the other subfamilies of Polynoidae. It is not clear, therefore, at this stage of the investigation, if either state can be called primitive with any degree of certainty.

Several descriptions of polynoids have been published which mention cilia on the parapodia, but cilia were not seen in the present study.

The parapodia bear chaetae (described below) and ventral cirri. They also bear either dorsal cirri or elytra. In one case, *Gesiella jameensis* (Hartmann-Schröder, 1974), the dorsal cirrophores also carry a structure unique among the polychaetes, called by Pettibone (1976) an accessory filamentous sensory organ. The presence or absence of this structure was used as a character in the numerical analyses, and presence was taken as the derived state.

Elytra

The elytra, singular elytron, are the scales which scale-worms carry dorsally. They are attached by short stalks or elytrophores to the dorsal surface of those parapodia which do not carry dorsal cirri. The elytrophores tend to be of greater diameter than the dorsal cirrophores and also to be nearer to the mid-line of the body. Thus the arrangement of the elytra can be discerned even when the elytra are missing.

The arrangement of the elytra has long been regarded as of great importance at the generic level. The arrangement is usually given as a list of the segments which carry the elytra. The

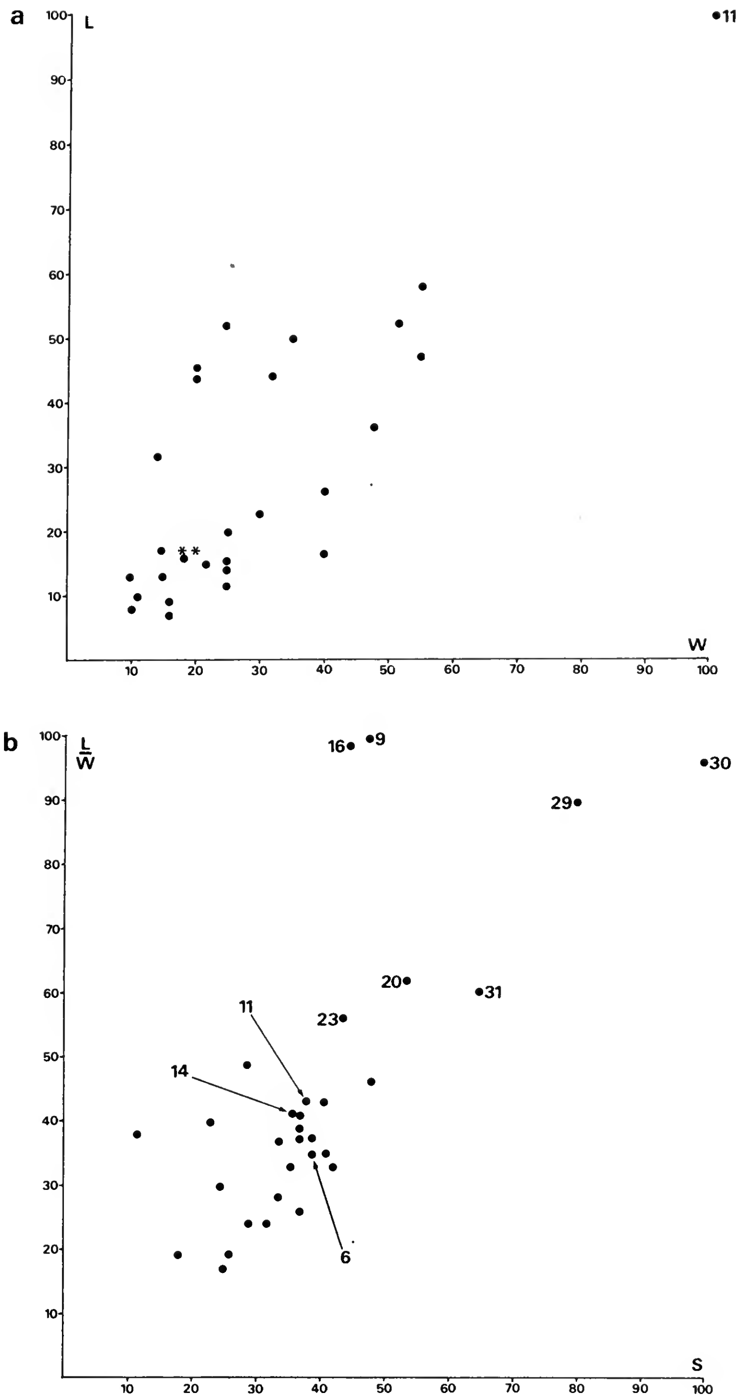

Fig. 1 (a) A scatter-diagram of ranged values of length (L) against ranged values of width (W). An asterisk represents two O.T.U.s. (b) A scatter-diagram of ranged values of length divided by width (L/W) against ranged values of number of segments (S). In both cases only those O.T.U.s especially mentioned in the text are numbered.

use of the term segment by itself is perhaps confusing in this situation, as it is not certain how many segments have been incorporated into the head (see Fauchald, 1974). Other authors have used the term setiger, meaning a segment which carries setae = chaetae. However, the tentacular cirrus segment may or may not display chaetae between the cirrophores, so that an elytron on the segment behind the tentacular cirri may be on setiger 1 or 2. I have therefore used the concept of the parapodial segment, i.e. a segment with distinct parapodia. Using this concept the most anterior elytra are always found on parapodial segment 1, and the standard arrangement of pairs of elytra is: 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31. A worm with only, say ten segments (including the tentacular cirrus segment) will only have nine parapodial segments, so the elytral arrangement will normally be: 1, 3, 4, 6, 8. This may explain why Darboux (1899) did not regard the number of elytra as a generic characteristic. Many polynoids have more than thirty-one parapodial segments, and these will normally either have a 'tail' region which does not bear elytra, or elytra will continue to be borne on every third segment.

The elytral arrangement has been scored as standard or non-standard in the numerical analyses, but there is a certain subjective element in judging whether an arrangement is standard or not when a minor variation is seen. The observations of Bergström (1916) on the posterior elytra of *Polyeunoa laevis* are of interest in this regard.

Five O.T.U.s were scored as non-standard, but their elytral arrangements were not the same as each other. Thus a certain amount of information has not been presented to the computer. The five arrangements are:

O.T.U. 9 *Enipo* (Right 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 25, 27, 30
(Left 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31
Asymmetrical, the right side being non-standard.
O.T.U. 12 *Gorekia* 1, 3, 4, 6, 8, 10, 12, (14?), 16, 18, 20, 23, 26, 29
O.T.U. 34 *Scalisetosus* 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 23, 26, 29, 32
Both change to every third segment after number 20 instead of number 22. Cirrophores of parapodial segment 14 of *Gorekia* not clear.
O.T.U. 18 *Leucia* 1, 3, 4, 6, 8, 10, 12, 14, 16 (17, 19, 23, 26, 29, 32)
Type broken at parapodial segment 16, but non-standard due to three non-elytrigerous segments in succession (i.e. 20, 21, 22).
O.T.U. 30 *Neohololepidella* 1, 3, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 25, 28, 31, 33, 35, 37, 39, 41, 43, 45, 47, 49, 51, 53, 55, 57, 59, 61, 63, 65, 67, 69, 71, 73, 75, 77, 79, 81, 83, 85, 87, 89, 91, 93, 95, 97, 99, 101, 103 (+?)
Returns to every second segment after number 31.

In descriptions of new genera or species of Polynoidae the elytra are usually described in some detail. The shape of any papillae, tubercles etc., on the surface is given, and any hairs or papillae forming a fringe on the postero-lateral rim are also described. It was found that, under increasing magnifications, a so-called hair became a papilla and a papilla could appear as a large tubercle. It was therefore decided to note 1) presence or absence of ornamentation on the dorsal surface. 2) presence or absence of fringe; at a magnification of ×60. The surface structure of the elytra of a range of scale-worms was investigated by Anton-Erxleben (1977) using a scanning electron microscope, and it appears that at very high magnifications the precise shapes of papillae, tubercles and scales, and the presence of pores in some of the Aphroditidae, can be a valuable taxonomic tool. It is not known which states of these characters concerning the elytra are primitive.

Body surfaces

The dorsal and ventral surfaces were both inspected, but no ciliation was observed. All the specimens in good condition showed a longitudinal ventral groove, however, which would be useful as a channel for a respiratory current as described by Dam (1940) for *Aphrodita aculeata*. Segrove (1938) and Lwebuga-Mukasa (1971) have described dorsal currents for some polynoids, and *Leucia* (O.T.U. 18) shows a dorsal groove from parapodial segment 12. Uschakov (1974) suggests that a dense grating of thin notochaetae (as in *Gattyana*) would protect this dorsal respiratory channel from obstruction in benthopelagic species which swim through water containing large amounts of detritus and suspended mineral particles.

Pettibone has described ciliated structures on O.T.U.s 6, 22 and 26, and other (non-ciliated) structures were seen on O.T.U.s 8, 11, 12 and 19, but these were not entered into the data matrix.

Nephridial Papillae

The nephridial papillae, seen at the postero-ventral base of the parapodia, were much more prominent in some specimens than in others, and this has been used as a character in the data matrix. The papillae were never dorsally directed as shown by Daly (1972) for a ripe female, and were never as elongated as he showed for a ripe male. Thus the specimens used in this study were probably not ripe. Specimens of *Polynoe scolopendrina* from North Uist (identified by McIntosh), Plymouth (Norman), Isles Chausey (Fauvel) and East London, South Africa (Stephenson) were examined, and all of them showed nephridial papillae enlarged but not elongated. As the specimens were of different sizes, and collected at different times from different places, it is unlikely that they were all collected at the beginning of the brief breeding season, and that the enlarged state is a developing stage of the elongated state. The enlarged state of the papillae is therefore probably a specific or generic characteristic rather than a seasonal or sexual one.

Daly (1972) states that the length of the nephridial papillae varies with the size of the individual for *Harmothoe imbricata.* This is shown in a general way by the data matrix, from which it can be seen that the specimens with small papillae have an average ranged length of 19·21, and those with large papillae have an average ranged length of 41·41. This latter figure is, of course, distorted by the presence of *Eunoe* (length 100), but also contains *Australaugeneria* (length 8). Enlarged papillae are shown by 12 (35·3%) of the O.T.U.s in the data matrix, and the distribution of this character in the other sub-families of the Polynoidae is not readily obtainable, so it cannot be said with confidence that one state is primitive or derived.

Colour

Colours and colour patterns are often seen in live and preserved polynoids. Daly (1973*b*), working with live animals, found intraspecific variation in the elytral patterns of *Harmothoe imbricata*. With preserved material, a dark surface can sometimes be seen flaking away from an otherwise colourless elytron. Again, with preserved material, colour is often leached out of the specimen by the preserving fluids. Alternatively, pigment may be dissolved out of the corks often used in the past to close containers and then transferred to the worm inside that container.

Chaetae, especially polynoid notochaetae, are sometimes coloured, and appear to keep their colour well when preserved. This colour varies from a pale yellow tint, through golden- or dark-brown, almost to black, but the range could not be subdivided because of the many intermediates seen.

For all these reasons, colour and colour patterns have not been considered useful taxonomic characters.

Chaetal diameter

Some authors, e.g. Darboux, 1899; Fauchald, 1977, use the relative thickness of the neurochaetae and notochaetae as a generic character. This can, of course, be very difficult to judge when there is a range of chaetae in both groups, and it has not been used as a character here. Bergström, 1916, considered this to be a useful character only at the specific level.

Neurochaetal shape

Unidentate

This common type has a long, thin shaft emerging from the surface of the neuropodium, abruptly widening to form a distinct 'shoulder' to the chaeta (Fig. 2a). The head of the chaeta, distal to the 'shoulder', is shorter than the shaft, and distinctly bent over at the tip, producing the unidentate effect. Between the tip and the 'shoulder' is a region which may bear quite large side-teeth, or may be serrated, or may merely bear faint striations on one side (see Fig. 2a). These states may all be present upon one parapodium, so they are not significant even at the specific level. It is probable that the side-teeth are usually fairly prominent in a newly secreted chaeta, but become worn in older chaetae.

Sesquidentate

This type is similar to the unidentate type (above), but bears a distinct hump below the bent-over tip (Fig. 2b). It is always found in conjunction with the unidentate or bidentate types.

Bidentate

This type is again similar to the unidentate type, but bears a distinct secondary tooth immediately below the bent-over tip (Fig. 2c).

Tridentate

This type is similar to the bidentate type (above), but bears a small tertiary tooth between the primary and secondary teeth (Fig. 2d).

Bergström, 1916 (p. 273 & Fig. 2), united the unidentate, sesquidentate and bidentate neurochaetae under the term 'Grundtypus'. The close relationship between these three types was shown in a startling manner by Hillger and Reish, 1970, in an experiment in which they converted a lepidonotine species with predominantly uni- and sesquidentate neurochaetae to one with predominantly sesqui- and bidentate neurochaetae (and vice versa) by letting amputated parapodia regenerate in warmer or colder water. Gaffney (1973) disagrees with some of the conclusions of Hillger and Reish, e.g. that temperature is the important factor, but it remains true to say that these chaetae are closely related. As Gaffney says, 'Examination of the setae reveals countless intermediates between the purely bifid and entire types, making the task of categorizing them a difficult one'. In my opinion, the tridentate neurochaetae (the *setae mucronatae* of Bergström) can be included with the above as a 'dentate series'. This series, as well as being common in the Polynoinae, is also commonly found in the Lepidonotinae, the other large sub-family of the Polynoidae. It may therefore be argued that possession of dentate neurochaetae can be regarded as a primitive trait.

Capillary Tip

These neurochaetae are similar to the unidentate type, except that the tip, instead of bending over to form a large, sharp tooth, extends into a long, thin filament (Fig. 2e).

Pointed Tip

Again, this is similar to the unidentate neurochaeta, but here the tip is not bent over (Fig. 2f).

Blunt Tip

This is as the pointed tip type, but blunt (Fig. 2g).

For the numerical part of this study I have united these three types as the 'simple tip' series. No work appears to have been published on the mode of formation of, or the effect of wear on, the chaetae of polynoids. However, Michaelis (1978) has shown that in spionid polychaetes chaetae with capillary tips do get worn down through a pointed stage to a blunt stage. This series, like the dentate series, is common to the Polynoinae and the Lepidonotinae, so presence may be a primitive trait, even though it is found less often than the dentate series in the specimens studied.

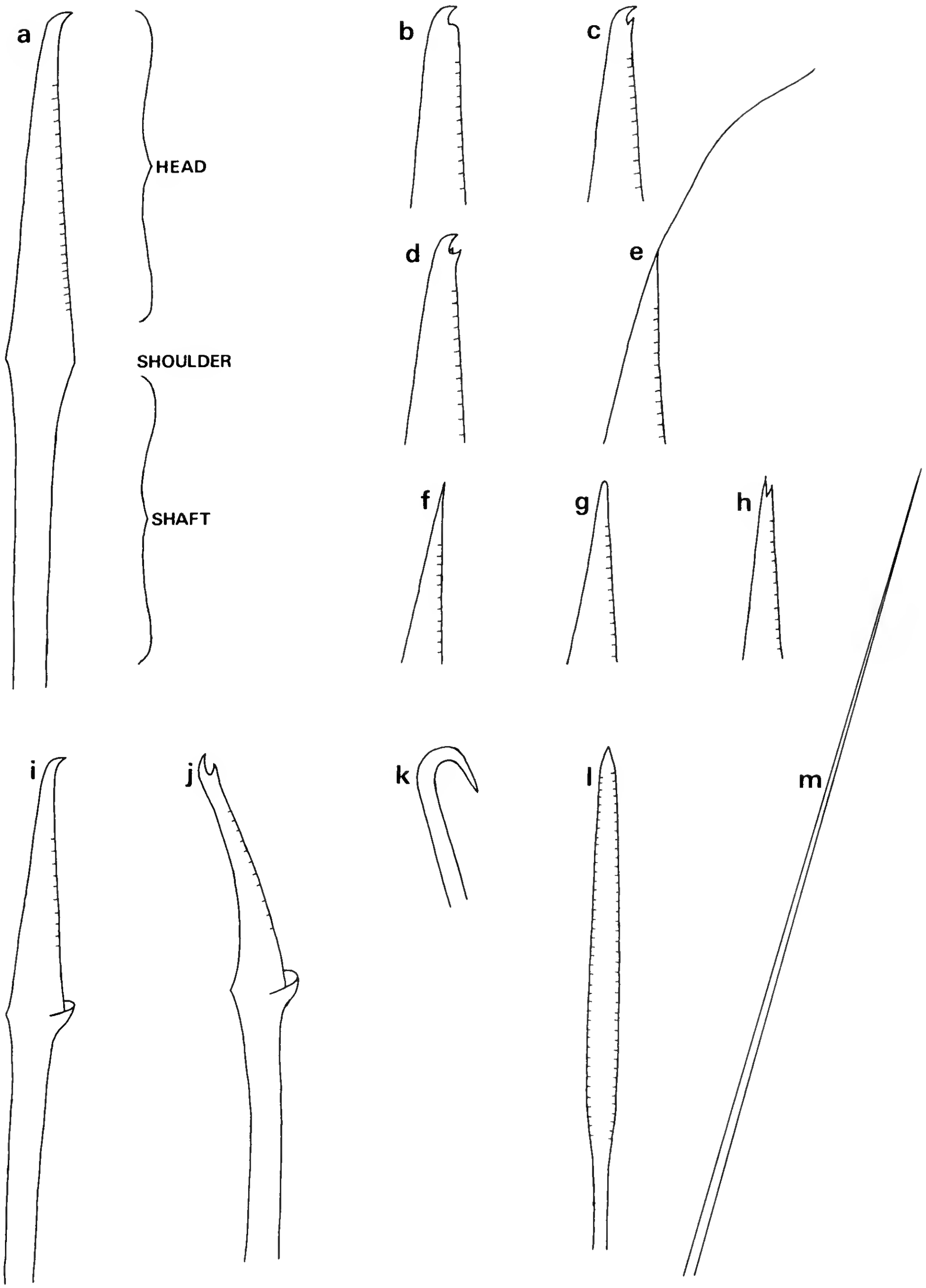

Fig. 2 Neurochaetal types. (a) Unidentate type. Complete chaeta showing regions. (b) Sesquidentate tip. (c) Bidentate tip. (d) Tridentate tip. (e) Capillary tip. (f) Pointed tip. (g) Blunt tip. (h) Unequal furcate tip. (i) Unidentate semi-lunar pocket type. (j) Bidentate, recurved, semi-lunar pocket type. (k) Anterior hook, after Pettibone, 1969*a*. (l) Flattened type, after Pettibone, 1976. (m) Capillary type.

Strong Type

This type is similar to the pointed, simple tip type, but is much more robust in appearance. It was seen only in *Polynoe scolopendrina*, where it is regarded as an advanced trait.

Unequal Furcate

These neurochaetae are similar to the pointed tip type (above), but in this case the tip is forked (Fig. 2h). The two forks are not divergent, and are not of the same length. The longer tip is not bent over as in the bidentate type. This character is unique to *Melaenis* amongst the Polynoinae. It is not found in the Lepidonotinae, although *Hermenia* is reported as having trifurcate neurochaetae. Its presence is therefore regarded as an advanced state.

Unidentate with Semilunar Pocket

This type is similar to the unidentate type described above, but on the 'shoulder', on the same side as the tooth points toward, bears a structure dubbed by Pettibone (1969*a*) 'basal semilunar cusp or pocket' (Fig. 2i).

Bidentate, Recurved with Semilunar Pocket

This type is like a bidentate form of the unidentate type with a semilunar pocket but it is usually strongly recurved (Fig. 2j).

I have united these two forms as the 'semilunar pocket' series in the numerical part of this paper. It is only found in two nominal genera of Polynoinae and not in the Lepidonotinae, and its presence is therefore likely to be an advanced trait.

Anterior Hook

Some polynoids possess, on the neuropodia of the first two or three segments, chaetae characterised by Pettibone (1969*a*) as 'stout golden hooks' (Fig. 2k). Being only found in the genus *Australaugeneria* its presence is an advanced trait.

Flattened

Gesiella jameensis (Hartmann-Schröder, 1974) is the only member of the Polynoinae to possess chaetae described by Pettibone (1976) as 'long, delicate, flattened, finely toothed along lateral borders, with tapered bare tips' (Fig. 2l).

Capillary

Herdmanella ascidioides (McIntosh, 1885) possesses capillary (i.e. long and very thin, see Fig. 2m) neurochaetae. I have regarded this as advanced in the Polynoinae, although it is found scattered throughout the Polychaeta, including *Frennia* (Lepidonotinae). The shape may have been produced many times independently, as it is a relatively simple structure.

Notochaetal shape

Bluntly Pointed

This is by far the most common type of notochaeta found in the Polynoidae, but does encompass a certain amount of variation. A typical member of this group will be the same diameter all along its length, slightly recurved, with a range of small side-teeth along the distal half of the convex side, and bluntly pointed at its tip (Fig. 3a). Members of this group may be slightly dilated in the region of the side-teeth, the side-teeth can be quite large or almost invisible, and the chaeta as a whole can be almost straight or strongly recurved in the region of the side-teeth. All these variations merge into one another, however, so I feel justified in calling them all one group of chaetae. Presence is a primitive trait in the Polynoidae.

Furcate

This type is similar to the bluntly pointed group of notochaetae, but the tip has a small though definite split which does not appear to be accidental damage (Fig. 3b, c). Its presence is rare and therefore probably an advanced trait in the Polynoinae.

Compressed

This group could be envisaged as flattened representatives of one of the previous two groups. They have fewer, but broader, side-teeth (Fig. 3d) and in *Adyte* and *Paradyte* can be furcate. Its presence is rare and therefore probably an advanced state in the Polynoinae.

Falciger

Fauchald (1977) defines falcigers as distally blunt and curved setae. *Eucranta*, as well as having the usual bluntly pointed notochaetae, has others which are straight almost until the distal end is reached, when they become strongly curved. These chaetae I have called falcigers, and their presence appears to be a derived trait.

Capillary

Several genera possess capillary notochaetae. As with the capillary neurochaetae, this may have been produced several times in the Polychaeta.

Paleae

These chaetae have a narrow proximal portion emerging from the parapodium which abruptly becomes widened and flattened before terminating in a blunt point (Fig. 3e). There are no side-teeth, and no 'shoulder' as seen in the neurochaetae. It is unique to *Antinoe* in the Polynoidae and can therefore be regarded as advanced.

Penicillate

Barrukia possesses normal, bluntly pointed notochaetae, and also others very similar to these but with the tip almost hidden by a mass of fine hairs. It is unique among the Polynoidae and therefore probably a derived character.

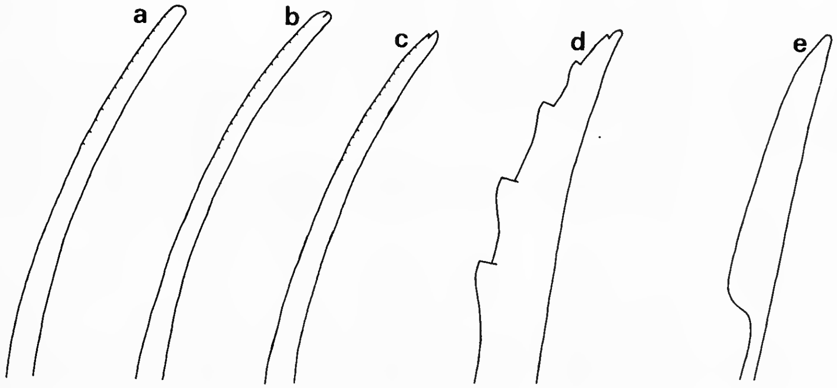

Fig. 3 Notochaetal types. (a) Bluntly pointed. (b) & (c) Two varieties of furcate tip. (d) Compressed type. (e) Palea.

Character coding

The characters used in the numerical part of this study are listed below, with their numbers and the coding used for their different states in the data matrix.

	Character	*Coding*
01	Neurochaetae, simple tip series	0 absent 1 present
02	Neurochaetae, dentate series	0 absent 1 present
03	Neurochaetae, unequal furcate	0 absent 1 present
04	Neurochaetae, semilunar pocket series	0 absent 1 present
05	Neurochaetae, anterior hooks	0 absent 1 present
06	Neurochaetae, flattened	0 absent 1 present
07	Neurochaetae, capillary	0 absent 1 present
08	Notochaetae, bluntly pointed	0 absent 1 present
09	Notochaetae, furcate	0 absent 1 present
10	Notochaetae, compressed	0 absent 1 present
11	Notochaetae, falcigers	0 absent 1 present
12	Notochaetae, capillary	0 absent 1 present
13	Notochaetae, paleae	0 absent 1 present
14	Notochaetae, penicillate	0 absent 1 present
15	Parapodial development	1 normal 2 elongated
16	Dorsal cirrus length: parapodium	1 shorter 2 equal 3 longer
17	Dorsal cirrus ornamentation	0 absent 1 present
18	Ventral cirrus length: parapodium	1 shorter 3 longer
19	Ventral cirrus ornamentation	0 absent 1 present
20	Length (including head and pygidium)	ranged from 0 to 100
21	Width (including parapodial lobes)	ranged from 0 to 100
22	Palp length: median antenna	1 shorter 3 longer
23	Tentacular cirrus length: median antenna	1 shorter 2 equal 3 longer
24	Antenna ornamentation	0 absent 1 present
25	Palp ornamentation	0 absent 1 present
26	Tentacular cirrus ornamentation	0 absent 1 present
27	Elytral arrangement	1 standard 2 non-standard
28	Elytral surface ornamentation	0 absent 1 present
29	Elytral fringe	0 absent 1 present
30	Nephridial papillae	1 small 2 enlarged
31	Accessory filamentous sensory organs	0 absent 1 present
32	Neurochaetae, strong	0 absent 1 present
33	Number of segments	ranged from 0 to 100

Computations and conclusions

Preliminary computations

The characters listed above are of three different types:

1. Those which are apparently derived, in which case absence of that character is not important from a phylogenetic point of view, i.e. two worms without that character are not necessarily similar and the computer will disregard those data. The characters in this group are numbered 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 31, 32. These are all binary characters (either present or absent) which are rarely present in the population under consideration.
2. Character 8 is a binary character which is almost always present in the population under consideration. It is also to be seen in other sub-families of the Polynoidae. This character is therefore regarded as primitive, and absence of this character may sometimes be significant. There are other characters for which it is not clear which states are primitive or

derived. It was therefore thought best that all states should be used in the calculations of overall similarity between the O.T.U.s. These characters are numbered 1, 2, 15, 16, 17, 18, 19, 22, 23, 24, 25, 26, 27, 28, 29, 30.

3. Characters 20, 21 and 33 are quantitative, and all values should be compared with all other values.

The character and O.T.U. codes have been given above. Descriptions of O.T.U.s and the resulting data matrix are available from the author. The data matrix was entered into the BM(NH) Varian mini-computer, a similarity matrix and the position of each O.T.U. on the first five principal coordinate axes were calculated, and the five nearest neighbours of each O.T.U. listed. The nearest neighbours are shown in Table 2.

The first and second coordinates of each O.T.U. were then plotted against each other (Fig. 4) in order to give the best graphical representation of similarities in two dimensions.

Table 2 List of first five nearest neighbours for each O.T.U. Thus the nearest neighbour of O.T.U. 1 is O.T.U. 13, with a similarity of 99·0%, and the second nearest neighbour is O.T.U. 3, with a similarity of 92·3%

	Nearest Neighbours									
O.T.U.	1		2		3		4		5	
01	13	99·0	03	92·3	33	90·9	18	88·3	05	87·3
02	21	99·7	32	76·0	16	72·0	28	71·9	26	69·2
03	01	92·3	13	88·9	28	87·5	05	85·6	33	85·4
04	33	77·6	01	76·7	14	72·7	07	72·7	03	72·3
05	28	92·7	18	92·6	16	92·1	13	92·0	33	91·5
06	24	72·9	09	70·4	32	69·1	33	67·1	12	65·6
07	13	98·4	01	84·9	08	83·9	33	83·5	25	81·3
08	13	90·4	01	86·4	07	83·9	33	82·7	17	80·7
09	15	78·6	06	70·4	24	68·5	32	64·2	26	61·9
10	27	73·9	01	68·7	33	67·3	13	66·0	17	65·4
11	07	80·7	13	78·8	27	74·7	29	73·7	08	73·7
12	18	94·3	28	88·2	30	84·3	16	84·3	05	83·0
13	01	99·0	07	98·4	05	92·0	08	90·4	18	90·2
14	04	72·7	22	65·8	19	64·8	07	61·3	03	58·5
15	09	78·6	24	71·1	32	69·9	28	64·0	16	63·8
16	28	97·2	05	92·1	32	90·7	33	90·3	31	87·3
17	33	87·8	08	80·7	13	80·3	27	78·9	07	75·4
18	12	94·3	05	92·6	28	91·8	30	91·0	13	90·2
19	20	69·5	14	64·8	04	64·3	28	63·2	10	62·6
20	11	72·9	19	69·5	07	67·7	22	64·1	04	62·3
21	02	99·7	32	79·0	16	74·5	28	74·3	26	71·1
22	24	79·3	01	70·8	04	67·2	14	65·8	20	64·1
23	25	79·9	28	72·9	05	71·6	18	70·8	16	70·8
24	22	79·3	05	76·9	32	76·8	25	74·8	28	73·2
25	28	89·7	05	88·8	13	87·5	16	86·8	07	81·3
26	28	83·9	16	78·9	32	78·5	31	77·4	05	77·4
27	13	85·1	33	84·0	17	78·9	08	77·1	01	76·2
28	16	97·2	05	92·7	32	92·4	33	91·8	18	91·8
29	11	73·7	07	70·3	04	70·1	13	67·2	01	64·6
30	18	91·0	16	84·9	12	84·3	01	83·5	13	81·8
31	28	88·8	16	87·3	34	84·2	05	83·7	33	79·4
32	28	92·4	16	90·7	05	86·3	18	85·6	31	84·2
33	28	91·8	05	91·5	01	90·9	16	90·3	13	89·6
34	18	74·2	33	74·0	32	71·8	12	69·1	27	67·0

Conclusions

It will be deduced from Table 2 and Fig. 4 that *Harmothoe* (O.T.U. 13) is very similar to O.T.U.s 1 (*Acanthicolepis*) and 7 (*Austrolaenilla*). *Austrolaenilla* is one of the genera that Hartmann-Schröder (1971) wished to make a sub-genus of *Harmothoe.* The other three genera that she specified (O.T.U.s 4, 10 and 11) are much more dissimilar. It is unfortunate that there are seven variates missing from the syntypes of *Harmothoe*, but as they and the types of *Austrolaenilla* are so similar, and as *Harmothoe* contains 120 species (*fide* Fauchald,

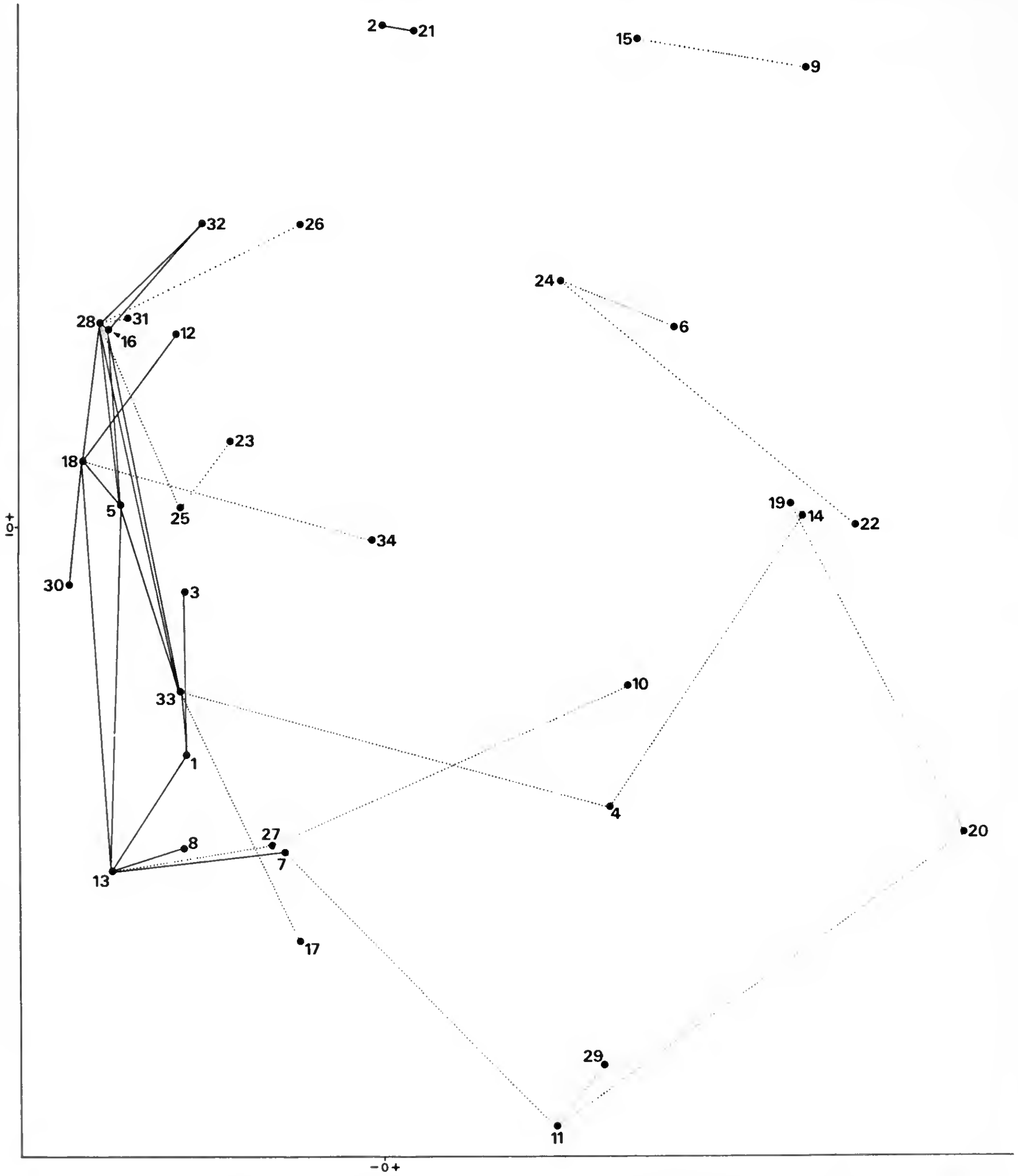

Fig. 4 A scatter-diagram of O.T.U.s plotted on principal coordinate axes 1 (vertical) and 2 (horizontal). Those O.T.U.s which are more than 90% similar to each other are joined by solid lines, the others are connected to their nearest neighbour by a broken line.

1977) and so probably covers a wide range of variation, I would agree with Hartmann-Schröder, who studied a wider range of specimens, that these two genera are synonymous. *Acanthicolepis* was considered a separate genus by Hartmann-Schröder, 1971, and Fauvel, 1923. The types of *Austrolaenilla* and *Harmothoe* are 98·4% similar, but those of *Acanthicolepis* and *Harmothoe* are 99·0% similar, so it would be sensible to synonymize *Acanthicolepis* as well. It would be of value to study the 130 or so species of this group to see if there are any noticeable phenetic gaps between them. *Harmothoe* is the oldest of these three genera, and is the central one in Fig. 4, so nomenclaturally and numerically it would be correct for *Harmothoe* to remain the name of a new enlarged genus.

O.T.U.s 2 (*Adyte*) and 21 (*Paradyte*) are even more similar to each other. *Paradyte* was erected by Pettibone (1969*a*) for three species with fewer segments than the only species left in *Adyte*, and with both types of semilunar pocket series chaetae (*Adyte* only has the bidentate, recurved type). The number of segments does not appear to be of importance at the generic level from a comparison of Figs. 1 and 4. The two types of semilunar pocket series chaetae are such complex structures, and yet so similar to each other, that I believe they must be closely related. I would therefore synonymize *Paradyte* Pettibone, 1969*a* with *Adyte* Saint-Joseph, 1899, although perhaps retaining *Paradyte* as a sub-genus.

O.T.U.s 16 (*Intoshella*) and 28 (*Kermadecella*) are also very similar to each other. The main differences between the types lie in the length and number of segments. The median antennae are missing from the types of *Kermadecella*, but the ratio of lengths of the palps and tentacular cirri seems similar to that shown by the types of *Intoshella*. Both genera were erected by Darboux, 1899, probably from the published descriptions of the type species by McIntosh, 1885. The defining characteristic of *Kermadecella* is that the dorsal cirri are alternately long and short. This is by no means obvious from the types, and as *Kermadecella* only has one species, it may safely become a junior synonym of *Intoshella*, which has three species.

O.T.U.s 16 and 28 are 97·2% similar. The next most similar pair of O.T.U.s are 12 and 18 (*Gorekia* and *Leucia*) at 94·3%. *Gorekia* possesses furcate notochaetae as well as the bluntly pointed type, *Leucia* does not. *Leucia* is distinctly wider than *Gorekia*. *Gorekia* shows two annuli per segment dorsally, while *Leucia* has a dorsal longitudinal groove from parapodial segment 12. It was therefore decided that these O.T.U.s represent distinct genera, and that 95% similarity would be a convenient cut-off point for generic identity in this study.

Secondary computations

Because O.T.U.s 1, 7, 21 and 28 have been synonymized with other O.T.U.s (above), it is necessary to run the data for the thirty remaining O.T.U.s through the computer again. Their nearest neighbours are shown in Table 3.

The first and second coordinates have been plotted against each other in Fig. 5. I have also plotted the first coordinates against the third in Fig. 6, to give a better idea of the O.T.U. distribution in multi-dimensional space, and to show why O.T.U.s 14, 19 and 22 are not directly connected to each other on a minimum spanning tree. A tree is a set of straight lines joining pairs of points such that all points are connected to each other, but no closed geometric shapes are formed. The minimum spanning tree uses the shortest possible set of lines in multi-dimensional space, i.e. it links O.T.U.s with high similarities.

Discussions

Previous theories on the inter-relationships of the Polynoinae

Darboux (1899), although considering the Polynoidae to be only one sub-family, split them up into five series. The genera of the Polynoinae that he knew of were put into his series D and E along with some Lepidonotinae. The members of series D were supposed to be long and cylindrical, while the members of series E are short and flattened.

The long, cylindrical group contained O.T.U.s 9, 20, 29 and 31, which are either in the top group or at the top of the lower group in Fig. 1b.

The short, flat group contained O.T.U.s 1, 3, 10, 11, 13, 15, 16, 17, 18, 19, 27, 28, 32, 33 and 34. This group therefore contained the longest genus (*Eunoe*, O.T.U. 11) and the relatively thinnest genus, O.T.U. 16, although this latter (*Intoshella*) was not mentioned in the discussion which followed the listing.

Not only is this division into two series therefore inconsistent with the definitions of the series, but the four genera of series D are well separated on Fig. 5. This shows that the other characters do not segregate along with body shape, and that the two series are therefore an artificial division.

Segrove (1938), basing his ideas on the surface ciliation, considered *Harmothoe* (O.T.U. 13) to show the primitive condition for all scale-worms, with one evolutionary line going through *Lagisca* (O.T.U. 17) to *Polynoe* (O.T.U. 29).

Uschakov (1974, 1977) is the latest author to discuss the phylogeny of this group, and he concentrates on shape and the arrangement of the elytra, which he relates to commensalism, especially commensalism of a polynoid in the tube of another organism. It is interesting to note here the work of Wagner, Phillips, Standing and Hand (1979), which shows that commensalism may not always be the correct term to describe the associations between polynoids and other organisms.

Table 3 List of first five nearest neighbours for each O.T.U. after removal of O.T.U.s 1, 7, 21 and 28

	Nearest Neighbours									
O.T.U.	1		2		3		4		5	
02	32	75·9	16	72·0	26	69·2	31	65·3	05	64·1
03	13	88·9	05	85·6	33	85·4	18	82·3	16	81·5
04	33	77·5	14	72·7	03	72·3	13	71·1	29	70·0
05	18	92·6	16	92·0	13	92·0	33	91·4	25	88·8
06	24	72·9	09	70·4	32	69·0	33	67·1	12	65·6
08	13	90·3	33	82·6	17	80·7	05	80·5	18	77·9
09	15	78·6	06	70·4	24	68·4	32	64·2	26	61·8
10	27	73·9	33	67·1	13	65·8	17	65·4	04	63·4
11	13	78·4	27	74·6	29	73·5	17	73·4	08	73·4
12	18	94·3	30	84·3	16	84·2	05	83·0	32	82·2
13	05	92·0	08	90·3	18	90·2	33	89·6	03	88·9
14	04	72·7	22	65·7	19	64·7	03	58·5	20	58·3
15	09	78·6	24	71·1	32	69·8	16	63·8	22	63·5
16	05	92·0	32	90·6	33	90·3	31	87·2	25	86·7
17	33	87·7	08	80·7	13	80·2	27	78·8	11	73·4
18	12	94·3	05	92·6	30	90·9	13	90·2	16	86·7
19	20	69·4	14	64·7	04	64·2	10	62·6	05	62·4
20	11	72·8	19	69·4	22	64·0	04	62·3	29	61·7
22	24	79·3	04	67·2	14	65·7	20	64·0	15	63·5
23	25	79·8	05	71·5	16	70·8	18	70·7	13	70·6
24	22	79·3	05	76·9	32	76·7	25	74·8	06	72·9
25	05	88·8	13	87·4	16	86·7	18	79·9	23	79·8
26	16	78·8	32	78·5	31	77·4	05	77·4	33	73·1
27	13	84·9	33	83·8	17	78·8	08	77·0	05	75·0
29	11	73·5	04	70·0	13	67·2	08	63·3	27	62·4
30	18	90·9	16	84·8	12	84·3	13	81·7	05	81·4
31	16	87·2	32	84·2	05	83·7	33	79·3	30	78·9
32	16	90·6	05	86·3	18	85·5	31	84·2	33	83·3
33	05	91·4	16	90·3	13	89·6	17	87·7	03	85·4
34	18	74·2	33	74·0	32	71·7	12	69·1	27	66·8

Hartmania (O.T.U. 14) is the only O.T.U. investigated which was found living in tubes (actually burrows of *Neanthes virens*), and it had a standard elytral arrangement. Other O.T.U.s with standard elytral arrangements were found in association with echinoderms (21, 23), ascidians (15), coelenterates (6), sponges (16) or living free (the other twenty-three O.T.U.s). Of the five O.T.U.s with non-standard elytral arrangements, one (30) was in the central cavity of a calcareous sponge. Thus 20% of the O.T.U.s with non-standard arrangements, and 20% of O.T.U.s with standard arrangements (after synonymizations) are 'commensals'. Statistically, therefore, elytral arrangement and 'commensalism' are not correlated.

Two of the 'commensal' O.T.U.s (16, 30) are in the relatively long and thin group of Fig. 1b, and one of the other four or five (23) is near the top of the other group. O.T.U.s 6 and 14 have lower values of ranged L/W. O.T.U.s 15 and 21 were incomplete. Again, this distribution is not statistically significant.

Uschakov actually cites *Polyeunoa* (O.T.U. 31) as a primitive type and *Polynoella* (O.T.U. 32) as an advanced type, but these two genera have similar coordinates (see Figs. 5 & 6).

Groupings within the Polynoinae

One of the obvious features of Figs. 5 and 6 is the 'back-bone' formed by the O.T.U.s which are 90–95% similar to each other. This group has a wide spread on axis 1 but a small spread on vectors 2 and 3.

The group includes O.T.U.s 12, 18 and 30, which have non-standard elytral arrangements. O.T.U. 34 is loosely attached to these three, but the fifth O.T.U. with a non-standard arrangement (O.T.U. 9) is widely separated on vector 2. The arrangement on O.T.U.s 12 and 34 is very similar, and O.T.U. 18 also has similarities. *Neohololepidella* (O.T.U. 30) has a normal arrangement up to parapodial segment 31, and then returns to every second segment rather than every third segment. O.T.U.s 12 and 18 (*Gorekia* and *Leucia*) have other similarities to each other, but O.T.U.s 30 and 34 (*Neohololepidella* and *Scalisetosus*) have many missing data. These O.T.U.s may all be regarded as being derived with respect to this character.

The other 'back-bone' genera with obviously derived character traits are O.T.U.s 8 and 32. O.T.U. 8 (*Barrukia*) has penicillate notochaetae in addition to the bluntly pointed type. These are very similar to each other, and the penicillate type could easily be derived from the usual type. O.T.U. 32 (*Polynoella*) has no notochaetae at all. Loss of a character, in this case bluntly pointed notochaetae, is generally regarded as of little importance from a phylogenetic point of view.

Of the four remaining 'back-bone' genera, O.T.U. 16 (*Intoshella*) has no ornamentation on the elytra, O.T.U. 5 (*Arcteobia*) has surface ornamentation but no fringe, and O.T.U. 13 (*Harmothoe*) has surface ornamentation and a fringe. These data are missing from O.T.U. 33 (*Robertianella*) which, however, has large nephridial papillae, whereas the others have small papillae. These four O.T.U.s could perhaps be regarded as primitive members of the Polynoinae, although none of them, of course, can be called an ancestral form.

A group of O.T.U.s which are weakly linked to each other, but which have important similarities to each other, consists of O.T.U.s 6, 9, 15, 22 and 24, which have positive first and second eigenvector coordinates but are widely spread on eigenvector 3. This group of five O.T.U.s all have elongated parapodia (a trait shared with O.T.U.s 23 and 25 which are also linked to O.T.U. 5; and O.T.U. 20) and do not have bluntly pointed notochaetae (a trait shared with O.T.U.s 2, 32 and 34). O.T.U. 32, as stated above, has no notochaetae, but it has dentate neurochaetae. O.T.U.s 2 (*Adyte*) and 34 (*Scalisetosus*) share character 10 (compressed notochaetae), but have other different, derived characters (semilunar pocket series neurochaetae for O.T.U. 2 and elytral arrangement for O.T.U. 34). O.T.U.s 23 and 25 (*Phyllosheila* and *Bathylevensteinia*) have dentate neurochaetae and bluntly pointed notochaetae (agreeing with the 'back-bone' genera) whereas O.T.U. 20 has simple-tip neurochaetae and bluntly pointed notochaetae (perhaps also a primitive arrangement).

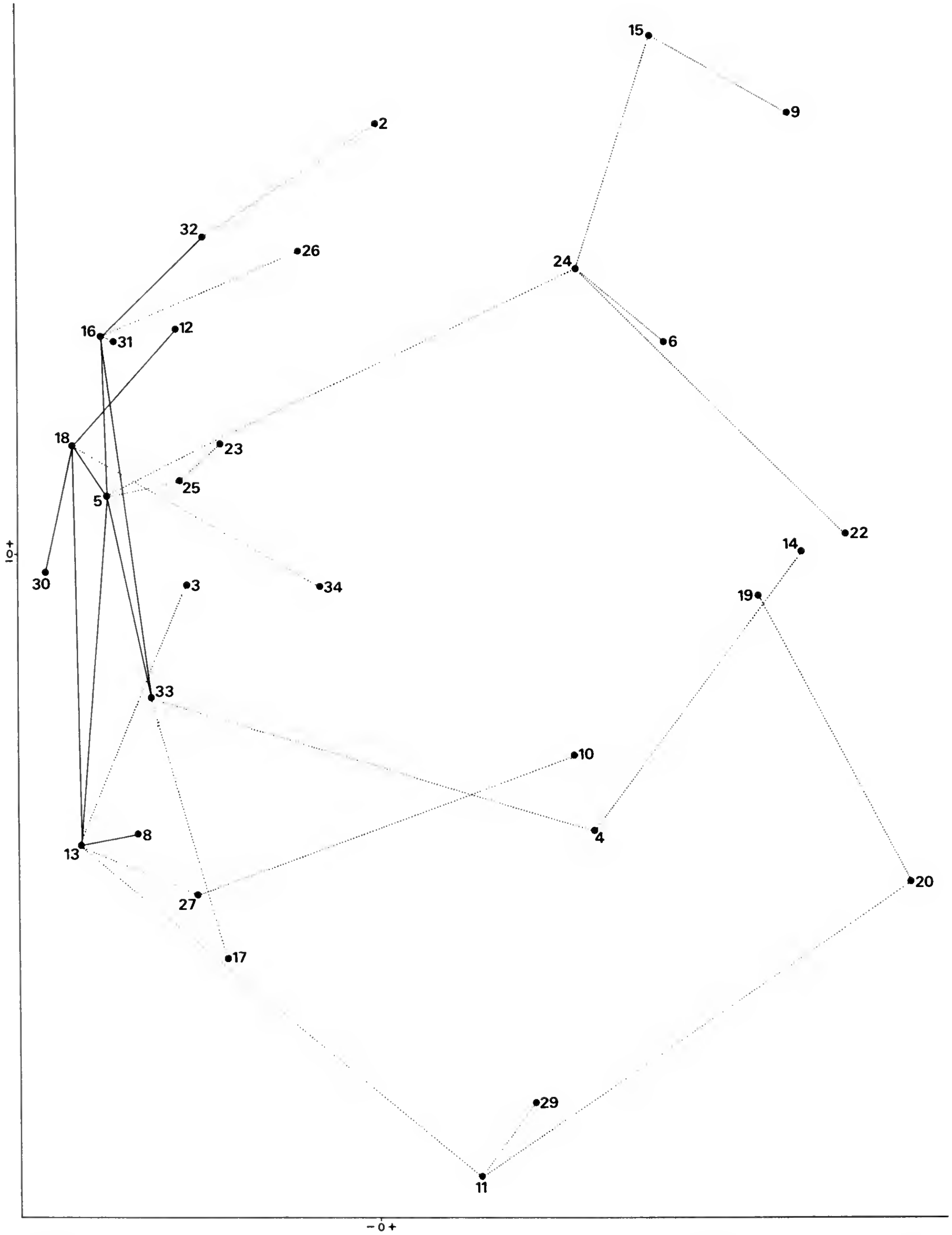

Fig. 5 A scatter-diagram of the 30 O.T.U.s which are less than 95% similar to each other, plotted on principal coordinate axes 1 (vertical) and 2 (horizontal). O.T.U.s 90–95% similar to each other are joined by solid lines, the others are linked in a minimum spanning tree by broken lines.

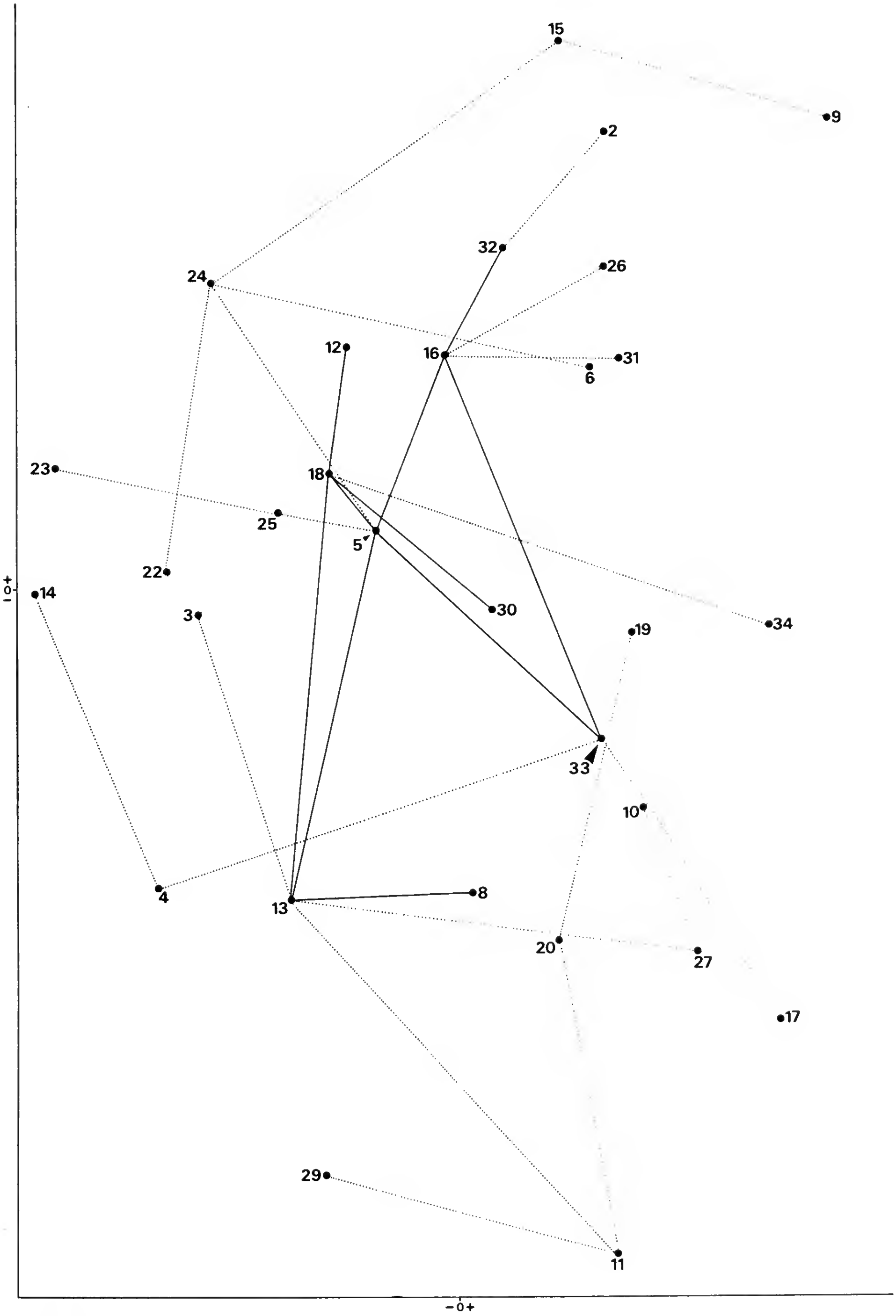

Fig. 6 As Fig. 5, but using principal coordinate axes 1 (vertical) and 3 (horizontal).

O.T.U.s 9 (*Enipo*), 15 (*Herdmanella*), 22 (*Phyllohartmania*) and 24 (*Tenonia*) have capillary notochaetae, whereas O.T.U. 6 (*Australaugeneria*) has furcate notochaetae. Thus they are all derived with regard to notochaetae as well as with regard to parapodial development. O.T.U.s 9, 22 and 24 have primitive neurochaetae. O.T.U. 6 has anterior hooks as well as primitive neurochaetae, and O.T.U. 15 has only got capillary neurochaetae. In my opinion these can be regarded as a distinct, derived group within the Polynoinae, with the possible exception of *Herdmanella*. There is a lot of missing data with regard to this O.T.U. In particular the anterior end is missing, which means that it cannot be referred with certainty to any polynoid sub-family. Pettibone (1976) refers to the genus and species as 'doubtful Polynoidae'.

Uschakov (1977), discussing the Macellicephalinae as defined by Hartmann-Schröder (1971, 1974) states that the characters (*a*) body consistency very soft; (*b*) elytra easily fall off; (*c*) bristles fine and long; (*d*) parapodia greatly elongated; (*e*) dorsal cirri extremely long; all facilitate swimming near the bottom in search of food at abyssal depths. *Herdmanella*, which has all these characters, was found at 2600 fathoms (4755 m) in the branchial chamber of an ascidian. It is possible that this was a hiding place used for protection between feeding forays. The other four members of this group appear slightly less specialized for abyssal life, and at least two of them (O.T.U.s 22 and 24) were found in shallow water. The depths were not given for O.T.U.s 6 and 9. O.T.U. 6 was found in association with the soft coral *Xenia*, so it is possible that the anterior hooks are an adaptation for attachment to the host.

In the bottom half of Fig. 5 there is a group of O.T.U.s which are loosely related phenetically to each other and to the 'back-bone' O.T.U.s. There are three lines of O.T.U.s attached to 'back-bone' O.T.U. 13, (*a*) 11, 29, 20, 19. (*b*) 27, 10. (*c*) 3. O.T.U. 33 gives rise to two lines, (*a*) 4, 14. (*b*) 17. In general, it will be noted that these O.T.U.s are greatly ornamented on some or all of the cirri, antennae, palps and elytra, although there is some missing information for O.T.U.s 3, 4, 10 and 27. All these O.T.U.s also have one or two derived character states and, or, large nephridial papillae. O.T.U. 33 is the only 'back-bone' O.T.U. with enlarged nephridial papillae, so perhaps this trait may also be regarded as derived.

O.T.U. 31 (*Polyeunoa*) is similarly phenetically related to the 'back-bone' at O.T.U. 16, neither of these displaying ornamentation. Again, O.T.U. 31 is not actually a member of the 'back-bone' group because it displays derived states for other characters, i.e. long ventral cirri, and perhaps the short palps and tentacular cirri are also derived.

O.T.U. 26 is similarly placed to O.T.U. 31 for similar reasons. However, whereas the derived states in O.T.U. 31 can be seen to be closely related to primitive states of the same characters in other O.T.U.s, the derived states seen in O.T.U. 26 (*Gesiella*) are completely new structures (flattened neurochaetae with fine lateral teeth and filamentous accessory organs on the dorsal cirrophores).

Out-group comparisons

Of the notochaetae, the bluntly pointed type is probably more primitive than the others, being much more common both in the Polynoinae and in the Lepidonotinae than the other notochaetal types. Of the neurochaetae, the dentate series is present in two-thirds of the specimens studied, and the simple-tip series is present in one-third, with, however, a degree of overlap occurring. The 'back-bone' O.T.U.s only possess dentate series neurochaetae, and the O.T.U.s which have simple-tip neurochaetae but not dentate neurochaetae (O.T.U.s 9, 10, 14, 19, 20 and 22) are far removed from the 'back-bone' because they have other, derived, character states. Does this mean that the dentate series is therefore the most primitive neurochaetal group in the Polynoinae? Both dentate series and simple-tip series neurochaetae are present in the Lepidonotinae, so one might presume that the common ancestor of these two sub-families possessed both types of chaetae. The next stage in this line of investigation is to look for a suitable out-group for comparison in the other families of scale-worms. The Sigalionidae and Peisidicidae both have composite neurochaetae and therefore are of no help. The Eulepethidae have a different complex of neurochaetae and also other differences from the Polynoidae such as the presence of branchiae and a single anal cirrus. The Aphroditidae again have a different complex of neurochaetae and other characters such as a papillate ventral surface to the body and parapodia, and absence of anal cirri. Several members of the family Polyodontidae have neurochaetae with a distinct 'shoulder', and some of these appear to be identical with the simple-tip neurochaetae with a capillary ending seen in the Polynoinae (see Strelzov, 1968, 1972). The only character which differs between all Polynoidae and all Polyodontidae is the spinning glands which are present in the Polyodontidae. These glands, found in the notopodia, secrete fibres which the worm uses to build a thick tube. Pflugfelder (1934) concluded that the fibres produced by the spinning glands are, in construction and origin, typical chaetae. Capillary notochaetae are also found in at least some polyodontids. The antennae are variable in number and point of insertion, but this is also true of the Polynoidae, especially since the erection of five new sub-families by Pettibone (1976). Some polyodontids have eyes on large ommatophores, but in others (e.g. *Eupanthalis kinbergi*) the eyes look similar to those found in polynoids. Polyodontids have two anal cirri, as do polynoids. The elytra are said to occur on parapodial segments, 1, 3, 4 and then every second segment, a situation seen in *Bathylevensteinia* and approached by *Neohololepidella* among the polynoids studied.

The presence of simple-tip neurochaetae in the Polyodontidae does not necessarily prove that they are more primitive than dentate series neurochaetae but does raise doubts as to the wisdom of retaining the Polyodontidae as a separate family.

A. If the Polyodontidae are defined by the presence of the spinning glands, then the Polynoidae can only be defined as polyodontids without spinning glands. As the polyodontids are the only polychaetes with spinning glands, this can be regarded as a derived character state. The Polynoidae then become a paraphyletic group, i.e. they consist of all the descendants of a common ancestor except those which evolved spinning glands.

B. If the Polyodontidae are accepted as a family because of their one unique derived character, why should *Gesiella*, with two unique derived structures as far as the Polynoinae are concerned, only be accepted as a genus?

Three of Pettibone's new sub-families are mono-specific (Pettibone, 1976). On the present evidence it would make sense to raise *Gesiella* to sub-familial status (as Gesiellinae) and to lower the Polyodontidae to the status of a sub-family within the Polynoidae (as Polyodontinae Pflugfelder, 1934 (1855)).

GESIELLINAE sub-fam. nov. Members of the Polynoidae with accessory filamentous sensory organs attached to the dorsal cirrophores. Type genus *Gesiella* Pettibone, 1976.

Key to families of Aphroditacea

1 Composite neurochaetae present 2
– All chaetae simple 3

2 Elytra, with concentric rings, present on alternate segments along body. One antenna present **PEISIDICIDAE**
– Elytra, without concentric rings, on alternate segments anteriorly and all segments posteriorly. One to three antennae present . . . . **SIGALIONIDAE**

3 Neuraciculae distally hammer-headed . . . . **EULEPETHIDAE**
– Neuraciculae distally pointed 4

4 Notochaetae including felt (covering dorsal surface) or erect, harpoon-shaped, flattened spines . . . . **APHRODITIDAE**
– Notochaetae, if present, never as felt or harpoon-shaped . . . . . **POLYNOIDAE**

The family-group name Peisidicidae Darboux, 1899 has priority over Pholoididae Fauchald, 1977 (International Code of Zoological Nomenclature 1964 (articles 36 and 40)).

Key to sub-families of Polynoidae

This key to sub-families is a provisional one. The genus *Cervilia*, according to Fauchald (1977) is of unknown sub-family. As the Polynoinae and Lepidonotinae were originally defined on the position of attachment of the lateral antennae, perhaps *Cervilia* should be placed in a new sub-family Cerviliinae. Alternatively, if the Polynoinae contains groups of species evolving in parallel with groups of species in the Lepidonotinae, perhaps the position of attachment of the lateral antennae is not important and these sub-families could be amalgamated and then broken down again in a more meaningful manner, e.g. *Polynoe scolopendrina* (a polynoine) and *Lepidasthenia elegans* (a lepidonotine) both have dentate neurochaetae with one or two stronger chaetae per segment, they are both long and thin, and they are both often found in terebellid tubes. Obviously much work remains to be done on these groupings.

1	Spinning glands present in some notopodia	**POLYODONTINAE**
–	Spinning glands absent	2
2	Antennae absent	3
–	Antennae present	4
3	Scale-lobe on parapodial segment 5. Elongate parapodia. 7 pairs of pharyngeal papillae	**POLARUSCHAKOVINAE**
–	Scale-lobe absent. Notopodia short. 9 pairs of pharyngeal papillae, two of them elongated	**BATHYEDITHINAE**
4	Median antenna absent	5
–	Median antenna present	6
5	Lateral antennae attached posteriorly	***Cervilia***
–	Lateral antennae attached anteriorly	**IPHIONINAE**
6	Only one antenna present (*note* frontal filaments may be present laterally to the antenna)	7
–	Three antennae present	9
7	Notochaetae present	**MACELLICEPHALINAE**
–	Notochaetae absent	8
8	Notopodia greatly reduced	**MACELLOIDINAE**
–	Notopodia forming very long, projecting acicular lobes enclosing a very stout acicula	**MACELLICEPHALOIDINAE**
9	Pharynx without papillae or jaws. Palps never visible dorsally	**BATHYMACELLINAE**
–	Pharynx with papillae and jaws. Palps usually visible dorsally	10
10	Lateral antennae attached distally on prostomium	11
–	Lateral antennae attached ventrally, sub-distally	12
11	Antennal scales, antennal sheath and tentacular sheath present	**ADMETELLINAE**
–	These structures absent	**LEPIDONOTINAE**
12	Accessory filamentous sensory organs present	**GESIELLINAE**
–	These organs absent	**POLYNOINAE**

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A new genus of ranine frog (Anura: Ranidae) from Somalia

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Introduction

Lanza (1978) described a new species of ranine frog from the Nogal Valley in northern Somalia and tentatively assigned it to the genus *Hildebrandtia* Nieden, 1907. However, he stressed that 'As the phylogenetic relationships between the various forms which have been included at one time or another under the name *Rana* are very questionable, I prefer to assign the new frog tentatively to *Hildebrandtia* rather than to a new genus'. Lanza consequently named his new species *Hildebrandtia* (?) *largeni*.

In a recent survey of African ranine frogs (Clarke, 1981) based on 22 osteological characters, evidence emerged for the recognition of a new genus to accommodate *H.* (?) *largeni*, but a formal description was delayed pending the examination of further material of Lanza's species. The external morphology and osteology of additional material confirm the necessity to recognize the new genus.

LANZARANA gen. nov.

TYPE SPECIES. *Hildebrandtia* (?) *largeni* Lanza, 1978 : 232.

DIAGNOSIS. (1) Small to moderate African ranine frogs, adult males 42·0–45·2 mm (n = 17); adult, gravid females 43·7–48·5 mm (n = 9) snout-vent length. (2) Skin of dorsum smooth or smooth with low pustules, no dorsolateral folds. (3) Males with external vocal sacs. (4) Fingers moderately long, 2nd shortest, 1st longer than or equal to 4th, 3rd longest. (5) Tips of fingers, 1st and 2nd rounded or slightly expanded; 3rd and 4th rounded or slightly to broadly expanded, truncate, 3rd showing most extreme condition. (6) Inner metatarsal tubercle moderately well developed not compressed. (7) Outer metatarsal tubercle present, distinct. (8) Outer metatarsals not separate, bound in a fleshy sole. (9) Nasals reduced, slip-like, widely separated. (10) Occipital canal absent. (11) Otic plate rudimentary. (12) Zygomatic ramus of squamosal shorter than otic ramus. (13) Preorbital process of pars fascialis of maxilla well developed, rectangular in lateral view. (14) Anterior end of maxilla convex. (15) Pterygoid process of maxilla absent. (16) Anterior process of prevomer moderate, separated from mesial maxilla/premaxilla articulation by a short gap. (17) Palatines present. (18) Distal end anterior ramus of pterygoid moderately long, separated from lateral border of planum antorbitale by short gap. (19) Cervical cotyles slightly separately mesially, type II sensu Lynch, 1971. (20) Base of omosternum moderately forked; greatest space between the arms is once to twice the width of one arm, state 2 of Liem, 1970. (21) Clavicles reduced, widely separated mesially. (22) Sternal style a short compact bony element, tapering slightly anteriorly to posteriorly. (23) 8th presacral and sacral vertebrae fused. (24) Dorsal protruberance of ilium not or slightly differentiated from dorsal prominence, smooth surfaced, confluent with dorsal ilial crest. (25) Distal ends of terminal phalanges of fingers slightly, moderately or markedly expanded, truncate, see (5) above; of toes cone-like.

ECOLOGY AND HABITAT. Specimens collected by Lanza were found in undulate subdesert regions characterized by grass, perennial herb and subshrub steppe. The type series of six males from ca. 10 km N of Garoe were found calling near a soil depression with shallow

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flowing water. Further collecting has shown that *L. largeni* is also associated with shallow wells (e.g. 20 km N of Garoe near a tiny well, 2 m deep, in evaporites), in surface puddles, deep wells (at El Ure, Sciu Manas and Rahole) and resevoirs. Lanza (1978) considered that *L. largeni* was 'Almost surely . . . a burrowing species . . .', but later revised this opinion 'I do not think it is a true digging animal' (Lanza, pers. comm.). *Lanzarana* apparently spends much of its life underground, particularly in the north, in burrows, crevices, vacuities and among shrub or tree roots. This mode of life accords with the structure of the inner metatarsal tubercle, moderately well developed but not compressed as in *Hildebrandtia* s.str., and with the bound metatarsals.

The information on ecology and habitat given above is derived from Lanza (1978 & pers. comm.).

Lanzarana should be looked for in those parts of Kenya and Ethiopia that afford similar habitats.

DISTRIBUTION. At present known only from Somalia, from Halin in the north to an area 30 km SSE of Dinsor in the south (See Fig. 1).

ETYMOLOGY OF GENERIC NAME. The genus is named after Professor Benedetto Lanza (Museo Zoologico de 'La Specola', Florence), in recognition of his many contributions to the herpetology of Somalia, and generosity in allowing me to describe this genus.

Relationships with *Ptychadena* and *Hildebrandtia*

Clarke (1981) noted that *Ptychadena*, *Hildebrandtia* and *H.* (?) *largeni* (= *Lanzarana*) share five derived character states not possessed by any other African ranine genera: loss of palatines; reduced clavicles; short, tapering sternal style, a compact bony element; fusion of 8th presacral and sacral vertebrae; dorsal protruberance of ilium not or slightly differentiated from dorsal prominence, smooth surfaced and confluent with dorsal ilial crest. *Ptychadena*, *Hildebrandtia* and *Lanzarana* are therefore considered a monophyletic group, distinctly separate from all other African ranines.

Comparisons based on external morphology as well as osteological characters suggest an evolutionary sequence: *Ptychadena*—*Lanzarana*—*Hildebrandtia*; with *Ptychadena* as the most primitive in the sequence, *Lanzarana* being an intermediate form but more closely related to *Hildebrandtia* than to *Ptychadena*.

(a). External morphology

(1) Dorsal skin folds. In *Ptychadena* there is considerable interspecific variation in the extent and arrangement, ranging from clearly defined to very fine or indistinct; in some species the paravertebral or even all the dorsal folds may be discontinuous, or fragmented. *Lanzarana* has neither paravertebral nor dorsolateral folds, but in some specimens smooth, low scattered pustules are present. In *Hildebrandtia* folds are usually absent although in some specimens of *H. ornata* smooth, low dorsolateral folds may be discernible. (2) Inner metatarsal tubercle. In *Ptychadena* present, poorly to well developed, in some species e.g. *Pt. trinodis* the tubercle may be moderately compressed; in *Lanzarana*, moderately developed, but not compressed; *Hildebrandtia*, well developed and compressed. (3) Outer metatarsal tubercle. Present, indistinct or absent in *Ptychadena*; present in *Lanzarana*; apparently absent in *Hildebrandtia*. (4) Terminal phalanges. *Ptychadena*, tapering, obtusely pointed, 3rd and 4th fingers not dilated, fingers usually moderately long; *Lanzarana* rounded, fingers variable, well rounded to strongly dilated, expecially 3rd and 4th (see Lanza, in prep.); *Hildebrandtia* tapering obtusely pointed, fingers usually short, not dilated. (5) Outer metatarsals, separated by web in *Ptychadena* but bound in a fleshy sole in both *Lanzarana* and *Hildebrandtia*.

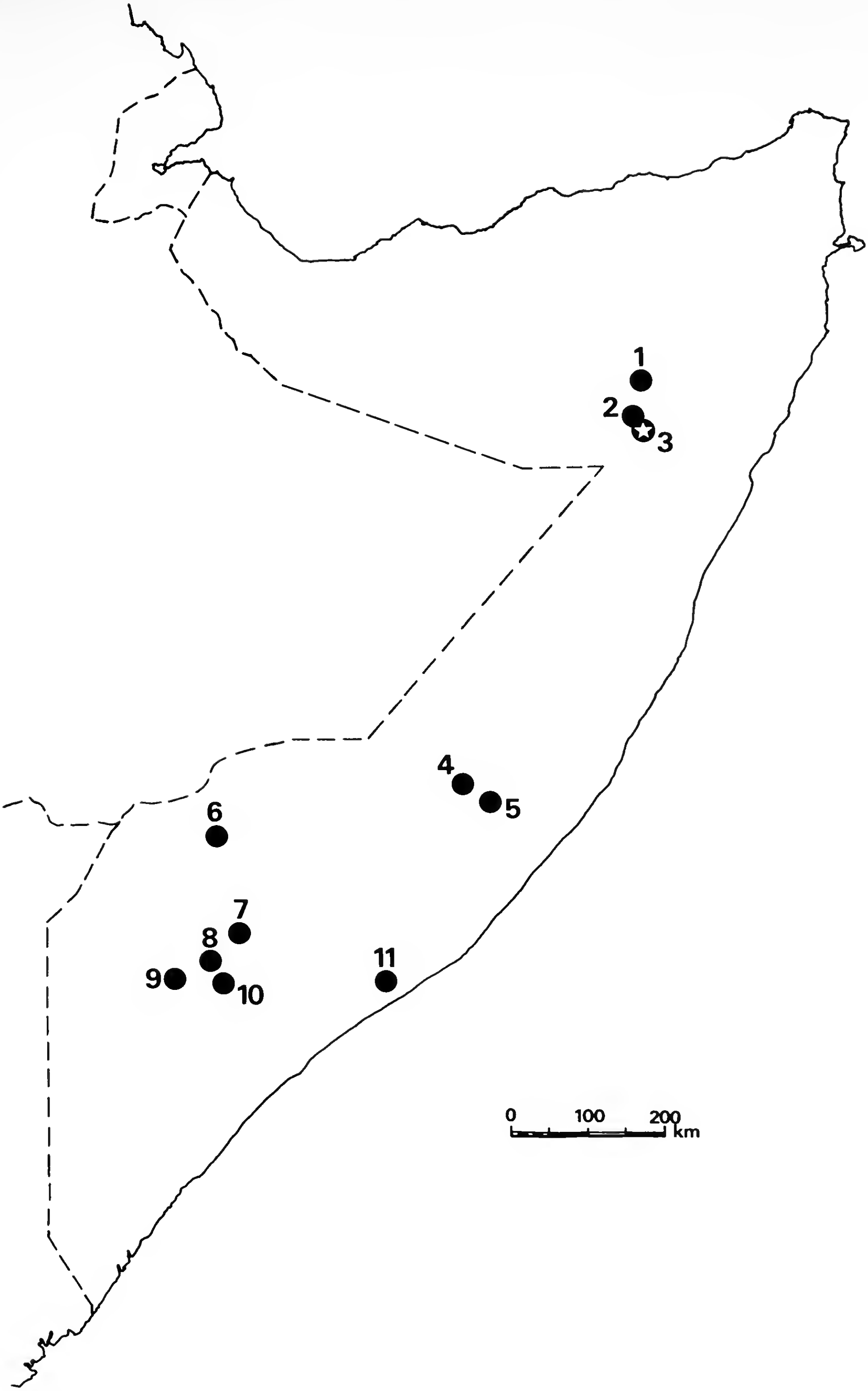

Fig. 1 Map showing present, known distribution of *Lanzarana* in Somalia. 1 = Lower wadi Halin, Nogal Valley, 09°00′ N 48°30′ E, 1550 m. 2 = About 20 km N of Garoe, Nogal Valley. 3 = About 10 km N of Garoe, Nogal Valley, about 08°25′ N 48°33′ E, c. 500 m (Type locality). 4 = Maas 04°23′ N 46°05′ E. 5 = Bud Bud 04°15′ N 46°30′ E. 6 = El Ure 03°50′ N 43°06′ E. 7 = Sciu Manas 02°48′ N 43°27′ E. 8 = Dinsor 02°24′ N 42°59′ E. 9 = Rahole 02°08′ N 42°37′ E. 10 = Between Dinsor and Jach Bravai (Jach Bravai is 01°56′ N 43°12′ E), about 30 km SSE of Dinsor. 11 = About 6 km E

(b). Osteology

Clarke (1981) attempted to infer relationships within the African Raninae at supraspecific level by a cladistic analysis of a sample of osteological characters. While the *Ptychadena—Lanzarana—Hildebrandtia* line emerged as a distinct, monophyletic unit, there was insufficient 'definition' in terms of the shared derived character state distributions, to permit any *firm* conclusion on interrelationships within the unit. The suggestion that *Hildebrandtia* (?) *largeni* (=*Lanzarana*) is more closely related to *Hildebrandtia* than to *Ptychadena* was made as much on the basis of character state polarities as on the sharing of one particular uniquely derived character state; viz. 13–3 'anterior ramus of pterygoid . . . separated from lateral border of planum antorbitale by a very small gap'.

In the present paper, it is suggested that external morphological evidence supports the theory that *Lanzarana* is more closely related to *Hildebrandtia*.

Generic status of *Lanzarana*

Lanzarana is here accorded full generic status because although it occupies, to some extent, an intermediate position between *Ptychadena* and *Hildebrandtia* it lacks the derived character states shown by *Ptychadena*, and more importantly lacks derived states shown by *Hildebrandtia* (see Clarke, 1981). *Lanzarana* is therefore a genus within the definition given by Mayr (1969) 'A genus is a taxonomic category containing a single species, . . . which is separated from other taxa of the same rank [other genera] by a decided gap'. Further, on present evidence *Ptychadena*, *Lanzarana* and *Hildebrandtia* occupy different ecological niches and may each therefore be regarded as a full genus; criterion of Inger (1958).

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Lanzarana study material

largeni: 94 specimens including 1 disarticulated dry skeleton (DS) and 1 cleared and stained preparation (C & S). MF 2733 (paratype: C & S), MF 2734–35 (paratypes), MF 2554, 2557, 2560–62, MF 10037–42, MF 11594–11611, MF 11631–37, MF 11640–56, MF 11667–68, MF 11689, MF 11830, MF 12004–12, 12014, 12016, MF (temporary numbers) 1980/1–1980/10, 8 unregistered MF specimens, BM 1931.8.1.67–68, BM 1980.1164–65, BM 1980.1166 (DS).

Abbreviations used:

BM	British Museum (Natural History)
MF	Museo Zoologico de 'La Specola', Florence.

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H. M. Platt

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Revision of the Ethmolaimidae (Nematoda: Chromadorida)

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Contents

Synopsis

Based on the proposed synapomorphic character of precloacal supplementary copulatory organs of a unique derived form, the family Ethmolaimidae now contains both the Ethmolaiminae of Filipjev & Stekhoven, 1941 and the Neotonchinae of Wieser & Hopper, 1966. A tentative cladogram is proposed to express a theory of the relationships within the family. Several other taxonomic changes are proposed, including the erection of four new genera and six new species. Figures and keys are provided to facilitate species identification.

Introduction

The work reported here, prompted by the discovery of further new species from Scotland and Ireland, began as a review of just those species contained in Wieser & Hopper's (1966) subfamily Neotonchinae (raised to family by Lorenzen, 1981). However, similarities between these organisms and species of the genus *Ethmolaimus* (Ethmolaimidae) and a species of *Spiliphera* suggested that the respective taxa should be united. This paper sets out the arguments for this new combination of taxa, although the main descriptive work concentrates on the marine neotonchids.

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In attempting to establish a sensible pattern of relationships among the ethmolaimids as a whole, cladistic methodology has been adopted in the belief that the concepts involved offer some hope of elucidating a coherent pattern in such a notoriously complicated group as the Nematoda. In this way, an attempt has been made to avoid providing taxonomic definitions based on a 'melange of primitive characters' (Rosen, Forey, Gardiner & Patterson, 1981), where many features appear to be included unnecessarily. It should also be pointed out that although a theory of relationships is presented here in terms of a branching diagram, no claim is made that this necessarily reflects the evolutionary history of the organisms concerned.

Materials and methods

Ethmolaimid specimens studied are those contained in the descriptive section of this paper. The outgroup material specifically examined in order to determine the status of various characters is listed below.

- Chromadoridae
  - Spilipherinae
    - *Spiliphera gracilicauda* De Man BMNH: 1980.4.20–21
  - Chromadorinae
    - *Atrochromadora microlaima* (De Man) BMNH: 1980.7.24–25
    - *Prochromadora oerleyi* (De Man) BMNH: 1958.12.5.20–27
    - *Prochromadorella septimpapillata* Platt BMNH: 1971.547
  - Euchromadorinae
    - *Graphonema scampae* (Coles) BMNH: 1963.616–17
    - *Rhips paraornata* Platt & Zhang BMNH: 1981.4.19–21
  - Hypodontolaiminae
    - *Dichromadora cephalata* (Steiner) BMNH: 1980.7.23
    - *Dichromadora hyalocheile* (De Coninck & Stekhoven) BMNH: 1980.7.22
    - *Hypodontolaimus balticus* (Schneider) BMNH: 1980.5.76
    - *Hypodontolaimus inaequalis* (Bastian) BMNH: 1981.12.103
    - *Neochromadora poecilosoma* (De Man) BMNH: 1981.12.100–101

- Cyatholaimidae
  - Pomponematinae
    - *Pomponema reductum* Warwick BMNH: 1968.274
    - *Pomponema sedecima* Platt BMNH: 1971.550
    - *Pomponema tautraense* (Allgen) BMNH: 1981.12.114
  - Paracanthonchinae
    - *Paracyatholaimus* sp. BMNH: 1980.7.1
  - Cyatholaiminae
    - *Marylynnia complexa* (Warwick) BMNH: 1980.6.49
    - *Praeacanthonchus punctatus* (Bastian) BMNH: 1981.12.104

- Selachinematidae
  - *Gammanema* sp. BMNH: 1981.1.1
  - *Synonchiella riemanni* Warwick BMNH: 1980.6.51

- Comesomatidae
  - Comesomatinae
    - *Metacomesoma* sp. BMNH: 1980.6.7
  - Sabatieriinae
    - *Sabatieria breviseta* Stekhoven BMNH: 1981.12.125
    - *Sabatieria celtica* Southern BMNH: 1981.12.124
    - *Sabatieria pulchra* (Schneider) BMNH: 1980.8.57
  - Dorylaimopsinae
    - *Dorylaimopsis punctata* Ditlevsen BMNH: 1980.6.26

Specimens were studied and photographed using microscopes fitted with interference contrast optics. Drawings, other than those taken from the literature, were made with a drawing tube.

The formula used in the description is a simplification of Filipjev's (1916) formula, itself a modification of Cobb's (1902) formula, where figures above the line indicate distance (in μm) from the anterior extremity to the posterior end of the oesophagus, vulva in females (or, in males and juveniles, and females where the vulva is not near the mid-point of the body, the letter 'M' designates the mid-point) and anus (cloaca in the male). Figures below the line represent corresponding body diameters at the head (conventionally taken at the level of the R_3 sensilla unless stated otherwise), base of oesophagus, mid-body and anus/cloaca. The total body length is placed after the line, followed by the De Man ratios 'a', 'b' and 'c' representing the ratio of total body length to maximum body diameter, oesophagus length and tail length respectively.

The following abbreviations are used: a.b.d. = anal/cloacal body diameter; c.d. = corresponding body diameter; h.d. = head diameter; R_1, R_2 and R_3 sensilla refer to the inner labial, outer labial and cephalic sensilla respectively; S = spicule length; V = position of vulva from the anterior as a percentage of the total body length; L = total body length.

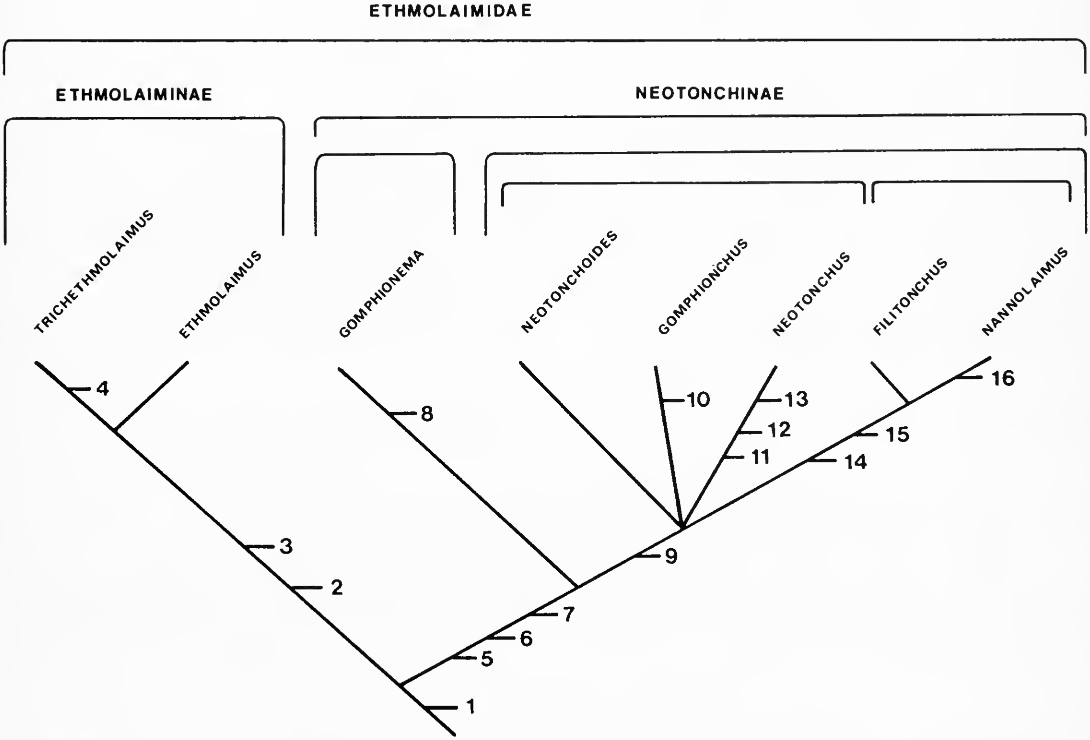

Fig. 1 Tentative cladogram expressing a theory of the relationships within the Ethmolaimidae. Numbered characters are those contained in the synapomorphy scheme in the text.

Synapomorphy scheme

At this stage the preferred theory of the interrelationships within the family Ethmolaimidae (as here defined) is introduced in order to facilitate discussion of the characters. The hypothesis is illustrated in Fig. 1. The following comparisons are based on the specimens contained in the descriptive section of this paper and the outgroups listed above.

A. Ethmolaiminae has the following derived feature which it shares with the Neotonchinae:
  1. Cup-shaped precloacal supplements with an external articulated flange.

B. *Trichethmolaimus* also has the following features which it shares with *Ethmolaimus:*
  2. Three large teeth, the subventral ones being as large or almost as large as the dorsal tooth.
  3. Amphid consists of one turn of the corpus gelatum.

C. *Trichethmolaimus* has the following autapomorphic feature:
  4. Extremely long somatic setae.

D. *Gomphionema* has the character of A and also shares with the clade consisting of *Neotonchoides*, *Gomphionchus*, *Neotonchus*, *Filitonchus* and *Nannolaimus*:
  5. Characteristically bent spicules.
  6. Dorso-sublateral subcephalic setae.
  7. Conical tail with rounded tip.

E. *Gomphionema* also has the following autapomorphic feature:
  8. Massive dorsal tooth only.

F. Genera of the clade consisting of *Neotonchoides*, *Gomphionchus*, *Neotonchus*, *Filitonchus* and *Nannolaimus* have the characters of A and D and also have the following feature:
  9. A patch of non-granulated cells in the vas deferens.

No features could be detected which *Neotonchus, Gomphionchus* and *Neotonchoides* uniquely share and so the three genera constitute an unresolved trichotomy.

G. *Gomphionchus* has the following autapomorphic feature:
  10. Large anteriorly situated dorsal tooth.

H. *Neotonchus* has the following autapomorphic features:
  11. Sublateral pore-seta complexes.
  12. Lateral longitudinal row of caudal punctations.
  13. Characteristically shaped dorsal tooth.

I. *Nannolaimus* has the characters of A, D and F and also shares with *Filitonchus*:
  14. Elongate R_2 sensilla (equal to or longer than 1 h.d.).
  15. Loss of structurally expanded buccal lumen.

J. *Nannolaimus* also has the following autapomorphic feature:
  16. R_1 sensilla setiform.

Morphology and character evaluation

In discussing the taxonomically important morphological characters an attempt has been made to suggest at which taxonomic level of universality each feature is operating. This has necessitated making several crucial decisions, many of which may, in the light of future evidence, prove erroneous. However, the exigencies of cladistics do not allow these judgements to be avoided. In following the discussion, it may be helpful to refer to the tentative theory of relationships expressed in Fig. 1 and the species drawings in Figs 2–5.

Body shape. Most ethmolaimids are usually 600–1200 μm long with an 'a' ratio of around 30. However, species of *Nannolaimus* and *Filitonchus* tend to be slimmer animals, with an 'a' ratio of 50–100. The fixation-shape, the typical body shape when subjected to *cold* formalin fixation, is usually uncoiled. There is some anterior attenuation in most species, the head typically being about 60% of the width at the base of the oesophagus. The tail is conical except in *Ethmolaimus*, where it is conico-cylindrical.

Most of the features of overall body shape are not unique statements for ethmolaimids and therefore of little phylogenetic use. However, the shape of the tail appears to be useful at a high taxonomic level. Many other chromadorid groups have conical tails although in most, the tip is pointed, e.g. *Neochromadora poecilosoma*, *Hypodontolaimus inaequalis* and *Praeacanthonchus punctatus*. Other groups such as the Pomponematinae have characteristic conico-cylindrical tails with swollen tips. However, it is the rounded tail tip of the Neotonchinae which appears to be unique within the Chromadoroidea.

Cuticle ornamentation. The cuticle is annulated with each annule bearing one or more transverse rows of dots – the punctated cuticle – which are in fact cuticle supporting rods viewed end-on. In most species, the rods are short but in the head and tail regions of *Trichethmolaimus* they are elongated. These long rods are very similar in appearance to those found in *Pomponema* and other cyatholaimids.

There are many species in which the rows become irregular or fewer in number and also somewhat larger in the lateral field. Where there are fewer lateral rows, this is referred to as lateral differentiation: it is known to occur in eight of the 26 valid species but is not confined to particular genera. This lateral differentiation usually begins level with the base of the oesophagus, but in *Ethmolaimus pratensis* and *Gomphionema typicum* it starts just posterior to the amphid. The discontinuous distribution of the lateral differentiation and an apparently homologous occurrence in other chromadoroid groups, e.g. Cyatholaimidae, suggests that it is the phenotypic expression of a symplesiomorphy. The alternative would be to assume that the condition had developed independently on many occasions, which seems less likely. In either case, the feature is phylogenetically irrelevant within the Ethmolaimidae.

In *Neotonchoides melotridus* studied here and as reported for *Neotonchus boucheri* by Boucher (1976), and for *Neotonchoides corcundus* and *Nannolaimus fusus* by Gerlach (1956), some species have certain complete rows consisting of larger dots. The presence of the character could not be verified in *Neotonchus boucheri* or *Nannolaimus fusus* specimens studied here. However, pending further information, its limited discontinuous distribution is probably best considered as representing analogous conditions.

In all four *Neotonchus* species there are lateral rows of irregular dots on the posterior third of the tail. This feature is considered synapomorphic for the genus since it was not detected in any of the other ethmolaimids nor in those specimens used as outgroup comparisons for the synapomorphy scheme.

Cuticle pores. Lateral and sublateral cuticle pores have been observed and documented many times (Sharma, Hopper & Webster, 1979). Cuticle pores were also observed in all the species studied with the exception of *Nannolaimus phaleratus*. The actual pattern of their distribution appears to vary among species and may be useful autapomorphic features characterising species, e.g. *Neotonchoides vitius*. However, there is no evidence that the pores in the Ethmolaimidae are different from those of other chromadorids or cyatholaimids, so their presence is considered phylogenetically irrelevant. In *Neotonchus* species, the sublateral pores posterior to the oesophagus each have a seta situated medially to them: called here pore-seta complexes. This combination appears to be a unique derived character, not detected in any other specimens studied.

Cephalic sensilla. Ethmolaimids have the plesiomorphic 6 + 6 + 4 cephalic sensilla arrangement (Lorenzen, 1981) so the character 'three circles of cephalic sensilla at different levels' is irrelevant. Only in groups such as the Cyatholaiminae, where the R_2 and R_3 sensilla are *always* at the same level, i.e. the relationship is stabilised, does this relationship become of phylogenetic significance. In the *Nannolaimus fusus* specimen studied, the sensilla were very close together although not exactly at the same level as depicted by Gerlach (1956). Within the Ethmolaimidae, there is a range in the degree of separation of the R_2 and R_3 sensilla, so the arrangement in *Nannolaimus fusus* can be considered convergent with that of the Cyatholaiminae. In most species, the R_3 sensilla are longer than the R_2 sensilla whilst the

R_1 sensilla are papilliform or not detectable. The R_1 sensilla are setiform in *Nannolaimus* species while in *N. fusus* the R_2 sensilla are longer than the R_3 sensilla. It will be argued below that the character 'setiform R_1 sensilla' is autopomorphic for the genus whilst the relative length of the two circles is probably irrelevant.

However, there is one character of the setation which does appear to be stabilised within a part of the Ethmolaimidae; the presence of a seta situated dorso-sublaterally just posterior to the level of the R_3 sensilla and often level with the amphid. The feature has been used to separate *Trichethmolaimus* and *Ethmolaimus* from the others (Fig. 1). In *Gomphionema* species, *Gomphionchus lutosus* and *Ethmolaimus pratensis*, the ventro-sublateral caudal setae appear to be particularly well developed and spine-like. The best interpretation is that the feature is not congruent since a clade containing these species requires a less parsimonious interpretation of other character states than that provided in Fig. 1.

Amphids. The amphids in all ethmolaimids are spiralled ventrally to the centre. Determining the exact number of 'turns' of the amphid is not easy: whereas the structure always appears to begin on the dorsal side, it is difficult to determine where the last turn ends. What is actually being observed, of course, is the wall of a spiralling groove in which lies the corpus gelatum. Following the course of the wall usually gives a count of one more than the turns of the corpus gelatum and is often reported as a count of 'n' plus a 'bit more'. Whether the 'bit more' is a $\frac{1}{4}$, $\frac{1}{2}$ or $\frac{3}{4}$ appears to vary among specimens even of the same species. However, the number of complete turns is a useful character at the species level. To simplify matters, in this work the amphids are described as 'n+', where 'n' is the number of complete turns of the wall. Most species have 3+ or 4+ amphids, although they may be up to 6+. In *Gomphionema*, both sexes have the same number of turns. However, in certain other genera where females are known, they have one less turn than the male. Unfortunately, most species are known from males only, so the extent of this sexual dimorphism and its phylogenetic importance remains unknown.

The amphids of *Trichethmolaimus* and *Ethmolaimus* have fewest turns of all, being apparently just one turn of the corpus gelatum (hence a possible wall count of 2+ turns), although the wall in *Ethmolaimus* may be only lightly cuticularised and therefore difficult to distinguish, particularly with normal light microscopy. Although essentially a multi-spiralled amphid, in these two genera, the number of turns, pending evidence to the contrary, is used here to characterise the subfamily to which these two genera will be consigned (Fig. 1). The apparently similar condition found in *Spiliphera* (Chromadoridae) must be considered homoplasic.

The widespread occurrence of multi-spiralled amphids among the outgroup comparisons and Chromadoria generally indicate that the character is plesiomorphic for the Ethmolaimidae. The amphid in the Ethmolaiminae may then possibly represent an example of reversal.

Buccal cavity. All species have the anterior part divided into twelve sections, a feature shared by all taxa within the suborder Chromadorina (Lorenzen, 1981). The degree of development of the dentition and the form of the buccal cavity posterior to the teeth are highly variable features and seem to show sufficient discontinuity to be of use in delimiting sets of genera (Fig. 1). The possession of a distinct dorsal tooth and a structurally expanded conical posterior part are characters found in all the chromadorid outgroups and so are judged to be plesiomorphic. If this is the case, the absence of an expanded buccal lumen in *Filitonchus* and *Nannolaimus* must be a derived feature, representing the terminal state of a transformation series in which the polarity is towards a reduction in cuticularisation, a simplification of the character.

Oesophagus. In all members of the Ethmolaimidae, the oesophagus ends in a muscular bulb. However, its degree of development is correlated with the size of the dorsal tooth, being poorly developed and difficult to detect in *Nannolaimus and Filitonchus* but large and conspicuous in *Gomphionema*, *Ethmolaimus* and *Trichethmolaimus*. The character 'oesophagus bulb present' is irrelevant phylogenetically within the Ethmolaimidae, being apparently homologous with the structures found in several other nematodes, e.g. Chromadoridae.

Copulatory structures. All ethmolaimids have paired spicules which in the known species are of equal size, mostly about the same length as the cloacal diameter. As pointed out by Wieser & Hopper (1966), in many species the shape viewed from a lateral perspective is rather characteristic, being bent about one-third of the distance from the distal end. This shape, typically as depicted in Figs 4a–c, appears to be unknown outside the set defined here as the subfamily Neotonchinae: it is not shared by species of *Trichethmolaimus* or *Ethmolaimus*. Those species within the Neotonchinae (on other grounds) which do not have this typical spicule shape are assumed, on grounds of parsimony, to display an autapomorphic condition.

The gubernaculum, as in most chromadoroid groups, is represented only by a lightly cuticularised rod-like structure, in lateral view, and is of no phylogenetic importance. However, lying lateral to the distal ends of the spicules in *Ethmolaimus*, *Gomphionema*, *Gomphionchus* and at least one species of *Neotonchoides*, there is an additional structure resembling a cone or triangular plate, possibly the cuticularised end of a duct. If homologous, the structure must be considered plesiomorphic since any group made up of those species in which the feature can be detected is not congruent with other characters. Well developed lateral pieces are also known in the Euchromadorinae.

All species studied here, and most of those described in the literature, possess a prominent ventral precloacal spine, a plesiomorphic character known to occur in other nematode groups, e.g. *Dichromadora* and *Pomponema* species.

Anterior to the precloacal spine in all ethmolaimid species there is a single ventral row of between 6 and 24 cup-shaped supplements occupying 7–30% of the total body length. Other chromadoroid groups have been described as having cup-shaped supplements, but in none of these other taxa do the supplements seem to be identical in detail. The 'cup' part of the supplement, when viewed laterally, is continuous, without the dorsal aperture seen in many other chromadoroid supplements, e.g. *Prochromadorella septempapillata.* The anterior and posterior ends of the 'cup' may be thickened, as in *Gomphionema*, but in many species the curve is the same thickness at all parts of the semi-circle. The external part of the cup is surrounded by a longitudinal oval flange with a pore in the middle (Fig. 30d). The anterior and posterior parts of this flange appear to be articulated, allowing the whole supplement to be protruded or retracted, and are particularly noticeable in *Ethmolaimus pratensis*, *Gomphionchus lutosus* and *Gomphionema fellator.*

The outgroup species investigated, in which the supplements are most similar to those of the ethmolaimids, were *Atrochromadora microlaima* which does not have external flanges and *Dichromadora cephalata* which does have external flanges. As far as can be ascertained, the supplements of *Dichromadora cephalata* are indistinguishable from those of certain ethmolaimids, e.g. *Neotonchoides vitius.* It may be that the flange is not articulated in *D. cephalata* but since it cannot be stated categorically that they are articulated in all ethmolaimid species this must remain only a possible difference. However, *Dichromadora* differs from the ethmolaimids on so many other grounds, e.g. cuticle ornamentation, amphid shape, number of testes and tail shape, that it must be concluded that the ethmolaimid supplement shape is the result of homoplasy in *D. cephalata.* Certainly, it is worth noting that within the Ethmolaimidae *all* species have the typical flanged supplement, whilst among the outgroups apparently similar structures occur only sporadically, even within a genus, cf. *Dichromadora cephalata* and *Dichromadora hyalocheile.* Therefore, it is suggested that the specific structure of the supplements is a crucial stable synapomorphic character indicating that the Ethmolaimidae is a monophyletic unit. Furthermore, the condition probably represents the terminal state of a transformation series in which polarity is determined by increasing complexity. The number of supplements may be of some use at the species level since in all but *Ethmolaimus pratensis* and *Gomphionema typicum* the range of variation appears to be n ± 1 (n = mode).

Reproductive system. All species have two opposed gonads. Females have both ovaries reflexed and of equal size. In the male, the testes are outstretched but the posterior one is smaller than the anterior in most species (Fig. 18f). The testes normally lie on opposite sides of the gut but there is no stability within genera as to whether the anterior gonad is to the left or right, although it is constant within species.

In at least eight of the species studied there appears to be a series of about five cells in the vas deferens which are of a non-granular appearance (Fig. 28d). They usually stand out as a distinct patch, generally located level with the fourth to sixth supplement from the cloaca. Within a species, not all specimens display the character, suggesting that it may be a feature appearing at a particular stage in development. However, when the feature is visible, it always occurs in the same place. Despite its discontinuous distribution, this character, here called simply the 'clear patch', has been used to delimit a set of genera within the Ethmolaimidae (Fig. 1). Nothing resembling this feature could be detected amongst the outgroups.

Ecology and distribution

Most ethmolaimids are found in marine sediments, particularly in fine sand, silt and muds with a relatively high organic content. They have been reported from intertidal locations down to 650 m and from the North Atlantic, the Mediterranean, Australia and South America. In most ecological investigations they seem to represent only a small proportion of the total nematode fauna. For example, in a recent study only 32 specimens of a species of *Neotonchoides* were found among 13,645 nematodes and so did not appear in tables of the most abundant species (Platt, 1977). However, in a study of Australian beach nematodes, a species of *Gomphionema* was one of the dominant species (Warwick, pers. comm.). It therefore seems that in keeping with our knowledge of most marine nematodes, we have yet to discover the preferred habitat of most ethmolaimid species. A practical consequence of this lack of knowledge is that most species descriptions are of necessity based on only a few specimens.

Unlike most of the genera, *Ethmolaimus* is found in freshwater and brackish habitats, which perhaps accounts for its failure in the past to be linked with some of those entities which are here considered to belong to the same group.

Taxonomic revision

In the following diagnoses, taxa above the family level are assumed to have the characters proposed as synapomorphies by Lorenzen (1981), namely:
Chromadorina: vestibule of buccal cavity divided into twelve parts.
Chromadoroidea: punctated cuticle.

Family **ETHMOLAIMIDAE** Filipjev & Stekhoven, 1941

Neotonchidae Wieser & Hopper, 1966 syn. nov.

Type genus. *Ethmolaimus* De Man, 1880

Diagnosis. Chromadoroidea. Ventral row of conspicuous cup-shaped supplements, each with an external articulated flange. Amphid multi-spiralled. Two testes.

Remarks. The subfamilies Ethmolaiminae and Neotonchinae were raised to family level by Lorenzen (1981) but in doing so he was unable to distinguish any synapomorphies and was therefore obliged to resort to a characteristic combination of primitive characters. None of these characters was a unique statement for the respective groups and monophyly was not established. Gerlach & Riemann (1973) had earlier placed the genera *Ethmolaimus* and *Spiliphera* in the same subfamily within the Chromadoridae. However, as discussed above, an examination of the supplements of *Ethmolaimus* and *Spiliphera hirsuta* (= *Trichethmolaimus*) suggests that they have a derived structure compared with those of the Chromadoridae. Therefore it is proposed that the group consisting of *Ethmolaimus*, *Trichethmolaimus* and the genera of the Neotonchinae be considered a monophyletic family, for which the senior synonym Ethmolaimidae is available.

Lorenzen (1981) refrained from establishing forms with a multi-spiralled amphids as a monophyletic group since he wanted to transfer the Comesomatidae to the order Monhysterida on the grounds of their ovaries being outstretched rather than reflexed. This somewhat controversial move assigns taxonomic supremacy to the reproductive system and has the consequence of requiring the condition 'spiral amphids and punctated cuticle' to have arisen independently on more than one occasion. Despite some reservations, for the purposes of this discussion Lorenzen's argument is accepted but the multi-spiralled amphid is treated as a plesiomorphic character for the Chromadoroidea since they also occur in the Desmodoroidea, e.g. *Eubostrichus*. The inclusion of multi-spiralled amphids in the diagnosis simply serves to draw attention to this unresolved problem.

Several species within the Ethmolaimidae have transverse rows of punctations which are discontinuous in the lateral field, a feature which appears to be homologous with that of certain members of the Cyatholaimidae and thus may constitute a synapomorphy linking the families, e.g. *Praeacanthonchus punctatus*.

Subfamily **ETHMOLAIMINAE** Filipjev & Stekhoven, 1941

TYPE GENUS. *Ethmolaimus* De Man, 1880.

DIAGNOSIS. Ethmolaimidae. Three large teeth, the subventral teeth being as large or almost as large as the dorsal tooth. Amphid consisting of one turn of the corpus gelatum.

REMARKS. This subfamily contains the genera *Ethmolaimus* and *Trichethmolaimus*. In addition to the diagnostic features, the genera also share the following characters: buccal cavity posterior to the level of the teeth cylindrical and cuticularised; tail has a pointed tip.

ETHMOLAIMUS De Man, 1880

SYNONYMY. See Gerlach & Riemann, 1973.

TYPE SPECIES. *Ethmolaimus pratensis* De Man, 1880.

DIAGNOSIS. Ethmolaimidae. R_2 sensilla papilliform.

REMARKS. No derived characters uniquely shared by species of this genus could be found which would also separate it unequivocally from *Trichethmolaimus* other than the lack of long somatic setae. As currently constituted, the genera can be separated on the relative size of the R_2 sensilla, although this may not prove very satisfactory in the future. Other characters of *Ethmolaimus* species, but not necessarily exclusive to them, are: R_3 sensilla papilliform or short setae; short (about 3 a.b.d.) conico-cylindrical tail. In addition, the species studied here (*E. pratensis*) had the following features which may or may not be shared with other species: lateral differentiation; cuticle pores; lateral spicule piece; two testes.

In Hirshmann's (1952) revision of the genus, the diagnosis only consisted of primitive characters which left its systematic position in some doubt (Jensen, 1979a). However, based on the form of the supplements they can now be linked with the Neotonchinae.

There are three valid species: *E. pratensis* De Man, 1880; *E. multipapillosus* Paramonov, 1926; *E. dahli* Gerlach, 1953 (see Table 1).

E. distaphanus De Cillis, 1917 is a *nomen nudum* (Goodey, 1963); and *E. faeroeensis*

Ditlevsen, 1928 and *E. caudatus* Alekseev, Naumova & Dymina, 1979, being based only on females, are here considered *species inquirenda. E. parapratensis* Alekseev, Naumova & Dymina, 1979 is morphometrically within the range of variation reported for *E. pratensis* by Hirshmann (1952); it has subventral teeth smaller than the dorsal tooth as reported for *E. pratensis* by Jensen (1979a) and appears to have supplements similar to those of *E. pratensis* described here. Therefore, the species should be synonomised.

TRICHETHMOLAIMUS gen. nov.

TYPE SPECIES. *Spiliphera hirsuta* Gerlach, 1956.

DIAGNOSIS. Ethmolaiminae. Extremely long somatic setae. Cuticle supporting rods elongated in head region. R_2 sensilla setiform and stout. Tail conical with pointed tip.

REMARKS. The species originally described as *Spiliphera hirsuta* by Gerlach (1956) from Kiel Bay differs from the other two valid species of *Spiliphera*, *S. dolichura* De Man, 1893 and *S. gracilicauda* De Man, 1893, in possessing two testes, lacking the characteristic pairs of sublateral setae level with the posterior end of the buccal cavity, having precloacal supplements and a short conical tail in addition to the long somatic setae. On these grounds, *S. hirsuta* has been removed from *Spiliphera*. In several respects the species is similar to *Ethmolaimus*, especially in buccal cavity structure. However, in view of the long somatic setae, elongated cuticle rods in the head region, setiform R_2 sensilla, conical tail and fully marine habitat, it seems there are sufficient differences to support the erection of a new genus, the only species becoming *Trichethmolaimus hirsutus* (Gerlach, 1956) (lapsus *hirsuta*).

Subfamily **NEOTONCHINAE** Wieser & Hopper, 1966

TYPE GENUS. *Neotonchus* Cobb, 1933.

DIAGNOSIS. Ethmolaimidae. Dorso-sublateral subcephalic setae. Spicules a characteristic shape, bent about one-third from the distal end. Conical tail with rounded tip.

REMARKS. This subfamily is the apomorphic sister group of the Ethmolaiminae (Fig. 1) and contains genera without large subventral teeth. All known neotonchids have an amphid consisting of more than one turn of the corpus gelatum (wall count of 3+ or more); a plesiomorphy, assuming the amphid found in the outgroups is homologous.

GOMPHIONEMA Wieser & Hopper, 1966

TYPE SPECIES: *Gomphionema typicum* Wieser & Hopper, 1966.

DIAGNOSIS. Neotonchinae. Massive dorsal tooth only. Large posterior oesophageal bulb. Spicule with lateral pieces. Tail in male with two or three stout ventro-sublateral spines. Supplements occupy about 30% of total body length.

REMARKS. The characters of the diagnosis, other than the size of the dorsal tooth, are not considered to be synapomorphies. Other features of the valid species, but not necessarily exclusive to them or shared by all, are: lateral differentiation; R_3 sensilla short; amphid 3+ turns in both sexes and situated well anterior; 14–24 supplements.

By including the proportion of the body length occupied by the supplements the intention is to draw attention to this as a possible differentiating feature. In other neotonchids with a large number of supplements, e.g. *Gomphionchus lutosus* and *Neotonchoides votadinii*, the proportion of the body occupied is less than in *Gomphionema* even when the number of supplements is the same. Perhaps it is the area to be occupied by supplements that is genetically programmed rather than the total number.

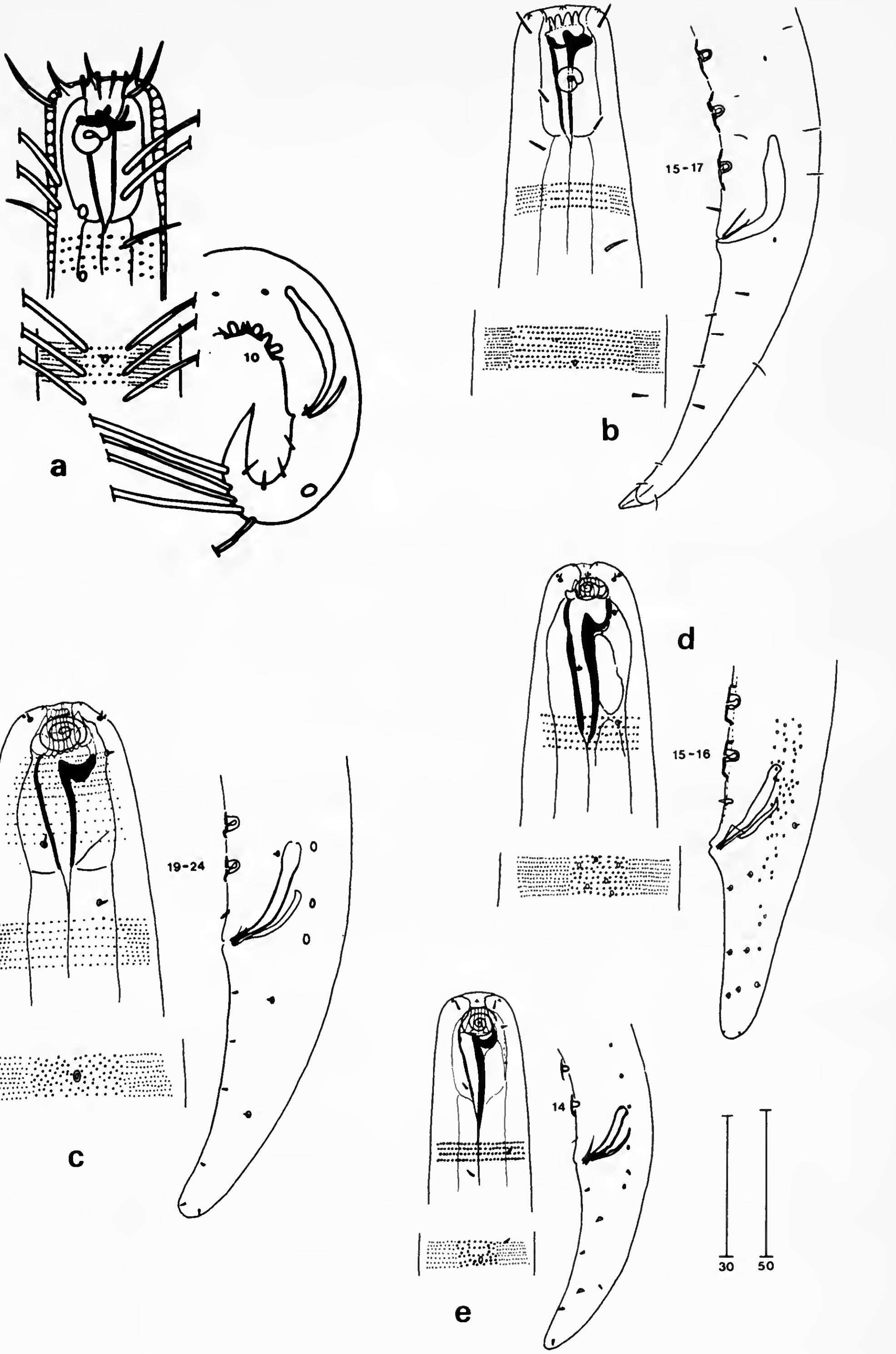

Fig. 2 (a) *Trichethmolaimus hirsutus*; (b) *Ethmolaimus pratensis*; (c) *Gomphionema typicum*; (d) *Gomphionema fellator*; (e) *Gomphionema* sp. Bar scales in microns; left bar for head, right bar for tail.

Table 1 Main differentiating data of *Ethmolaimus*, Gomphionema and *Gomphionchus* species (measurements in μm)

Species	L	a	b	c	R_3	A♂	A♀	S	Ps	T	Distribution
Ethmolaimus pratensis	385–1200	13–35	4–8	5–14	7–8	2+	2+	40–43	9–17	l/r	Europe & USSR
*Ethmolaimus multipapillosus**	830–1230	17–28	7–8	8–14	pap.	2+	2+	32	21–24	?	Europe
*Ethmolaimus dahli**	710–775	19	5–6	9–13	pap.	2+	?	36	20–21	?	Chile
Gomphionema typicum	1240–1530	18–22	6–7	13–15	2	3+	3+	41–47	19–24	l/r	E. coast USA
Gomphionema fellator	645–1035	15–26	4–6	11–17	1	3+	3+	36–38	15–16	l/r	E. coast USA
Gomphionema euripus	920	26	6	13	5	3+	?	23	16	?	Suez Canal
Gomphionema sp.	835	22	6	12	2	3+	?	25	14	r/l	Australia
Gomphionchus lutosus	870–1020	21–24	8	12–14	3	4+	?	29	20	l/r	E. coast USA

Abbreviations: L = total body length; a, b and c = De Man ratios; R_3 = length of R_3 sensilla; A ♂ and A♀ = number of turns of ♂ and ♀ amphid; S = absolute length of spicule; Ps = number of precloacal supplements; T = disposition of testes relative to gut (l = left, r = right), anterior/posterior; pap. = papilliform sensilla. Data from own observations and/or published descriptions.

*Specimens not seen.

Gerlach (1957) described *G. compactum* (as *Neotonchus compactus*) from Brazil, based on a single juvenile female: this species is here considered dubious. Riemann & Rachor (1972) subsequently described a single male from the Suez Canal as *G. compacta*. However, the specimen cannot be Gerlach's *G. compacta* since it lacks lateral differentiation: it also lacks the cuticle pores found in other *Gomphionema* species. The Suez specimen therefore warrants recognition as a separate species, named *Gomphionema euripus* sp. nov. (*euripus* L=canal), the holotype being the specimen on which Riemann & Rachor's (1972) description was based.

Gomphionema now contains three valid named species, *G. typicum* Wieser & Hopper, 1966, *G. fellator* Wieser & Hopper, 1966 and *G. euripus* sp. nov. plus a new species from Australia to be described by Dr R. M. Warwick. These valid species may be distinguished by using the information in Table 1 and Fig. 2.

Clade: *NEOTONCHOIDES/GOMPHIONCHUS/NEOTONCHUS/ FILITONCHUS/NANNOLAIMUS*

These five genera, discussed below, all share the occurrence of a clear patch in the vas deferens. Together, they form the apomorphic sister group of *Gomphionema* and could be designated a tribe. However, it seems inappropriate at this stage to formalise taxonomically such groups since they are based on what must at best be considered only tentative information.

Clade: *NEOTONCHOIDES/GOMPHIONCHUS/NEOTONCHUS*

In these three genera there is a well-developed buccal cavity with a distinct dorsal tooth which, by comparison with outgroups, is taken to be a plesiomorphic feature. As remarked earlier, no synapomorphies could be found for these genera so they must remain an unresolved trichotomy separated from the clade consisting of *Filitonchus* and *Nannolaimus* by the absence of those features which characterise the latter.

NEOTONCHUS Cobb, 1933

Heterocyatholaimus Allgen, 1935 syn. nov.

TYPE SPECIES. *Neotonchus punctatus* Cobb, 1933.

DIAGNOSIS. Neotonchinae. Cuticle has sublateral pores each associated with a seta. Posterior third of tail with lateral row of small punctations. Buccal cavity wide with a characteristic triangular dorsal tooth and two small subventral teeth. Clear patch in vas deferens.

REMARKS. As here redefined, the genus contains only four valid species: *N. punctatus* Cobb, 1933; *N. chamberlaini* Wieser & Hopper, 1966; *N. boucheri* sp. nov. (syn. *N. chamberlaini sensu* Boucher, 1976 *nec* Wieser & Hopper, 1966); *N. meeki* Warwick, 1971. Jensen (pers. comm.) considered *Heterocyatholaimus* Allgen, 1935 congeneric with *Neotonchus* although the only species, *H. macrolaimus*, is so poorly described from a single female that it should be regarded as a dubious species. *N. hapalus* Vitiello, 1974 and *N. spiralis* Vitiello, 1974 are both *nomena nuda*.

In addition to the diagnostic features, valid species have the following characters: lateral differentiation (except *N. boucheri*); R_3 sensilla 30–35% h.d.; amphid 3+ to 5+ turns, 50–70% c.d. and at least in *N. boucheri* the female has one fewer turns than the male; 6–8 precloacal supplements. With the exception of *N. punctatus*, all species had a clear patch in the vas deferens. *N. punctatus* had a vas deferens in which there was an area of cells which had a different appearance from the rest of the vas deferens (Fig. 16). Since this was in a position where a clear patch might be expected, perhaps in freshly preserved specimens it would be the clear patch.

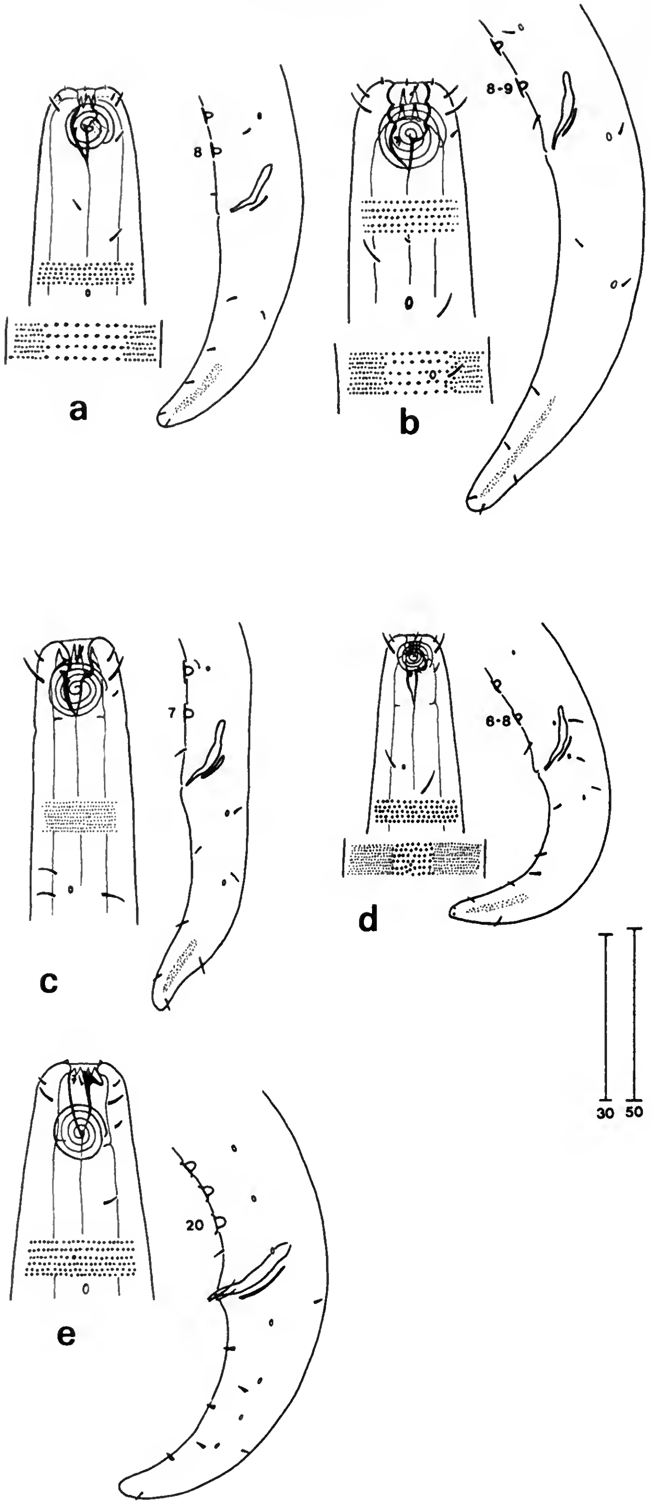

Fig. 3 (a) *Neotonchus punctatus*; (b) *Neotonchus chamberlaini*; (c) *Neotonchus boucheri*; (d) *Neotonchus meeki*; (e) *Gomphionchus lutosus*. Bar scales as in Fig. 2.

Table 2 Main differentiating data of *Neotonchus* species (measurements in μm)

Species	L	a	b	c	R_2	R_3	A♂	A♀	T	Cp	Ps	Location
N. punctatus	722	28	7	11	1·5	3	3+	?	r/r	–	8–9	E. coast USA
N. chamberlaini	960	29	7	8	4	6	5+	?	r/l	+	8–9	E. coast USA
N. boucheri	590–755	24–34	6–7	9–11	2–3	5–6	4+	3+	l/?	+	7	English Channel
N. meeki	710–750	25–29	6–7	9	2–3	6–7	4+	4+	l/r	+	6–8	North Sea

Abbreviations: R_2 = length of R_2 sensilla; Cp = presence (+) or absence (–) of clear patch in vas deferens; others as Table 1.

The shape of the dorsal tooth is rather characteristic but difficult to put into words. It is like an equilateral triangle projecting out from the wall of the buccal cavity and, compared with *Neotonchoides*, it is not forward-pointing (cf. Figs 3 a–d & 4 a–j).

The species may be distinguished using the information in Table 2 and Fig. 3.

GOMPHIONCHUS gen. nov.

TYPE SPECIES. *Neotonchus lutosus* Wieser & Hopper, 1966.

DIAGNOSIS. Neotonchinae. Large forward-pointing dorsal tooth situated anteriorly in the buccal cavity and protruding into the vestibule. Clear patch in vas deferens.

REMARKS. The form of the buccal cavity appears to be so different from the other neotonchids that a distinct genus is justified for *Neotonchus lutosus*. The buccal cavity form is the only autapomorphy which could be detected, the clear patch being synapomorphic. Other, non-exclusive, features are: lateral cuticle pores; amphid 4+ turns, situated posterior to R_3 sensilla; spicule with lateral pieces; male with ventro-sublateral caudal spines. Characters of use in identification are contained in Table 1 and Fig. 3e.

NEOTONCHOIDES gen. nov.

Comesa Gerlach, 1956 syn. nov.

TYPE SPECIES. *Neotonchoides cuanensis* sp. nov.

DIAGNOSIS. Neotonchinae. Buccal cavity with a distinct forward-pointing tooth and ventral ridges but no definite subventral teeth. Clear patch in vas deferens.

REMARKS. In 1956, Gerlach described a specimen from Kiel Bay as *Comesa corcunda* gen. et sp. nov. Wieser & Hopper (1966) noted the similarity between Gerlach's description and Cobb's specimens of *Neotonchus punctatus*, which they deemed congeneric. However, Gerlach's (1956) description gives no indication that *Comesa corcunda* fits the new definition of *Neotonchus* given above, so in the absence of specimens it is removed from *Neotonchus*. It would be possible to make Gerlach's species the type of a genus to hold all those taxa transferred from *Neotonchus*, which would then become *Comesa* species. But since the opportunity presents itself, it seems more sensible to base the genus on a species for which there is a good series of type specimens available. Such a species would be the one described here from Ireland, for which the new genus *Neotonchoides* is erected. Until specimens become available which might prove to the contrary, *Comesa corcunda* is transferred to the new genus.

Vitiello (1970) described a species as '*Neotonchus aff. corcundus*' which differed from Gerlach's (1956) species on the relative size of the spicule and its less heavily cuticularised buccal cavity, in addition to the other minor differences pointed out by Vitiello (1970). Vitiello's specimens warrant recognition as a separate species, which is named after him as *Neotonchoides vitielloii* sp. nov., the holotype being the male specimen on which Vitiello's (1970) description was based.

Warwick & Buchanan (1970) also recorded the presence of '*Neotonchus corcundus*' from the Northumberland coast. Examination of their material showed it to represent a distinct species new to science which is named *Neotonchoides warwicki* sp. nov. and described below.

The following species are considered valid: *N. melotridus* (Wieser & Hopper, 1966) comb. nov.; *N. corcundus* (Gerlach, 1956) comb. nov.; *N. vitius* (Warwick, 1971) comb. nov.; *N. interruptus* (Warwick, 1971) comb. nov.; *N. votadinii* (Warwick, 1971) comb. nov.; *N. pseudocorcundus* (Vitiello, 1971) comb. nov.; *N. cupulatus* (Vitiello, 1970) comb. nov.; *N. cuanensis* sp. nov.; *N. warwicki* sp. nov.; *N. vitielloii* sp. nov.

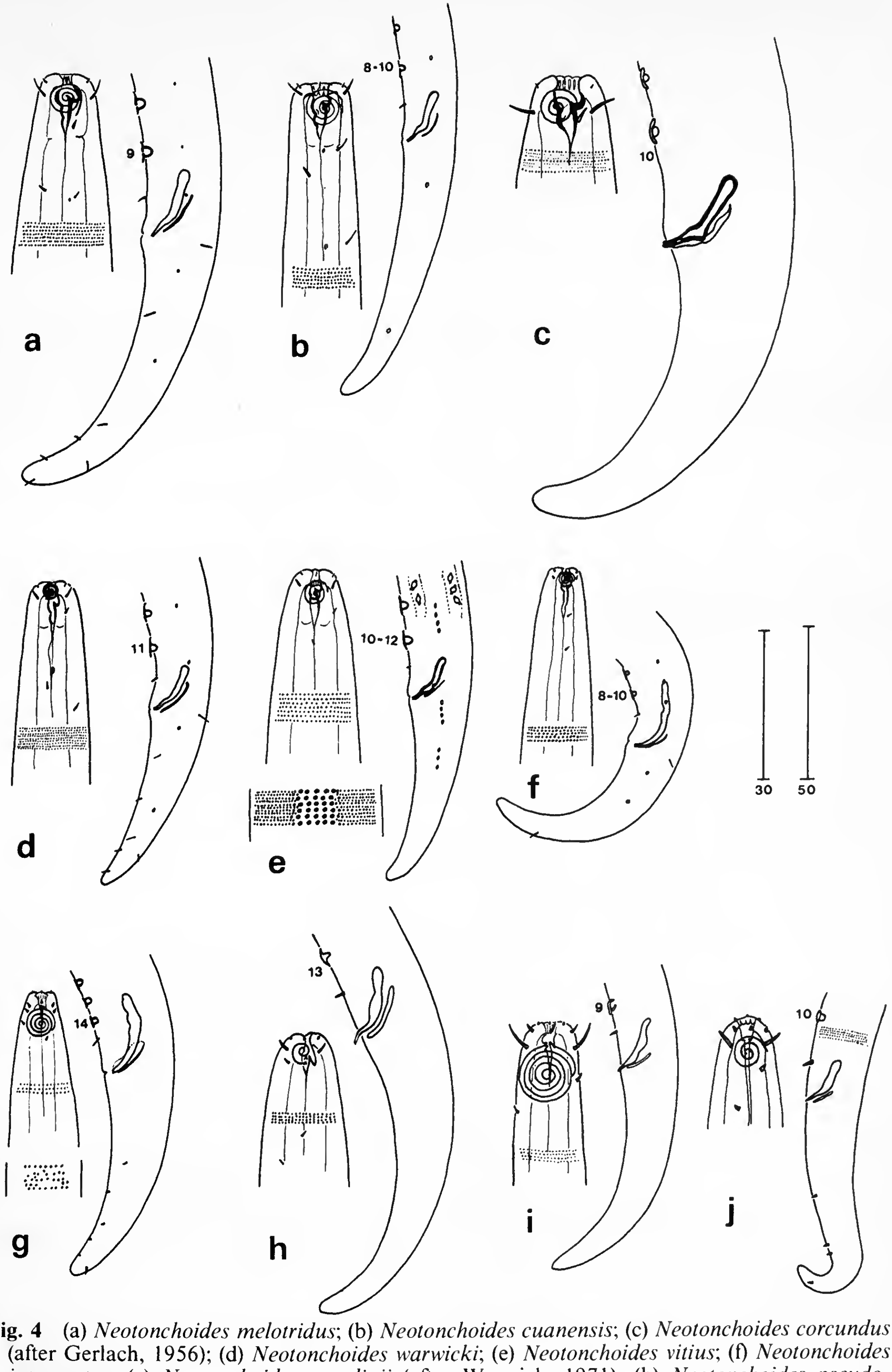

Fig. 4 (a) *Neotonchoides melotridus*; (b) *Neotonchoides cuanensis*; (c) *Neotonchoides corcundus* (after Gerlach, 1956); (d) *Neotonchoides warwicki*; (e) *Neotonchoides vitius*; (f) *Neotonchoides interruptus*; (g) *Neotonchoides votadinii* (after Warwick, 1971); (h) *Neotonchoides pseudocorcundus* (after Vitiello, 1971); (i) *Neotonchoides cupulatus* (after Vitiello, 1970); (j) *Neotonchoides vitielloii* (after Vitiello, 1970). Bar scales as in Fig. 2.

The proposed diagnostic feature for *Neotonchoides*, absence of definite subventral teeth, is admittedly a weak character but no positive autapomorphies could be found for the genus. In addition to the diagnostic characters, other features of the valid species, not necessarily shared by all, are: lack of lateral differentiation, except *N. vitius* and *N. votadinii*; R_3 sensilla 20–50% h.d., except *N. interruptus*; amphids 3+ or 4+ turns, except *N. cupulatus* with 5+ turns; amphid 30–70% c.d., except *N. cupulatus*; 8–14 precloacal supplements. In the only species in which females are known, *N. cuanensis*, the amphid of the female has one less turn than that of the male.

N. pseudocorcundus was described as having just over two turns of the amphid (Vitiello, 1971), but since the amphid is depicted as spiralling in the 'wrong' direction (Fig. 4h) one may assume that it was not clearly visible and a reinvestigation may show the species to have more turns of the amphid.

The species may be distinguished using the information in Table 3 and Fig. 4.

Clade: ***FILITONCHUS/NANNOLAIMUS***

These two genera form the apomorphic sister group of *Neotonchoides/Gomphionchus/Neotonchus*. Synapomorphies are: buccal cavity not structurally expanded; R_2 sensilla elongate, one or more head diameters. Other characters currently displayed by the constituent species are: slender body, 'a' ratio about or greater than 50; long R_3 sensilla; dorsal tooth, if present, only a small peg; 4–6 amphid turns in male; no lateral differentiation of cuticle.

NANNOLAIMUS Cobb, 1920

TYPE SPECIES. *Nannolaimus guttatus* Cobb, 1920.

DIAGNOSIS. Neotonchinae. R_1 sensilla setiform. R_2 sensilla elongate. Buccal cavity not structurally expanded. Clear patch in vas deferens.

REMARKS. This genus is transferred from the Cyatholaimidae. According to Lorenzen (1981) the monophyly of the Cyatholaimidae is based on the R_2 and R_3 sensilla being at the same level. Whilst in the type and in *Nannolaimus fusus* described by Gerlach (1956) the two circles are close together, in the specimens of *N. fusus* studied here they were not at exactly the same level and there are grounds for questioning the setal arrangement in *N. guttatus* (see below). As discussed earlier, the setal arrangement in some *Nannolaimus* species is considered as convergent with the condition found in the Cyatholaimidae since the presence of typical supplements and a posterior oesophageal bulb, albeit weak, supports their position within the Ethmolaimidae. A connection between *Nannolaimus* and *Gomphionema* was also noted by Riemann & Rachor (1972).

N. guttatus Cobb, 1920 was described from a single female specimen and should be considered a *species inquirenda*. However, there are a number of interesting points contained in Cobb's description: he figures the cuticle as having lateral differentiation; the R_1 sensilla are very long and depicted in a position posterior to the lips, i.e. not where they normally occur, which suggests that the disposition of the cephalic setae may have been misinterpreted; the intestinal cells had granules with 'the appearance of hollow shells', a description which would fit the structures found in *Neotonchoides vitius* (see below).

Nannolaimus complicatus Gerlach, 1957 does not belong to this genus: the tail is conico-cylindrical; R_1 sensilla are not setiform; supplements are absent. The species shows more similarity with *Paralongicyatholaimus* Stekhoven, 1950 to which genus it is proposed to transfer it: *Paralongicyatholaimus complicatus* (Gerlach, 1957) comb. nov., syn. *Nannolaimus complicatus* Gerlach, 1957. *Nannolaimus volutus* Gerlach, 1956 is transferred to *Filitonchus*. *Nannolaimus labiosus* Vitiello, 1974 is a *nomen nudum*.

Neotonchus phaleratus Wieser & Hopper, 1966 has the characters of *Nannolaimus* as now defined and is transferred to this genus. The only two valid species therefore are *N. phaleratus* (Wieser & Hopper, 1966) comb. nov. and *N. fusus* Gerlach, 1956. In addition to

Table 3 Main differentiating data of *Neotonchoides* species (measurements in μm)

Species	L	a	b	c	R_2	R_3	A♂	A♀	Sp	Ps	T	Cp	Location
N. melotridus	1140	42	10	12	0·7	4	3+	?	0·9	9	l/r	–	E. coast USA
N. cuanensis	810–1115	37–64	8–10	9–16	2	4–5	4+	3+	0·9	8–10	l/r	–	Irish Sea
*N. corcundus**	1280	28	7	12	1	7	3+	?	0·9	10	?	?	Baltic
N. warwicki	750–785	31–33	7–8	12–13	0·5	3	3+	?	0·9	11	r/l	+	North Sea
N. vitius	690–780	23–29	6–7	12	1	2	3+	?	0·9	10–12	l/r	+	North Sea
N. interruptus	630–680	30	7–8	10–11	1	1	3+	?	1·5	8–10	l/r	–	North Sea
*N. votadinii**	820	23–33	7	10–11	1·5	1·5	4+	?	1·5	14	?	?	North Sea
*N. pseudocorcundus**	1115–1345	35–42	9–11	10–13	+	3	2+	?	0·9	13	?	?	Mediterranean
*N. cupulatus**	745	35	8	11	2·6	6	5+	?	0·9	9	?	?	Mediterranean
*N. vitielloii**	915	44	8	12	+	4·5	3+	?	0·5	10	?	?	Mediterranean

Abbreviations: Sp = approximate length of spicule as proportion of distance from cloaca to first precloacal supplement; others as Tables 1 & 2.
*Specimens not seen.

Table 4 Main differentiating data of *Nannolaimus* (*N.*) and *Filitonchus* (*F.*) species (measurements in μm)

Species	L	a	b	c	R_2	R_3	A♂	A♀	T	Cp	Ps	Location
N. fusus	1245	66	9	11	11	6	6+	?	l/r	–	9–10	Irish Sea; Baltic
N. phaleratus	960–1000	51	8	9	9–10	12–14	4+	3+	l/l	+	8	E. coast USA
N. filiformis	1190–1300	86–99	12	16	5–6	9	4+	?	r/l	+	8–9	North Sea
F. ewensis	1370	81	13	14	6	8	6+	?	r/l	+	7	W. coast Scotland
*F. volutus**	1555	48	7	10	15	15	5+	?	?	?	8	Baltic

Abbreviations: See Tables 1 & 2.
*Specimens not seen.

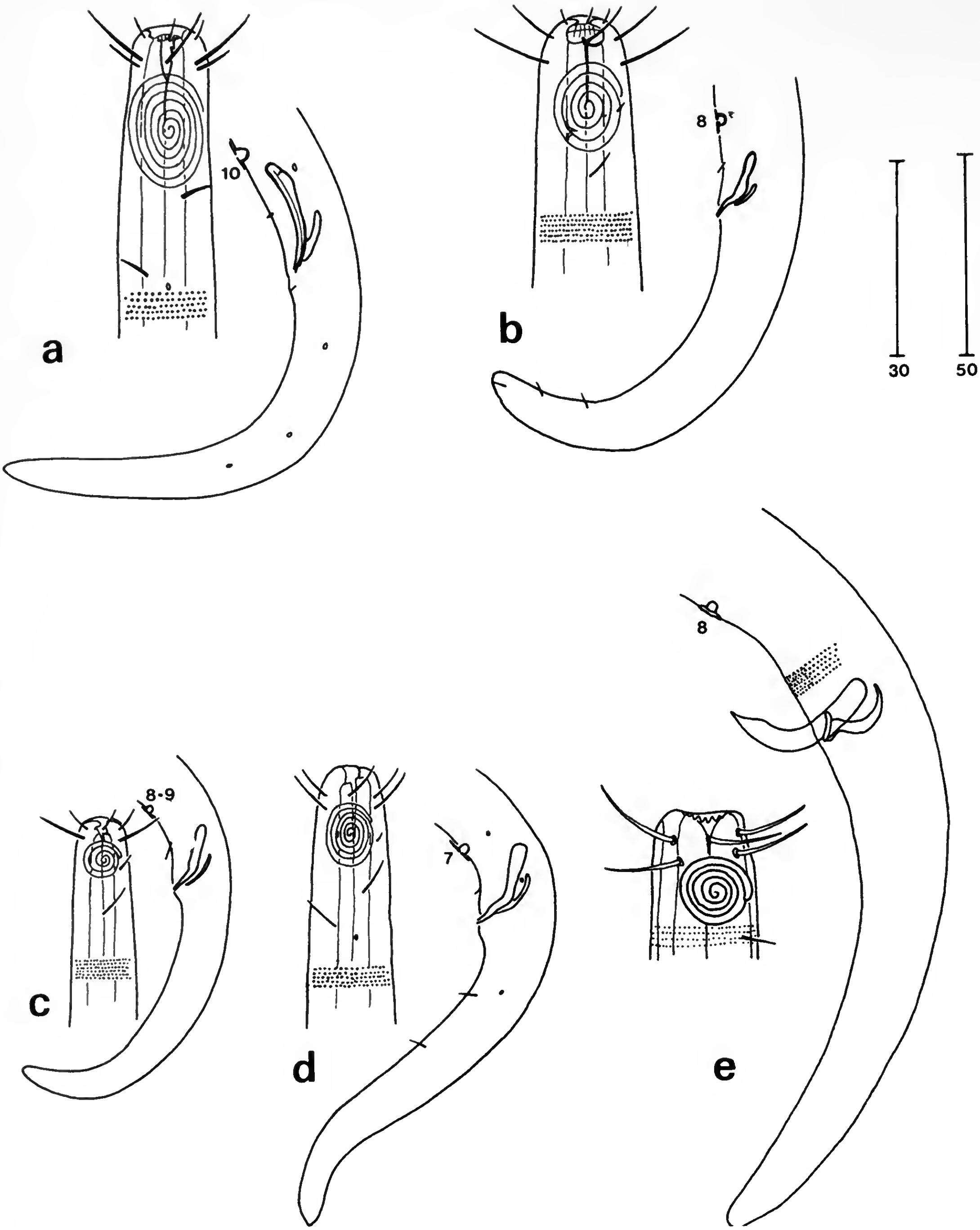

Fig. 5 (a) *Nannolaimus fusus*; (b) *Nannolaimus phaleratus*; (c) *Filitonchus filiformis*; (d) *Filitonchus ewensis*; (e) *Filitonchus volutus* (after Gerlach, 1956). Bar scales as in Fig. 2.

the diagnostic characters, other features shown by the species are: no lateral differentiation; slender body ('a' >50); R_2 and R_3 sensilla long ($>50\%$ c.d.); amphid large (about 80% c.d. in males); 8–10 supplements. The species can be distinguished using the information in Table 4 and Fig. 5.

The two species of *Nannolaimus* constitute one of the least satisfactory grouping within the Ethmolaimidae. It could be argued that the condition 'R_2 sensilla longer than R_3 sensilla', if discontinuously distinct from 'R_3 sensilla longer than R_2 sensilla', is sufficient grounds for assigning *N. fusus* to different genus from *N. phaleratus*. However, if the length of the two circles of sensilla can vary independently then the condition found in *N. fusus* may be towards one end of a range of variation. With but two valid species, only the discovery of further species will provide an answer to this problem.

FILITONCHUS gen. nov.

TYPE SPECIES. *Neotonchus filiformis* Warwick, 1971.

DIAGNOSIS. Neotonchinae. R_1 sensilla papilliform. R_2 sensilla elongate. Buccal cavity not structurally expanded. Clear patch in vas deferens.

REMARKS. The new genus can be distinguished from *Nannolaimus* only through the absence of setiform R_1 sensilla. There are three valid species: *F. filiformis* (Warwick, 1971) comb. nov., syn. *Neotonchus filiformis* Warwick, 1971; *F. ewensis* sp. nov.; *F. volutus* (Gerlach, 1956) comb. nov., syn. *Nannolaimus volutus* Gerlach, 1956.

In addition to the characters used in the diagnosis, other features of the genus as presently constituted are: no lateral differentiation; slender body ('a' >80); R_3 sensilla long ($>80\%$ c.d.); amphid large ($>70\%$ c.d. in male); 7–9 supplements. The species may be distinguished using the information given in Table 4 and Fig. 5.

Key to the genera of Neotonchinae

The six genera contained in the subfamily may be distinguished by means of the lattice key (Table 5) based on the valid species contained in each genus.

Table 5 Lattice key to genera of the Neotonchinae

Genus	Character							
	A	B	C	D	E	F	G	H
Gomphionema	1	1	2	2	2	1	2	2
Gomphionchus	2	2	1	2	2	1	2	2
Neotonchus	2	2	2	2	2	2	1	1
Neotonchoides	2	2	2	2	2	2	2	2
Nannolaimus	2	2	2	1	1	2	2	2
Filitonchus	2	2	2	2	1	2	2	2

A: 1. Oesophagus bulb $\geqslant 30\%$ total oesophagus length; 2. Oesophagus bulb $<25\%$ total oesophagus length.
B: 1. Massive dorsal tooth, buccal cavity length $\geqslant 1{\cdot}3 \times$ h.d. at mid-amphid level; 2. Dorsal tooth not massive, buccal cavity length $\leqslant 1{\cdot}0 \times$ h.d. at mid-amphid level.
C: 1. Dorsal tooth extends anteriorly into vestibule; 2. Dorsal tooth does not enter vestibule.
D: 1. R_1 sensilla setiform; 2. R_1 sensilla papilliform or not visible.
E: 1. R_2 sensilla $\geqslant 6\ \mu m$; 2. R_2 sensilla $\leqslant 5\ \mu m$.
F: 1. Spicule with lateral piece; 2. Spicule without lateral piece.
G: 1. Tail end with lateral file small dots; 2. Tail end without lateral file small dots.
H: 1. Sublateral pore-setae present; 2. Sublateral pore-setae absent.

Summary of proposed taxonomic changes and additions

Valid name	Synonymy
Ethmolaimidae Filipjev & Stekhoven, 1941	Neotonchidae Wieser & Hopper, 1966
Ethmolaimus pratensis De Man, 1880	*Ethmolaimus parapratensis* Alekseev, Naumova & Dymina, 1979
Trichethmolaimus gen. nov.	
Trichethmolaimus hirsutus (Gerlach, 1956)	*Spiliphera hirsuta* Gerlach, 1956
Gomphionema euripus sp. nov.	*Gomphionema compacta* sensu Riemann & Rachor, 1972 nec Gerlach, 1957
Neotonchus Cobb, 1933	*Heterocyatholaimus* Allgen, 1935
Neotonchus boucheri sp. nov.	*Neotonchus chamberlaini* sensu Boucher, 1976 nec Wieser & Hopper, 1966
Gomphionchus gen. nov.	
Gomphionchus lutosus (Wieser & Hopper, 1966)	*Neotonchus lutosus* Wieser & Hopper, 1966
Neotonchoides gen. nov.	*Comesa* Gerlach, 1956
Neotonchoides melotridus (Wieser & Hopper, 1966)	*Neotonchus melotridus* Wieser & Hopper, 1966
Neotonchoides corcundus (Gerlach, 1956)	*Neotonchus corcundus* (Gerlach, 1956)
Neotonchoides vitius (Warwick, 1971)	*Neotonchus vitius* Warwick, 1971
Neotonchoides interruptus (Warwick, 1971)	*Neotonchus interruptus* Warwick, 1971
Neotonchoides votadinii (Warwick, 1971)	*Neotonchus votadinii* Warwick, 1971
Neotonchoides pseudocorcundus (Vitiello, 1971)	*Neotonchus pseudocorcundus* Vitiello, 1971
Neotonchoides cupulatus (Vitiello, 1971)	*Neotonchus cupulatus* Vitiello, 1971
Neotonchoides vitielloii sp. nov.	*Neotonchus aff. corcundus* sensu Vitiello, 1970 nec Gerlach, 1956
Neotonchoides cuanensis sp. nov.	
Neotonchoides warwicki sp. nov.	*Neotonchus corcundus* sensu Warwick & Buchanan, 1970 nec Gerlach, 1956
Nannolaimus phaleratus (Wieser & Hopper, 1966)	*Neotonchus phaleratus* Wieser & Hopper, 1966
Filitonchus gen. nov.	
Filitonchus filiformis (Warwick, 1971)	*Neotonchus filiformis* Warwick, 1971
Filitonchus volutus (Gerlach, 1956)	*Nannolaimus volutus* Gerlach, 1956
Filitonchus ewensis sp. nov.	
Paralongicyatholaimus complicatus (Gerlach, 1957)	*Nannolaimus complicatus* Gerlach, 1957

Doubtful taxa

Ethmolaimus faeroeensis Ditlevsen, 1928 sp. inq.
Ethmolaimus caudatus Alekseev, Naumova & Dymina, 1979 sp. inq.
Gomphionema compactum Gerlach, 1957 sp. dub.
Neotonchus macrolaimus (Allgen, 1935) sp. dub.
Neotonchus hapalus Vitiello, 1974 nomen nudum
Neotonchus spiralis Vitiello 1974 nomen nudum
Nannolaimus guttatus Cobb, 1920 sp. inq.
Nannolaimus labiosus Vitiello, 1974 nomen nudum

Species descriptions

Trichethmolaimus hirsutus (Gerlach, 1956) comb. nov.
(Fig. 2a)

Spiliphera hirsuta Gerlach, 1956

MATERIAL STUDIED. Several ♂♂, collected by Mr P. J. D. Lambshead.

LOCALITY. Clyde Sea, Scotland.

REMARKS. The specimens were only studied in sufficient detail to ascertain the following features: 10 typical cup-shaped precloacal supplements present; two opposed testes. The fixation-shape is characteristically a tight coil, so that detailed study will be difficult: thus far, few uncoiled specimens have been encountered.

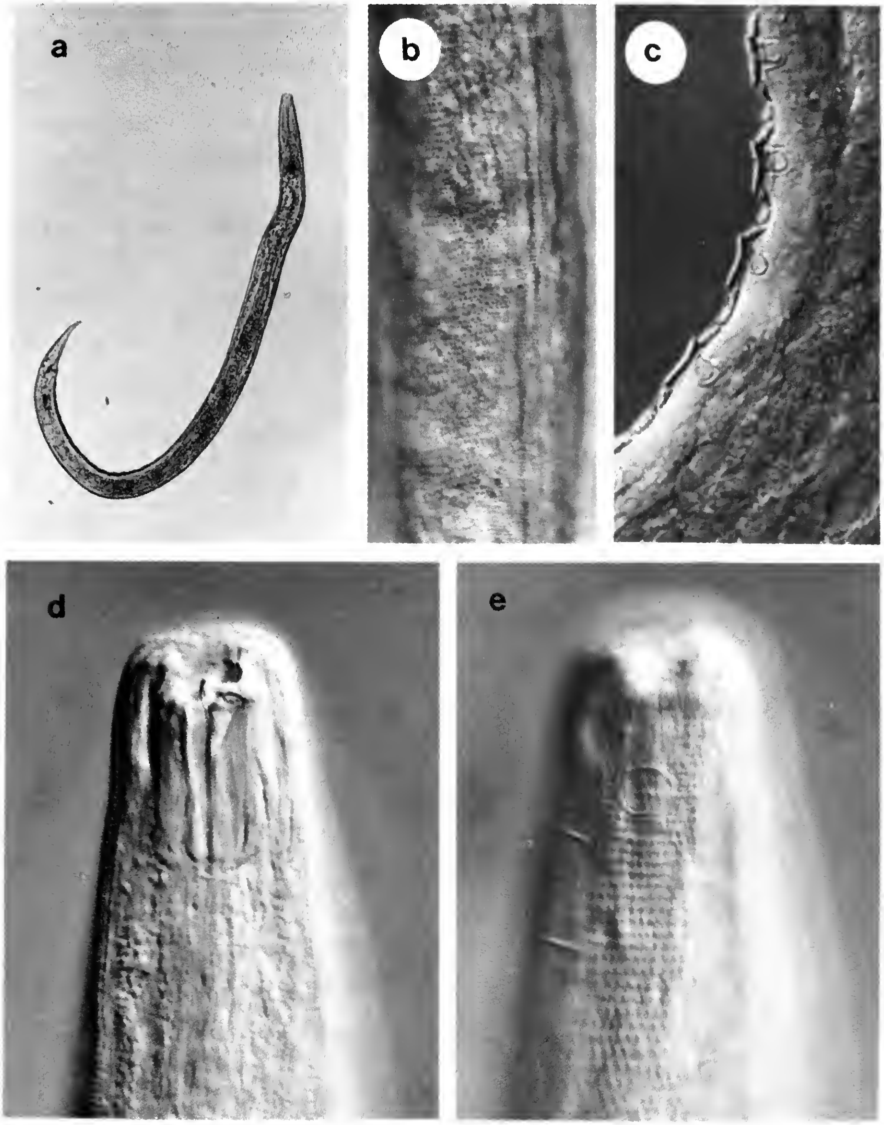

Fig. 6 *Ethmolaimus pratensis*: (a) ♂ whole body; (b) cuticle pattern at mid-body; (c) precloacal supplements; (d) anterior showing buccal cavity; (e) anterior showing amphid.

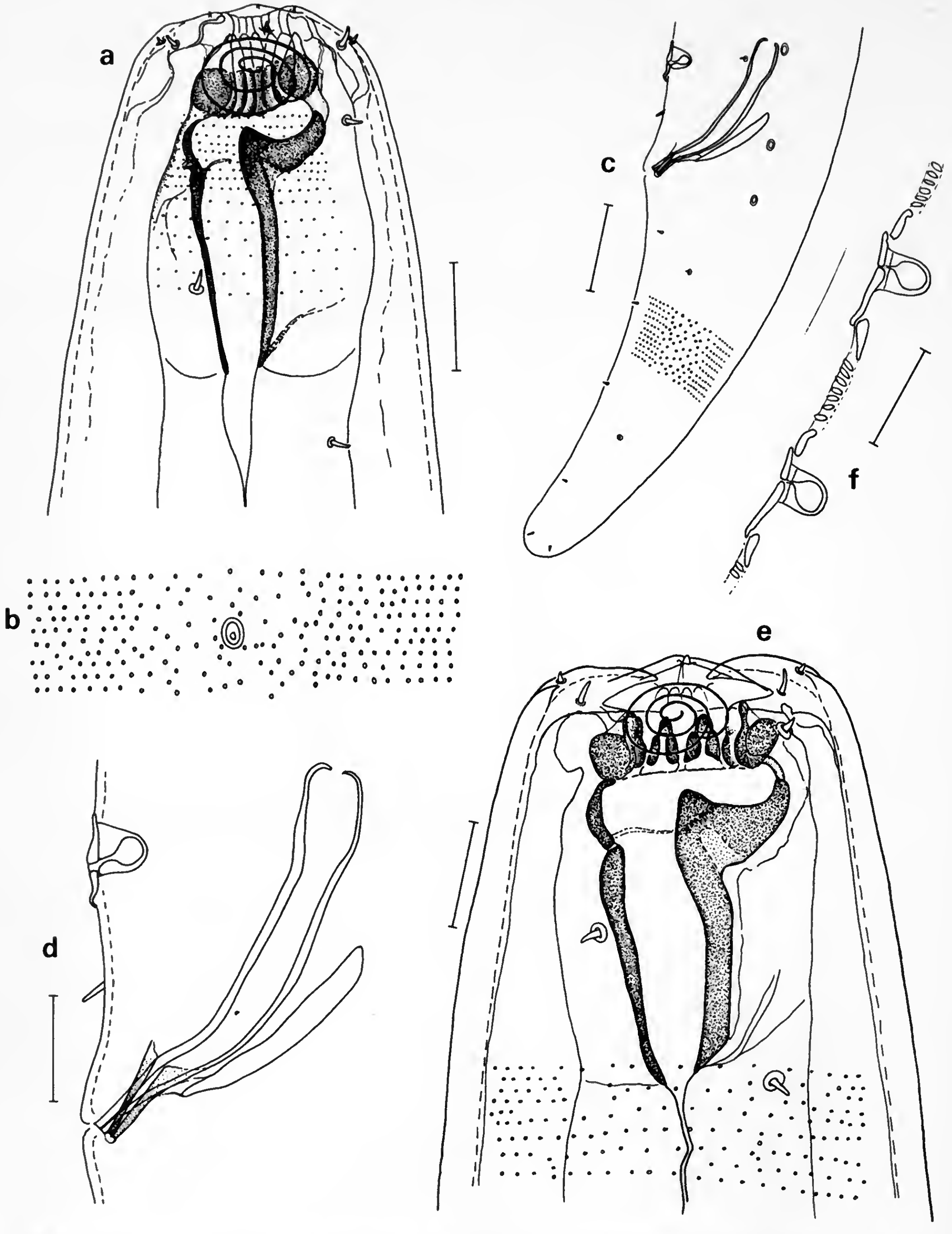

Fig. 7 *Gomphionema typicum*: (a) holotype ♂ head; (b) cuticle pattern at mid-body; (c) ♂ tail; (d) copulatory apparatus; (e) ♀ head. *Ethmolaimus pratensis*: (f) supplements. Bar scales: c = 20 μm; others = 10 μm.

Ethmolaimus pratensis De Man, 1880
(Figs 2b, 6, 7f)

MATERIAL STUDIED. 1♂ (slide Tv 134 p), 3♀♀ (slides Tv 134c, e, g) in the collection of Dr P. Jensen.

LOCALITY. Pojoviken, southern Finnish archipelago.

DESCRIPTION. Cuticle with transverse rows of punctations which in the lateral field are larger and arranged in fewer rows, although in places tending to be irregular. This lateral differentiation of fewer rows of larger dots is most noticeable in the region between the amphid and the nerve ring. There is a single lateral file of small cuticle pores; difficult to distinguish. In the male studied, there were 15 supplements which extended 350 µm anterior to the cloaca, 30% of total body length. The anterior testis is to the left, posterior to the right of the gut.

REMARKS. Apart from this additional data, the specimens agree with the redescription by Jensen (1979*a*). Cobb (1914) noted the more conspicuous lateral punctations near the head of the female specimen he called *E. americanus* (= *E. pratensis*) but could not detect any lateral differentiation.

Gomphionema typicum Wieser & Hopper, 1966
(Figs 2c, 7a–e, 8, 9)

MATERIAL STUDIED. Holotype ♂, slide 121 and allotype ♀, slide 121a, Canadian National Collection of Nematodes.

LOCALITY. Sandflat, Key Biscayne, Florida, U.S.A.

DESCRIPTION.

Holotype ♂: $\dfrac{-\quad 200\quad M\quad 1238}{21\quad 53\quad 62\quad 41}$ 1335 µm; $a = 22$; $b = 7$; $c = 14$; $S = 41$ µm

Allotype ♀: $\dfrac{-\quad 220\quad 710\quad 1242}{29\quad 72\quad 77\quad 49}$ 1350 µm; $a = 18$; $b = 6$; $c = 13$; $V = 53\%$

Cuticle bears transverse rows of punctations and there is a lateral differentiation of fewer rows which begins about the level of the buccal cavity and continues to the tail tip (Figs 7b, 9b). The lateral punctations are irregular throughout most of the body, but in the oesophageal region they are in relatively regular transverse rows. Conspicuous lateral cuticle pores are present: the male had a total of 12 on the right side, 4 in oesophageal region, and 13 on left side, 5 in oesophageal region; the female had a total of 34 on right side, 9 in oesophageal region, and 31 on left side, 8 in oesophageal region. Sparse sublateral spine-like somatic setae present. R_1 sensilla minute papillae. R_2 sensilla papilliform, about 1 µm. R_3 sensilla short setae, about 2 µm, situated only slightly posterior to R_2 sensilla (Figs 7a, e). Short dorso-sublateral subcephalic setae present. Amphid 3+ turns in both sexes, situated anteriorly on head and therefore appearing oval in lateral view: 10·5 µm (45% c.d.) wide in male; 10 µm (30% c.d.) wide in female. Buccal cavity larger and more heavily cuticularised in female than male (Figs 7a, e). 12 well-developed rugae at anterior of buccal cavity which appear to be organised in six pairs at certain depths of focus (Fig. 7e). Massive dorsal tooth. Large oesophageal bulb, constituting 33% and 44% of oesophagus length in male and female respectively. Tail conical with two small ventro-sublateral spines in both sexes and short subventral setae in male (Fig. 7c). Spicules slightly cephalate proximally and in addition to the dorsal gubernaculum there is an extra structure lying lateral to the distal end of each spicule (Fig. 7d). Precloacal spine present and 22 precloacal supplements extending 395 µm anterior to cloaca (Figs 9c, d). No clear patch in vas deferens detected. Two opposed testes; anterior left, posterior right of gut. Two opposed, reflexed ovaries; anterior lies left of gut and is reflexed to the right, posterior lies right of gut and is reflexed to the left.

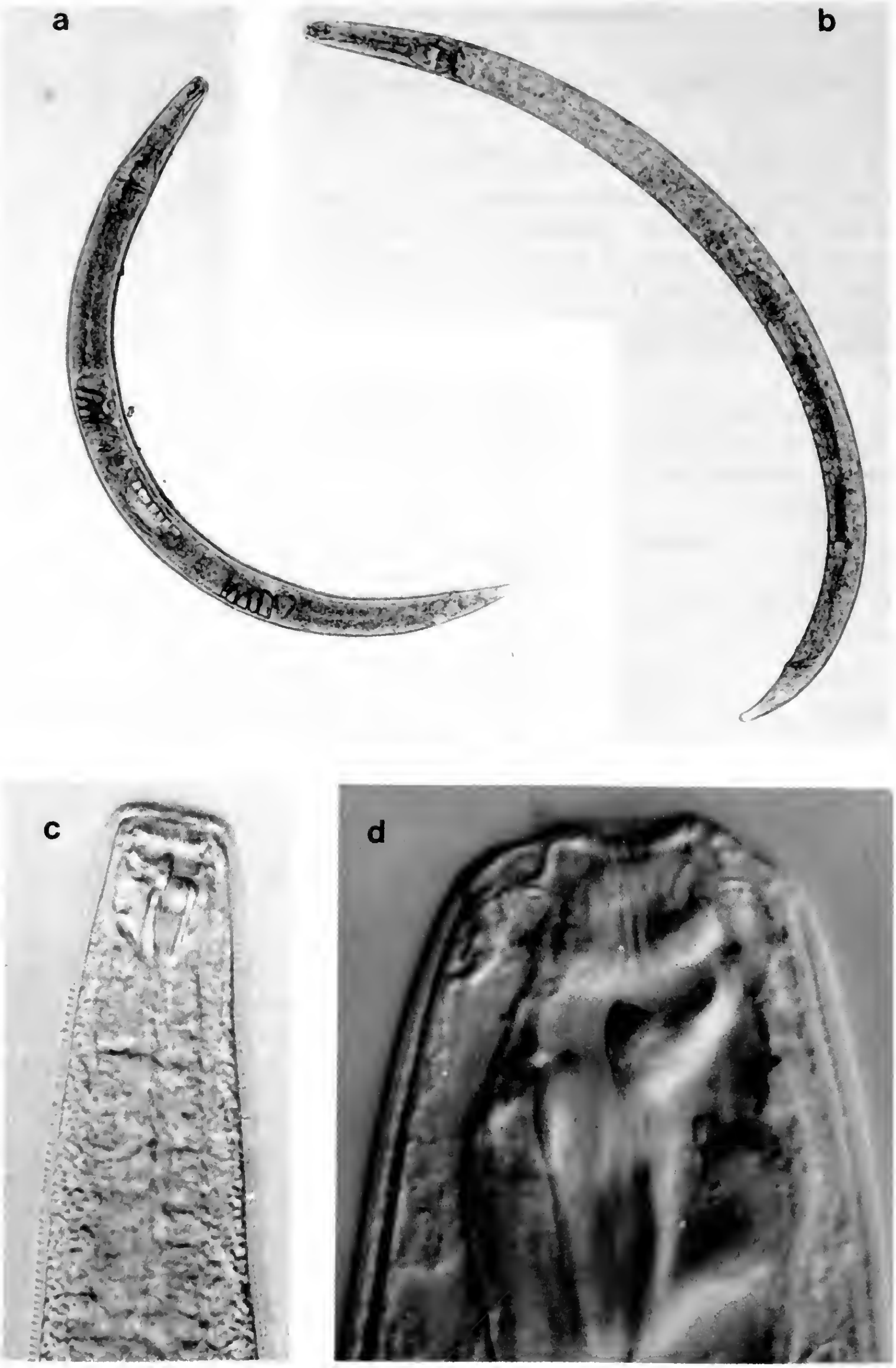

Fig. 8 *Gomphionema typicum*: (a) allotype ♀ whole body; (b) holotype ♂ whole body; (c) allotype anterior region; (d) holotype head.

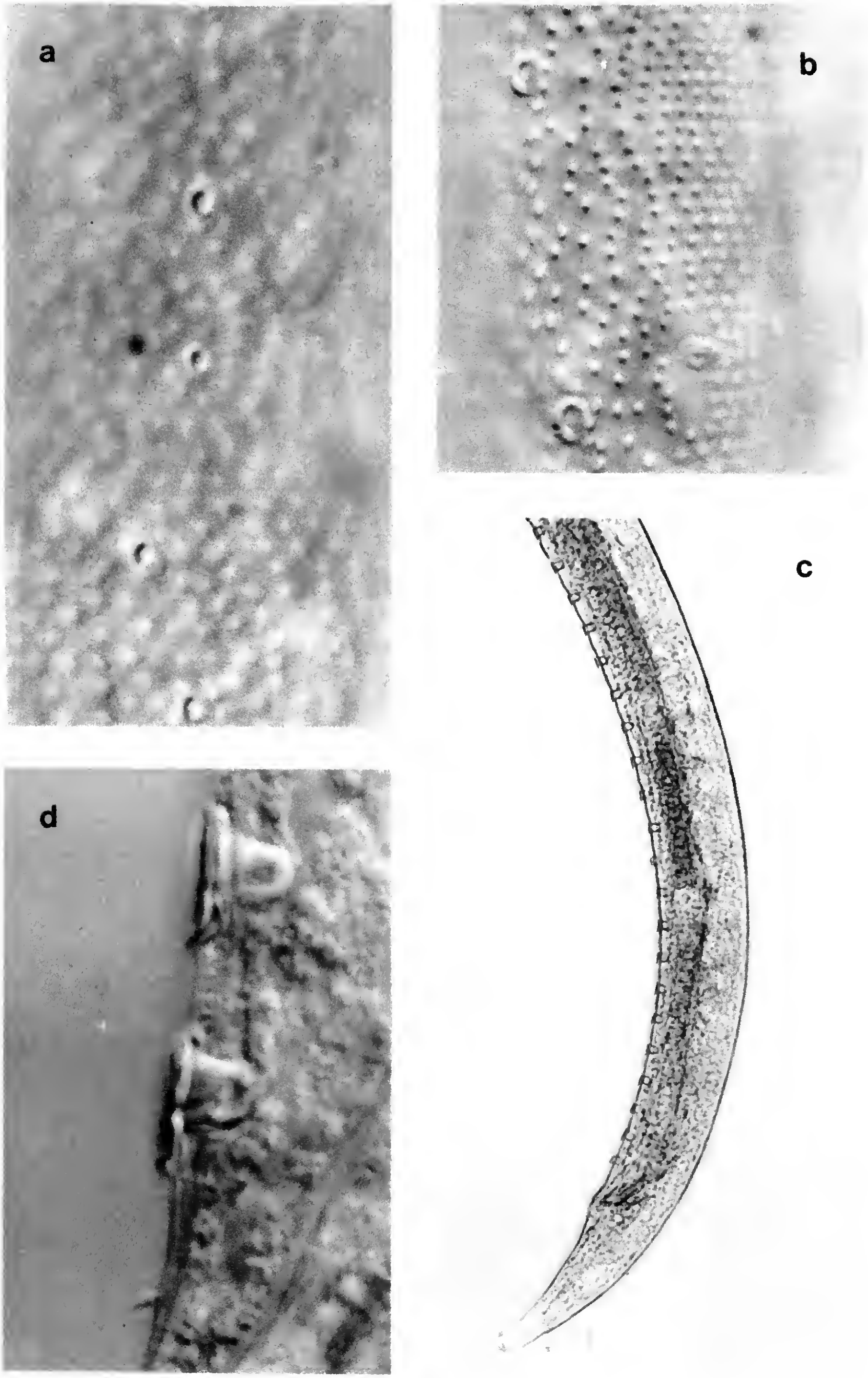

Fig. 9 *Gomphionema typicum*: (a) ♀ lateral cuticle showing pores; (b) ♀ lateral cuticle showing differentiation; (c) ♂ posterior region; (d) precloacal spine and two precloacal supplements.

Remarks. There are some points of difference between the description given above and that of Wieser & Hopper (1966), although the latter is based on a large number of specimens. The R_2 and R_3 sensilla are not in one circle; the R_3 are slightly posterior to the R_2. The cuticular punctation is not of 'uniform distribution over entire body', if this statement is taken to imply an absence of lateral differentiation. Wiesser & Hopper (1966) quote the range of maximum width as 78–90 μm: the holotype has a maximum diameter of 62 μm. The female studied here had almost three times as many cuticle pores as the male but whether this reflects a true sexual dimorphism is obviously unclear. Also, the allotype has a more substantial buccal cavity. Finally, there are two testes, not one.

Gomphionema fellator Wieser & Hopper, 1966

(Figs 2d, 10–12)

Material studied. Holotype ♂$_1$ (slide 122), allotype ♀$_1$ (slide 122a), paratype ♂$_2$ (slide 122b) and paratypes ♂$_3$, ♀$_{2-5}$ (slide 122e), Canadian National Collection of Nematodes.

Locality. ♂$_{1-2}$, ♀$_1$ from muddy sand, Charleston, South Carolina, U.S.A.; ♂$_3$, ♀$_{2-5}$ from Sapelo Island, Georgia, U.S.A.

Description.

Holotype ♂$_1$: $\frac{-\quad 203\quad \mathrm{M}\quad 974}{16\quad 41\quad 41\quad 30}$ 1040 μm; a = 25; b = 5; c = 16; S = 36 μm.

Allotype ♀$_1$: $\frac{-\quad 215\quad 486\quad 865}{17\quad 49\quad 56\quad 35}$ 930 μm; a = 17; b = 4; c = 14; V = 52%

Paratype ♂$_2$: L = 1035 μm; a = 26; b = 5; c = 15; S = 38 μm
Paratype ♂$_3$: L = 645 μm; a = 18; b = 5; c = 13; S = 36 μm
Paratype ♀$_2$: L = 593 μm; a = 15; b = 4; c = 11; V = 54%
Paratype ♀$_3$: L = 672 μm; a = 18; b = 5; c = 14; V = 57%
Paratype ♀$_4$: L = 734 μm; a = 18; b = 5; c = 15; V = 55%
Paratype ♀$_5$: L = 924 μm; a = 21; b = 6; c = 17; V = 66%

Cuticle bears transverse rows of punctations and the lateral dots are larger. The lateral dots are not much larger in most of the oesophageal region but towards the end of the oesophagus, the lateral dots become larger and slightly irregular (Fig. 10b). By about the middle of the body, the lateral dots are conspicuously larger and although irregular, give the appearance of being in fewer transverse rows (Fig. 10c). This lateral differentiation of fewer rows ends just anterior to the tail, although the lateral dots are still larger on the tail. There are numerous small lateral cuticle pores present from the mid-oesophageal level to mid-caudal level (Figs 10b, d and 12b). Short sublateral spine-like somatic setae present. R_1 sensilla minute. R_2 sensilla papillate. R_3 sensilla short, about 1 μm. Short dorso-sublateral subcephalic seta present. Amphid 3+ turns in both sexes, about 8–9 μm wide and transversely oval in Charleston specimens (Fig. 10a), but more rounded in Sapelo Island specimens (Fig. 10f). Buccal cavity similar to *G. typicum*, although the large dorsal tooth is more pointed and anteriorly directed (Fig. 11d). Large oesophageal bulb (Fig. 11c), 31–36% of oesophageal length with no apparent sexual dimorphism. Tail conical with 3 ventro-sublateral and 2 dorso-sublateral spines. In the males, there are also 3, sometimes 4, subventral spines (Fig. 10d); absent in females. Spicules have extra lateral pieces at the distal ends (Figs 10e, g). Precloacal spine present, emanating from a conspicuous base structure (Fig. 10e). 15 precloacal supplements, extending in ♂$_1$ 298 μm, in ♂$_2$ 320 μm and in ♂$_3$ 192 μm anterior to cloaca, but occupying about 30% of the total body length in each case. Two opposed testes; anterior left, posterior right of gut. No clear patch in vas deferens. Two opposed, reflexed ovaries; anterior lies left of gut and reflexed to the left, posterior lies right of gut and reflexed to the right.

REMARKS. There are some points of difference between the description given above and that of Wieser & Hopper (1966): the cephalic setae are not in one circle; the cuticle punctation is not uniform all along the body; cuticle pores are present. Otherwise the information given in Wieser & Hopper (1966) is corroborated here. *G. fellator* can be distinguished from *G. typica* in having more numerous cuticle pores, lateral differentiation not present in oesophageal region, fewer precloacal supplements and a precloacal spine with a conspicuous base.

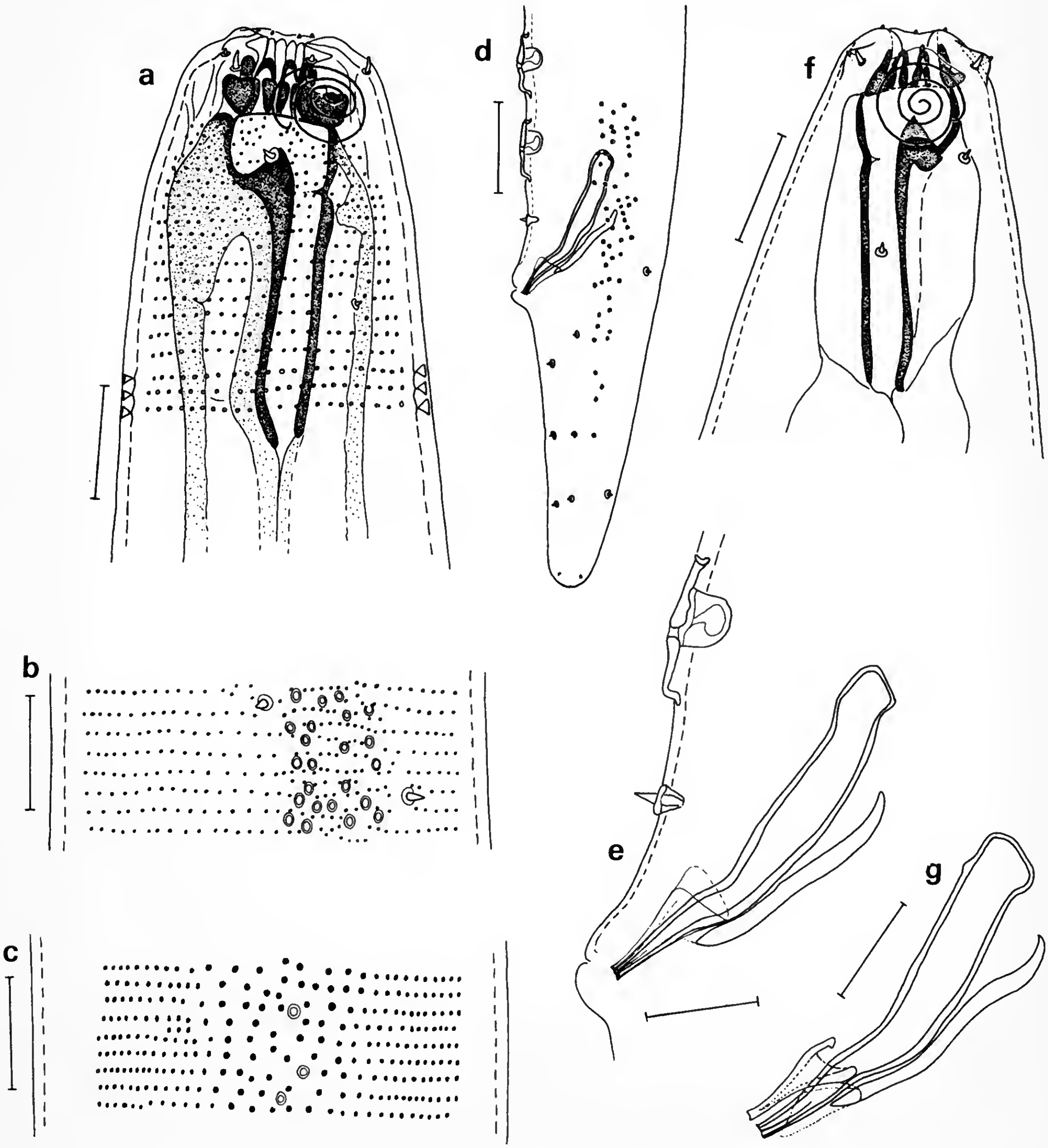

Fig. 10 *Gomphionema fellator:* (a) holotype ♂ head; (b) cuticle pattern level with anterior of oesophageal bulb, dorso-sublateral view showing cuticle pores and sublateral spines; (c) cuticle pattern mid-body, lateral view showing differentiation; (d) holotype ♂ tail; (e) holotype copulatory apparatus; (f) paratype $♂_3$ head; (g) paratype $♂_3$ copulatory apparatus. Bar scales: d = 20 μm; others = 10 μm.

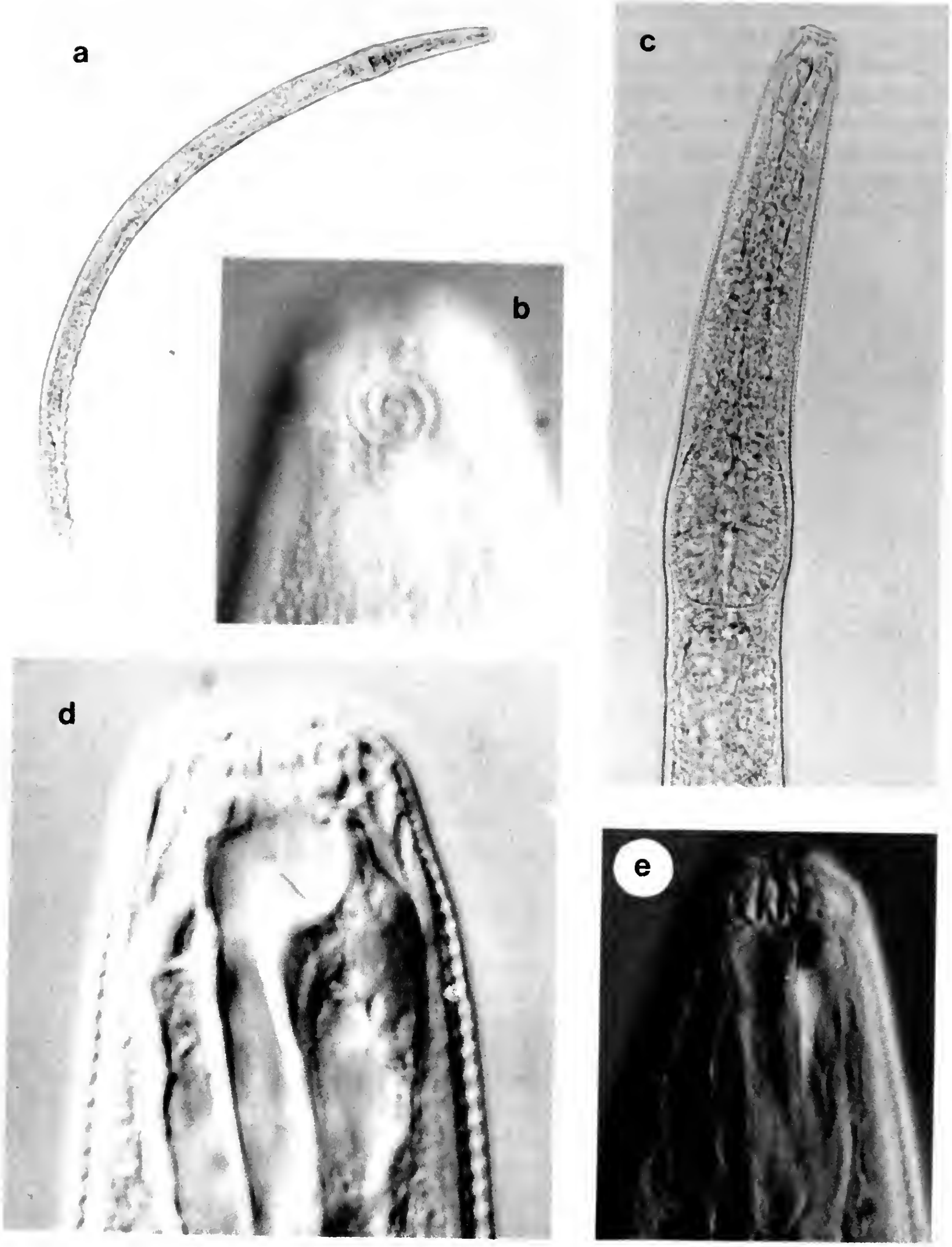

Fig. 11 *Gomphionema fellator:* (a) holotype ♂ whole body; (b) head showing amphid; (c) anterior region; (d) head showing buccal cavity; (e) head showing rugae.

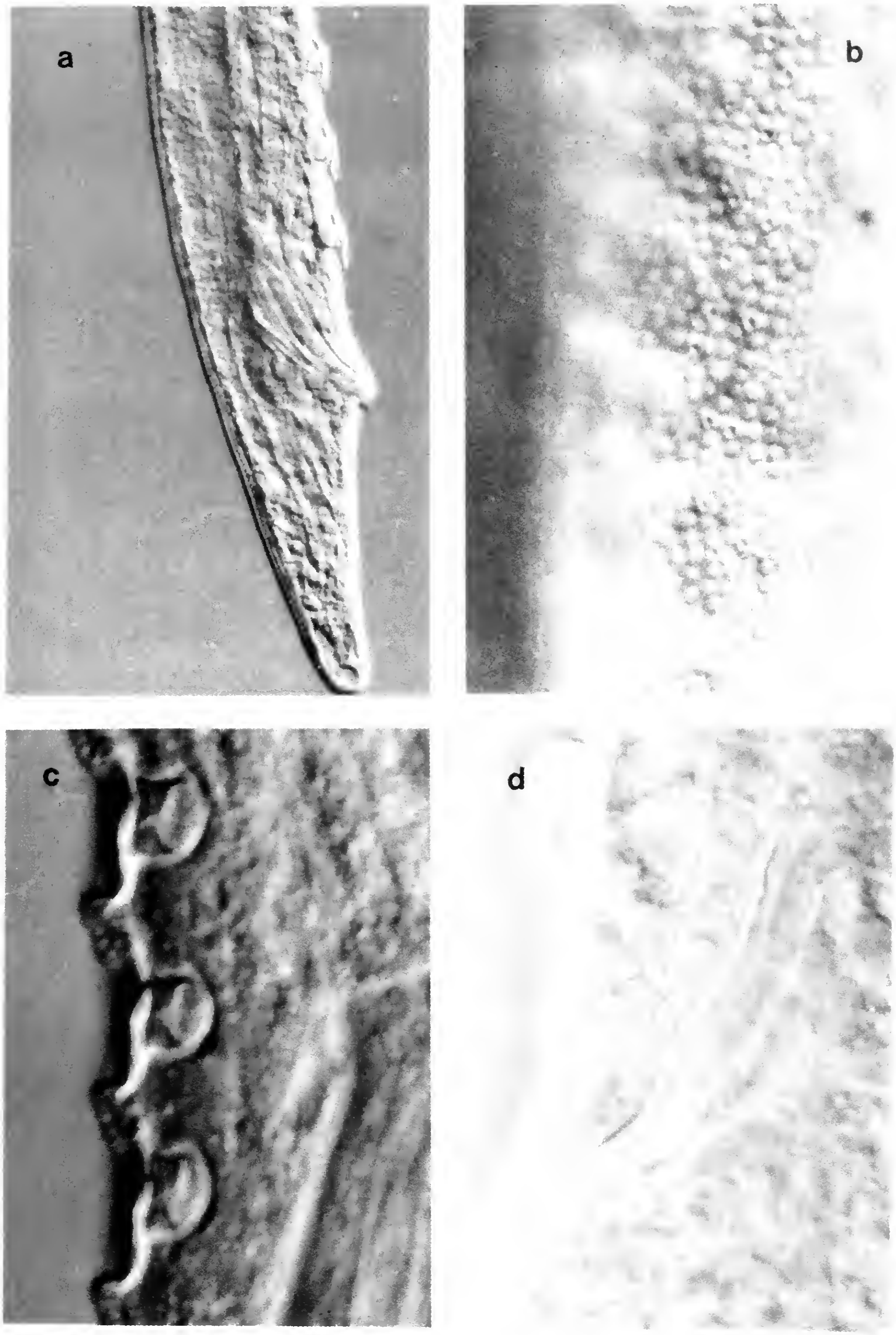

Fig. 12 *Gomphionema fellator*: (a) holotype ♂ tail; (b) lateral cuticle showing pores; (c) precloacal supplements of another ♂; (d) spicule.

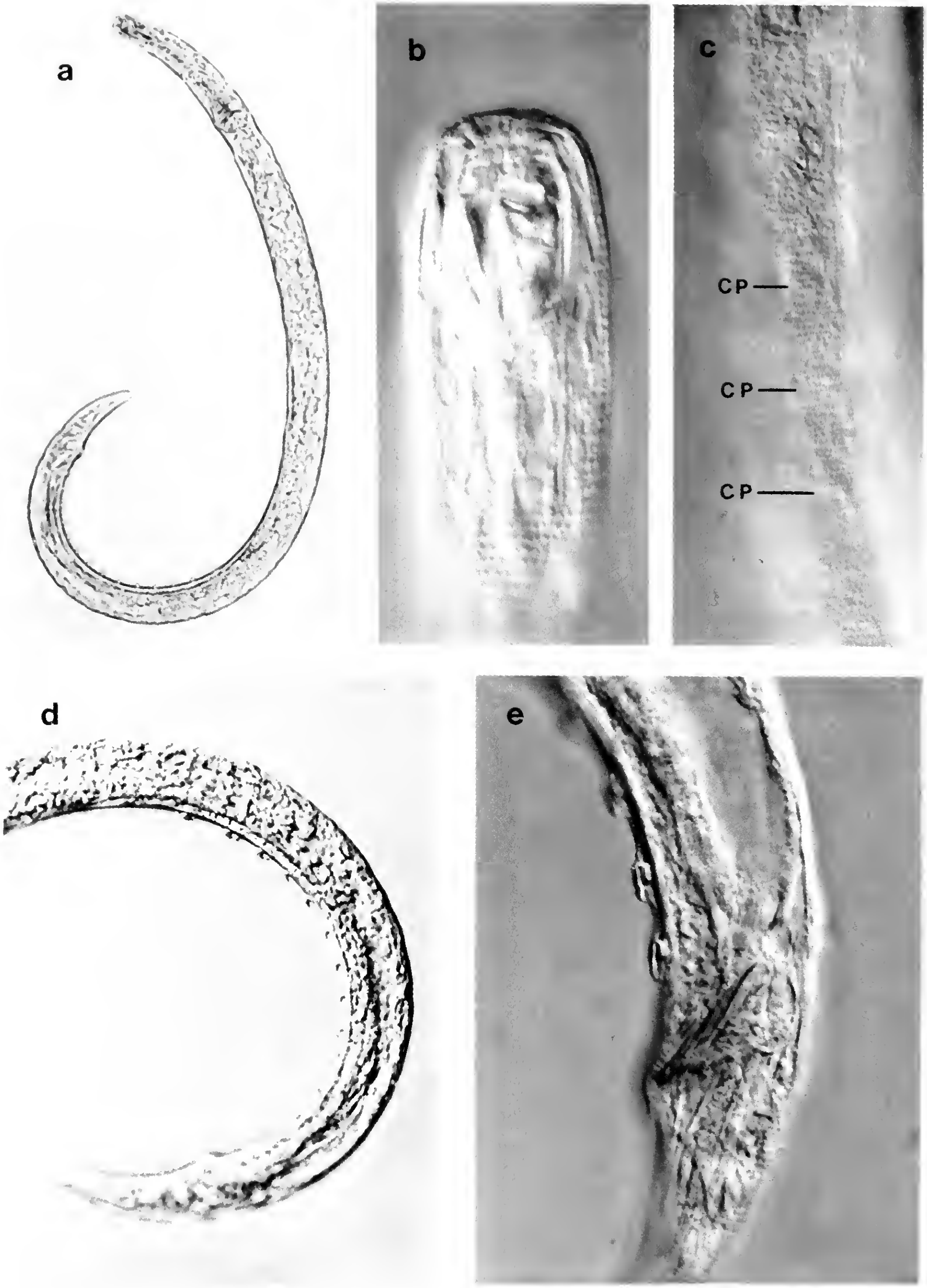

Fig. 13 *Gomphionema* sp.: (a) ♂ whole body; (b) head showing buccal cavity; (c) lateral cuticle punctations, CP = cuticle pore; (d) ♂ posterior region; (e) cloacal region.

Gomphionema sp.
(Figs 2e, 13)

A new species of *Gomphionema* was found by Dr R. M. Warwick in Australia and he will be providing a description. However, he kindly allowed some specimens to be observed and photographed in order that the species could be included in this work. The following information is given simply to indicate the state of those characters of phylogenetic importance.

DESCRIPTION. Lateral differentiation present, consisting of larger dots and fewer transverse rows (Fig. 13c) and beginning posterior to oesophageal region. The lateral rows of dots appear to anastomose in places. Minute cuticle pores present as a single lateral row 13–15 μm apart (Fig. 13c): difficult to detect. Sublateral somatic spine-like setae present. Lateral spicule pieces present. Precloacal spine and 14 precloacal supplements present. Two opposed testes; anterior right, posterior left of gut. No clear patch in vas deferens. The male tail has two dorso-sublateral, two larger ventro-sublateral spines and three sub-ventral spines.

REMARKS. The specimens can be distinguished from the other two valid species by the cuticle pores, fewer than *G. fellator* and smaller than *G. typica*, in addition to several other minor differences.

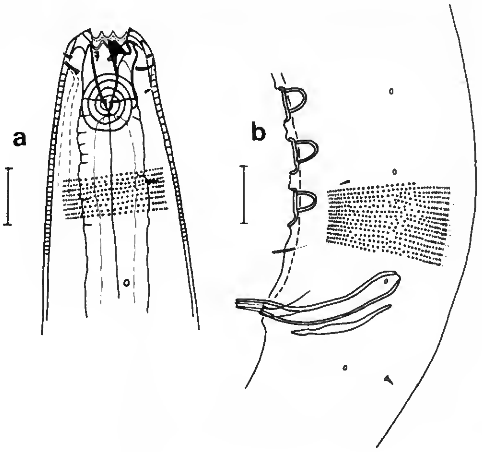

Fig. 14 *Gomphionchus lutosus*: (a) holotype ♂ head; (b) holotype cloacal region. Bar scales: 10 μm.

Gomphionchus lutosus (Wieser & Hopper, 1966) comb. nov.
(Figs 3e, 14, 15)

Neotonchus lutosus Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype ♂, slide 91, Canadian National Collection of Nematodes.

LOCALITY. Mud, Virginia Key, Florida, U.S.A.

DESCRIPTION. Cuticle with transverse rows of punctations. True lateral differentiation of fewer rows of dots is absent although in the lateral field the rows tend to anastomose, so that in places there can seem like fewer rows. A lateral file of small cuticle pores present, about 15 μm apart, from the anterior oesophageal region to the tail (Figs 3e, 14b, 15b, c). Sublateral somatic setae present. Dorso-sublateral subcephalic seta present situated just anterior to the middle of the amphid (Fig. 15e). R_3 sensilla situated level with the anterior of the amphid. Amphid of 4+ turns. Excretory pore 7 μm from anterior (Fig. 14a). Spicules have an extra piece lateral to distal end (Fig. 15h). The precloacal spine is situated closer to the first supplement than the cloaca (Fig. 14b). 20 precloacal supplements. Two opposed testes; anterior left, posterior right of gut. A possible clear patch in the vas deferens was observed lying between the levels of supplements 5–7 (Fig. 15d).

REMARKS. The disposition of the cephalic sensilla reported here is slightly different from that depicted by Wieser & Hopper (1966); the latter placed the two R_3 sensilla at the level where the dorso-sublateral subcephalic seta were observed here. Wieser & Hopper (1966) also depicted the excretory pore 40 μm from the anterior whilst it was found only 7 μm from the anterior in this study, level with the R_2 sensilla. Otherwise, the observations reported here conform well with the original description.

Neotonchus punctatus Cobb, 1933
(Figs 3a, 16, 17)

MATERIAL STUDIED. 1♂, slide T-69 t (Lectotype), U.S. Department of Agriculture Nematode Collection.

LOCALITY. Cuttyhunk Hole, Woods Hole, Massachusetts, U.S.A.

DESCRIPTION.

$$♂ : \frac{- \quad 102 \quad M \quad 646}{13 \quad 30 \quad [26] \quad 24} 722\,\mu\text{m}; a = 28; b = 7; c = 10$$

Body slightly larger than reported by Wieser & Hopper (1966). The specimen is clearly somewhat squashed: since its present maximum dorso-ventral diameter is about 30 μm and the lateral diameter at that point is 22 μm the original diameter is estimated to have been about 26 μm (if the body was cylindrical), giving a higher ‘a’ ratio – this figure is used in the formula given above. The transverse rows of punctations show no lateral differentiation in the anterior oesophageal region (Fig. 17b), but about the level of the posterior oesophageal bulb the transverse rows become more widely spaced and irregular. On the posterior part of the tail, there is a lateral longitudinal file of small, closely spaced punctations (Fig. 16a). There are several sublateral cuticle pores, each associated with a more medial and anteriorly situated stout seta – the sublateral pore-seta complexes. The condition of the specimen, covered by oil-droplets, made these structures difficult to observed but the pore-complexes seem to be bilaterally arranged and the distribution observed is shown in Fig. 16a. R_1 sensilla fine, less than 1 μm. R_2 sensilla setiform, 1·5 μm. R_3 sensilla setiform, 3 μm. Dorso-sublateral subcephalic seta 2 μm, level with posterior margin of amphid (Fig. 16b). Amphid of 3+ turns (♂), 9 μm wide (60% c.d.). Spicules 20 μm long with proximal end level with posterior supplement. Short precloacal spine present. 8 typical precloacal supplements extending 110 μm anterior to cloaca. Two testes, both situated to right of gut, opposed and outstretched: anterior testis larger than posterior testis (Fig. 16a). A clear patch in the vas deferens could not be detected, although a small number of differentiated cells was present where a clear patch might be expected.

REMARKS. This species was first described by Cobb (1933) without any illustrations and subsequently redescribed well by Wieser & Hopper (1966) from Cobb's original material. The foregoing is therefore only a brief redescription based on Cobb's material intended to highlight new information or where observations here are at variance with those of Wieser & Hopper (1966). For example, the cuticle pores had not been detected previously but the lateral file of punctations on the tail had been reported by Cobb (1933) although not by Wieser & Hopper (1966).

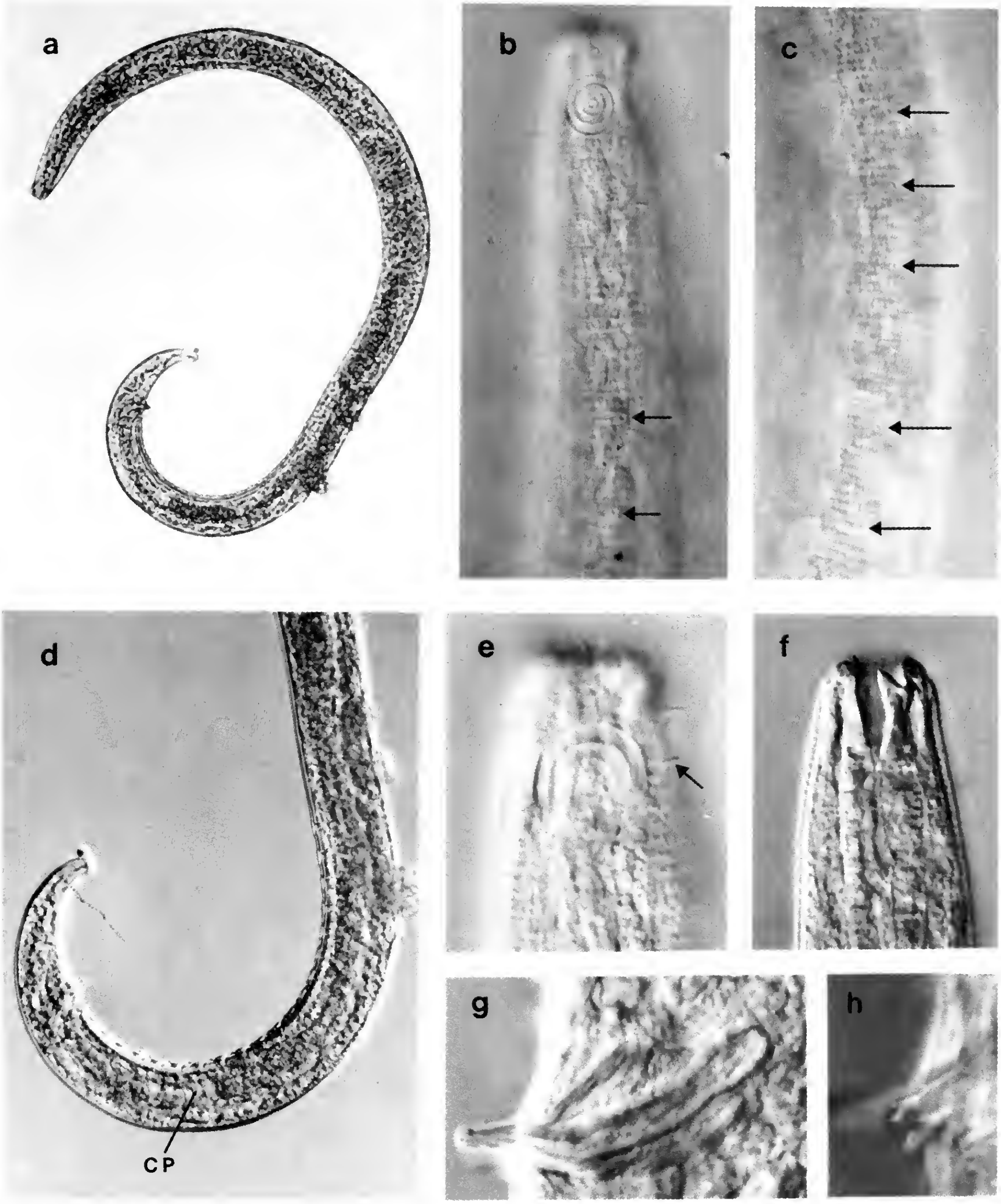

Fig. 15 *Gomphionchus lutosus*: (a) whole body; (b) anterior region, cuticle pores arrowed; (c) lateral mid-body cuticle, cuticle pores arrowed; (d) ♂ posterior region, CP = clear patch; (e) head showing R_3 sensilla and dorso-sublateral subcephalic seta (arrowed); (f) head showing buccal cavity; (g) spicule; (h) lateral spicule piece.

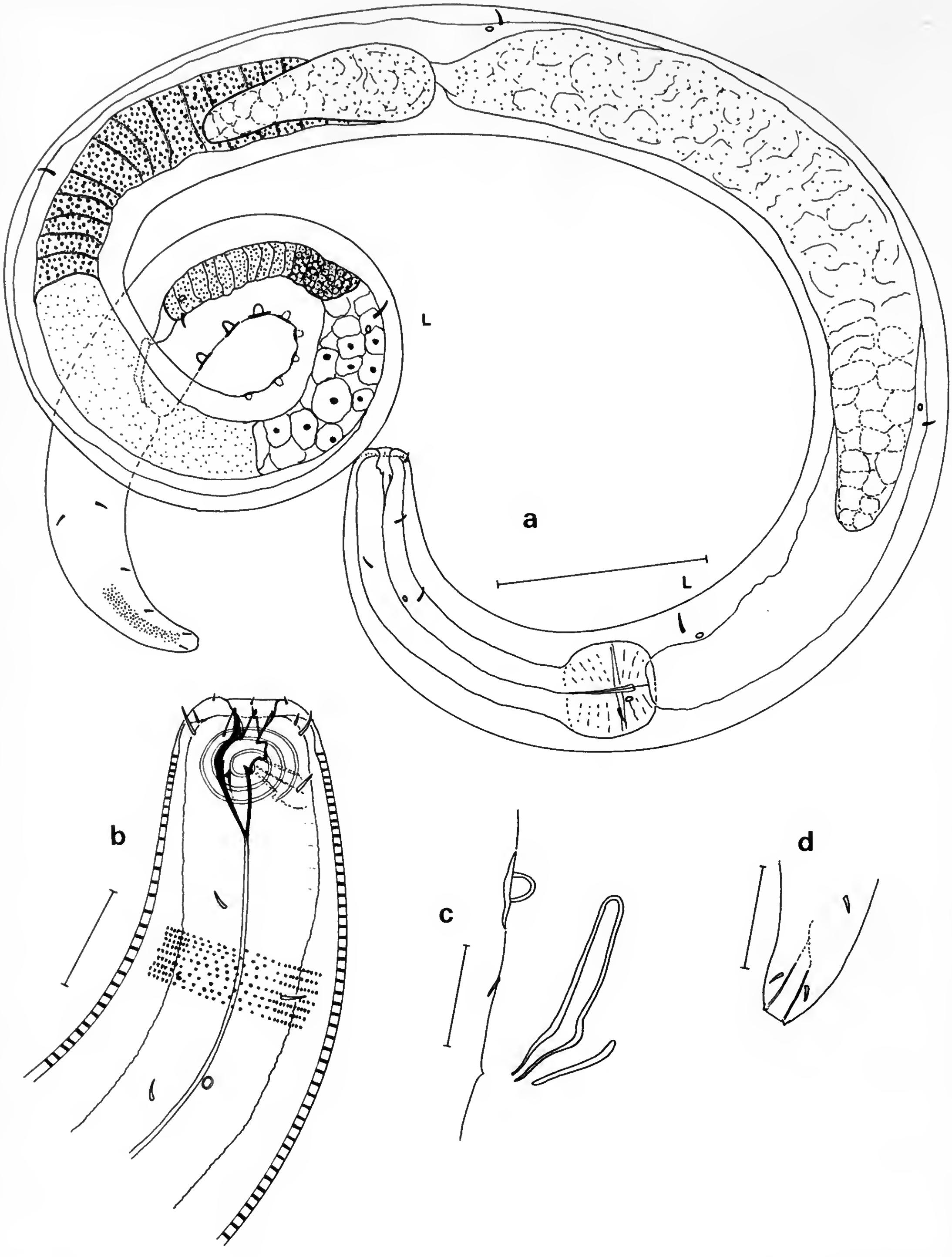

Fig. 16 *Neotonchus punctatus*: (a) whole body (L = position of pore-seta complexes seen on left side only); (b) ♂ head; (c) copulatory apparatus; (d) tail tip. Bar scales: a = 50 μm; b–d = 10 μm.

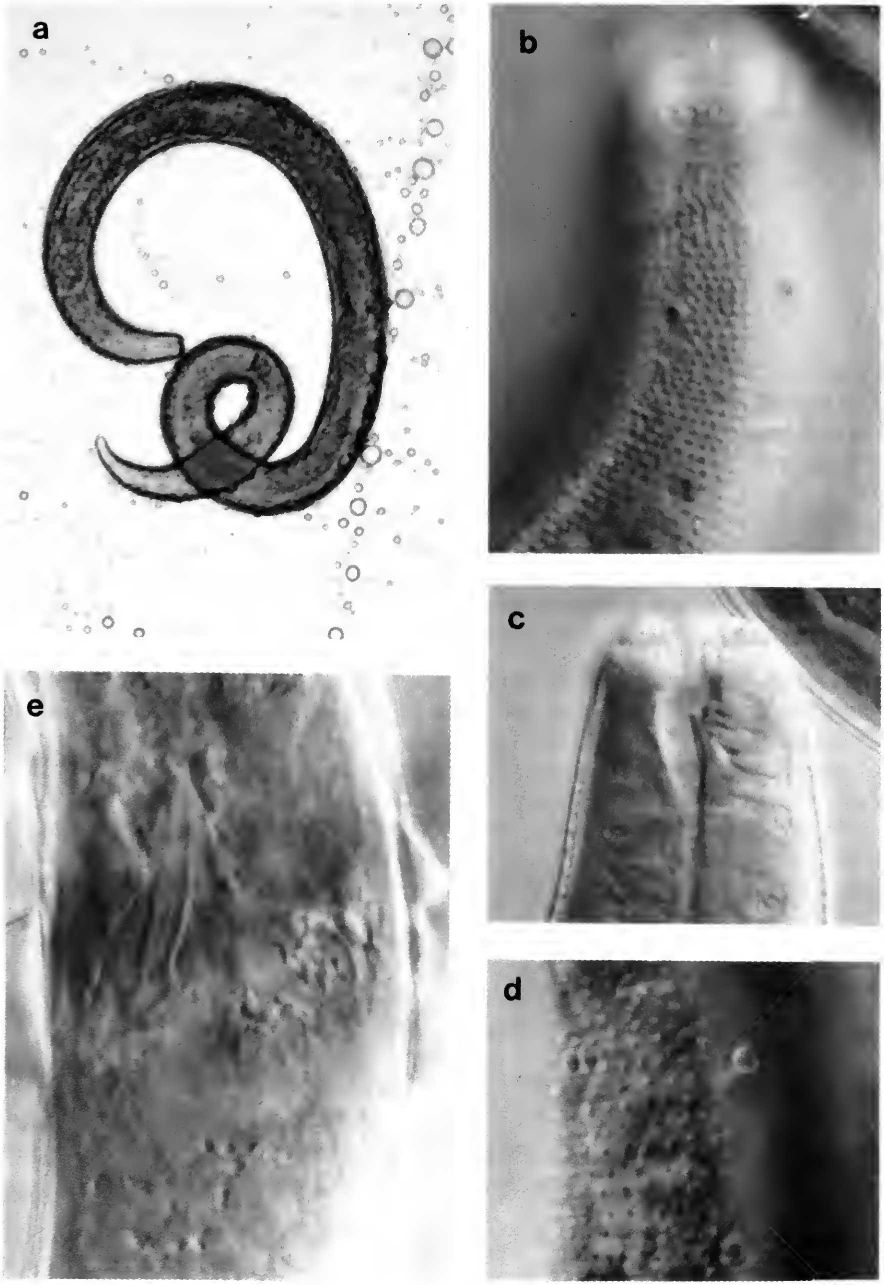

Fig. 17 *Neotonchus punctatus*: (a) whole body; (b) amphid and anterior oesophageal cuticle punctation; (c) buccal cavity; (d) lateral cuticle punctation at mid-body; (e) cloacal region showing spicule.

Neotonchus chamberlaini Wieser & Hopper, 1966
(Figs 3b, 18, 19)

MATERIAL STUDIED. Holotype ♂, slide 118 and paratype ♂, slide 118a; Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A. at a depth of 12 m.

DESCRIPTION.

Holotype ♂: $\dfrac{-\quad 130\quad \mathrm{M}\quad 840}{18\quad 28\quad 33\quad 26}$ 960 μm; a = 29; b = 7; c = 8

Lateral differentiation of fewer transverse rows of punctations begins level with the posterior end of the oesophagus. Posterior third of tail has lateral longitudinal file of punctations (Fig. 19g). There is a single row of lateral cuticle pores in the oesophageal region and posterior to the oesophagus, sublateral pore-seta complexes are present (Figs 18d, 19c–d). R_1 sensilla are short setae. R_2 sensilla 4 μm. R_3 sensilla 5·5 μm. Short dorso-sublateral subcephalic seta present (Fig. 18a). Male amphid 5+ turns, 14 μm (72% c.d.) wide. Buccal cavity with dorsal and two subventral teeth (Figs 18a, 19f). Spicules 27 μm. 8 (holotype) or 9 (paratype) precloacal supplements extending 125 μm anterior to cloaca (holotype). Precloacal spine present. Clear patch in vas deferens situated level with supplements 5–6. Two opposed testes; anterior to right, posterior to left of gut.

REMARKS. Wieser & Hopper (1966) depicted a single cuticular pore just posterior to the amphid (their Fig. 3) but did not draw attention to it in the text. Neither did they mention the lateral differentiation but they did see the dorso-sublateral subcephalic setae. The amphid has almost one more turn than originally depicted and the paratype one more precloacal supplement. Wieser & Hopper (1966) considered the species was closely related to *Nannolaimus phaleratus* (= *Neotonchus phaleratus*), which it is clearly not. In fact, *N. chamberlaini* is most similar to *N. punctatus* (buccal cavity, lateral differentiation, tail punctations) although it can be easily distinguished using the information in Table 2.

Neotonchus boucheri sp. nov.
(Figs 3c, 20–22)

Neotonchus chamberlaini sensu Boucher, 1976 nec Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype: ♂R1010, BM(NH)1981.6.63; allotype ♀R162, BM(NH)1981.6.64; paratype ♀R549, BM(NH)1981.6.65; paratype ♂R528, in possession of Dr Boucher.

LOCALITY. Pierre Noire (West Channel), France, sublittoral fine sand; collected by Dr Boucher.

DESCRIPTION.

Holotype ♂: $\dfrac{-\quad 120\quad \mathrm{M}\quad 683}{15\quad 21\quad 22\quad 20}$ 755 μm; a = 34; b = 6; c = 11

Paratype ♂: $\dfrac{-\quad 110\quad \mathrm{M}\quad 643}{16\quad 20\quad 22\quad 19}$ 710 μm; a = 32; b = 7; c = 11

Allotype ♀: $\dfrac{-\quad 91\quad 312\quad 528}{15\quad 21\quad 25\quad 19}$ 590 μm; a = 24; b = 7; c = 9

Paratype ♀: $\dfrac{-\quad 110\quad 360\quad 597}{16\quad 24\quad 25\quad 20}$ 665 μm; a = 27; b = 6; c = 10

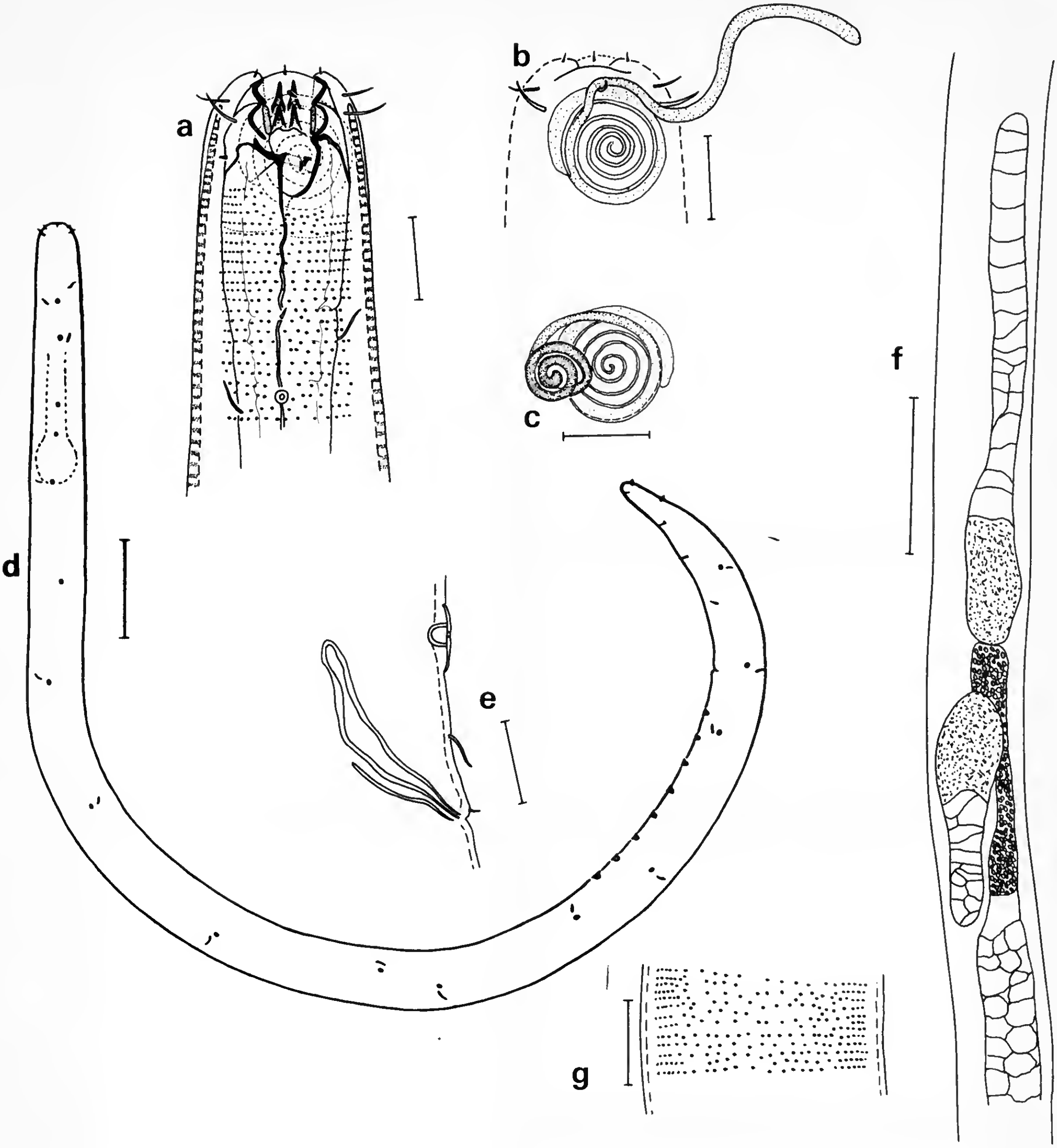

Fig. 18 *Neotonchus chamberlaini*: (a) holotype head; (b) holotype right amphid; (c) holotype left amphid; (d) holotype whole body showing distribution of cuticle pores; (e) holotype copulatory apparatus; (f) paratype ♂ reproductive system, ventral view, anterior to top; (g) cuticle punctation in cloacal region. Bar scales: a, b, c, e, g = 10 μm; d, f = 50 μm.

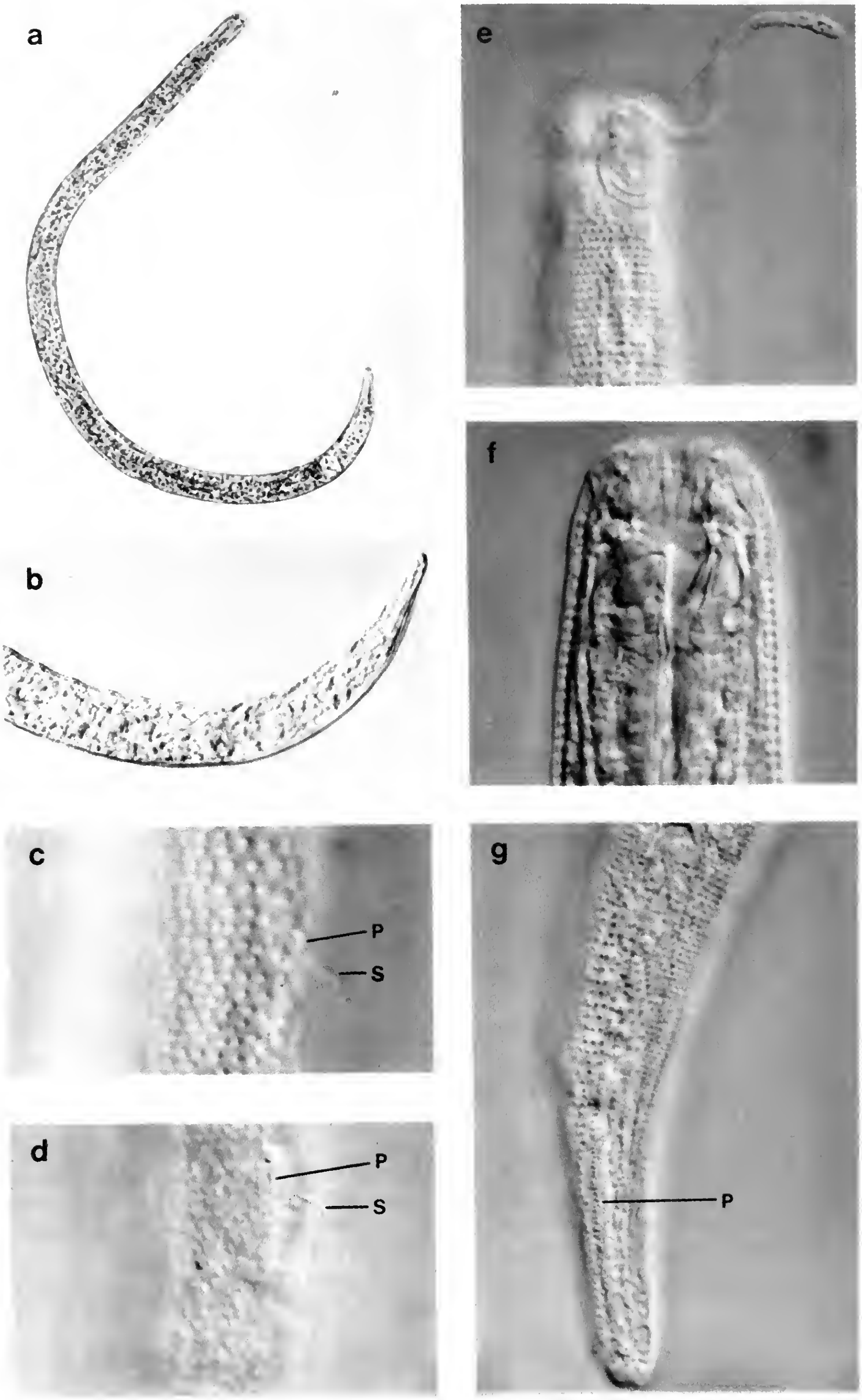

Fig. 19 *Neotonchus chamberlaini*: (a) whole body; (b) tail region; (c) lateral cuticle punctations and pore (P)–seta (S) complex; (d) pore (P)–seta (S) complex; (e) head region showing amphid and anterior cuticle pattern; (f) buccal cavity; (g) tail showing lateral punctations (P).

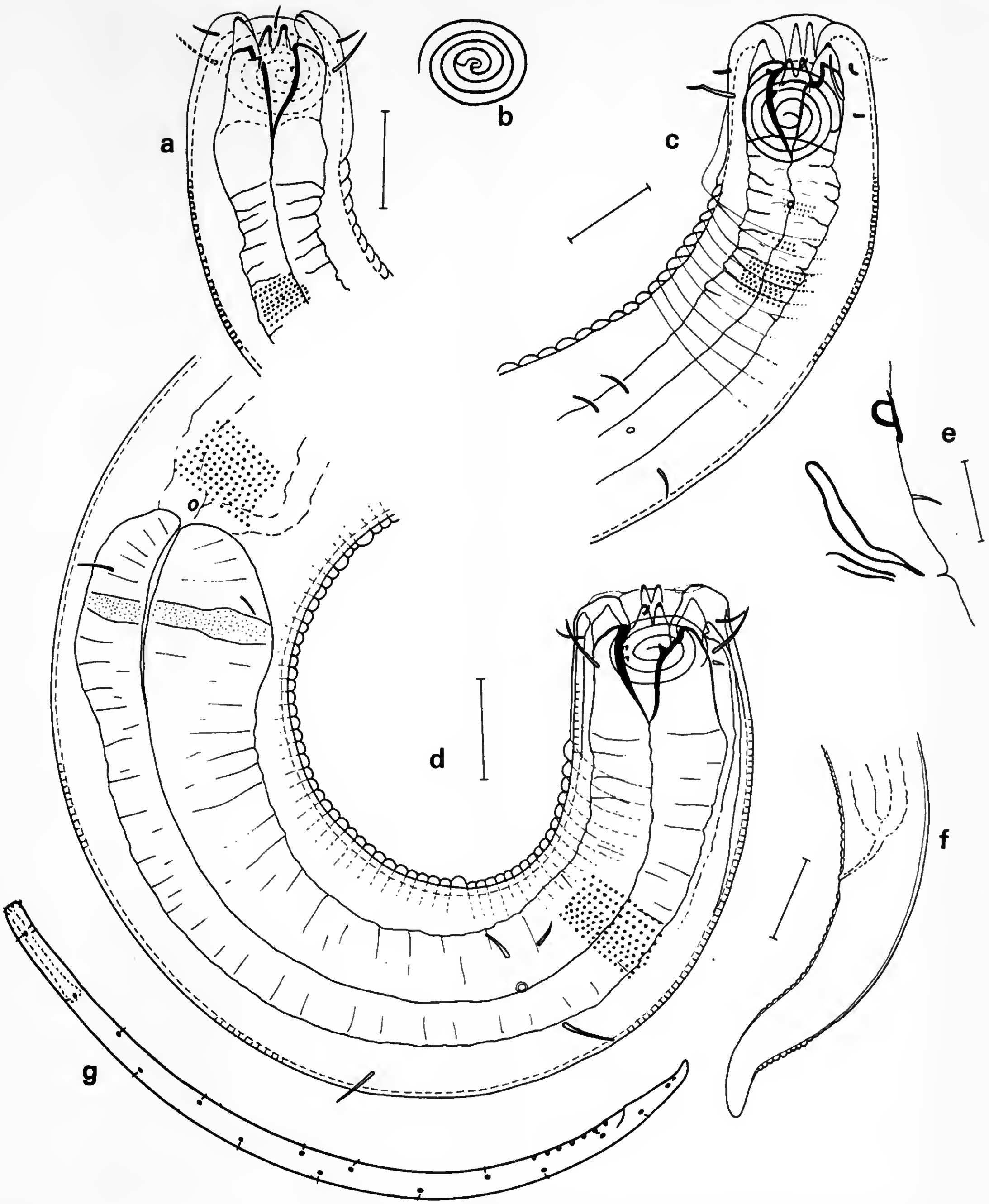

Fig. 20 *Neotonchus boucheri*: (a) head ♂ 528; (b) amphid ♂ 528; (c) head ♂ 1010; (d) anterior ♀ 549; (e) copulatory apparatus ♂ 528; (f) tail ♀ 549; (g) diagrammatic whole body to show distribution of pore-setae (not to scale). Bar scales: a, c, d, e = 10 μm; f = 20 μm.

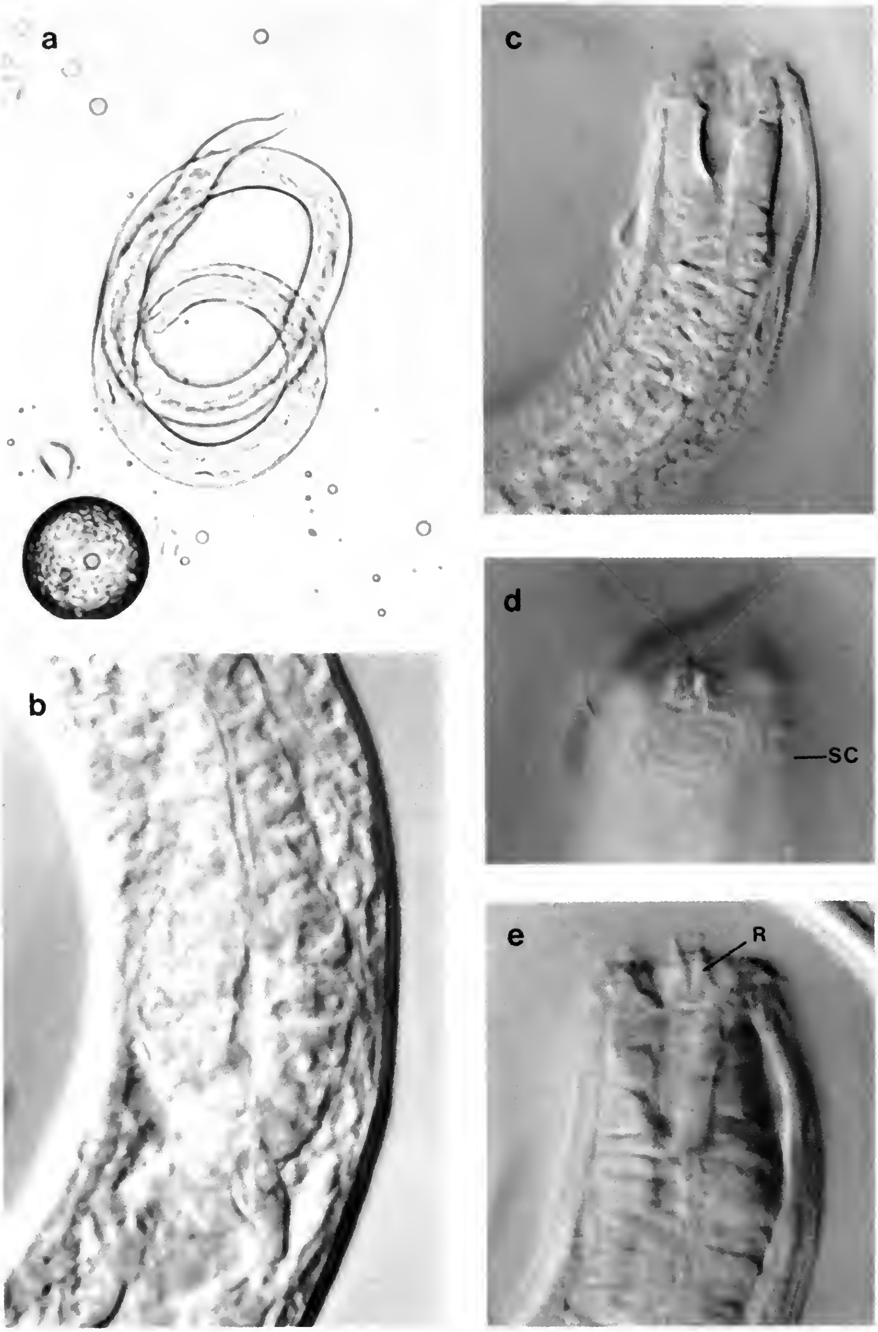

Fig. 21 *Neotonchus boucheri*: (a) whole body; (b) posterior oesophagus bulb; (c) buccal cavity; (d) amphid, cephalic setae and dorso-sublateral subcephalic seta (SC); (e) anterior part of buccal cavity showing buccal rugae (R).

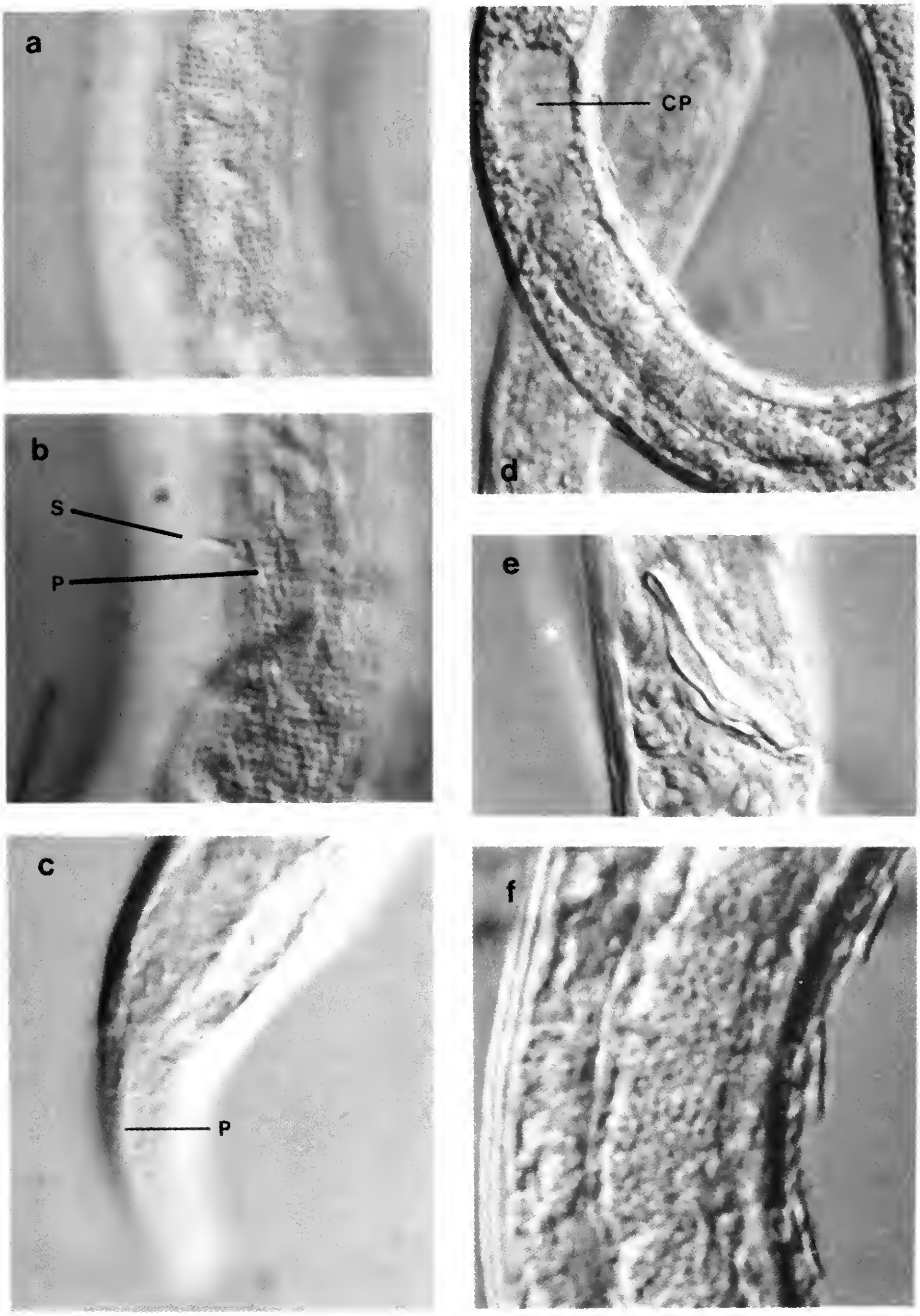

Fig. 22 *Neotonchus boucheri*: (a) lateral cuticle punctations; (b) lateral cuticle showing pore (P) – seta (S) complex; (c) posterior tail showing lateral file of punctations (P); (d) anterior cloacal region showing position of clear patch (CP) of vas deferens opposite supplement 7; (e) spicule; (f) precloacal supplements.

Fixation-shape usually coiled. Cuticle carries transverse rows of punctations which may appear anastomosing laterally (Fig. 22a) but lateral differentiation of wider spaced rows absent. About 13 sublateral pore-seta complexes situated posterior to oesophagus region and lateral pores present in oesophagus region (Figs 20d, g, and 22b). The holotype had a small cuticle pore situated about 4 μm posterior to amphid (Fig. 20c): not detected in other specimens. The cuticle pore located in all of the specimens about 45 μm from anterior was accompanied by three characteristically arranged setae: two ventro-sublateral and one dorso-sublateral. R_1 sensilla not detected. R_2 sensilla 2–3 μm. R_3 sensilla 5–6 μm, located level with middle of amphid. Short dorso-sublateral subcephalic seta present. Male amphids of 4+ turns, 10·5–11·5 μm (68–73% c.d.) wide. Female amphids of 3+ turns, 9 μm (56–60% c.d.) wide. Buccal cavity wide with dorsal tooth and two smaller subventral teeth and anteriorly twelve rugae arranged in six pairs. Oesophagus has a 20–22 μm posterior bulb (18–23% oesophagus length) (Fig. 21b). Tail conical, characteristically dorsally bent at tip (Fig. 20f). Lateral file of caudal punctations present (Fig. 22c) but difficult to distinguish due to curvature of the posterior section of tail and lack of lateral differentiation, from which it can be distinguished in the two species described above. Spicules 20–22 μm long. 3 μm precloacal spine and 7 supplements extending about 100 μm anterior to cloaca. A clear patch in the vas deferens is located opposite the anteriormost supplement. Two opposed testes; anterior to left of gut but relative position of posterior testis difficult to determine. Female: V = 53–54%. Two ovaries, opposed, reflexed: anterior to right, posterior to left.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchus boucheri* sp. nov. can be distinguished from other members of the genus by its lack of lateral cuticle differentiation, the presence of three characteristic setae situated around the cuticle pore in the anterior oesophageal region, the paired buccal rugae and shape of the tail tip. *N. boucheri* is most similar to *N. chamberlaini* in size and spicule structure, but can be separated on the more posterior position of R_3 sensilla and position of anterior testis relative to gut.

ETYMOLOGY. The species is named after Dr G. Boucher, who first described the specimens.

REMARKS. Boucher (1976) considered these specimens conspecific with *N. chamberlaini* Wieser & Hopper, 1966, although he recognised several differences. However, examination of representatives of both material revealed evidence to support Boucher's specimens being a new species. In addition to those features mentioined in the diagnosis and Table 2, other possible characters aiding separation are the somewhat smaller dorsal tooth and the absence (?) of R_1 sensilla. The presence of transverse rows of larger punctations at every third row as depicted by Boucher (1976 : Fig. 10B) could not be detected in the specimens studied here. However, the condition described by Boucher (1976) is not unknown in this group; see *Neotonchoides melotridus*.

Neotonchus meeki Warwick, 1971
(Figs 3d, 23, 24)

MATERIAL STUDIED. 2♂♂ BM(NH) 1970.245–246 and 1♀, BM(NH)1970.247: syntypes.

LOCALITY. Northumberland coast (North Sea), sublittoral very fine sand and silt.

DESCRIPTION. Body length 710–750 μm: a = 25–29; b = 6–7; c = 9; V = 49%. Cuticle has well-developed lateral differentiation of fewer rows of larger dots beginning level with the posterior oesophageal bulb (Figs 23c, 24d). Lateral cuticle pores are present but small and difficult to detect (Fig. 23c). Posterior to the oesophageal region, the larger sublateral pores, mainly dorso-sublateral and at the edge of the area of lateral differentiation, are each associated with a seta, the pore-seta complexes (Fig. 24e): there are about 10. Male amphids have 4+ turns: the female amphid was obscured. A dorso-sublateral subcephalic seta is present (Fig. 23a). Two testes present; anterior to left of gut, posterior basically ventral to gut with perhaps a little bias to the right. Clear patch in vas deferens opposite supplements 4/5 (Fig. 24b). Tail bears a lateral longitudinal row of punctations (Fig. 3d).

REMARKS. The foregoing is based on Warwick (1971) with some additional information. Jensen (pers. comm.) found specimens of this species in the Øresund, which is the type locality of Allgen's (1935) poorly described monotypic genus *Heterocyatholaimus*. Ventral views of *N. meeki*, as Dr Jensen pointed out to me, appear identical with Allgen's drawing of the head of *H. macrolaimus*. Since there are no other characters separating the genera, at Jensen's suggestion, it is proposed that *Heterocyatholaimus* Allgen, 1935 becomes a junior synonym to *Neotonchus* Cobb, 1933. Nevertheless, Allgen's species is so badly described and based only on one female it should best be regarded as dubious. The species has also been reported from Helgoland by Lorenzen (1974).

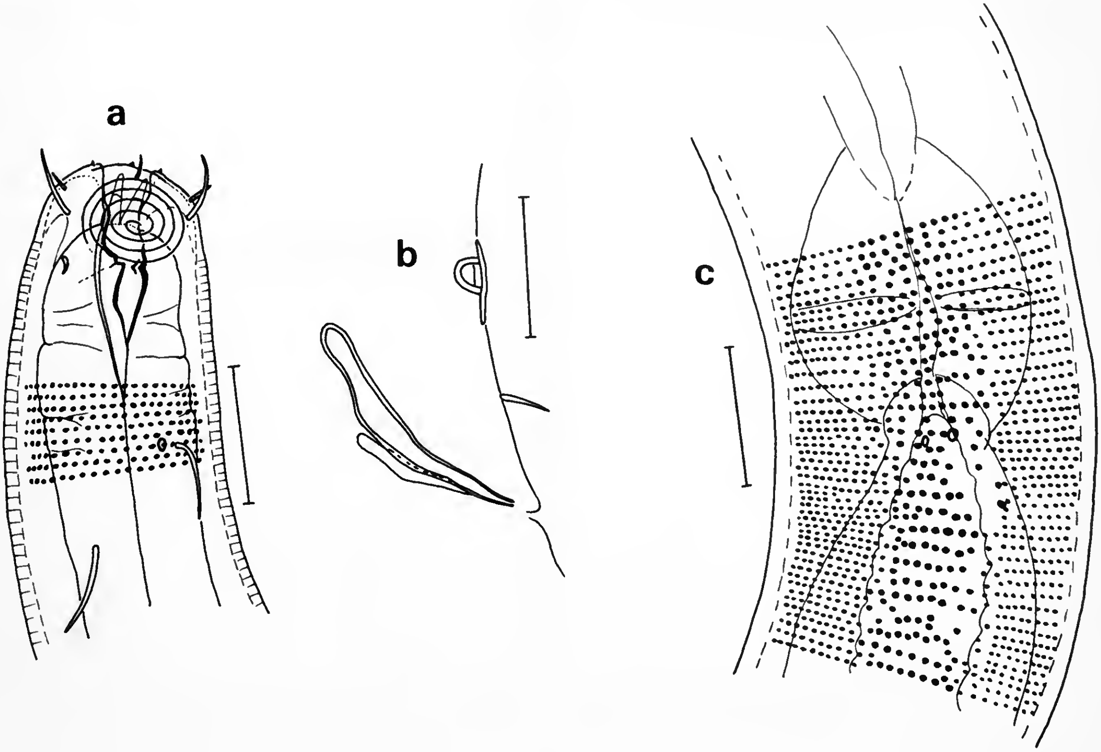

Fig. 23 *Neotonchus meeki*: (a) ♂ head; (b) copulatory apparatus; (c) cuticle pattern at oesophageal-intestinal junction showing beginning of lateral differentiation. Bar scales = 10 μm.

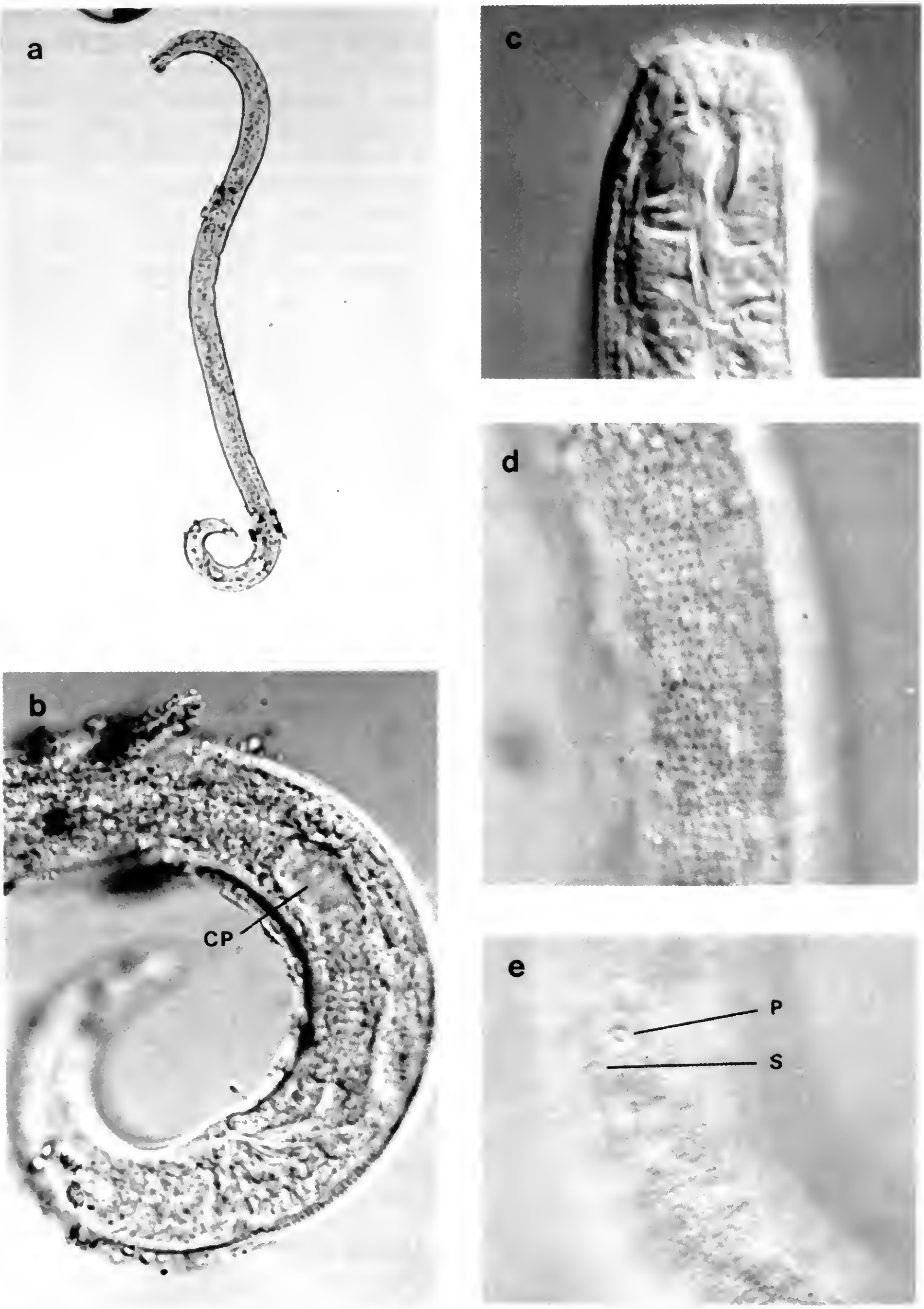

Fig. 24 *Neotonchus meeki*: (a) whole body; (b) ♂ posterior region showing position of clear patch (CP); (c) buccal cavity; (d) cuticle pattern mid-body; (e) pore (P) – seta (S) complex.

Neotonchoides melotridus (Wieser & Hopper, 1966) comb. nov.
(Figs 4a, 25a–b, 26)

Neotonchus melotridus Wieser & Hopper, 1966.

MATERIAL STUDIED. Holotype ♂, slide 119, Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A., at a depth of 12 m.

DESCRIPTION. Body length 1140 μm; a = 42; b = 10; c = 12 (from Wieser & Hopper, 1966). Posterior to the oesophageal region, every third transverse row tends to consist of larger, more closely spaced dots (Fig. 26e) although this is not regular: sometimes every other row is larger. In the lateral field, there is some anastomosing of the transverse rows but lateral differentiation of fewer rows is absent. Small lateral cuticle pores are present, evenly spaced throughout the body. Subventral somatic setae are present: subdorsal setae were only detected on the tail. Head diameter 12 μm. R_2 sensilla 0·7 μm. R_3 sensilla 4 μm. Dorso-sublateral subcephalic seta situated posterior to amphid (Fig. 25a). Amphid 3+ turns, 6·5 μm (55% c.d.) wide, situated between R_3 sensilla (Figs 25a, 26b). Buccal cavity well developed with prominent rugae (Fig. 26d). Spicule 25 μm, typical neotonchid shape (Fig. 26g). Feint lateral pieces detected at the distal ends of the spicule. Relatively prominent precloacal spine (Fig. 26g) and 9 precloacal supplements extending 170 μm anterior to cloaca. Prominent cuticular ridges between supplements which continue some distance anterior to last supplement. Testes opposed; anterior left, posterior right of gut. Clear patch not distinct but possibly opposite supplement 6 (Fig. 26f).

REMARKS. The R_3 sensilla appear to be slightly shorter and the amphids smaller than reported by Wieser & Hopper (1966). As Wieser & Hopper (1966) suggested, this species seems quite similar to *N. corcundus* (Gerlach, 1956) from which it can be distinguished by the more slender body (a=42 vs 28), longer spicule (25 μm vs 15·5 μm) and more posterior position of the dorso-sublateral subcephalic seta. Gerlach (1956) did not depict a precloacal spine but this was probably an oversight. There is no information for *N. corcundus* on the presence of cuticle pores, but the cuticle in the postcephalic region is depicted as having every third row larger (Fig. 4c). Decraemer & Coomans (1978) also recorded *N. melotridus* from Australia.

Neotonchoides interruptus (Warwick, 1971) comb. nov.
(Figs 4f, 25c–e, 27)

Neotonchus interruptus Warwick, 1971.

MATERIAL STUDIED. 3♂♂, BM(NH)1970.241–243 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt and fine sand.

DESCRIPTION. Body length 630–680 μm; a = 30; b = 7–8; c = 10–11 (from Warwick, 1971). Cuticle lacks differentiation but in some areas there appears to be a tendency for every third row or every other row to be of larger dots. Lateral row of small cuticle pores beginning in posterior third of oesophagus and continuing to tail: most numerous in oesophageal bulb and precloacal regions (Figs 25d, e & 27f). Dorso-sublateral subcephalic seta could not be detected. Two testes; anterior left, posterior right of gut. Clear patch in vas deferens was not detected.

REMARKS. There is little to add to the description given by Warwick (1971) except for the cuticle pores and testes configuration. Warwick (1971) depicts the amphid spiralling dorsally to the centre, which is not the case. The spicule shape (Fig. 27c) clearly distinguishes this form other known species; otherwise it seems to belong to the group characterised by small cephalic sensilla, narrow buccal cavity and small amphids.

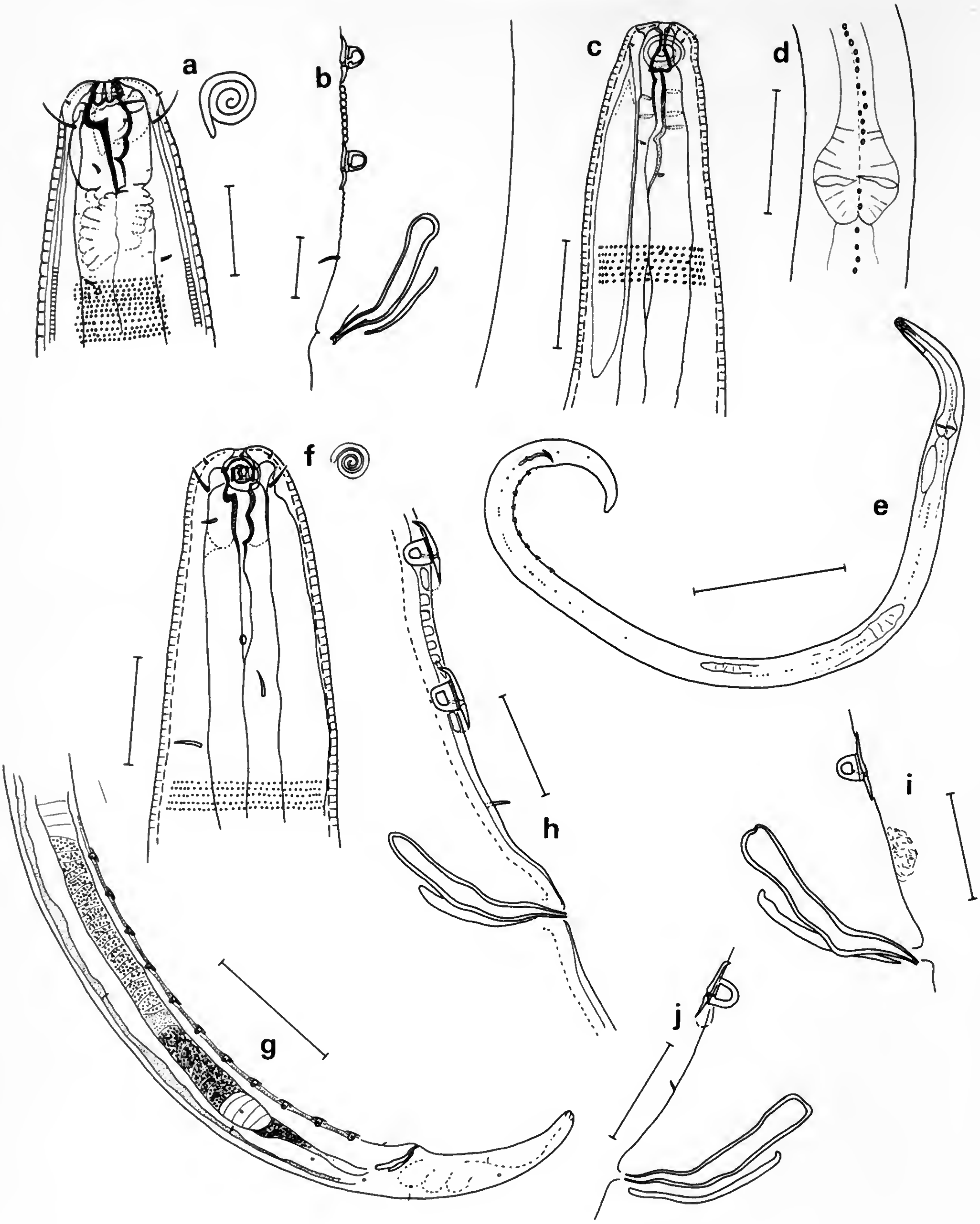

Fig. 25 *Neotonchoides melotridus*: (a) ♂ head, amphid shown separately; (b) cloacal region. *Neotonchoides interruptus*: (c) ♂ head; (d) oesophageal region; (e) whole body to show distribution of cuticle pores. *Neotonchoides warwicki*: (f) ♂ head, amphid shown separately; (g) posterior region; (h) $♂_1$ copulatory apparatus; (i) $♂_3$ copulatory apparatus (dirt obscuring precloacal spine); (j) $♂_2$ copulatory apparatus. Bar scales: e = 100 μm; g = 50 μm; others = 10 μm.

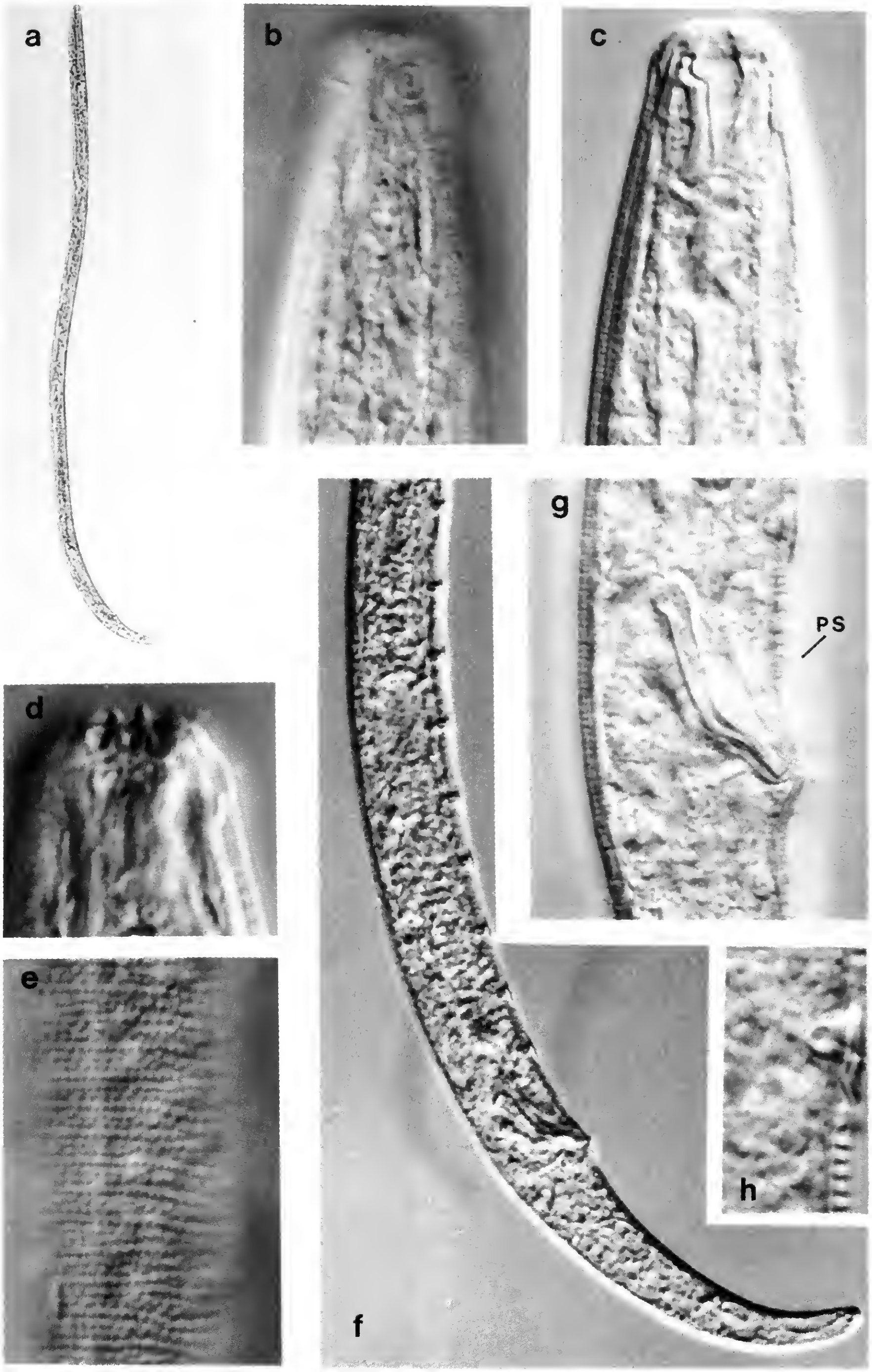

Fig. 26 *Neotonchoides melotridus*: (a) whole body; (b) anterior view showing amphid; (c) anterior view showing buccal cavity; (d) anterior view showing rugae; (e) cuticle pattern mid-body; (f) posterior region; (g) cloacal region (PS = precloacal spine); (h) detail of precloacal supplement.

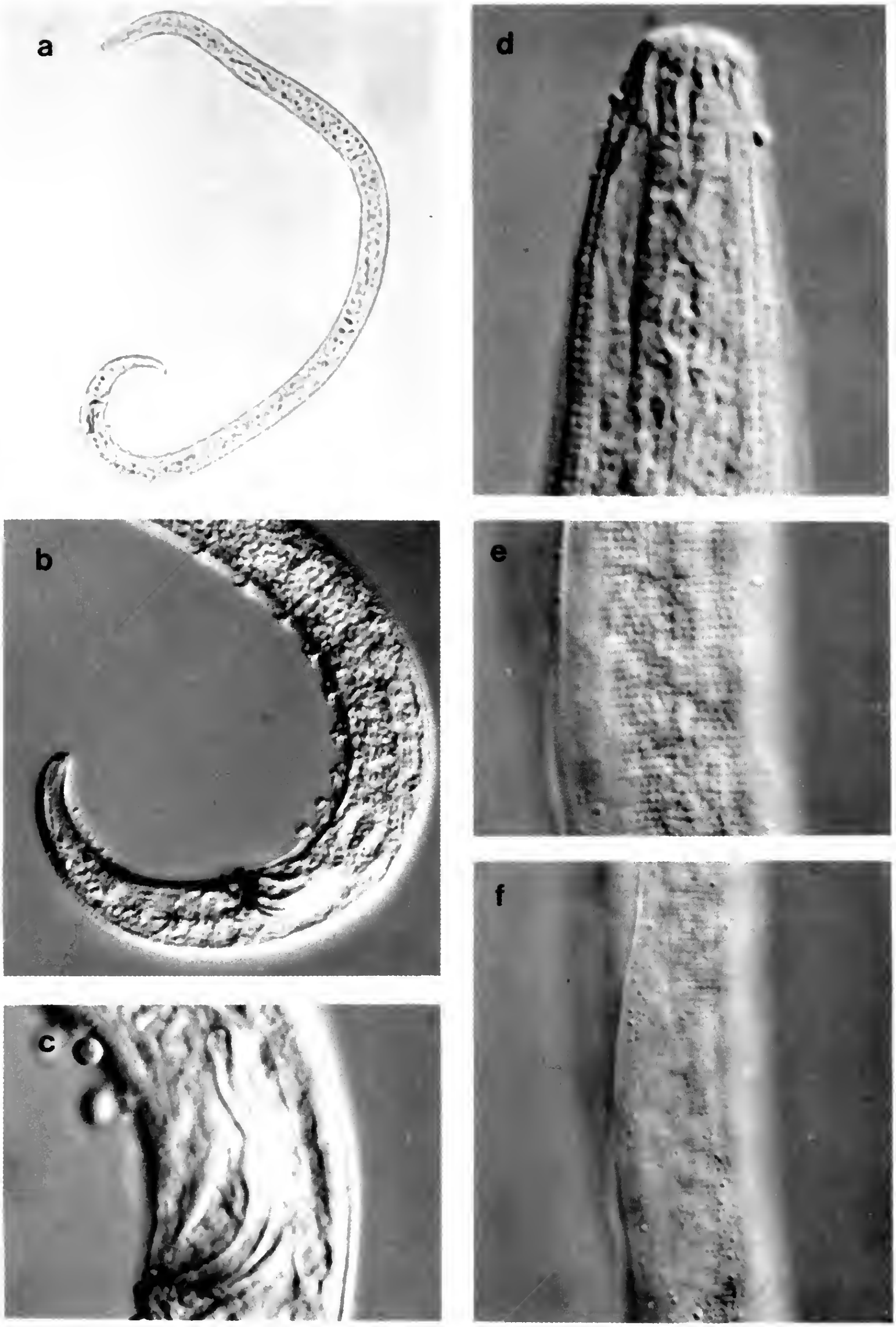

Fig. 27 *Neotonchoides interruptus*: (a) whole body; (b) posterior region showing distribution of precloacal supplements; (c) spicule; (d) anterior region showing buccal cavity; (e) lateral cuticle pattern; (f) lateral cuticle showing pores.

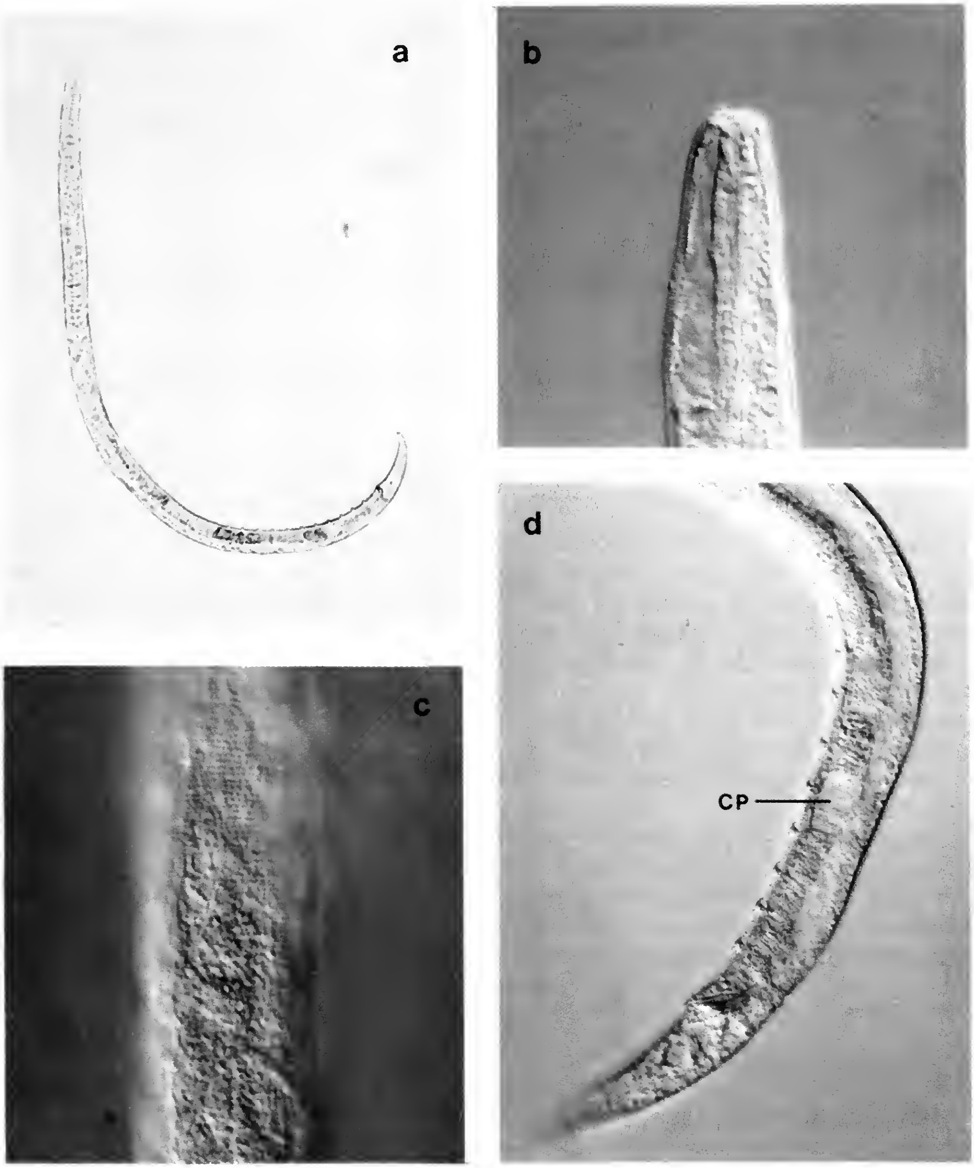

Fig. 28 *Neotonchoides warwicki*: (a) whole body; (b) anterior region showing buccal cavity and ventral excretory ampulla; (c) lateral cuticle pattern mid-body; (d) posterior region showing distribution of precloacal supplements and position of clear patch (CP).

Neotonchoides warwicki sp. nov.

(Figs 4d, 25f–j, 28)

Neotonchus corcundus sensu Warwick & Buchanan (1970) nec Gerlach, 1956.

MATERIAL STUDIED. Holotype ♂$_1$, paratype ♂$_2$, paratype ♂$_3$: on slide BM(NH)1981.6.66.

LOCALITY. Northumberland coast (North Sea), sublittoral silt and fine sand.

DESCRIPTION.

Holotype ♂$_1$: $\frac{-\quad 102\quad M\quad 721}{10\quad 22\quad 24\quad 20}$ 785 μm; a = 31; b = 8; c = 12; S = 18 μm.

Paratype ♂$_2$: $\frac{-\quad 95\quad M\quad 704}{10\quad 22\quad 24\quad 20}$ 765 μm; a = 32; b = 8; c = 13; S = 18 μm.

Paratype ♂$_3$: $\frac{-\quad 102\quad M\quad 687}{10\quad 21\quad 23\quad 19}$ 750 μm; a = 33; b = 7; c = 12; S = 20 μm.

Cuticle has transverse rows of small punctations: lateral dots in mid-body appear larger than medial dots (Fig. 28c) although lateral differentiation of fewer rows is absent. Very small cuticle pores are present as a lateral row, apparently evenly spaced but not easy to resolve. Few somatic setae resembling small sublateral spines. R_1 sensilla not detected. R_2 sensilla very short about 0·5 μm. R_3 sensilla 3 μm long. Short dorso-sublateral subcephalic seta present situated posterior to amphid. Male amphids 3+ turns, 3–4 μm wide, situated between R_2 and R_3 sensilla (Fig. 25f). Buccal cavity narrow, containing medium sized dorsal tooth (Figs 25f, 28b) but no ventral teeth detected. Ventral excretory ampulla prominent and opens level with amphid. Nerve ring at 60–70% oesophagus length. Oesophagus has a posterior bulb; approximately 20 μm long, 16 μm wide. Tail conical; caudal glands confined to tail. Spicules 18–20 μm long; typical neotonchid shape (Figs 25h–j). Small ventral precloacal spine. 11 precloacal supplements extending 125–165 μm anterior to cloaca. Ventral cuticle between supplements has prominent ridges. Prominent clear patch in vas deferens present level with supplement 4 in ♂$_1$ (Fig. 25g), supplement 5 in ♂$_2$ (Fig. 28d) but not detectable in ♂$_3$. Two opposed testes; anterior right, posterior left of gut in all three specimens. Females unknown.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchoides warwicki* sp. nov. may be distinguished from other members of the genus by the small, anteriorly situated amphids. *Neotonchoides interruptus* (Warwick, 1971) also has small amphids, but they are not so far forward, the R_3 sensilla are smaller, the spicule has a different shape and the gonads are not orientated to the gut in the same way. *Neotonchoides pseudocorcundus* (Vitiello, 1971) is similar in many ways but can be separated on the position of the excretory pore, which is posterior to the nerve ring in *N. pseudocorcundus*.

ETYMOLOGY. The species is named after Dr R. M. Warwick, who had the foresight to keep a reference collection.

REMARKS. Warwick & Buchanan (1970) reported the presence of *Neotonchus corcundus* Gerlach, 1956 from off the Northumberland coast. Fortunately, the material was retained and an examination of this material revealed several important differences between it and the original description of *N. corcundus* given by Gerlach (1956): the amphid of *N. corcundus* is larger and not so anteriorly situated, the buccal cavity is much wider and more heavily cuticularised and the cephalic setae are longer. In the light of the known infraspecific variation, these differences are considered sufficient to warrant the erection of a new species.

Neotonchoides cuanensis sp. nov.
(Figs 4b, 29, 30)

MATERIAL STUDIED. 11♂♂ (Holotype ♂$_5$: BM(NH)1981.6.67) and 6♀♀ (Allotype ♀$_2$: BM(NH)1981.6.68).

LOCALITY. Intertidal sandflat, Strangford Lough, Northern Ireland (see Platt, 1977).

DESCRIPTION.

Holotype ♂$_5$: $\dfrac{-\quad 112\quad \mathrm{M}\quad 1028}{13\quad 18\quad 21\quad 18}$ 1115 μm; a = 54; b = 10; c = 13; S = 19 μm

Allotype ♀$_2$: $\dfrac{-\quad 96\quad 462\quad 752}{13\quad 20\quad 21\quad 16}$ 823 μm; a = 39; b = 9; c = 12; V = 56%

Paratypes

♂$_1$: L = 1100 μm; a = 58; b = 9; c = 16; S = 21 μm
♂$_2$: L = 1010 μm; a = 53; b = 9; c = 15; S = 20 μm
♂$_3$: L = 1015 μm; a = 54; b = 9; c = 14; S = 20 μm
♂$_4$: L = 1080 μm; a = 64; b = 9; c = 13; S = 20 μm
♂$_6$: L = 1015 μm; a = 54; b = 9; c = 12; S = 19 μm
♂$_7$: L = 1015 μm; a = 53; b = 10; c = 12; S = 20 μm
♂$_8$: L = 930 μm; a = 52; b = 9; c = 11; S = 20 μm
♂$_9$: L = 1010 μm; a = 53; b = 9; c = 13; S = 20 μm
♂$_{10}$: L = 915 μm; a = 48; b = 10; c = 12; S = 20 μm
♂$_{11}$: L = 1005 μm; a = 53; b = 10; c = 13; S = 19 μm
♀$_1$: L = 905 μm; a = 45; b = 8; c = 11; V = 54%
♀$_3$: L = 830 μm; a = 38; b = 9; c = 12; V = 56%
♀$_4$: L = 810 μm; a = 37; b = 9; c = 9; V = 55%
♀$_5$: L = 810 μm; a = 37; b = 9; c = 11; V = 59%

Cuticle bears transverse rows of fine punctations, no lateral differentiation. Transverse rows more numerous in oesophageal region of males than females (cf. Figs 29b and 29c): rows in female become more numerous posterior to oesophageal region. Very small lateral cuticle pores present throughout the body, regularly spaced but difficult to detect except in head and tail regions. Short stout sublateral somatic setae present (Fig. 29a). R$_1$ sensilla present as minute papillae. R$_2$ sensilla 1·5–2·5 μm. R$_3$ sensilla 4–5 μm. Dorso-sublateral subcephalic seta (?) situated posterior to level of amphid and buccal cavity. Male amphids 4+ turns, 7·5–8 μm (62–63% c.d.) wide. Female amphids 3+ turns, 6–6·5 μm (46–50% c.d.) wide. Middle of amphids situated posterior to level of R$_3$ cephalic setae. Head not attenuated anteriorly, giving a rather square appearance (Fig. 30c). Buccal cavity relatively wide with twelve rugae anteriorly, a pointed dorsal tooth and subventral ridges: subventral teeth could not be detected. Nerve ring 50–70 μm from the anterior, 40–60% of oesophagus length. Posterior oesophagus bulb present, 17–21 μm long, 15–20% of oesophagus length. Tail conical, 3·8–5·5 a.b.d. long with characteristic ventral bend at tail tip (Fig. 29h–m). Spicules 'L' shaped; gubernaculum a short rod lying dorsal to spicules (Figs 29e–g, 30e). Short ventral precloacal spine, 9–11 μm from cloaca. 8–10 typical precloacal supplements: in males with 10 supplements, they extended 99, 126 and 140 μm anterior to cloaca; in males with 9 supplements, they extended 81, 119, 110 and 109 μm anterior to cloaca; in males with 8 supplements, they extended 96, 86 and 98 μm anterior to cloaca. The first supplement is situated 16–23 μm (mean = 20 μm) from cloaca, so that in most specimens it lies slightly anterior to the level of the proximal end of the spicules. The cuticle is more conspicuously annulated in the areas betweeen the supplements than elsewhere. Two testes, opposed, posterior smaller and more difficult to distinguish than the anterior; anterior left, posterior right of gut. Clear patch in vas deferens not detected. Two opposed, reflexed ovaries.

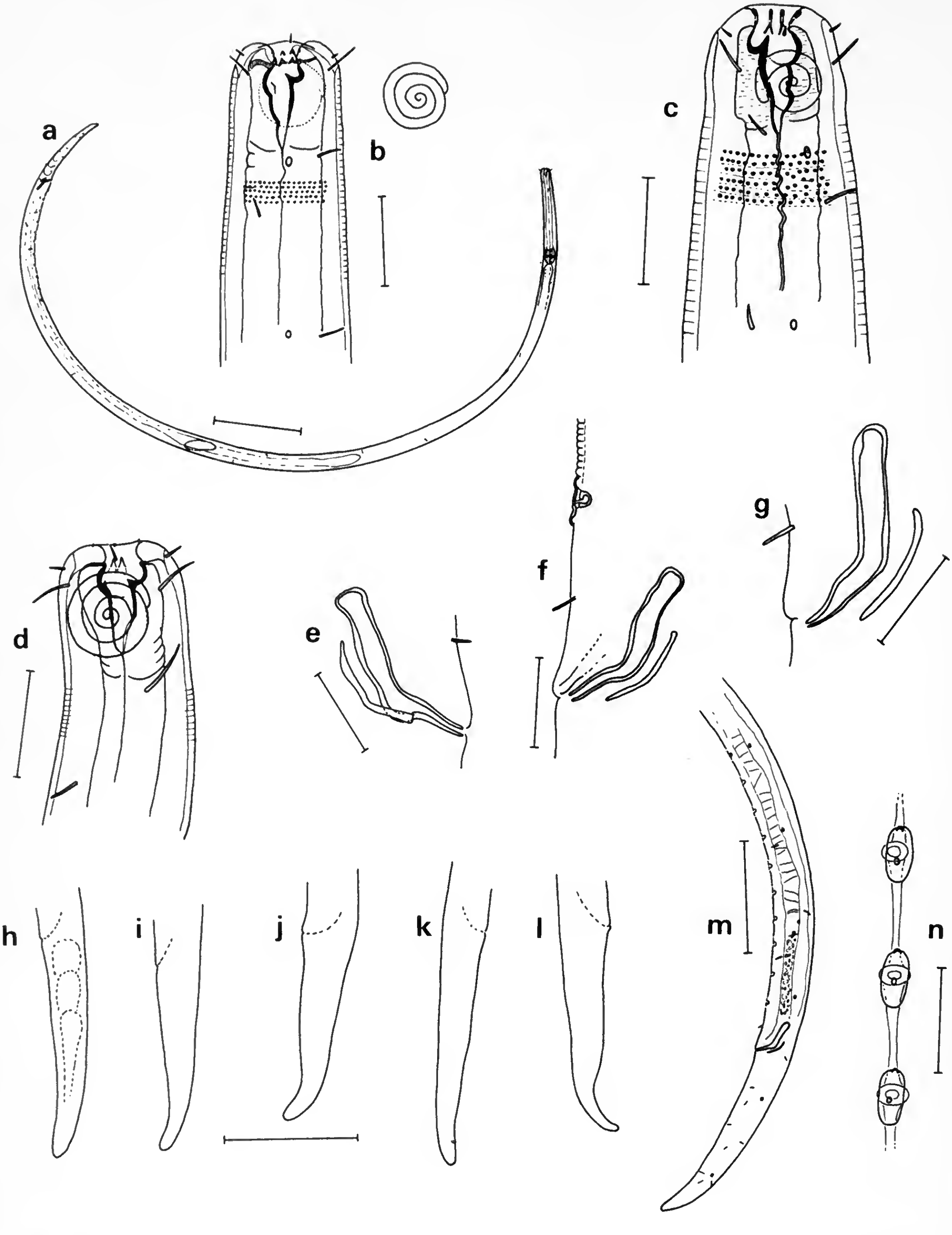

Fig. 29 *Neotonchoides cuanensis*: (a) holotype whole body; (b) holotype head; (c) allotype head; (d) ♂$_4$ head; (e) ♂$_6$ copulatory apparatus; (f) holotype copulatory apparatus; (g) ♂$_4$ copulatory apparatus; (h) ♀$_5$ tail; (i–l) tails of four different males; (m) holotype posterior region; (n) ventral view of three precloacal supplements, anterior to top. Bar scales: a = 100 μm; h–l, m = 50 μm; others = 10 μm.

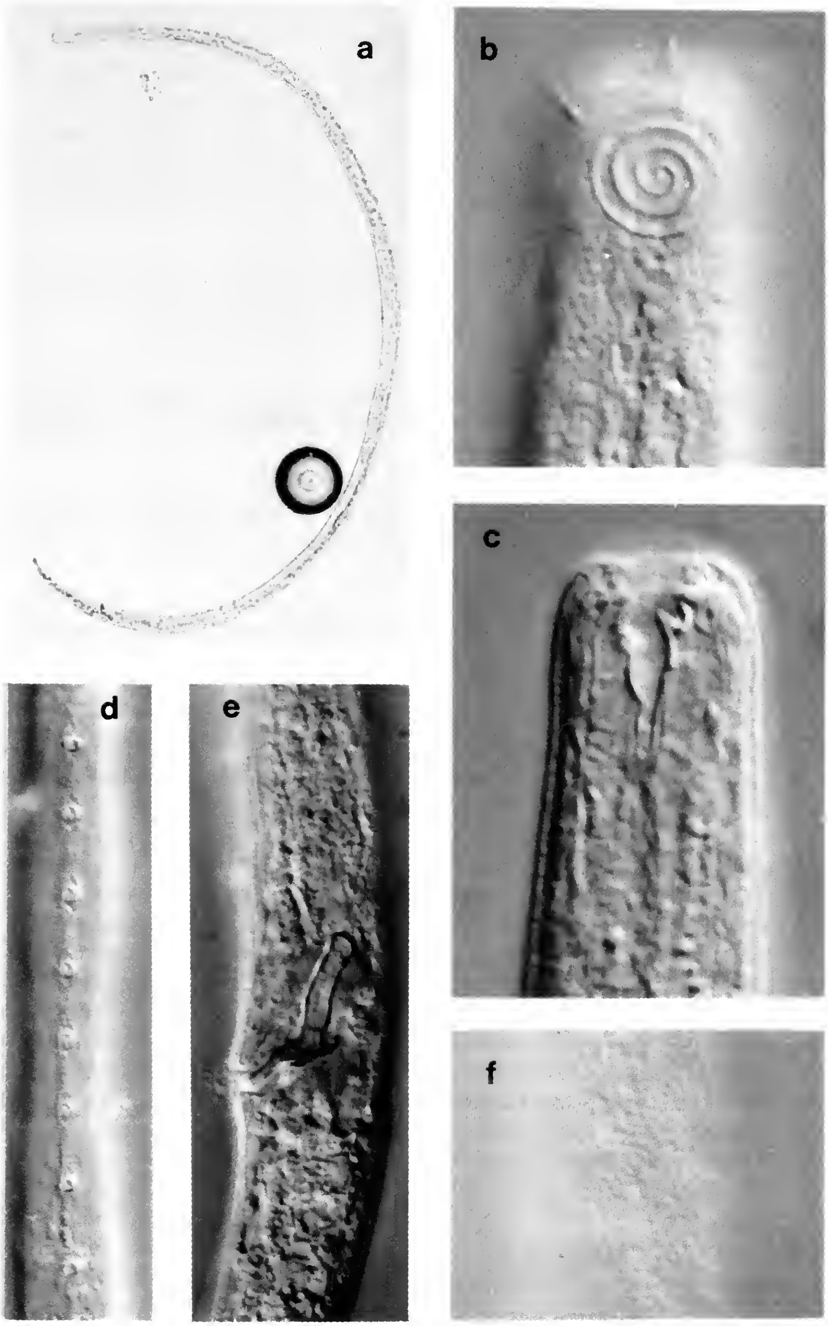

Fig. 30 *Neotonchoides cuanensis*: (a) whole body; (b) ♂ anterior region showing amphid; (c) ♂ anterior region showing buccal cavity; (d) ventral view of precloacal supplements; (e) cloacal region showing spicule shape; (f) lateral cuticle showing punctations.

DIFFERENTIAL DIAGNOSIS. Neotonchinae. *Neotonchoides cuanensis* sp. nov. most closely resembles *N. melotridus* (Wieser & Hopper, 1966) and *N. corcundus* (Gerlach, 1956) in size of R_3 sensilla, buccal cavity development, supplement number, spicule shape and tail shape. However, the males of *N. cuanensis* have larger amphids with one more turn, a different head shape, lack the cuticle pattern of larger punctations every third row and have smaller spicules and supplements.

ETYMOLOGY. The species name comes from the old Irish name for Strangford Lough: Lough Cuan.

REMARKS. The sensillum which was interpreted above as the dorso-sublateral subcephalic seta typical of the neotonchids is in a more posterior position and somewhat longer than is usual and could as easily be the first of the 'true' sublateral somatic setae; in which case the dorso-sublateral subcephalic seta would be absent or not detectable by light microscopy. In the absence of further evidence, the interpretation given in the description is preferred. *N. cuanensis* and the two species which most closely resemble it, *N. melotridus* and *N. corcundus*, were all found in shallow sediment; *N. cuanensis* from fine intertidal sand in Strangford Lough, *N. corcundus* from sand at 12 m in Kiel Bay and *N. melotridus* from 12 m depth off the North Edisto River, South Carolina, although the type of sediment was not stated. Wieser and Hopper (1966) noted that the South Carolina specimens had a 'round inflection between the proximal and distal portions of the spicules': this distinction can be seen by comparing Figs 4a and 4c. However, it is worth noting that the angularity of the spicule can also vary because of the angle from which the structure is viewed; this can be seen for *N. cuanensis* in Figs 29e–g. Wieser & Hopper (1966) also point out the difference in spicule size relative to the cloacal body diameter, but it is suspected that Gerlach's (1956) figure redrawn here as Fig 4c, may have been of a squashed specimen. *N. melotridus* and *N. corcundus* are also distinguishable on the position of the dorso-sublateral subcephalic seta. A redescription of *N. corcundus* would be useful to provide information on somatic setation, cuticle pores and gonad configuration in addition to confirming the presence of a precloacal spine.

The description of *N. cuanensis* is based on a fairly large number of individuals bearing in mind their rarity in the total nematode population. The mean length of the males, 1020 μm, was significantly greater than the mean length of the females, 836 μm, at the 0·1% level of probability. The standard deviation as a percentage of the mean, i.e. coefficient of variation, was 6·1 for males and 4·8 for females, which is within the range of infraspecific variation in body length previously reported for marine nematodes (Jensen, 1979*b*; Lambshead, 1982). However, a high coefficient of variation was present in the measurement 'anterior supplement to cloaca', surprisingly independent of the total number of supplements. The CV was 17%, similar to the 14% CV reported by Lambshead (1982) for the measurement 'supplement to cloaca' in *Odontophoroides paramonhystera.* This range of variation indicates that this character may be of little value in distinguishing between species.

Neotonchoides vitius (Warwick, 1971) comb. nov.

(Figs 4e, 31)

Neotonchus vitius Warwick, 1971.

MATERIAL STUDIED. 3♂♂ BM(NH)1970.236–238 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt.

DESCRIPTION. Body length 690–780 μm; a = 23–29; b = 6–7; c = 12 (from Warwick, 1971). Cuticle punctated, with lateral differentiation of fewer rows of larger dots (Fig. 31b) beginning posterior to oesophagus. The lateral cuticle pores are most numerous in oesophagus bulb region (Fig. 31c) and throughout the rest of the body are found in groups of two, three or occasionally four (Figs 31d, e). There are small hollow lemon-shaped granules in the cells of the intestine (Fig. 4e). Two testes, opposed; anterior left, posterior right of gut. Clear patch in vas deferens situated opposite supplement 5 (Fig. 31f).

REMARKS. As pointed out by Warwick (1971), what he refers to as lateral punctations are indeed the cuticle pores. However, they could not be resolved into paired structures as depicted by Warwick (1971). *N. vitius* can be distinguished from other species in the genus by the presence of groups of pores, the lateral differentiation and the ventral kink in the dorsal surface of the spicule (Fig. 31g). The only other reference to lemon-shaped granules in the intestine wall appears to be that of Cobb (1920) in his description of *Nannolaimus guttatus*, where he describes them as 'hollow shells, more or less thick-walled'.

Nannolaimus fusus Gerlach, 1956
(Fig. 5a, 32)

MATERIAL STUDIED. 1♂, BM(NH)1981.6.69.

LOCATION. South Bay, Co. Down, Northern Ireland (Boaden & Platt, 1971).

DESCRIPTION.

$$♂\!: \quad \frac{-}{12}\;\frac{140}{17}\;\frac{M}{19}\;\frac{1132}{18}\,1245\,\mu\text{m};\ a = 66;\ b = 9;\ c = 11;\ S = 26\,\mu\text{m}$$

Body relatively elongated (Fig. 32a). Cuticle has transverse rows of small punctations but lateral differentiation absent. Lateral file of cuticle pores present, about 30 μm apart. Sparse somatic setae. R_1 sensilla setose, 3·5 μm long. R_2 sensilla 11 μm. R_3 sensilla 6 μm, situated only very slightly posterior to R_2 sensilla. Dorso-sublateral subcephalic seta not detected at mid-amphid level and the long seta situated level with the posterior margin of the amphid is probably the first of the sublateral somatic setae. Amphid large, 6+ turns and longitudinally elongated; 18 μm long and 11 μm (85% c.d.) wide. Oesophagus widens posteriorly to a bulb but the latter not easy to detect. Tail cylindrical with rounded tip; 6 a.b.d. long. Spicules relatively long, 1·4 a.b.d., with a central division. Gubernaculum lies parallel to spicules. Small ventral precloacal spine and two subventral postcloacal spines (Fig. 32e). 10 typical precloacal supplements, extending 218 μm anterior to cloaca: first supplement 33 μm from cloaca and remainder about 20 μm apart. Two opposed testes; anterior left, posterior probably right of gut but difficult to be certain. No clear patch observed in vas deferens.

REMARKS. There are two apparent differences between the specimen from South Bay and the only other description, that of Gerlach (1956). Gerlach (1956) found alternating rows of large and small dots whereas this could not be detected here. However, Gerlach depicted this from a medial view whereas the Irish specimen was laterally orientated. Since it was decided not to risk damaging the only specimen by rolling it to observe a medial view, this difficulty will have to remain unresolved. The spicule was similar in general outline shape but Gerlach (1956) did not depict a central division and drew the gubernaculum strongly, lying lateral to the distal end of the spicule. Since both Gerlach's interpretation and that given here differ from the usual neotonchid spicule and gubernaculum, it seems preferable to await further evidence before using this difference to create a separation. Gerlach (1956) quotes the length of the spicule as 20 μm, but if his measurement of the cloacal diameter is correct (25 μm), the spicule is also about this length. In most other respects, the specimen from South Bay conforms well with Gerlach's description, especially in terms of body size and shape, setose R_1 sensilla, relative lengths of R_2 and R_3 sensilla, amphid size and number of turns and supplement number (9 vs. 10).

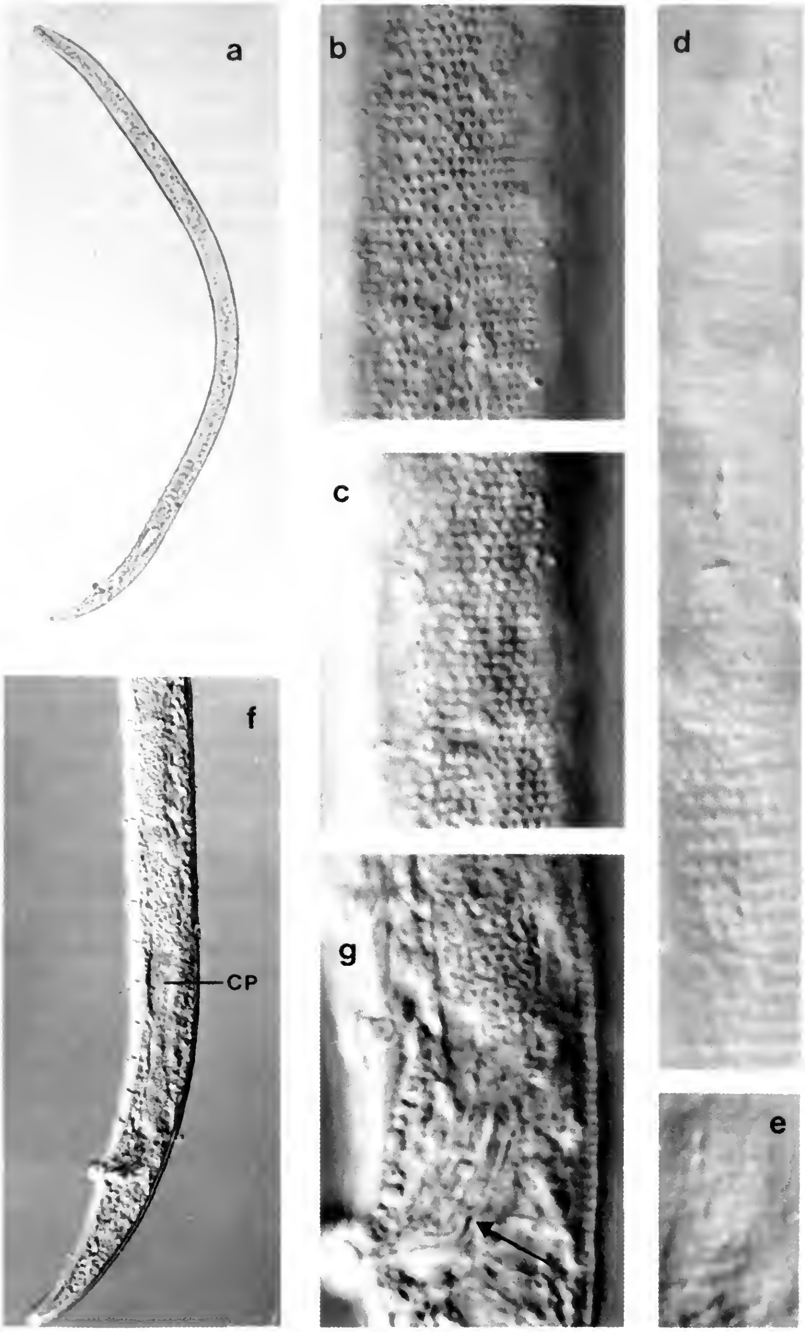

Fig. 31 *Neotonchoides vitius*: (a) whole body; (b) lateral cuticle pattern mid-body; (c) lateral cuticle showing pores level with oesophagus bulb; (d) cuticle pores mid-body; (e) group of four cuticle pores from cloacal region; (f) posterior region showing supplements and clear patch (CP); (g) cloacal region, arrow showing position of kink in spicule.

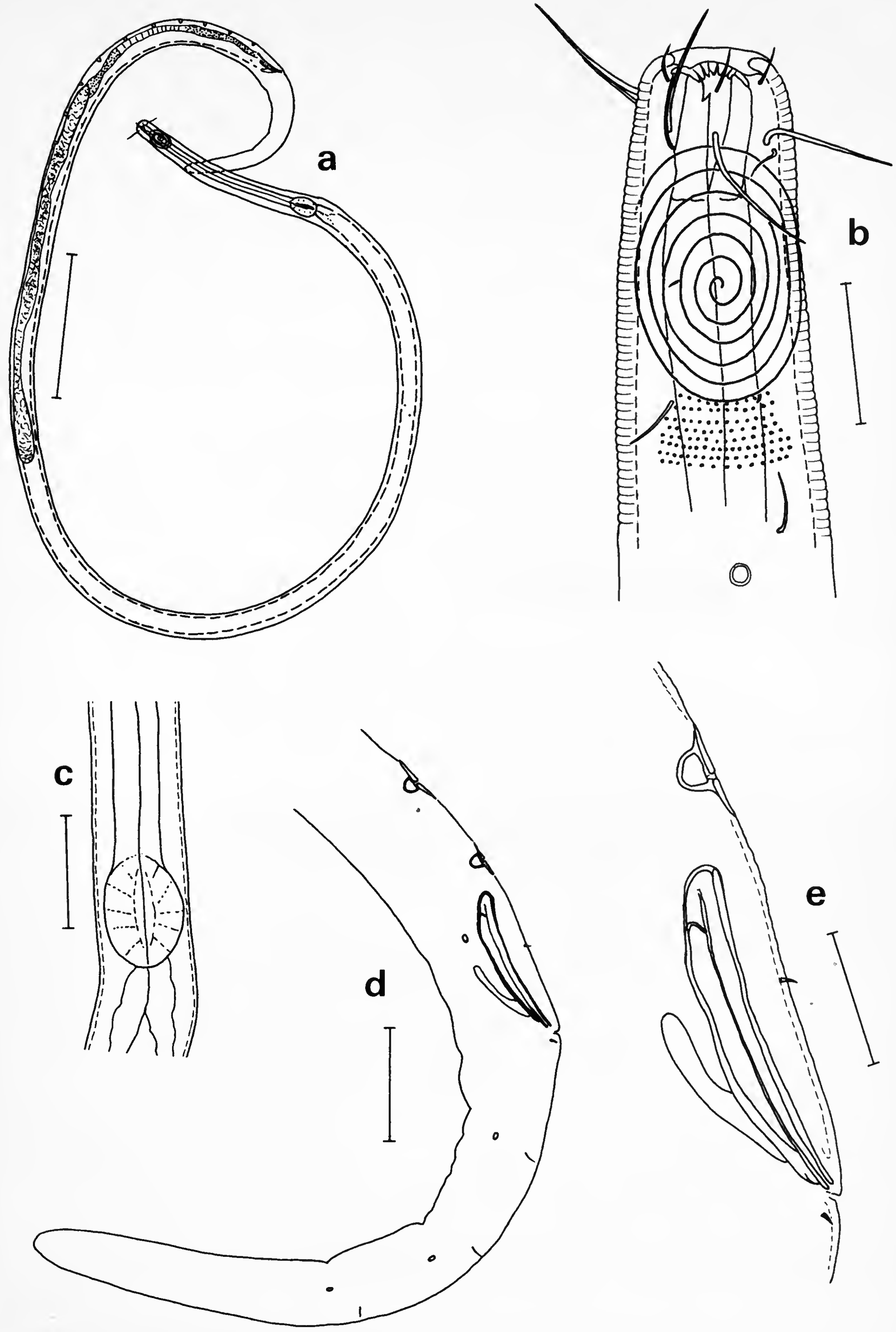

Fig. 32 *Nannolaimus fusus*: (a) ♂ whole body; (b) ♂ head; (c) posterior oesophageal region; (d) ♂ posterior region; (e) copulatory apparatus. Bar scales: a = 100 μm; c, d = 20 μm; b, e = 10 μm.

Nannolaimus phaleratus (Wieser & Hopper, 1966) comb. nov.
(Figs 5b, 33a–c, 34)

Neotonchus phaleratus Wieser & Hopper, 1966

MATERIAL STUDIED. Holotype ♂, slide 120, Canadian National Collection of Nematodes.

LOCALITY. 4 miles southeast of the mouth of the North Edisto River, South Carolina, U.S.A., at a depth of 12 m.

DESCRIPTION. Body length = 970 μm. Maximum body diameter 19 μm (a = 51). Cuticle has transverse rows of punctations; no lateral differentiation. The punctations are less pronounced and smaller posterior to the oesophagus with a clear discontinuity in annule width level with the posterior of the oesophagus. In mid-oesophagus, there are 14 rows of dots per 10 μm whilst in the mid-body area, there are 19–20 rows per 10 μm. Cuticle pores could not be detected. Apart from setae situated laterally just posterior to the amphid and on the tail, somatic setae were also not detected. R_1 sensilla setiform, 2 μm long. R_2 sensilla 8 μm. R_3 sensilla 12 μm. Dorso-sublateral subcephalic seta present level with the amphid centre. Amphid 4+ turns, longitudinally elongate. Buccal cavity with rugae anteriorly, a short vestibule and then narrow with a small dorsal tooth-like projection at the entrance to the narrow section (Figs 33b, 34b). Oesophagus 116 μm long (b = 8) with a 19 μm long posterior bulb (16% of total oesophagus length). Tail 96 μm long (c = 10). 8 precloacal supplements. Two testes, both situated left of gut and apparently lying in tandem, although it is difficult to be sure. There appears to be a clear patch in the vas deferens situated opposite supplement 6.

REMARKS. The specimen studied conformed well with the description given by Wieser & Hopper (1966), based on two males and one female, although the holotype appeared to be somewhat narrower than reported by them. According to Wieser & Hopper (1966), the female amphids are smaller and only 3+ turns. Wieser & Hopper (1966) considered that this species most closely resembled *Neotonchus chamberlaini*, having similar shaped spicules. However, there are sufficient differences at the generic level as discussed earlier which suggest that *N. phaleratus* should be placed in a different genus together with *Nannolaimus fusus*, the two being easily distinguished by the relative lengths of the R_2 and R_3 sensilla.

Filitonchus filiformis (Warwick, 1971) comb. nov.
(Figs 5c, 33d–e, 35)

Neotonchus filiformis Warwick, 1971

MATERIAL STUDIED. 3♂♂, BM(NH)1970.233–235 (syntypes).

LOCALITY. Northumberland coast (North Sea), sublittoral silt.

DESCRIPTION. Body length 1190–1300 μm; a = 86–99; b = 12; c = 16, S = 15–16 μm (from Warwick, 1971). Cuticle with transverse rows of small punctations; no lateral differentiation. Minute cuticle pores can be detected; difficult to distinguish any pattern and appear to be few in number. R_1 sensilla not detected; R_2 and R_3 sensilla setose. Dorso-sublateral subcephalic seta present level with the posterior part of the amphid (Fig. 33d). Long sublateral cervical setae present (Figs 33d & 35b) but somatic setae otherwise sparse. Amphids 4+ turns. Two opposed testes; anterior right, posterior left of gut. An obvious clear patch in the vas deferens is present level with supplements 4 and 5 (Fig. 35c).

REMARKS. The foregoing conforms well with the original description by Warwick (1971). The sharp pointed dorsal tooth described by Warwick (1971) could not be detected but the specimens were not in good condition at the anterior.

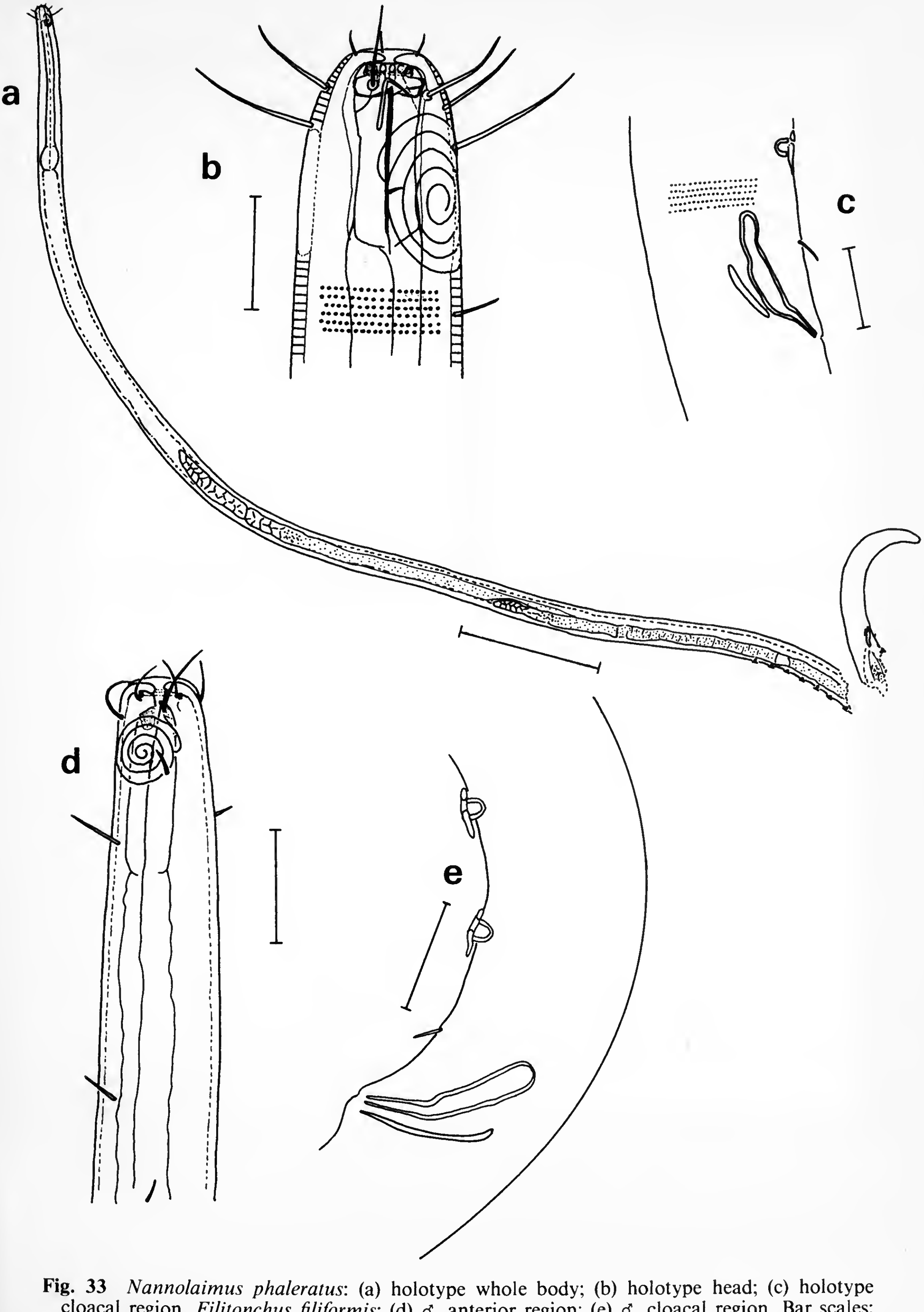

Fig. 33 *Nannolaimus phaleratus*: (a) holotype whole body; (b) holotype head; (c) holotype cloacal region. *Filitonchus filiformis*: (d) ♂$_1$ anterior region; (e) ♂$_1$ cloacal region. Bar scales: a = 100 μm; others = 10 μm.

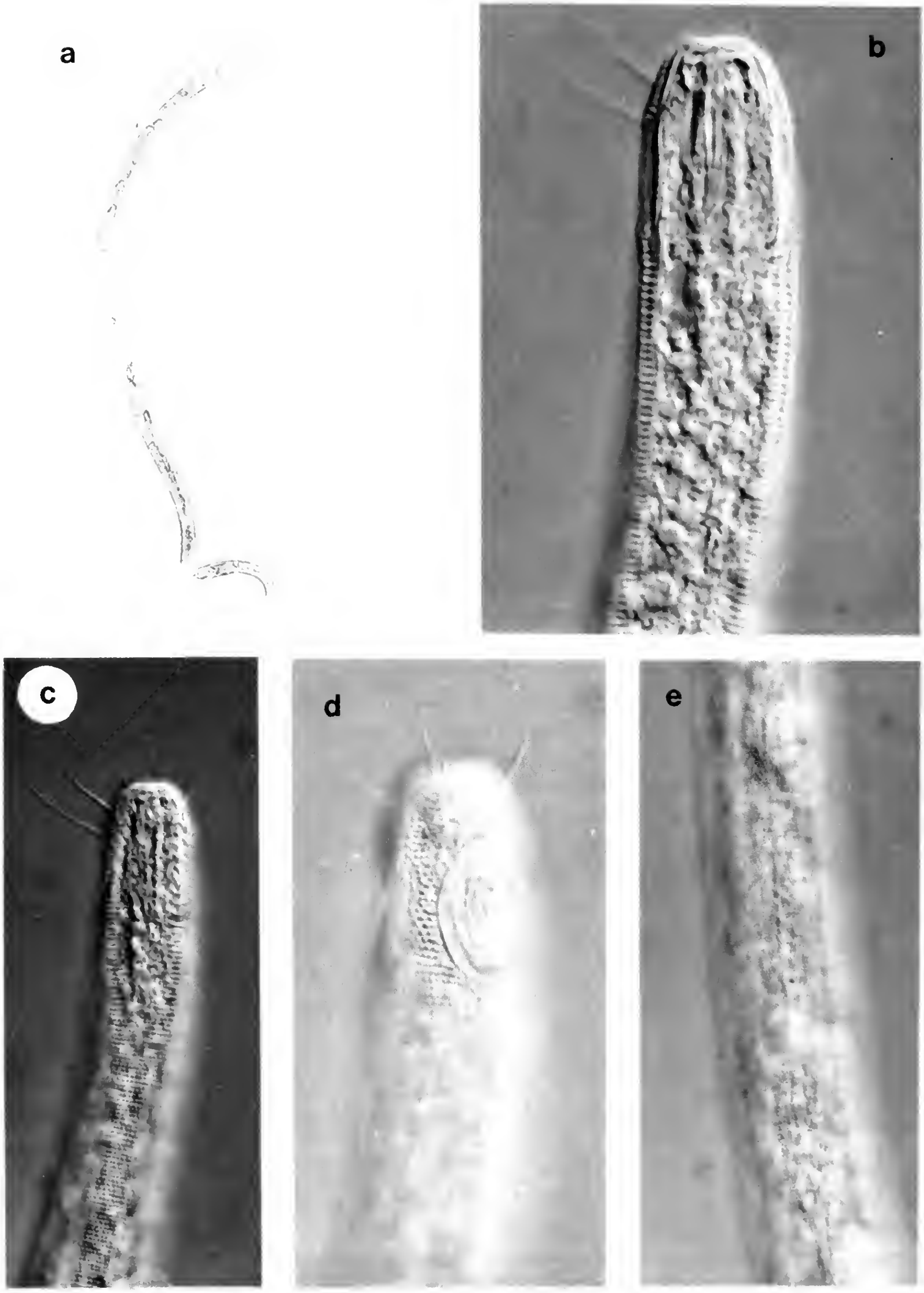

Fig. 34 *Nannolaimus phaleratus*: (a) whole body; (b) anterior region showing R_1 sensilla and buccal cavity; (c) anterior region showing cephalic sensilla and cuticle punctations; (d) anterior region showing amphid and cephalic punctations; (e) lateral cuticle punctations mid-body.

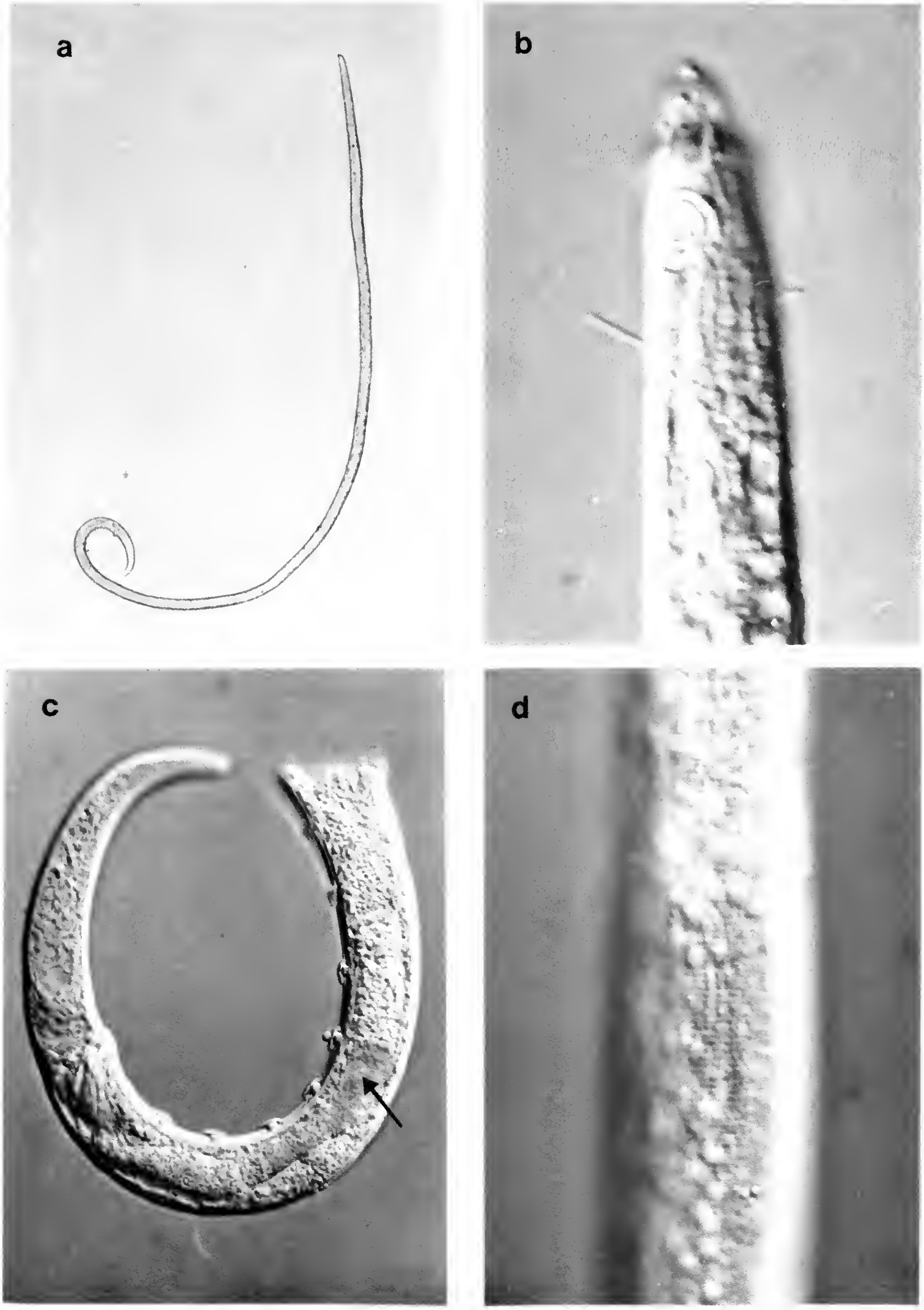

Fig. 35 *Filitonchus filiformis*: (a) whole body; (b) anterior region showing amphid; (c) posterior region showing supplements and clear patch (arrowed); (d) lateral cuticle markings.

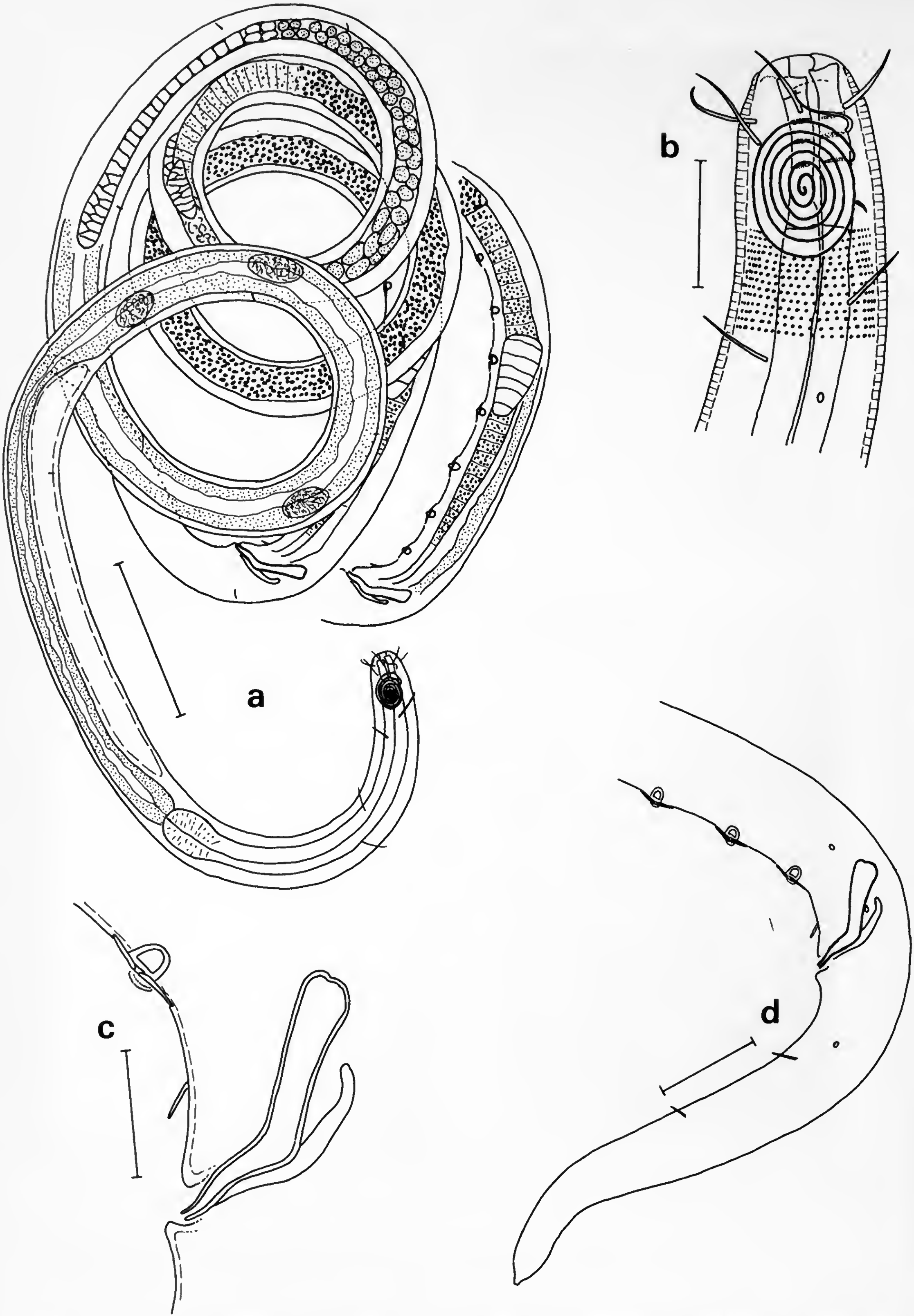

Fig. 36 *Filitonchus ewensis*: (a) whole body; (b) head; (c) copulatory apparatus; (d) posterior region. Bar scales: a = 50 μm; d = 20 μm; b, c = 10 μm.

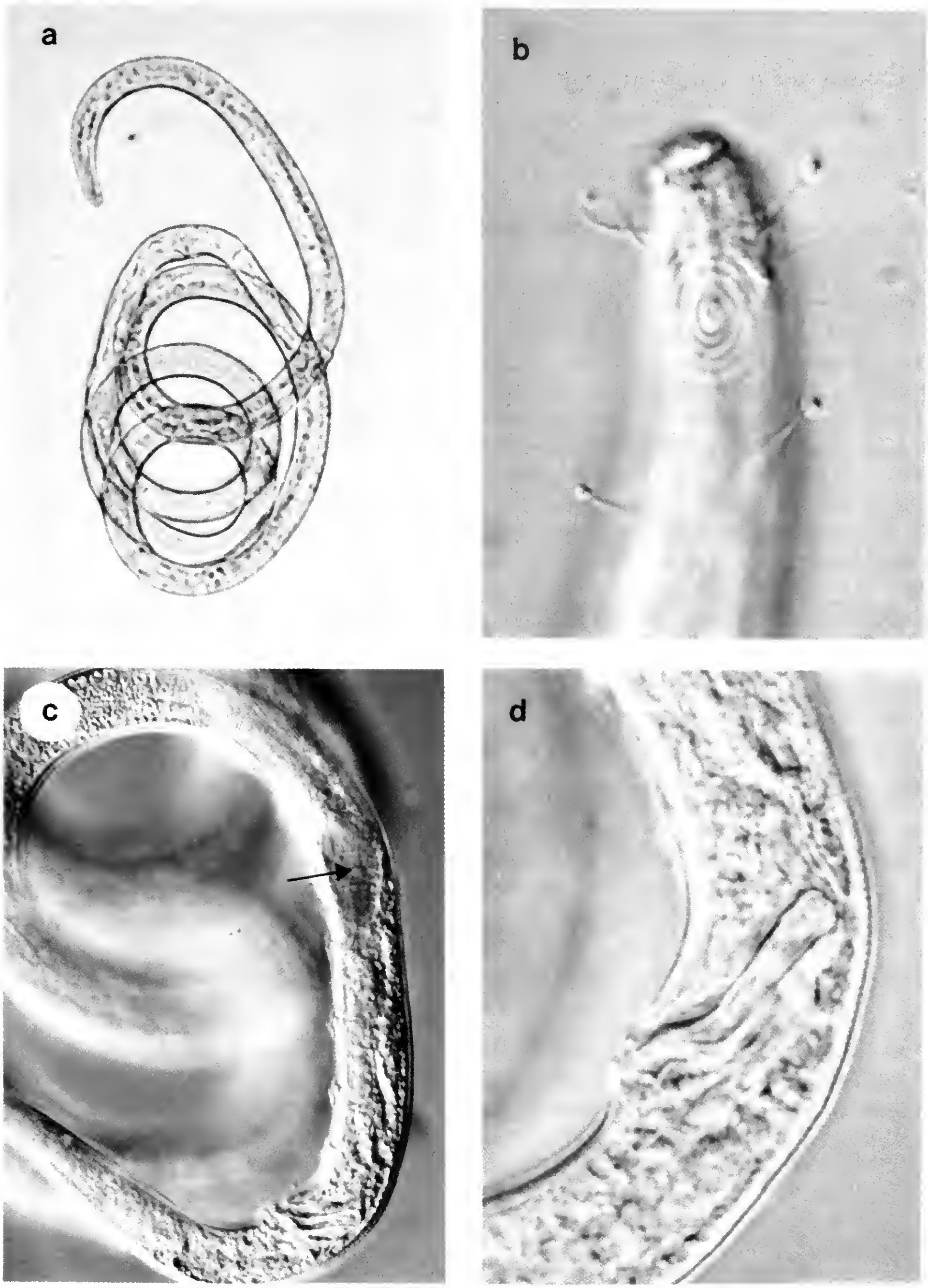

Fig. 37 *Filitonchus ewensis*: (a) whole body; (b) anterior region showing amphid and cervical setae; (c) posterior region showing clear patch (arrowed); (d) cloacal region showing spicule shape.

Filitonchus ewensis sp. nov.
(Figs 5d, 36, 37)

MATERIAL STUDIED. Holotype ♂: BM(NH)1981.6.70.

LOCALITY. Intertidal sand, Firemore Bay, Loch Ewe, Wester Ross, Scotland.

DESCRIPTION.

Holotype ♂: $\dfrac{-\quad 103\quad M\quad 1275}{10\quad 17\quad 17\quad 18}$ 1370 μm; a = 81; b = 13; c = 14; S = 23 μm

Cuticle bears transverse rows of punctations; no lateral differentiation. Small cuticle pores present as a lateral file throughout the body. Long cervical setae present on the anterior half of the oesophageal region which are bilaterally symmetrical. Sparse short somatic setae present on the rest of the body. R_1 sensilla not detected. R_2 sensilla 6 μm. R_3 sensilla 8 μm, situated slightly posterior to R_2 sensilla. Short dorso-sublateral subcephalic seta present level with middle of amphid. Amphids large, 6+ turns and longitudinally oval; 11 μm long and 8 μm (70% c.d.) wide. Buccal cavity narrow with no sign of a cuticularised dorsal tooth. Oesophagus ends in a 17 μm long bulb (17% of total oesophagus length). Long renette cell situated posterior to oesophagus (Fig. 36a). Tail gently tapering; 5 a.b.d. long. Spicules typical neotonchid shape and broad proximally (Fig. 37d). Precloacal spine situated 9 μm anteriorly. 7 typical precloacal supplements extending 115 μm from cloaca. Two opposed testes; anterior right, posterior left of gut. A prominent clear patch is situated between supplements 4 and 6 (Figs 36a & 37c).

DIFFERENTIAL DIAGNOSIS: Neotonchinae. *Filitonchus ewensis* sp. nov. may be distinguished from the other species in the genus by the larger amphid with a greater number of turns and shape of the spicules.

ETYMOLOGY. The species name comes from the type locality; Loch Ewe.

REMARKS. Despite only one specimen being available, it seems well enough characterised to warrant the erection of a separate species. However, the condition of the buccal cavity was not very good and needs further investigation when more specimens become available. The presence of a long renette cell was also found in *Nannolaimus guttatus* by Cobb, 1920.

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by R. J. Lincoln

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The work has been carefully edited to bring corresponding descriptions, keys and figures into close proximity within the text. The systematic section is supported by chapters dealing with morphology, systematics, geographical distribution, biology and ecology, the latter being presented in the form of an annotated subject index of research literature. Finally, there is an extensive bibliography of about 1,200 references that includes most of the British marine amphipod literature published to date.

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Revision of the eastern African earthworm genus *Polytoreutus* (Eudrilidae : Oligochaeta)

R. W. Sims
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Contents

Synopsis

Fifty-three nominal species and subspecies of the genus *Polytoreutus* are revised; descriptions and a key are provided to seven species groups here recognized and 27 species now regarded as valid (five being new to science).

Introduction

The earthworm genus *Polytoreutus* was described by Michaelsen in 1890 to accommodate a highly variable eudriline species, *coeruleus,* from Tanzania. Its distinguishing characters are: a single male pore, a single spermathedal pore in furrow 18/19, the absence of penial setae and a single pair of testes in segment *xi.* During the first five years following its description, another seven species were recognized on other characters (Beddard, 1895) and altogether eleven species and six subspecies were known by the end of the century (Michaelsen, 1900); at the time that Stephenson published his monograph (1930), the genus contained 32 species compared with the 53 nominal taxa from central and eastern Africa examined during the studies reported below. During the ninety years or so that have elapsed since the description of *Polytoreutus,* the included taxa have not been reviewed nor have intraspecific and other variations been recorded with the result that several species have been described as new more than once. This present report contains the first revisions of the nominal taxa assigned to the genus, seven species groups are recognized containing 27 species now regarded as valid (five being described as new).

The current revision became essential in order to identify material of the genus *Polytoreutus* among the collections of earthworms made in eastern Africa by Miss Edna Oxtoby. In 1964 Miss Oxtoby was appointed to the staff of Kenyatta College, Nairobi and resumed teaching biology after fifteen years as an Education Officer (later Senior Education

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Officer) first in Zanzibar then later in Hong Kong. During her career she had encountered problems in teaching about earthworms. The fundamental difficulty was that the boreal species *Lumbricus terrestris* was frequently the only oligochaete described and figured in textbooks. Now she became determined that Kenyan students should be taught from representatives of their own country. The new problem was to select a suitable teaching type. An appropriate species needed to be fairly plentiful and to produce large individuals so that the worms could be examined without the use of a low-power dissecting microscope. To achieve her ambition, Miss Oxtoby collected samples of earthworms from many localities in Kenya and some in nearby territories. Eventually she selected a species of the highly specialized genus *Polytoreutus* and produced a dissection guide describing its anatomy but did not provide the species with a name as the genus was overdue for revision (Oxtoby, 1975). The species is identified below as *P. huebneri* Michaelsen, 1913.

Miss Oxtoby had always been anxious to stimulate research on Kenyan earthworms, especially the genus *Polytoreutus,* due to its frequency of occurrence and to establish the name of her teaching type. She donated many samples of earthworms to the British Museum (Natural History) containing numerous representatives of the families Alluroididae, Sygenodrilidae, Acanthodrilidae, Eudrilidae and Almidae in addition to introduced species of Megascolecidae and Glossoscolecidae. As *Polytoreutus* was the most commonly represented genus in her large collections, little progress could be made with studying the material until this taxon and its component species were re-examined. Clearly the revision reported below represents the realization of Miss Oxtoby's more recent ambition, made possible solely by her dedication. Sadly in 1979 Miss Oxtoby died in Nairobi before the completion of this present study.

During the course of this investigation material was examined from collections in several institutions. The following abbreviations cited with catalogue numbers denote those specimens and indicate the institution in which they are deposited.

BM(NH)	British Museum (Natural History), London.
Berlin	Zoologisches Museum, Museum für Naturkunde der Humboldt Universität, Berlin.
Brussels	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels.
Hamburg	Zoologisches Institut und Zoologisches Museum, Universität Hamburg.
Harvard	Museum of Comparative Zoology, Harvard University.
Stockholm	Naturhistoriska Riksmuseet, Stockholm.
Turin	Museo ed Istituto di Zoologia Sistematica dell Universitá di Torino.
USNM	National Museum of Natural History, Smithsonian Institution, Washington.

Variation

In earthworms of the genus *Polytoreutus* many structures are morphologically stable, especially those diagnostic of the genus (single male pore in *xvii* or 17/18, single spermathecal pore in 19/19, alimentary tract and the presence of only a single pair of testes in *xi*), yet other structures, particularly the spermathecal system, are highly variable. The differences, however, cannot always be attributed to specific variation; sometimes extensive modifications in morphology may be associated with growth and sexual activity while the effects of employing (frequently *mis*employing) different techniques to relax, kill, fix and preserve series, have added to the variations which need to be discounted when identifying material. Unfortunately there has been a lack of awareness of individual variation but this has not been the only factor resulting in many nominal species being recognized, there has been too a regrettable oversight of the literature by authors who in addition, apparently seldom re-examined type-series, often their own.

Size. The lengths of clitellate specimens vary between 52 mm for a small individual of *coeruleus* (*minutus* at 80 mm is usually regarded as the smallest species in the genus) and 390 mm recorded for the largest specimen of *huebneri*. But length is not a reliable taxonomic character as the range of sizes of any single species usually overlaps those of several others. Differences in size could be caused, as in some Lumbricidae, by growth ceasing at the onset of the first period of aestivation after hatching (breeding, not growth, activity following the diapause). Thus, the earlier that cocoons hatch after the end of a dry season, the longer is the period available for growth before the onset of the next dry season. Often a disparity in size between conspecific series can be attributed to divergent collecting and curatorial techniques, these may result in preserved specimens being excessively contracted, relaxed or subsequently starting to macerate so becoming abnormally long.

Segments. The numbers of segments forming the bodies of the majority of species are 200–300 but only 102 are recorded for a (non-regenerating) individual of *minutus* whereas 670 were present in a specimen of *multiporus* (a member of the *kilindinensis* species group that contains other species with numerous segments).

Prostomium. This structure is basically prolobous but occasionally additional longitudinal furrows occur in the peristomium causing the prostomium to appear to be pro-epilobous or tanylobous. These furrows seem to be associated mainly with a larger body size and may be a function of growth. In some cases they may be no more than wrinkling caused by epidermal shrinkage during preservation.

Setae. The setal ratios (segmental inter-setal distances) are constant among conspecific series which have received comparable treatments during collection and storage. However, by subjecting specimens of a single species to differing techniques for relaxing, fixing and preserving, variations can be produced in the setal ratios of greater magnitude than the differences recorded between species. The reason for these discrepancies appears to lie in the non-uniformity of the thickness of the longitudinal muscles around the body, in particular along the setal lines where the muscles are reduced. Depending on the treatment applied to a specimen, the contractions of the longitudinal and the opposing circular muscles will vary to affect the inter-setal distances sufficiently to reduce the taxonomic usefulness of the measurements. Nevertheless, the positions of setal lines *c* and *d* remain constant relative to the nephridiopores which are located midway between them, i.e. $\frac{1}{2}$ cd; the nephridiopores being invariably $\frac{1}{2}$ circumference apart.

Clitellum. A clitellum is present at least on *xiv–xvii* (four segments) in all adults and with increasing maturity extends forwards onto *xiii* and, in many species, also backwards onto *xviii*. It is usually annular but occasionally (*multiporus* and *violaceus*) only poorly developed ventrally and, for taxonomic purposes, is regarded as being saddle-shaped. In addition, the clitellum may fail to develop ventrally in the vicinity of the male pore so although it may be annular over *xiii–xvi*, it becomes saddle-shaped posteriorly.

Male and spermathecal pores. Most species have the true male pore carried by a penis lying within a male pouch. The penis often protrudes externally, the extent of the protrusion depending upon the length of the penis and the collection and preservation techniques to which a specimen has been subjected. The secondary male pore (orifice to the male pouch) is located either on *xvii* or in 17/18. It is often carried on a porophore.

In preserved specimens, the sizes of both the secondary male pore and the porophore can be affected by the degree of relaxation. In contracted specimens the pore may be small (inconspicuous) and circular with the porophore raised whereas if a specimen is relaxed, the pore can be slit-like to rounded (commonly with the penis protruding) and the porophore difficult to detect.

The spermathecal pore is usually an inconspicuous, simple, lateral slit midventrally in 18/19 but it may become enlarged and modified when a spermatophore is present within the orifice. (The presence of a spermatophore may produce a temporary thickening in the wall of the ectal region of the receptaculum seminis. Authors have mistaken this modification for a 'bursa copulatrix'.)

The male and spermathecal pores are accommodated within a single, common pouch in the adults of the *arningi* species group. Mature individuals possess a large, single pore occupying most the midventral region of *xviii* and sometimes part of *xvii* too. Within the pouch the male pores (possibly the paired ectal ends of the prostatic ducts) are located anteriorly, often concealed under the lips of the orifice; while the spermathecal pore is situated towards the posterior wall.

Female pores. The external apertures of the oviducts are invariably small, simple pores located laterally on the posterior half of *xiv* between setal lines *c* and *d* where their precise location can vary individually. The variation appears to be connected with growth and sexual activity. The oviducts pass obliquely through the lateral parietal walls and as the clitellum thickens with increasing sexual maturity, so the oviducts lengthen correspondingly and maintain the oblique line of flow for the discharging zygotes. The result is for the pores to become located slightly more dorsally and posteriorly.

External genital structures. Most species lack external genital features apart from the clitellum and a porophore. However, a midventral longitudinal seminal groove leads posteriorly for several segments behind the spermathecal pore in *usambariensis* (*coeruleus* species group) and all members of the *kenyaensis* species group. While a single genital pad is present in *pulvillatus* (*meruanus* species group), a series of pads in *gregorianus* (*kilindinensis* species group), a single papilla occasionally in *arningi* and several papillae in *meruanus* and *papillatus* (*magilensis* species group). In addition, raised glandular (?pigmented) areas occur ventrally in *kilindinensis* and *hindei* (*kilindinensis* species group). Other random markings, neither midventral nor bilaterally symmetrically arranged, sometimes occur in the vicinity of the male and spermathecal pores; it is suggested that in some specimens of *coeruleus* such markings may be cyst-like bodies produced by parasites infesting the body wall.

Alimentary canal. Differences in collecting and curatorial techniques can cause superficial differences in the alimentary canal of conspecific individuals from separate series. In preserved specimens, contraction or relaxation of the alimentary canal often fails to correspond with the contraction or relaxation of other systems. Considerable displacement can occur with the paired calciferous glands in *xiii* lying within the parietes of more anteriorly situated segments or of those behind that segment. (In one extreme specimen the calciferous glands were lying over the prostrates with septum 11/12 and the anterior portions of the seminal vesicles covering the male pouch.) When the septa are correctly identified, the disparate relative positions of the organs do not cause confusion.

Seminal vesicles. There is considerable individual variation in the gross morphology and extent of the seminal vesicles due to growth and sexual activity. The seminal vesicles lead posteriorly from septum 11/12 as slender ducts, near the hinder ends of the prostates they expand and extend for a varying number of segments as dilated, sperm-filled sacs. Infrequently the slender anterior duct-like portions may also be filled with sperm. Posteriorly the vesicles may be flat and commonly expanded segmentally with a moniliform appearance; sometimes they become almost tubular. Throughout their lengths, their locations in relation to the prostates, intestine and to each other are fortuitous as they often become entwined with one another. In detail, the morphologies of the seminal vesicles of any two conspecific individuals are never alike.

Prostates. Tubular in structure, the prostates are usually long and pass posteriorly through several segments, possibly up to ten or more, with intersegmental constrictions: occasionally small and almond-shaped. Variations in structure are mainly specific so causing them to be taxonomically significant. The common variations are seen at the site of entry of the vasa deferentia. These ducts may lead into the prostates either terminally or subterminally at the ectal ends where the lateral wall of the glands may be raised to become papillate or cornuate in structure. When the lateral process is cornuate and long, the paired prostates together appear to form an 'H' with the horizontal member leading into the male pouch. When the vasa diferentia pass subterminally into the prostates, the region of the prostates anteriad to the union with the ducts, may be flexed forwards or perhaps laterally depending largely on whether a specimen is grossly or moderately contracted.

Male pouch. In most species a penis may be seen within this structure which seems to function as a penial sheath. The size may vary both individually and specifically. In species with a small male pouch, internally there is little sign of the pouch when a specimen is contracted due to the pouch itself being contracted and forced externally by the contracted muscles of the body wall to produce (externally) a raised porophore but in a relaxed specimen the male pouch can be seen internally on the ventral parietes of *xvii* while externally the porophore may be difficult to detect. In species with a large male pouch, the structure is readily evident regardless of the degree of relaxation (or otherwise) of a specimen. In a minority of species, a single or a pair of accessory glands or pouches of unknown function are associated with the male pouch.

Spermathecal System. In the Eudrilidae the female and spermathecal systems are highly specialized, being commonly united. In most the spermathecae have been replaced by coelomic (mesodermal) sacs which communicate entally with the paired oviducts at the 'fertilization chambers' where the ova are fertilized before being discharged through the female pores. In each species group of the genus *Polytoreutus* (and often in individual species) the spermathecal system forms a discrete pattern of major taxonomic importance yet wide ranges of individual variation are often present in the gross morphology (Fig. 1).

Variations are caused by a seeming adventitious development of the coelomic membranes forming the system due to growth, sexual activity and, on occasions, techniques of collection

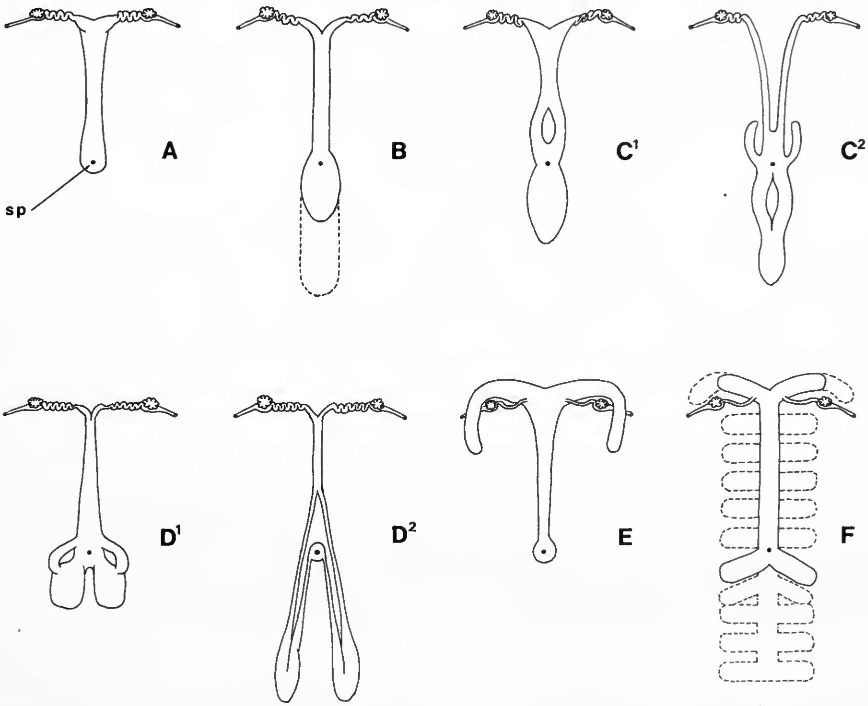


Fig. 1 *Polytoreutus* spp. Female and spermathecal systems (schematic dorsal views, not to scale). (A) *kenyaensis* species group; (B) *meruanus* species group; (C. 1–2) *magilensis* species group; (D. 1–2) *kirimaensis* species group; (E) *kilindinensis* species group; (F) *coeruleus* species group. *sp*, ventral location of the spermathecal pore.

and preservation. A lack of appreciation of the causes of the variations has, in the past, contributed towards some of the species being described as new more than once, sometimes by the same author. In the genus *Polytoreutus* the spermathecal system fundamentally comprises a simple median duct (receptaculum seminis) passing anteriorly from the spermathecal pore in furrow 18/19 to segment *xiii* where it bifurcates with each furca passing laterally to a fertilization chamber which communicates with the exterior by way of an oviduct. In some species the anterior furcae are massive and flexed posteriorly but with proximal, basal, ducts leading to the fertilization chambers (*kilindinensis* species group and, to a lesser extent, *coeruleus* species group). Otherwise the anterior furcae are usually slender, often convoluted, with the fertilization chambers located distally, i.e. terminally. The receptaculum seminis may be simple between *xiii* and 18/19 rarely to *xxi (kenyaensis* species group), simple but extending several segments behind the spermathecal pore (*meruanus* species group), divided by the spermathecal pore then reunited so forming a foramen for the ventral nerve cord (*magilensis* species group) or have several pairs of lateral diverticula *coeruleus* species group or have the diverticula unite distally on each side when proximally part of the median duct may fail to develop (*kirimaensis* species group). In all of these conditions there are many variations, some specific, others individual. Variations in the morphology of the spermathecal systems between conspecific individuals depend largely on the volume of received sperm being stored or having been stored previously but now expended. This kind of variation not only affects the gross size of the receptaculum seminis but in the case of diverticulate species, the proportions and number of diverticula. In *magilensis* the furcation occurs more posteriorly with the furcae sweeping forwards to *xiii* before flexing laterally, here partial union of the furcae commonly occurs anteriorly in individuals possessing a large volume of received sperm to give the receptaculum seminis a ladder-like appearance.

In *kilindinensis* the single, unpaired longitudinal portion of the receptaculum seminis is adiverticulate and always slender; it is suggested below that it may function as a vagina with received sperm being stored in the massive furcae. In other species the receptaculum seminis may be modified locally in the region of the external orifice. The changes are seen usually as a slight thickening of the wall of the sac and can be associated with the presence, or recent presence (?), of a spermatophore; the ectal region thus modified has, on occasions, been identified as a bursa copulatrix. Beddard (1901 & 1902) reported the presence and structures of spermatophores in five species, their occurrence and morphologies were confirmed during this present study. The function of these bodies is obscure. In all of the species concerned, there is an intromittant penis for transferring sperm products directly into the receptaculum seminis of a concopulant, while fertilization presumably takes place in the lumena of the anteriorly situated paired fertilization chambers from whence the zygotes pass into the slender oviducts to be discharged through the small paired female pores on *xiv*. The spermatophores of these eudrilids do not therefore seemingly have the same function as the structures of the same present, for example, in many Lumbricidae. Their production gives rise to the possibility that they are perhaps concerned with cell multiplication before cell division and the production of the haploid spermatozoa. Clearly the production of the male gametes in this group of earthworms needs to be investigated, especially whether received male sexual products consist of diploid spermatogonoid cells.

Taxonomy

Members of the family Eudrilidae (Megascolecoidea lacking pretesticular spermathecae) are unique in having complex spermathecal systems derived from coelomic (mesodermal) tissue, which usually unite with the oviducts to permit ova to be fertilized internally by received spermatozoa (Clausen, 1965; Sims, 1964, 1969 & 1980). Apart from allochthonous species, the family is confined to central Africa where two subfamilies are recognized: Pareudrilinae mostly in the east and the Eudrilinae mostly in the west. The latter is characterized by the presence of single, suboesophageal pouches in *x* and *xi*, or *ix*, *x* and *xi* with paired stalked (extramural) calciferous glands in *xii* or *xiii* respectively and the vasa deferentia investing the testes to form 'sperm reservoirs' which are continuous with the seminal vesicles; the subfamily Pareudrilinae is defined negatively on the absence of the characters diagnostic of the Eudrilinae. The included genera in the subfamily Eudrilinae form two groups on the number of male and spermathecal pores: a minority with paired pores and a larger group of which *Polytoreutus* is a member, with single, midventral pores. The inter-relationships of the individual genera are marked partly by the situation of the spermathecal pore(s) (Sims, 1971). The genus *Polytoreutus* Michaelsen, 1890 (eastern Africa) with the single spermathecal pore located one segment behind the single male pore has seemingly greater affinity with *Teleutoreutus* Michaelsen, 1913 (Ethiopia) and the doubtfully distinct *Eupolytoreutus* Michaelsen, 1910 (western Tanzania, Zaire and Togo) with the spermathecal pore near (before, same segment or behind) the male pore than with *Schubotziella* Michaelsen, 1915 (eastern Zaire) with the spermathecal pore several segments in front of the male pore although *Polytoreutus* and *Schubotziella* are metandric (testes in *xi* only) and *Teleutoreutus* and *Eupolytoreutus* are holandric (testes in both *x* and *xi*). On the other hand, the genus *Polytoreutus* has a low affinity with the holandric *Eutoreutus* Michaelsen, 1922 (synonym *Agrotoreutus* Segun, 1976) from Nigeria and Zaire with rolled penial setae yet the spermathecal pore is behind the male pore and no significant level of similarity with *Keffia* Clausen, 1963 (Nigeria) with rolled penial setae and paired spermathecal pores behind paired male pores.

Genus ***POLYTOREUTUS*** Michaelsen, 1890

Polytoreutus Michaelsen, 1890 : 24; Michaelsen, 1891 : 55; Beddard, 1895 : 608; Michaelsen, 1900 : 412; Stephenson, 1930 : 877.

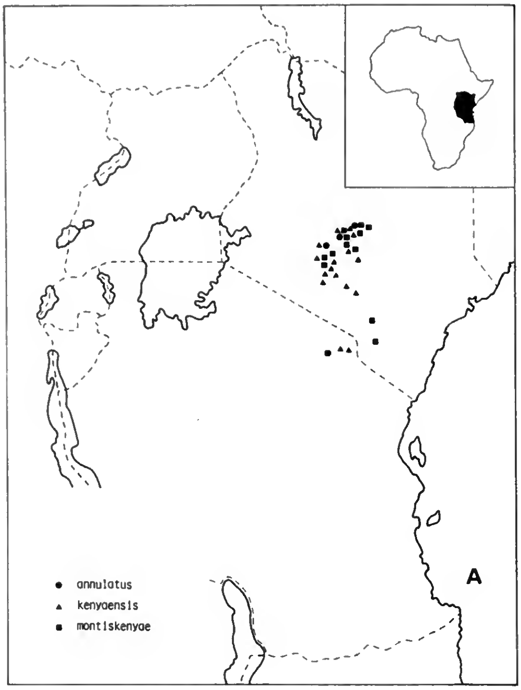
TYPE SPECIES. *Polytoreutus coeruleus* Michaelsen, 1890 by monotypy.

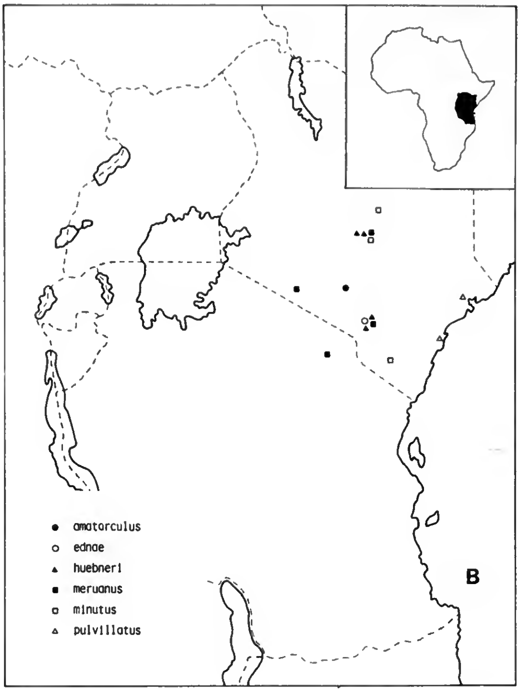
DIAGNOSIS. Metandric Eudrilinae with male pore single, penial setae absent, spermathecal pore single behind the male pore.

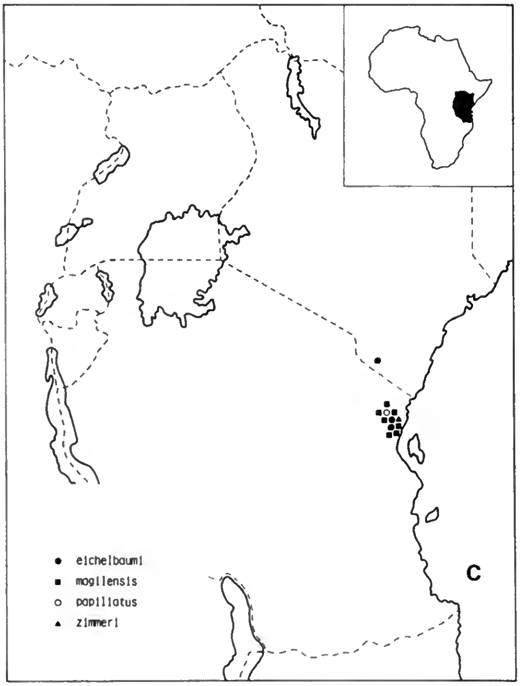
DESCRIPTION. Prostomium commonly prolobous, rarely pro-epilobous or tanylobous. Setae *ab* widely paired, setae *cd* closely paired. Dorsal pores absent. Nephridiopores midway between setal lines *c* and *d*, 0·5 body circumference apart. Clitellum commonly annular *xiii*, *xiv–xvii*, *xviii*. Secondary male pore (orifice to the male pouch containing the penis), single, midventral *xvii* or 17/18; penial setae absent. Female pores paired on hinder part of *xiv* between setal lines *c* and *d*. Spermathecal pore single, midventral 18/19. Oesophageal gizzard *v*; single sub-oesophageal sacs *ix*, *x*, *xi*; paired supra-oesophageal (dorso-lateral) stalked calciferous glands *xiii*. Testes single pair *xi* (metandric) enclosed by 'sperm reservoirs' formed from the anterior ends of the vasa deferentia and continuous with the seminal vesicles; seminal vesicles single pair originating in *xii* and extending posteriorly usually as slender ducts before dilating near the hinder ends of the prostates and continuing for several segments as expanded sacs. Prostates tubular. Ovaries paired *xiii*, occasionally displaced into *xiv*; rosette-shaped with several egg-strings, usually invested by ovisacs; ovisacs infrequently dependent from septum 12/13 with an ovarian duct leading to the antero-lateral regions of the spermathecal system or (commonly) united with the antero-lateral regions of the spermathecal system. Spermathecal system derived from coelomic tissues, morphology highly variable but essentially a single median sac, the receptaculum seminis, leading forwards from the spermathecal pore to a bifurcation usually in *xiii* (sometimes more posteriorly) with the furcae passing laterally to combine with the ovisacs (or ovarian ducts) to form paired fertilization chambers with oviducts discharging onto *xiv*. Holonephridial.

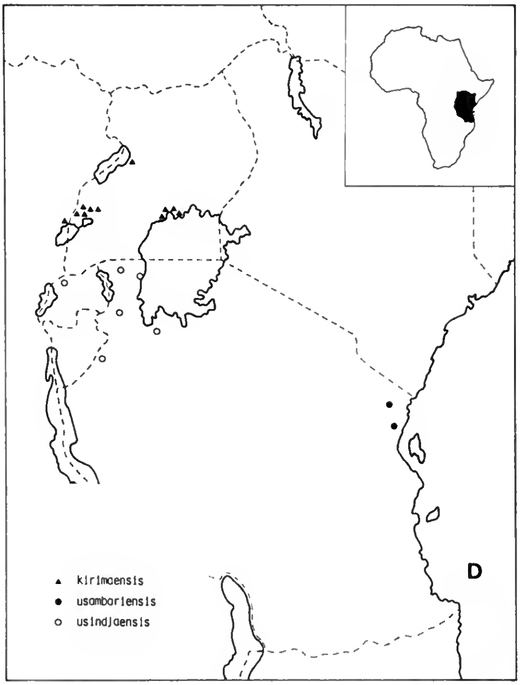
Note 1. The name *male pouch* is preferred for the muscular structure containing the penis and sometimes termed the 'bursa propulsoria'.

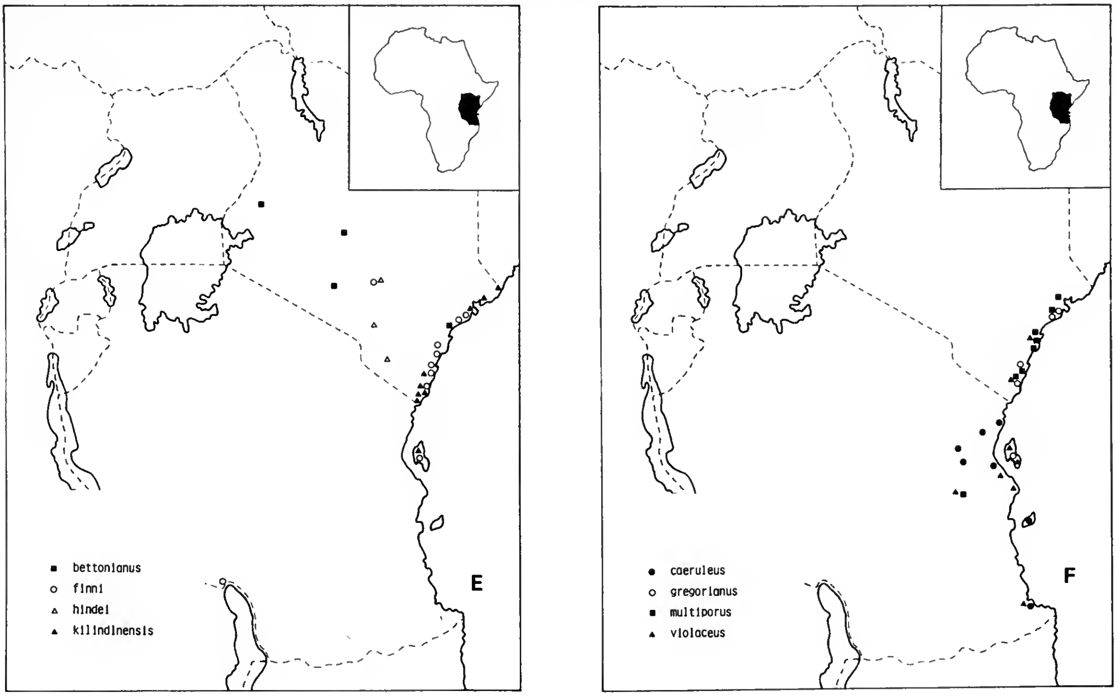
Note 2. The paired, highly specialized structures formed at the union of the anterior furcae


● annulatus
▲ kenyaensis
■ montiskenyae
A


● amatorculus
○ ednae
▲ huebneri
■ meruanus
□ minutus
△ pulvillatus
B


● eichelbaumi
■ mogiliensis
○ papillatus
▲ zimmeri
C


▲ kirimaensis
● usambariensis
○ usindjaensis
D



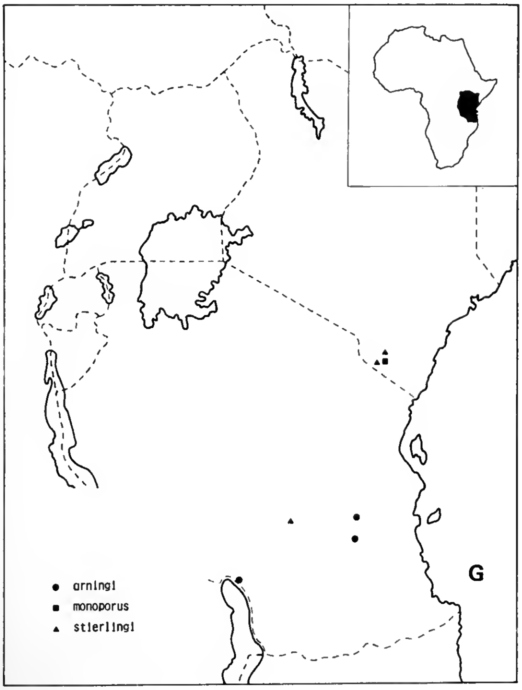


Fig. 2 Distributions of species of the genus *Polytoreutus*. Collecting localities: (A) *kenyaensis* species group; (B) *meruanus* species group; (C) *magilensis* species group; (D) *kirimaensis* species group; (E) *kilindinensis* species group; (F) *coeruleus* species group; (G) *arningi* species group.

of the single spermathecal system with the oviducts of the paired female systems are here termed *fertilization chambers* to reflect their primary function.

DISTRIBUTION. Uganda, Rwanda, eastern Zaire, Kenya and Tanzania (Fig. 2).

REMARKS. An outstanding aspect of the morphology of members of this genus is the reduction in the constraints imposed by metameric segmentation on the development of the reproductive systems. Although the testes are located in *xi* and the ovaries usually in *xiii*, the seminal vesicles, prostates and spermathecal systems are extensive and pass through many segments (in some species, perhaps 30 segments). As discussed above, the spermathecal systems are diverse yet the specializations can be categorized to permit six of the seven species groups to be recognized (Fig. 1). (The *arningi* species group, taxonomically the least satisfying of the species groups recognized, is separated on the male and spermathecal pores opening within a common orifice.)

(*a*) Anterior furcae of the receptaculum seminis slender leading to distally located fertilization chambers.

kenyaensis species group. Receptaculum seminis single, adiverticulate, only occasionally slightly pouched posteriorly (to *xx* or *xxi*) behind the spermathecal pore.

meruanus species group. Receptaculum seminis single, adiverticulate, extending posteriorly for several segments behind the spermathecal pore.

magilensis species group. Receptaculum seminis divided near the spermathecal pore to form a foramen for the passage of the ventral nerve cord, united posteriorly to form a single sac; diverticula may be present.

kirimaensis species group. Receptaculum seminis with paired lateral sacs formed by the distal coalescence of diverticula.

(*b*) Anterior furcae of the receptaculum seminis with basal (proximal) ducts leading to the fertilization chambers.

kilindinensis species group. Receptaculum seminis adiverticulate.

coeruleus species group. Receptaculum seminis diverticulate.

Key to the adults of species of the genus *Polytoreutus*

1	Male and spermathecal pores open into a common orifice (*arningi* species group)	2
–	Male pore *xvii* or 17/18, spermathecal pore 18/19	4
2	A pair of accessory pouches present internally posterolaterally to the male pouch	3
–	Accessory pouches absent	***monoporus*** (p. 296)
3	Receptaculum seminis short (*xiii–xix*), male pouch large	***arningi*** (p. 295)
–	Receptaculum seminis long (*xiii–xxii* or longer), male pouch small	***stierlingi*** (p. 296)
4(1)	Anterior furcae of the receptaculum seminis usually slender, often convoluted, leading distally to the fertilization chambers	5
–	Anterior furcae of the receptaculum seminis often massive, proximal ducts lead to the fertilization chambers	20
5	Receptaculum seminis simple, adiverticulate	6
–	Receptaculum seminis complex, forming a ring near the spermathecal pore and/or diverticulate at least posteriorly, diverticula may coalesce distally	14
6	External median ventral seminal groove present behind the spermathecal pore, internally receptaculum seminis not extending behind *xxi* (*keynaensis* species group)	7
–	External median ventral seminal groove absent, internally receptaculum seminis extending several segments behind the spermathecal pore (*meruanus* species group)	9
7	Seminal groove interrupted by a pad-like papilla in *xxii*	***annulatus*** (p. 266)
–	Seminal groove without papilla	8
8	Prostates with subterminal ectal cornu receiving the vasa deferentia	***montiskenyae*** (p. 268)
–	Prostates simple ectally	***kenyaensis*** (p. 266)

9(6)	External genital markings (papillae or pad) present ventrally behind the spermathecal pore	10
–	External genital markings absent from behind the spermathecal pore	11
10	Large single pad *xxiii–xxvi* between setal lines *bb*	***pulvillatus*** (p. 274)
–	Midventral papilla present in two or three furrows (20/21, 21/22 and often 22/23)	***meruanus*** (p. 272)
11(9)	Prostates simple ectally	***minutus**** (p. 273)
–	Prostates with either a low anterolateral process or a long anterior cornu receiving the vas deferens	12
12	Prostates ectally with a small papilliform process receiving a vas deferens (vasa deferentia lying over the dorsolateral surfaces of a large male pouch)	***amatorculus*** (p. 270)
–	Prostates with a distinct anterior cornu receiving the vas deferens (when relaxed, together the two prostates form an 'H')	13
13	Body length less than 150 mm (posterior, glandular region of the prostate less than twice the length of the anterior cornu)	***ednae*** (p. 271)
–	Body length over 150 mm (posterior, glandular region of the prostates about five times the length of the anterior cornu)	***huebneri*** (p. 272)
14(5)	Receptaculum seminis with median posterior sac, divided to form a ring near the spermathecal pore (*magilensis* species group)	15
–	Receptaculum seminis without median posterior sac but with paired lateral sacs formed by the distal coalescence of diverticula (*kirimaensis* species group)	18
15	Externally median ventral papillae present on several segments behind the spermathecal pore	***papillatus*** (p. 277)
–	External papillae absent	16
16	Receptaculum seminis with a single pair of diverticula in *xix,* (one side may fail to develop)	***magilensis*** (p. 277)
–	Receptaculum seminis adiverticulate	17
17	Prostates with a subterminal ectal cornu receiving the vas deferens	***zimmeri*** (p. 278)
–	Prostates simple ectally	***eichelbaumi*** (p. 276)
18(14)	External median ventral seminal groove present behind the spermathecal pore	***usambariensis*** (p. 281)
–	External median ventral seminal groove absent	19
19	A pair of accessory pouches associated with the male pouch, prostates often almond-shaped	***kirimaensis*** (p. 280)
–	Paired accessory pouches absent, prostates always tubular	***usindjaensis*** (p. 282)
20(4)	Receptaculum seminis adiverticulate (*kilindinensis* species group)	21
–	Receptaculum seminis diverticulate (*coeruleus* species group)	24
21	Anterior bifurcation of the receptaculum seminis *xiv–xvi*	***bettonianus*** (p. 284)
–	Anterior bifurcation of the receptaculum seminis *xiii*	22
22	Male pouch with single anterior accessory pouch	***hindei*** (p. 286)
–	Male pouch lacking accessory pouch	23
23	Secondary male and spermathecal pores small (male pouch small)	***kilindinensis*** (p. 286)
–	Secondary male and spermathecal pores large (male pouch large)	***finni*** (p. 285)
24(20)	Receptaculum seminis with a single pair of diverticula (*xix*)	***gregorianus*** (p. 291)
–	Receptaculum seminis with several pairs of diverticula	25
25	Receptaculum seminis short with the last pair of diverticula in *xix*	***coeruleus*** (p. 288)
–	Receptaculum seminis long extending several segments behind the spermathecal pore	26
26	Receptaculum seminis extends *xiii–xxiv, xxv* or *xxvi,* diverticulate only behind (?) *xviii* or *xix*	***multiporus*** (p. 292)
–	Receptaculum seminis extends *xiii–xxi, xxii* or *xxiii,* diverticulate throughout	***violaceus*** (p. 292)

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*Specimens of *eichelbaumi* (*magilensis* species group) will key out as *minutus* when the foramen of the receptaculum seminis is reduced and overlooked (See *Remarks* p. 276).

Polytoreutus kenyaensis species group
(Figs 3, 4 & 5)

DIAGNOSIS. Male and spermathecal pores separate. Receptaculum seminis adiverticulate, rarely distended slightly behind the spermathecal pore; anterior furcae slender, fertilization chambers distal (terminal). Externally a median ventral, longitudinal seminal groove present extending posteriorly from the spermathecal pore.

DISTINGUISHING CHARACTERS. The species group comprises three sympatric species: *kenyaensis* Beddard, 1902; *montiskenyae* Beddard, 1902 and *annulatus* Michaelsen, 1912. They are readily separable externally on the characters of the secondary male pore and the genital field also internally on the morphology of the ectal ends of the prostates.

kenyaensis. The perigenital ridge bordering the seminal groove and genital field is separate from and continues anteriorly around a large secondary male pore bounded by fleshy lips; ectal ends of the prostates simple, vasa deferentia received subterminally.

montiskenyae. The right and left elements of the perigenital ridge bordering the seminal groove, arise anteriorly from the conical porophore bearing a small secondary male pore; ectal end of each prostate with a small lateral cornu receiving the vas deferens (in relaxed specimens, the ectal ends of the prostates are 'Y'-shaped).

annulatus. The right and left elements of the perigenital ridge bordering the seminal groove arise anteriorly from the conical porophore bearing a small secondary male pore (as in *montiskenyae*); seminal groove interrupted in *xxii* by a pad-like papilla joining the right and left elements of the perigenital ridge; ectal end of each prostate with a small lateral bulbous process receiving a vas deferens.

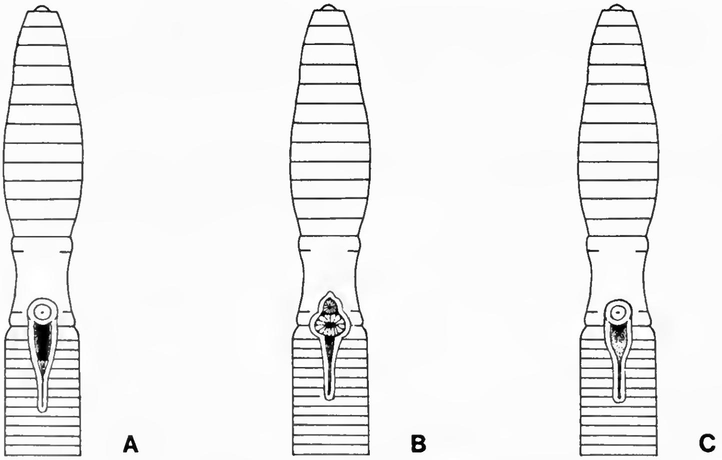

Fig. 3 *Polytoreutus kenyaensis* species group. Genital fields, (external ventral views, schematic): (A) *annulatus*; (B) *kenyaensis*; (C) *montiskenyae*.

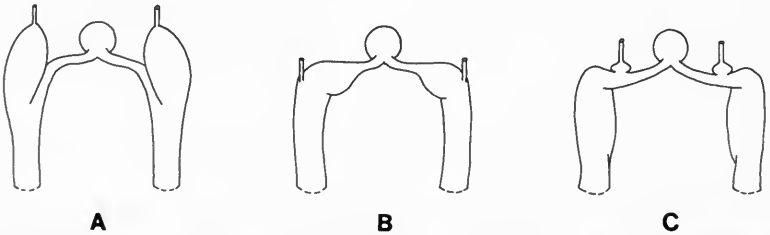

Fig. 4 *Polytoreutus kenyaensis* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *annulatus*; (B) *kenyaensis*; (C) *montiskenyae*.

Variation. Knowledge of *annulatus* is based on only two specimens and variation is unknown. However, two kinds of morphological variability, natural and artificial, can be observed in series of the other two species. Natural variation is seen in the considerable ranges in body size and segment numbers but more perplexing taxonomically is the significance of differences in the length of the seminal groove. In most series of both *kenyaensis* and *montiskenyae* the seminal groove terminates at about segment *xxv,* sometimes more anteriorly in *xxiv* or *xxiii* or posteriorly in *xxvi* to *xxviii* or *xxix* even *xxx,* i.e. it is nearly as long as the seminal groove in *usambariensis* (*coeruleus* species group). The length of the seminal groove in each sample is constant to within two segments but the variation in length between one sample and another, perhaps collected at the same altitude on the same mountain, can be much greater. As these variations cannot be correlated either geographically or altitudinally, they are not considered to be subspecifically significant while evidence is inadequate for believing that species swarms have evolved on each mountain in the region.

The second group of variations, here termed artificial, are the products of the various techniques employed to relax, kill, fix and preserve material. Several nominal species described by Michaelsen and now regarded as junior synonyms, were separated originally on the length and shape of the genital field, mostly the area between the spermathecal pore and the anterior end of the seminal groove. In contracted individuals, the genital field is broader but the perigenital ridges of the posterior part of the field become closely applied so apparently extending the seminal groove forwards. In addition, by the genital field contracting and causing the glandular area to become more concave externally, it produces a corresponding convexity of glandular tissue internally on the parietal wall. These encroachments, products of the preservation techniques employed, have been interpreted as being internal accessory glands and accorded taxonomic significance. The size (and apparent presence) of the male pouch is also affected by the degree of contraction or relaxation of preserved specimens. Preservation techniques can independently affect the size of the penis. In relaxed specimens the penis protrudes through the secondary male pore, if only slightly in *kenyaensis.* Whereas in contracted specimens, the male pouch needs to be dissected to observe the male intromittant organ which may be turgid and filling most of the pouch, slim or, exceptionally, very small and perhaps shrivelled as in Beddard's syntypes of *kenyaensis* and *montiskenyae.*

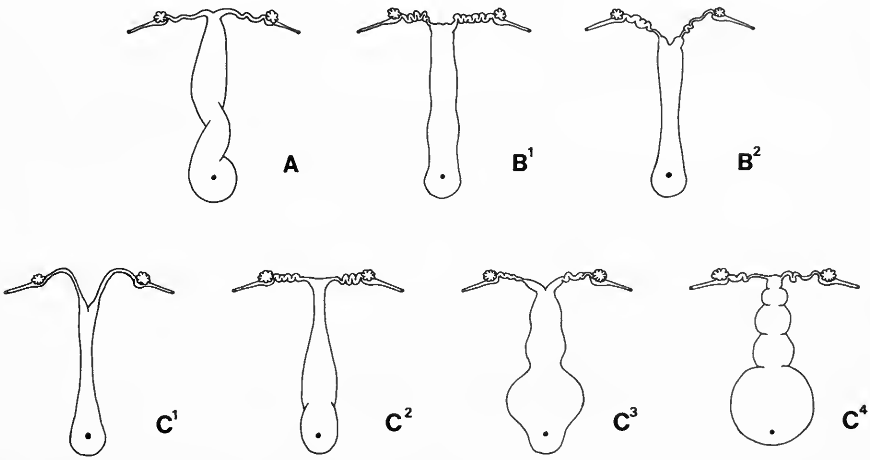

Fig. 5 *Polytoreutus kenyaensis* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *annulatus* (holotype); (B) *kenyaensis* (1. syn *sjoestedti* syntype, 2 *kenyaensis* syntype); (C) *montiskenyae* (1–3. *montiskenyae* syntypes, 4 syn. *alluaudi* holotype).

Polytoreutus annulatus Michaelsen, 1912
(Figs 3A, 4A & 5A)

Polytoreutus annulatus Michaelsen, 1912 : 3; Michaelsen, 1913 : 5; Michaelsen, 1914 : 122; Michaelsen, 1915 : 38.

DESCRIPTION. *External characters.* Length 65, 66 mm, diameter 4 mm, segments 186, 191. Prostomium combined pro- and epilobous. Clitellum ½*xiii–xvii*, annular. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 5 : 3 : 4 : 1. Secondary male pore small on a low porophore in 17/18 or displaced somewhat anteriorly, the pore is a small transverse slit (holotype) or rounded with the penis protruding (paratype). Spermathecal pore 18/19, small transverse slit. Genital field extends posteriorly from the porophore as a slender, deeply depressed glandular zone which narrows in *xxii* to form a longitudinal seminal groove terminating in *xxvii–xxx*. A perigenital ridge borders the genital field, the left and right elements arise anteriorly in the porophore and unite posteriorly in *xxvii–xxx*. Uniquely a midventral raised pad, or papilla, unites the two elements of the perigenital ridge in *xxii*. Female pores paired ¾*xiv* at ⅓*cd* above setal line *c*.

Internal characters. Prostates tubular, extending back to *lii, liii*; they tend to be clavate with the ental diameter about twice the ectal diameter. The ectal end of each prostate is bifid, the vas deferens enters the lateral limb which is bulbous with a diameter similar to the adjacent main body of the prostate; the medial limb which passes to the male pouch, is more slender. Spermathecal system consists of a simple adiverticulate, longitudinal receptaculum seminis passing from the spermathecal pore to the anterior bifurcation in *xiii* where paired lateral ducts pass with few convulations to terminally situated fertilization chambers. Receptaculum seminis slightly pouched posteriorly extending behind the spermathecal pore for one or two segments. The parietal wall is highly glandular internally to the area contained by the external ridge. It tends to invest the ventral nerve cord although the glandular area is interrupted in *xxii* corresponding to the external location of the pad-like papilla separating the genital field from the seminal groove.

TYPE LOCALITY. 'Boma' Meru, Mount Kenya*.

MATERIAL EXAMINED. *Previous record.* 2C Under a fallen tree trunk in woodland, near Meru, northeastern Mount Kenya (0° 03′ N, 37° 39′ E), +2000 m; Hamburg V. 6730 (dissected holotype of *annulatus*) and Stockholm 136 (undissected paratype of *annulatus*).

OTHER RECORD. 1C Clearing in bamboo forest, northeastern slope of Mount Kenya (0° 10′ S, 37° 20′ E), 2870 m (Michaelsen, 1914 & 1915).

DISTRIBUTION. Known only from the northeastern slopes of Mount Kenya (Fig. 2A).

Polytoreutus kenyaensis Beddard, 1902
(Figs 3B, 4B & 5B)

Polytoreutus kenyaensis Beddard, 1902 : 191; Michaelsen, 1912 : 3.
Polytoreutus sjoestedi Michaelsen, 1907 : 4.
Polytoreutus gracilis Michaelsen, 1907 : 6; Michaelsen, 1914 : 120; Michaelsen, 1915 : 36.

DESCRIPTION. *External characters.* Length 75–190 mm, diameter 1·5–5·5 mm, segments 125 (regenerating), 135–256. Prostomium epilobous. Clitellum ½*xiii*–½*xviii, xviii*, annular but incomplete ventrally *xvii*–½*xviii, xviii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 2·5 : 2 : 2·5 : 1. Secondary male pore large, posterior region of *xvii* (adults) surrounded by raised, swollen tissue, circular in relaxed specimens but seen as a transverse slit in contracted individuals; the pore leads into the male pouch containing a papilliform penis which may protrude through the orifice. (The extent to which the penis is visible depends on its degree of dilation and the extent that the male pouch is evaginated.) Spermathecal pore 18/19, large lateral slit with glandular lips, commonly holding a spermatophore. Both the male and spermathecal pores lie within the genital field bordered by a perigenital ridge. Genital field is an elongate hour-glass shape beginning 16/17 and drawn out posteriorly to extend backwards to about *xxii* whence a seminal groove continues to *xxii–xviii*. Behind the spermathecal pore, the

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*Throughout this report Mount Kirinyaga is referred to by its widely known name of Mount Kenya.

genital field becomes highly glandular and concave, especially midventrally at 19/20 where often superficially it forms a pore-like depression. Female pores paired ⅔*xiv* in setal line *c*.

Internal characters. Prostates tubular, extending back to about *xxv–xvii,* simple ectally where they receive the vasa deferentia; they enter into the posterolateral surfaces of the male pouch. The size of the male pouch depends on the degree of contraction of specimen, large (penis retracted and not seen externally) or small (penis protruding externally). Spermathecal system comprises a single adiverticulate receptaculum seminis passing from the spermathecal pore to the anterior bifurcation in *xiii* where the lateral furcae extend with few convolutions to paired distal (terminal) fertilization chambers. The receptaculum seminis may be regular and slender or irregularly dilated and massive in size according to the volume of received sperm within; when massive it seldom pouches posteriorly behind the spermathecal pore and then only slightly. In contracted specimens the parietal wall internally to the genital field may be raised appearing superficially as if an accessory gland.

TYPE LOCALITY. Mount Kenya (1300–1600 m), Kenya.

MATERIAL EXAMINED. *Previous records.* 6C 22A ?Mount Kenya ('Kenya District') (0° 10′ S, 37° 20′ E) 1200–1400 m ('4000–4800 ft'); BM(NH) 1902.11.26, 6–15, 1902.11.26.19–20 & 1904.10.5.1003–1004 (syntypes of *kenyaensis*). 1C Under decaying leaf mould, tropical rain forest, on the western slope of Kilimanjaro, above Kibonoto station, Tanzania (3° 04′ S, 37° 22′ E), 2000 m; Hamburg V. 6955 (holotype of *gracilis*). 3C 4A Mountain grassland, Mount Kilimanjaro, Kiboscho, Tanzania (3° 04′ S, 37° 22′ E), 3000–3800 m; Hamburg V. 6954 & Stockholm 135 (syntypes of *sjostedti*).

New Records. Kenya (*Coll.* E. Oxtoby): 2C 4A Leaf mould, garden, Kenyatta College, Thika road, 12 miles outside Nairobi (1° 17′ S, 36° 49′ E), 1500–2500 m, Nov. 1973; BM(NH) 1981.6.876–881. 74C 68A Mbooni, Machakos District (1° 40′ S, 37° 28′ E), 1·000–1·500 m, Nov. 1974 & Sept. 1974; BM(NH) 1981.6.892–973 & 1981.6.975–1033. 16C 1A Cultivation, plant nursery, Kenyatta College, Nairobi (1° 13′ S, 36° 55′ E), 1500–2000 m, Oct. 1974; BM(NH) 1981.6.1034–1045. 1C Forest fishing post near side of road between Gatanga (0° 56′ S, 36° 58′ E) and Thika (1° 03′ S, 37° 05′ E), 1000–2000 m, 24 Nov. 1974; BM(NH) 1981.6.974. 3C 6A Leaf litter under eucalyptus trees, Kamiti Forest road, Ruiru, 35 km north of Nairobi (1° 09′ S, 36° 53′ E), 1500–2000 m, 22 Jul. 1974; BM(NH) 1981.6.1050–1093. 4C 'Black Cotton' soil, Sukari ranch, opposite Kenyatta College, Nairobi (1° 17′ S, 36° 49′ E), 1500–2500 m, May 1974; BM(NH) 1981.6.888–891. 4C Roots of giant lobelia, grassland, Aberdare Mountains (0° 25′ S, 36° 38′ E), 3000 m ('10 000 ft') June 1971; BM(NH) 1981.6.798–801. 3C Garden soil, Thogoto Teacher Training College, Kikuyu, Nairobi (1° 15′ S, 36° S, 36° 40′ E), 2000–3000 m, 14 July 1974; BM(NH) 1981.6.885–887. 3C Sirimon Track, Mount Kenya (0° 03° 17′ E) 3000–4000 m 19 Nov. 1974; BM(NH) 1981.6.882–884. 45A Aberdare Mountains (0° 25′ S, 36° 38′ E), 3000 m, 18 Nov. 1974; BM(NH) 1981.6.811–856. 2C Among arrowroot cultivation near swamp, Machakos Club (1° 31′ S, 37° 16′ E), 1500–2000 m, Jul. 1971; BM(NH) 1981.6.874–875. 9A Oxtoby's homestead, Kimande, Muranga District (0° 49′ S, 36° 48′ E), 2800 m ('7500 ft'), Nov. 1976; BM(NH) 1981.6.802–810. 1C 3A Grassland, Mwea (0° 455, 37° 29′ E), 1500 m, 7 Mar. 1978; BM(NH) 1981.6.1046–1049. 6A Forest above Oxtoby's homestead Kimande, Muranga District (0° 49′ S, 36° 48′ E), 2800 m ('7500 ft'), Dec. 1976; BM(NH) 1981.6.779–784. 14 C 12A Beneath leaf litter near soil surface, very wet conditions, Kenya National Museum grounds, Nairobi (1° 17′ S, 36° 50′ E), 1500–2500 m, 4 May 1977; BM(NH) 1981.6.1094–1119. 6C 7A Roots of giant lobelias and forest loam, Aberdare Mountains, National Park (0° 25′ S, 36° 38′ S), 3000 m ('10 000 ft'), Jun. 1972; BM(NH) 1981.6.785–797.

(*Coll.* I Jabbal, University College, Nairobi): 2C 1A Kazita, western slopes of Mount Kenya (0° 25′ S, 37° 05′ E), 4150 m ('12 500 ft'); BM(NH) 1967.4.219–226.

OTHER RECORDS. Eastern slopes, Mount Kenya (0° 10′ S, 37° 20′ E), +2000 m; (Michaelsen, 1912). In an area of large *Senecio,* Mount Kenya (0° 10′ S, 37° 20′ E), 4000 m; (Michaelsen, 1914 : 120; 1915 : 36).

DISTRIBUTION. Kenya and Tanzania (Mount Kilimanjaro), above 1500 m (Fig. 2A).

Polytoreutus montiskenyae Beddard, 1902
(Figs 3C, 4C & 5C)

Polytoreutus montiskenyae Beddard, 1902 : 194.
Polytoreutus montiskenyae jeanneli Michaelsen, 1914 : 120; Michaelsen, 1915 : 37.
Polytoreutus alluaudi Michaelsen, 1914 : 122; Michaelsen, 1915 : 39.

DESCRIPTION. *External characters.* Length (immature 59 mm) 170–235 mm, diameter 3·0–5·5 mm, segments 109–235. Prostomium epilobous, infrequently tanylobous. Clitellum ½*xiii–xvii*, annular. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4·5 : 3 : 4 : 1. Secondary male pore small on a low porophore 17/18 from which the penis or only the tip, may protrude. Spermathecal pore 18/19, small to moderate in size (sometimes containing a spermatophore). Genital field extends posteriorly from the male porophore as a scutate to lanceolate depressed glandular zone that narrows posteriorly to form a median, longitudinal seminal groove terminating *xxiii–xxx*; the field is bounded laterally by a perigenital ridge with its right and left elements terminating anteriorly in the porophore. Female pores ⅓*xiv* at ⅓*cd* above setal line *c*.

Internal characters. Prostates tubular extending back to the region of *xxv–xxvii*. Each has a subterminal ectal cornuate process receiving the vas deferens of its side, in contracted specimens the cornu are located at the flexture of the glands whereas in relaxed specimens the ectal end of each gland appears to be Y-shaped. The prostates enter into the male pouch posterolaterally, in contracted specimens (penis not seen externally) the male pouch forms only a slight swelling internally. Spermathecal system comprises a simple, adiverticulate receptaculum seminis passing from the spermathecal pore to the anterior bifurcation in *xiii* where the furcae pass laterally with few convolutions to terminally situated fertilization chambers. The receptaculum seminis may be regular and slender or have irregular swellings and be massive depending on the volume of received sperm; when massive it seldom pouches posteriorly behind the spermathecal pore and then only slightly. In contracted specimens, the parietal wall internal to the genital field may be raised as if forming an accessory gland.

TYPE LOCALITY. Mount Kenya (1300–1600 m), Kenya.

MATERIAL EXAMINED. *Previous records.* Kenya: 20C 30A ?Mount Kenya ('Kenya District') 0° 10′ S, 37° 20′ E), 1200–1400, ('4000–4800 ft'); BM(NH) 1902.11.12.1–5 & 1902.11.16–18 (syntypes of *montiskenyae*). 2C Foot of northern slopes ('lowland forest to the west' [Michaelsen, 1915 : 39]), Mount Kenya (0° 10′ S, 37° 20′ E), 2400 m; Hamburg V. 8351 (holotype of *alluaudi*). Fragment of 1C Upper limit of grasslands near *Senecio*, Mount Kenya (0° 10′ S, 37° 20′ E), 4000 m; Hamburg V. 8347 (fragment of holotype of *montiskenyae* var. *jeanneli*).

New records. Kenya (*Coll.* Oxtoby): 7C 8A Forest, mainly podocarps, Meru, Mount Kenya (0° 05′ N, 37° 37′ E), 1500–2000 m; BM(NH) 1981.6.1324–1340. 13C 9A Near river, Castle Forest Station, Kirinyaga District, north of Nairobi (0° 23′ S, 37° 18′ E), 2250 m ('6800 ft'), 30 Jan. 1974; BM(NH) 1981.6.1211–1232. 1C Roadside forest between Thika (1° 03′ S, 37° 05′ E) and Ilkinangop (0° 38′ S, 36° 42′ E), 2000 m ('6000 ft'), 23 Jul. 1974; BM(NH) 1981.6.1348. 3C 4A Forest, Nyambeni ('Nyambera') Hill, near Meru, (0° 15′ N, 37° 55′ E), 1·000–2000 m, 15 Jun. 1974; BM(NH) 1981.6.1341–1347. 9C 11A Forest, Kionyo, Nkubu, Meru (0° 07′ S, 37° 35′ E), 1000–2000 m, 14.8.1974; BM(NH) 1981.6.1304–1323. 13C 1A Forest, Kikuyu escarpment, near Nairobi (0° 55′ S, 36° 40′ E), 2000–3000 m, Mar. 1972; BM(NH) 1981.6.1281–1294. 20C 13A Sirimon Track, Mount Kenya (0° 03′ S, 37° 17′ E), 3500 m & 4000 m, 19 Nov. 1974; BM(NH) 1981.6.1233–1266. 4C 5A Aberdare Mountains (0° 25′ S, 36° 38′ E), 3000 m, 18 Nov. 1974; BM(NH) 1981.6.1267–1271 & 1981.6.1273–1276. 9A Karuruma, Aberdare Mountains (0° 41′ S, 36° 50′ E), 2000 m, 12 Dec. 1974; BM(NH) 1981.6.1295–1299 & 1981.6.1300–1303. 4A Among grass roots, Oxtoby's homestead, Kimandi, Muranga District (0° 49′ S, 36° 48′ E), 2800 m ('7500 ft'), Nov. 1976; BM(NH) 1981.6.1277–1280. 1A Bushwackers camp, 20 km northeast of Kibwezi (2° 25′ S, 38° 0′ E) 500–1000 m, Apr. 1977; BM(NH) 1981.6.1272.

Other new records. 1C Mount Kenya (0° 10′ S, 37° 20′ E), +2000 m; USNM 24587. 1A ?Mambu ('Nambu') Region, Eastern Kenya (2° 55′ S, 38° 11′ E), 1500 m; Stockholm 279. 3C 5A Kazita, west of valley of Mount Kenya, 4150–4500 m ('12 500–13 500 ft'), Coll. I Jabbal; BM(NH) 1967.4.216–218.

DISTRIBUTION. Kenya, usually above 1500 m (Fig. 2A).

Polytoreutus meruanus species-group
(Figs 6 & 7)

DIAGNOSIS. Male and spermathecal pores separate. Receptaculum seminis single, adiverticulate, extending for several segments behind the spermathecal pore; anterior furcae slender or truncate with short ducts or absent when replaced by short ducts leading to distally situated (terminal) fertilization chambers. (External median ventral, longitudinal seminal groove absent.)

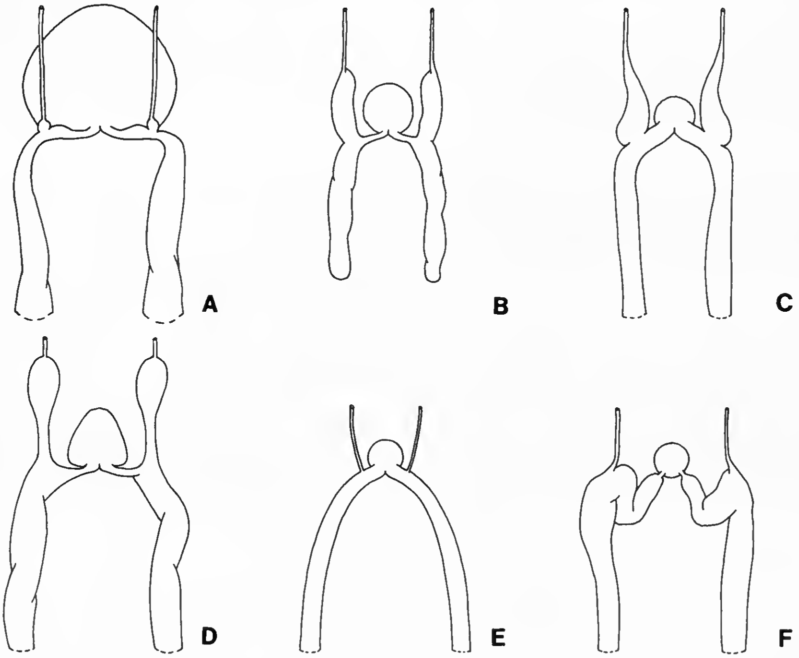

Fig. 6 *Polytoreutus meruanus* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *amatorculus*; (B) *ednae*; (C) *huebneri*; (D) *meruanus*; (E) *minutus*; (F) *pulvillatus*.

DISTINGUISHING CHARACTERS. The species-group is formed from six species: *meruanus* Michaelsen, 1907; *minutus* Michaelsen, 1912; *huebneri* Michaelsen, 1913; *amatorculus* sp. nov.; *ednae* sp. nov. and *pulvillatus* sp. nov. They may be separated on the following characters:

pulvillatus. Externally a genital pad present *xxiii–xxvi* between setal lines *bb*; prostates simple ectally, receiving the vasa deferentia subterminally (ectally often 'S'-shaped with the vasa deferentia entering at the penultimate flexures); anterior furcae of the receptaculum seminis seen as short ducts.

meruanus. Externally single, median porophores present in 20/21, 21/22 and often 22/23; prostates ectally each with a long anterior cornu receiving the vas deferens of its side (together the prostates form an 'H'); anterior furcae of the receptaculum seminis truncate with short ducts.

minutus. Prostates ectally simple with the vasa deferentia joining terminally; anterior furcae of the receptaculum seminis truncate with short ducts. (Perhaps the smallest species in the genus.)

amatorculus. Externally with a large secondary male pore (possibly with a midventral papilla on the anterior margin); prostates each flexed ectally with a small antero-lateral papilliform process receiving a vas deferens; male bursa large with the vasa deferentia lying over its dorso-lateral surfaces; anterior furcae of the receptaculum seminis tapering gradually, with convolutions, into the fertilization chambers.

huebneri. Prostates long, each with a long anterior cornu receiving a vas deferens (together the prostates form an 'H'), the cornu being less that one quarter of the length of the prostate; anterior furcae of the receptaculum seminis slender, tapering gradually. (One of the largest species in the genus.)

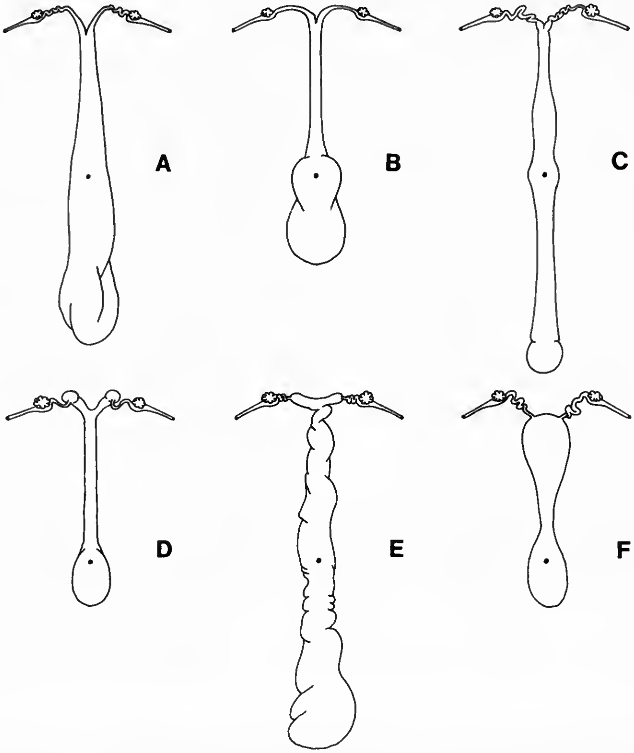

Fig. 7 *Polytoreutus meruanus* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *amatorculus* (syntype); (B) *ednae* (syntype); (C) *huebneri* (new record); (D) *meruanus* (syntype); (E) *minutus* (holotype); (F) *pulvillatus* (syntype).

ednae. Prostates short, each with a long anterior cornu receiving a vas deferens (together the prostates form an 'H'), the cornu being nearly the same length as the prostates; anterior furcae of the receptaculum seminis slender, tapering gradually.

Polytoreutus amatorculus sp. nov.
(Figs 6A & 7A)

DESCRIPTION. *External characters*. Length 112, 142 mm, diameter 4, 5 mm, segments 153, 211 (2 adults), (1 juvenile: length 55 mm, diameter 2 mm, segments 89). Prostomium prolobous. Clitellum annular *xiii*–$\frac{1}{2}$*xviii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 6 : 1. Secondary male pore large 17/18, in relaxed specimens $\frac{1}{2}$*xvii*–$\frac{1}{2}$*xviii*, laterally with the body wall swollen between setal lines *bb* and glandular between setal lines *aa*; in the fully developed specimen (the largest), there is a low, domed pad midventrally on the anterior lip of the male orifice. (Within the secondary male pore paired pads are present on either side of a penis in the anterior wall and paired pads in the lateral and the posterior walls.) Spermathecal pore small but conspicuous due to the ventral surface of *xix* being raised and curving around the posterior margin of the pore. Apart from the domed pad anteriad to the secondary male pore, genital papillae and markings absent. Female pores paired $\frac{2}{3}$*xiv* slightly above $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular passing back to about *xxx,* slightly constricted intersegmentally; anteriorly they flex medially along the posterior wall of a large male pouch and held by mesenteries, they unite medially and enter the male pouch. A small papilliform process is present on the antero-lateral surface of the flexure of each prostate and receives the vas deferens of its side. The male pouch is large (in dissected, displayed specimens it occupies one-third of the width of the body) and triangular with the apex anteriorly and the ectal ends of the prostates lying along part of the basal, posterior wall of the pouch, the width is so great that the vasa deferentia lie over its lateral regions.

The spermathecal system comprises a single, median adiverticulate receptaculum seminis which extends from the anterior bifurcation in *xiii* (?*xiv*) to a few segments behind the spermathecal pore (18/19) to about *xxiii*; the anterior furcae lead without modification into terminally situated, distal fertilization chambers.

TYPE LOCALITY. Masra, near Machakos, Kenya, 1500 m.

MATERIAL EXAMINED. (Coll. E. Oxtoby): 5C (2 specimens complete, 3 specimens broken posteriorly) 1A (juvenile with a trace of a clitellum) Cultivation, Masra, near Machakos, Kenya (1° 31′ S, 37° 16′ E), 1500 m ('4500 ft'), July 1971; BM(NH) 1981.6.427–433 (syntypes of *amatorculus*).

DISTRIBUTION. Known only from the type locality (Fig. 2B).

Polytoreutus ednae sp. nov.

(Figs 6B & 7B)

DESCRIPTION. *External characters.* Length 75 mm, diameter 2 mm, segments 165–295. Prostomium prolobous. Clitellum annular *xiii–xviii.* Setae at *xxx,* *aa* : *ab* : *bc* : *cd* = 6 : 3 : 4 : 1. Secondary male pore carried on a low porophore $\frac{3}{4}$*xvii* near 17/18, circular with tumid lips sometimes with the distal end of the penis protruding. Spermathecal pore transversely oval 18/19 with an anterior and a posterior lip, larger than the male pore. A raised glandular area surrounds the spermathecal pore and extends forwards across *xviii* to the male porophore. Genital markings absent. Female pores $\frac{1}{2}$*xiv* in setal line *d.*

Internal characters. Prostates tubular, short, reaching back only to *xxi–xxiii,* each with an anterior cornu extending forward to near 15/16 to receive the vas deferens of its side; together the prostates and the cornu form an 'H' with the transverse horizontal limb passing into the posterior surface of a large male pouch lying between 15/16–$\frac{2}{3}$*xviii*; each cornu is approximately half to one-third of the total length of the prostate. The spermathecal system comprises a single, adiverculate receptaculum seminis passing back from the anterior bifurcation to the spermathecal pore where it dilates to form a blind sac extending posteriorly to *xxi* or *xxii*; anterior furcae with distal (terminal) fertilization chambers. Each chamber is attached entally by connective tissue to septum 12/13 and has a short, coiled ovarian duct leading forwards into an ovarian capsule containing the ovary. The ovary is rosette-shaped with several egg strings.

TYPE LOCALITY. Bushwackers, 20 km northeast of Kibwesi, Kamba, Kenya, 600 m.

MATERIAL EXAMINED. (*Coll.* E. Oxtoby): 9C 2A Bushwackers camp, 20 km northeast of Kibwesi, Kenya (2° 25′ S, 38° 00′ E), 500 m, Apr. & Nov. 1977; BM(NH) 1981.6.440–447 & 1981.6.448–450 (syntypes of *ednae*).

DISTRIBUTION. Known only from the type locality (Fig. 2B).

REMARKS. Named in memory of the late Miss Edna Oxtoby who by collecting this series and many other earthworms in eastern Africa, stimulated research leading to the present revision.

Polytoreutus huebneri Michaelsen, 1913
(Figs 6C & 7C)

Polytoreutus Hübneri Michaelsen, 1913 : 48; 1931 : 556.
Polytoreutus sp. nov. (Meru) Oxtoby, 1975 : 27.

DESCRIPTION. *External characters.* Length 210–390 mm (damaged holotype 150 mm *vide* Michaelsen, 1913 : 48), diameter 5–7 mm, segments 288–340. Prostomium prolobous to pro-epilobous. Clitellum annular, *xiii*–½*xviii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore ⅔*xvii* to 17/18 being more anteriorly located in breeding individuals, usually on a low porophore; distal end of the penis may protrude. Spermathecal pore 18/19, a narrow transverse slit with tumid lips. Genital papillae and markings absent. Female pores paired ⅔*xiv* near setal line *c*.

Internal characters. Prostates tubular, extending posteriorly to the region of *xxx*, anteriorly (lateral) cornu receive the vasa deferentia and together the two prostates and their cornu form an 'H' with the cornu forming the upper limbs which extend forwards to 15/16 while the anterior parts of the prostates form the horizontal limbs which lead into the posterior surface of a low male pouch lying between 15/16 and ⅔*xviii*; each cornu is approximately one-sixth of the total length of the prostate. The spermathecal system comprises a single, median adiverticulate receptaculum seminis extending posteriorly from the anterior bifurcation in *xiii* to far beyond the spermathecal pore, possibly to *xxx*; the anterior furcae are slender, frequently convoluted, with distal (terminally situated) fertilization chambers.

MATERIAL EXAMINED. *Previous records.* Fragment (prostates) Kibwezi, Kenya, (2° 25′ S, 37° 58′ E), 500–1000 m; Hamburg V. 7641 (remnant of holotype of *huebneri*).

New records. Kenya (*Coll.* E. Oxtoby): 4C 1A Among grass roots, in undergrowth of broad leafed woodland, Nduru, near Kisii (0° 41′ S, 34° 46′ E), 1500–2000 m, Jun. 1971; BM(NH) 1981.6.774–778. 6C 2A Bushwackers camp, 20 km northeast of Kibwezi (12° 25′ S, 38° 00′ E), 500–1000 m, Nov. & Apr. 1977; BM(NH) 1981.6.766–767 & 1981.6.768–773. 63C 31A Vegetation mainly comprised of podocarps, Kionyo Forest Station, near Nkubu, Meru District, (0° 04′ S, 37° 40′ E), 1500 m, June 1974; BM(NH) 1981.6.672–765. 2C Evergreen rain forest, Kionyo, 15 miles from Meru, on southeast slopes of Mount Kenya (0° 08′ S, 37° 35′ E), +2100 m ('7000–8000 ft'), Dec. 1970; BM(NH) 1981.6.670–671.

OTHER RECORD. Kibwezi, Kenya (2° 25′ S, 37° 58′ E), 500–1000 m; Michaelsen, 1931 : 556).

DISTRIBUTION. Forests of Kenya, above 500 m (Fig. 2B).

REMARKS. Individuals of *eichelbaumi*, (*magilensis* species group), may occasionally have the receptaculum seminis modified and cause confusion with this species. The two species can be readily separated on other characters, especially the morphology of the prostates (*see* Remarks, p. 276).

Polytoreutus meruanus Michaelsen, 1907
(Figs 6D & 7D)

Polytoreutus meruanus Michaelsen, 1907 : 8.

DESCRIPTION. *External characters.* Length 60–100 mm, diameter 2·0–2·5 mm, segments 144–180. Prostomium prolobous. Clitellum annular, *xiii–xviii.* Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore 17/18 on a low circular porophore with a raised rim or elevated to form a low papilliform (?) intromittant organ. Spermathecal pore small in 18/19. Genital field (adults) with single, midventral porophores 20/21, 21/22 and sometimes 22/23. Female pores ¾*xiv* slightly above setal line *c*.

Internal characters. Prostates tubular, together they form an 'H' with somewhat clavate upper limbs extending anteriorly beyond the male pouch to receive the vasa deferentia. The horizontal limb of the 'H' leads into the posterior surface of the male pouch while the paired posterior limbs form the main bodies of the prostates and extend posteriorly, sometimes with flextures, perhaps to *xxxvi.* The spermathecal system comprises a median, adiverticulate receptaculum seminis passing posteriorly from the anterior bifurcation in *xiii* to beyond the spermathecal where it forms a blind sac extending back to *xxi* or *xxii*; anterior furcae somewhat convoluted with ducts to the fertilization chambers located slightly subterminally. Additionally, the adults from Kenya possess two or three, median accessory glands that discharge anteriorly through the midventral porophores in 20/21, 21/22 and sometimes 22/23; in appearance they resemble small euprostates by being smooth and clavate, each is long and passes through four or five segments.

TYPE LOCALITY. Mount Meru, Tanzania.

MATERIAL EXAMINED. *Previous record.* 2C (immature) Rainforest, southern slopes of Mount Meru, Tanzania (3° 15′ S, 36° 44′ E), 3000 m; Hamburg V. 6951 & Stockholm 139 (syntypes of *meruanus*).

New records. Kenya (*Coll.* E. Oxtoby): 1C Nanyuki Road, Meru Forest, (0° 05′ N, 37° 37′ E), 2000–3000 m, 13 Dec. 1976; BM(NH) 1981.6.1204. 1A Bushwackers camp, 20 km northeast of Kibwezi, (2° 25′ S, 38° 00′ E), 500–1000 m, Apr. 1977; BM(NH) 1981.6.1203. 4C 1A Stream bed, temporary water by road side, 'Narosera' (?Narosura = Subukloita), Loita Hills (1° 32′ S, 35° 52′ E), 2000–3000 m, Dec. 1977; BM(NH) 1981.6.1198–1202.

DISTRIBUTION. Higher altitudes in forest of Kenya and Tanzania (Fig. 2B).

REMARKS. The adult specimens newly recorded from Kenya agree with the immature syntypes of *meruanus* apart from additionally possessing accessory glands. The glands are assumed to develop with maturity.

Polytoreutus minutus Michaelsen, 1912
(Figs 6E & 7E)

Polytoreutus minutus Michaelsen, 1912 : 2; Michaelsen, 1913 : 53; Michaelsen, 1937 : 473.

DESCRIPTION. *External characters.* Length 32–70 mm, diameter 1·8–3·0 mm, segments (84, 95 regenerating) 102–134. Prostomium prolobous to pro-epilobous. Clitellum annular (*xiii*) *xiv–xvii* (½*xviii*). Setae at *xxx, aa* : *ab* : *bc* : *cd* = 4·5 : 3 : 4 : 1. Secondary male pore on a low, broad cushion-like porophore, ⅔*xvii*; the ectal ends of the paired prostatic ducts may be seen within the male orifice (penis apparently absent). Spermathecal pore inconspicuous, small, circular in 18/19. Genital papillae and markings absent. Female pores paired ⅔*xiv* near setal line *c.*

Internal characters. Prostates tubular extending posteriorly for about ten segments; ectally each is simple and receives the vas deferens of its side directly into the antero-lateral surface; low male pouch present (penis not seen, ?absent). The spermathecal system comprises a single median, adiverticulate receptaculum seminis that extends from the anterior bifurcation in *xiii* posteriorly to far beyond the spermathecal pore to about *xl*; the anterior furcae are truncate narrowing sharply into slender ducts with distal (terminally situated) fertilization chambers.

TYPE LOCALITY. Kenya Province, Kenya; subsequently restricted to the vicinity of Mount Kenya (Michaelsen, 1937).

MATERIAL EXAMINED. *Previous records.* 1C 'Kenya Province' (?near Mount Kenya), Kenya; Stockholm 1949 (dissected holotype of *minutus*) and Hamburg V. 7631 (prostates of holotype of *minutus*).

New records. (*Coll.* E. Oxtoby): 4C Nanyuki road, Meru Forest, Kenya (0° 05′ N, 37° 10′ E), 2000–3000 m, 13 Dec. 1976; BM(NH) 1981.6.1205–1208.

OTHER RECORD. 1C Mount Mbololo 'Teita' (?Taita), Kenya, (3° 20′ S, 38° 30′ E), 1400 m ('4800 ft'); Michaelsen, 1937 : 473, specimen not located April 1980, Museum of Comparative Zoology, Harvard).

Distribution. Higher altitudes, Mount Kenya area, Kenya (Fig. 2B).

Remarks. Individuals of *eichelbaumi* (*magilensis* species group) may occasionally have the receptaculum seminis modified and be confused with this species. The two species can be readily separated on other characters (*see* Remarks, p. 276).

Polytoreutus pulvillatus sp. nov.

(Figs 6F & 7F)

Description. *External characters.* Length 73–92 mm, diameter 1·5–2·0 mm, segments 228–254. Prostomium proepilobous with two indistinct longitudinal striations leading from the 'tongue' back to 1/2 giving superficially a tanylobic appearance. Clitellum annular $\frac{1}{2}$*xiii*–$\frac{1}{2}$*xvii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore 17/18 carried on a low porophore extending $\frac{1}{2}$*xvii*–$\frac{1}{2}$*xviii*; pore circular with crenulated lips, penis present. Spermathecal pore crescentic with the extremities of the crescent in 18/19 and the arc extending anteriorly to $\frac{3}{4}$*xviii*; the anterior lip is raised and the concavity so formed is occupied by a papilla formed midventrally from the anterior wall of *xix*. Raised genital pad present *xxiii–xxvi*, pigmented, between setal lines *bb*. Female pores paired $\frac{3}{4}$*xiv* at $\frac{1}{2}$*cd*.

Internal characters. Prostates tubular extending back to about *xxvii*; anteriorly they have a double flexure producing a S-shape in segments *xvii–xix* where the vas deferens of the side enters into the second (ental) flexure. Male pouch large, receiving the prostates into its dorso-lateral surfaces. Spermathecal system comprises a simple, adiverticulate receptaculum seminis lying between *xiii* and *xx*(*xxi*) becoming somewhat constricted in *xvii* where it passes to one side (left side in the two syntypes) of the male pouch; anterior bifurcation lacking, replaced by paired ducts leading directly into the fertilization chambers from the lateral surfaces at the anterior end of the receptaculum.

Type locality. Near Gede, south of Malindi, Kenya.

Material examined. Kenya (*Coll.* E. Oxtoby): 2C Under coconut palms, cultivated sandy soil, near Gede, south of Malindi (3° 13′ S, 40° 07′ E), –200 m, 29 June 1974; BM(NH) 1981.6.1367–1368 (syntypes of *pulvillatus*). 1C Road side bush between Majengo (1° 45′ S, 40° 20′ E) and Kiunga (1° 44′ S, 41° 30′ W), –200 m, 12 June 1978; BM(NH) 1981.6.1366.

Distribution. Coastal lowlands, southeastern Kenya (Fig. 2B).

Polytoreutus magilensis species group

(Figs 8 & 9)

Diagnosis. Male and spermathecal pores separate. Receptaculum seminis forming a ring near the spermathecal pore and a single blind sac posteriorly to the spermathecal pore, diverticula sometimes present; anterior furcae slender, fertilization chambers distal (terminal).

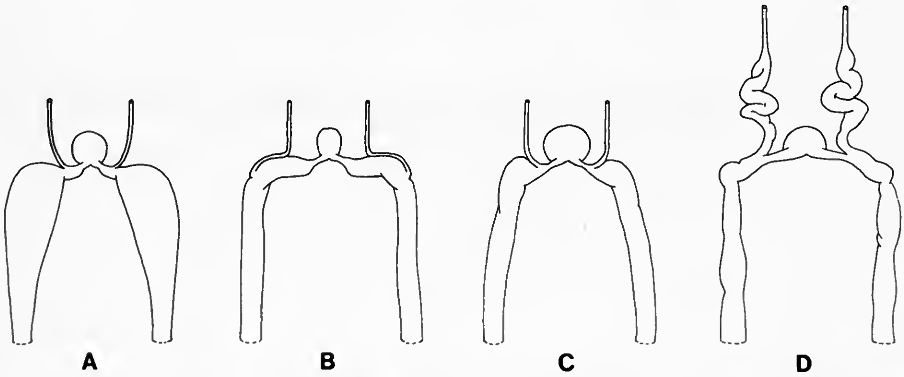

Fig. 8 *Polytoreutus magilensis* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *eichelbaumi*; (B) *magilensis*; (C) *papillatus*; (D) *zimmeri*.

DISTINGUISHING CHARACTERS. The species group contains four sympatric species mainly from northeastern Tanzania: *magilensis* Beddard, 1893; *eichelbaumi* Michaelsen, 1905; *zimmeri* Michaelsen, 1914 and *papillatus* sp. nov. They form two couplets: *magilensis* and *papillatus* with the anterior furcation deeply incised originating in *xv* or *xvi*, penis large; *eichelbaumi* and *zimmeri* with the anterior furcation usually in *xiii*, seldom *xiv*, penis small or not seen. The four species are separable on the following characters:

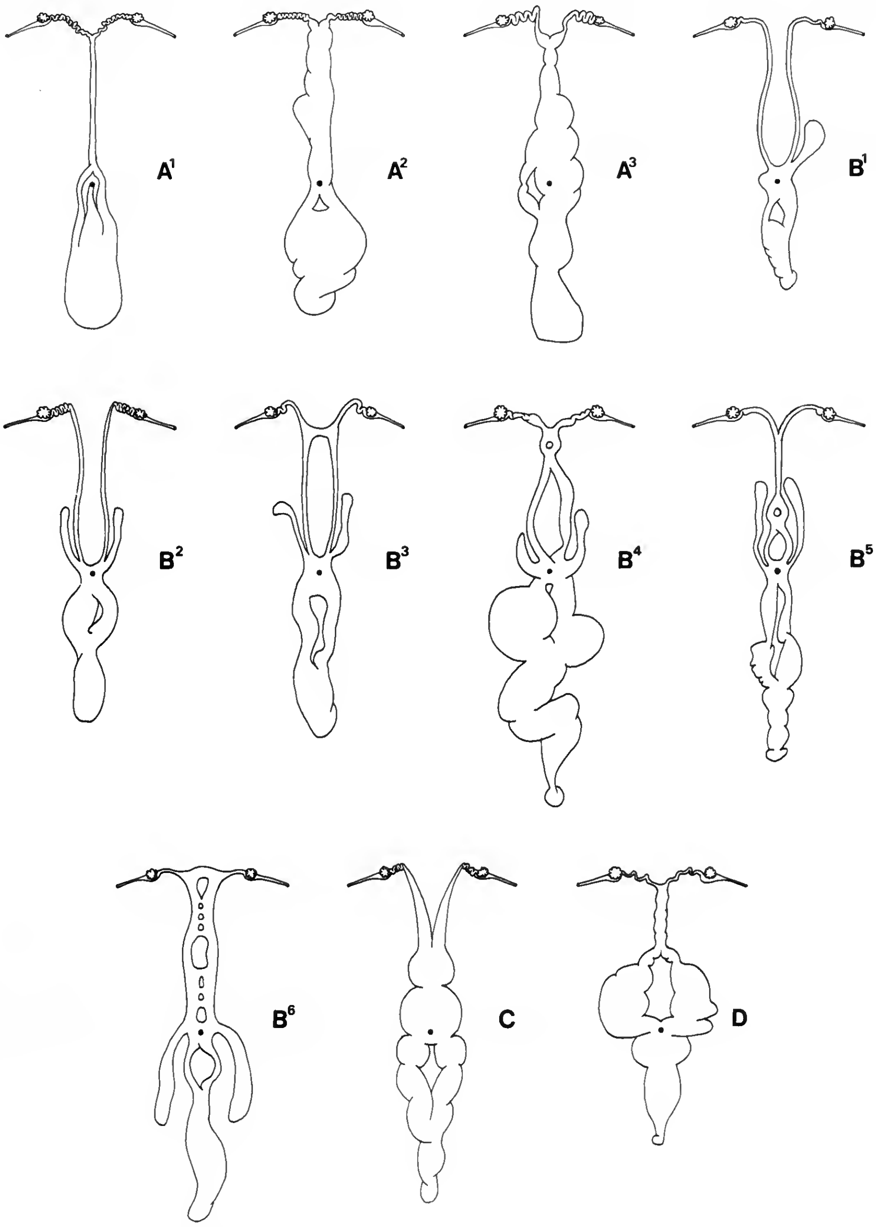

Fig. 9 *Polytoreutus magilensis* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *eichelbaumi* (1 new record, 2–3 syntypes); (B) *magilensis* (1 syn. *ehlersi monozyga* (sic) syntype, 2–4 syn. *ehlersi typica* (sic) syntypes, 5 syn. *ehlersi dizyga* (sic) syntype, 6 *magilensis* holotype); (C) *papillatus* (syntype); (D) *zimmeri* (syntype).

papillatus. Genital papillae present, midventral, one on each of several segments behind the spermathecal pore; receptaculum seminis with 'ring' posterior to the spermathecal pore, adiverticulate; prostates simple ectally, vasa deferentia terminal.

magilensis. Genital papillae absent; receptaculum seminis with 'ring' posterior to the spermathecal pore, single pair of diverticula *xix* (one may fail to develop); prostates simple ectally, vasa deferentia terminal.

zimmeri. Genital papillae absent; receptaculum seminis with 'ring' anterior to the spermathecal pore, adiverticulate; prostates each with a long, subterminal, lateral cornu receiving the vas deferens of its side.

eichelbaumi. Genital papillae absent; receptaculum seminis with 'ring' either anterior or posterior to the spermathecal pore, adiverticulate; prostates simple ectally, vasa deferentia terminal.

Polytoreutus eichelbaumi Michaelsen, 1905
(Figs 8A & 9A)

Polytoreutus eichelbaumi Michaelsen, 1905 : 357.

DESCRIPTION. *External characters.* Length 125–360 mm, diameter 2–3 mm, segments 370–512. Prostomium proepilobous. Clitellum annular *xiii–xvii*. Setae at *xxx*, $aa : ab : bc : cd = 3{\cdot}5 : 3{\cdot}0 : 3{\cdot}0 : 1{\cdot}0$. Secondary male pore 17/18 small on a low porophore sometimes with the penis protruding, surrounded by an oval glandular area. Spermathecal pore small 18/19 with adjacent areas of *xviii* and *xix* modified, glandular. Female pores $\frac{1}{3}$ *xiv* in line with the nephridiopores at $\frac{1}{2}cd$.

Internal characters. Prostates tubular, long, convoluted extending to *xxx* with the vasa deferentia passing simply into the ectal ends. Male pouch small. Spermathecal system adiverticulate with a short, blind posterior sac; single apart from the anterior bifurcation where the fertilization chambers are located distally (terminal) and near the spermathecal pore where the receptaculum divides briefly to form a 'ring' and provide an orifice for the ventral nerve cord. (Occasionally one of the limbs of the 'ring' may be reduced or possibly missing.)

TYPE LOCALITY. Amani, Usambara, Tanzania.

MATERIAL EXAMINED. *Previous records.* 5C 2A Amani, Usambara, Tanzania (5° 09′ S, 38° 36′ E), 1000 m; Hamburg V. 6665 & V. 6667 (syntypes of *eichelbaumi*). 2C 4A Coastal stream, near Amani, Usambara, Tanzania (5° 09′ S, 38° 36′ E), 1000 m; Hamburg V. 6481 (syntypes of *eichelbaumi*).

New records. (*Coll.* E. Oxtoby): 5C 21A Among white roots of plantains, in black volcanic soil, Vuria radio station, Taita Hills, Kenya (?3° 25′ S, 38° 18′ E), –1500 m, 13 Aug. 1978; BM(NH) 1981.6.451–476.

OTHER RECORD. Sakarre, Usambara, Tanzania (4° 59′ S, 38° 26′ E), –1500 m; (syntypes of *eichelbaumi*, not located September 1978, Zoologisches Museum, Hamburg).

DISTRIBUTION. Southeastern Kenya and northeastern Tanzania (Fig. 2C).

REMARKS. The foramen of the receptaculum seminis may be reduced, possibly becoming an indistinct longitudinal slit and overlooked when specimens are extended. Hence the morphology of the receptaculum seminis may superficially resemble that of *huebneri* or the worms mistaken for exceptionally large individuals of *minutus* (both members of the *meruanus* species group). The species *eichelbaumi* and *huebneri* can be separated on the characters of the prostates: in *eichelbaumi* the vasa deferentia pass simply into the anterior ends of the prostates while in *huebneri* each vas deferens enters into a long subterminal, anterolateral cornu of the prostate. The characters of the prostates are similar in *eichelbaumi* and *minutus* but these species are separable on segment number, the positions of the female pores and preserved specimens of *eichelbaumi* commonly having the penis protruding.

Polytoreutus magilensis Beddard, 1893
(Figs 8B & 9B)

Polytoreutus magilensis Beddard, 1893 : 243; Beddard, 1895 : 610; Michaelsen, 1900 : 415.
Polytoreutus ehlersi f. *typica* [sic] Michaelsen, 1905 : 346.
Polytoreutus ehlersi f. *monozyga* [sic] Michaelsen, 1905 : 350; 1910 : 81.
Polytoreutus ehlersi var. *dizyga* [sic] Michaelsen, 1905 : 350.

DESCRIPTION. *External characters.* Length 120–370 mm, diameter 6–8 mm, segments *160*–270. Prostomium prolobous, Clitellum annular $\frac{1}{3}$*xiii–xvii.* Setae at *xxx, aa* : *ab* : *bc* : *cd*= 5·7 : 2·5 : 5·0 : 1·0. Secondary male pore wide with anterior and posterior tumid lips, often raised giving a sucker-like appearance 17/18. Spermathecal pore small, broadly oval 18/19. Genital field smooth and elongate *xvii–xix.* Female pores paired $\frac{1}{3}$*xiv* in line with the nephridiopores at $\frac{1}{2}$*cd.*

Internal characters. Prostatic glands tubular, long, somewhat convoluted and frequently extending throughout most of segments *xii–xxx*; slender ectally, simple receiving the vasa deferentia subterminally but becoming more massive entally. Male pouch small but posteriorly with a penial sheath joined entally to the parietal wall between the male pouch and the spermathecal pore (in poorly relaxed specimens, the penial sheath may be contracted into a U-shape). Spermathecal system highly variable but basically the receptaculum seminis consists of a pair of 'ducts' uniting only at the spermathecal pore and again more posteriorly to form a single median posterior sac; paired diverticula (as lateral sacs or pouches) present dorsolaterally on the main 'ducts' above the spermathecal pore, often with one of the pair failing to develop. Although essentially paired, the two 'ducts' frequently coalesce and in an extreme condition form an apparently single receptaculum seminis perforated by numerous medial foramina which give a ladder-like appearance. The fertilization chambers are distal (terminally situated) on the anterior furcae.

TYPE LOCALITY. Magila, Tanga, Tanzania.

MATERIAL EXAMINED. *Previous records.* Tanzania: 9C Magila, Tanga (5° 08′ S, 38° 46′ E), 200 m; BM(NH) 1904.10.5.442–450 (holotype and paratypes of *magilensis*). 5C 3A Wugiri, western Usambara (4° 45′ S, 38° 30′ E), 1000–2000 m; Hamburg V. 6656 & Stockholm 127 (syntypes of *ehlersi* f. *typica*). 2C Mkusa ?Valley ('Tal'), western Usambara (approx. 5° 00′ S, 38° 20′ E), 1100 m; Hamburg V. 6214 (syntypes of *ehlersi* f. *typica*). 1C Msimni ?Valley ('Tal'), western Usambara (approx. 5° 00′ S, 38° 20′ E), 1000 m; Hamburg V. 6243 (syntypes of *ehlersi* f. *monozyga*). 2C Sakarani, western Usambara (4° 49′ S, 38° 24′ E), 1500 m; Hamburg V. 6722 (syntypes of *ehlersi* f. *monozyga*). 4C Mombo, western Usambara (4° 52′ S, 38° 14′ E), 1400 m; Hamburg V. 6207 (syntypes of *ehlersi* v. *dizyga*). 5C 1A River bank, Muhesa, near Tanga (approx. 5° 10′ S, 38° 40′ E), – 500 m; (*ehlersi* f. *monozyga*: Michaelsen, 1910). 5C 3A Potwe, native village near Magila and Muhesa (5° 08′ S, 38° 46′ E), – 500 m; (*ehlersi* f. *monozyga*: Michaelsen, 1910).

New records. 1C Musambara (approx. 4° 45′ S, 38° 30′ E), + 1000 m; Turin OL. 197.

DISTRIBUTION. Northeastern Tanzania (Fig. 2C).

REMARKS. Variation in the extent of the coalescence between the paired main 'ducts' forming the receptaculum seminis led Michaelsen to separate these growth (sexual or seasonal) phases as separate taxa. The basic paired condition he named *ehlersi* f. *typica,* further coalescence he recognized as *ehlersi* var *dizyga* and the fully mature state, receptaculum seminis superficially single but with medial perforations giving a ladderlike appearance, he identified as *magilensis* Beddard. He separated the asymmetry when one of the paired dorsolateral diverticula failed to develop as *ehlersi* f. *monozyga.*

Polytoreutus papillatus sp. nov.
(Figs 8C & 9C)

DESCRIPTION. *External characters.* Length (19, 24 mm aclitellate) 50, 60 mm, diameter

1–1·5 mm, segments (71, 100 aclitellate) 128, 146. Prostomium epilobous. Clitellum annular *xiii–xvii.* Setae at *xxx, aa* : *ab* : *bc* : *cd* = 6 : 2 : 4 : 1. Secondary male pore on a low porophore $\frac{2}{3}$*xvii,* penis, when seen, tapered uniformly and protruding to a length equal to the diameter of the *xvii.* Spermathecal pore inconspicuous, small lateral slit 18/19. Genital papillae present (clitellate syntypes), median ventral, one per segment, *xviii, xxi–xxiii* (smaller clitellate syntype) and *xx–xxvi* (larger clitellate syntype); each papilla is circular and cushion-like being flattened centrally with the lateral borders investing setae *aa.* Female pores $\frac{2}{3}$*xiv* in line with the nephridiopores in $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular, extending posteriorly nearly to *xxx*; anteriorly each narrows slightly before passing into the posterior surface of the male pouch, the vasa deferentia enter the prostates simply at the ectal constriction. Spermathecal system consists of a single median, adiverticulate receptaculum seminis, the anterior bifurcation with distal (terminally located) fertilization chambers, arises only two or three segments anteriad to the spermathecal pore, posteriad to the spermathecal pore the receptaculum seminis divides briefly only to form a ring and reunite after two or three segments then to terminate in a small blind sac.

TYPE LOCALITY. Baga 1 Forest Reserve, Lushoto District, Tanzania.

MATERIAL EXAMINED. (*Coll.* K. M. Howell): 2C 2A Baga II Forest Reserve, Lushoto District, Tanzania (4° 48′ S, 38° 23′ E), 1000–2000 m, June 1980; BM(NH) 1981.7.1–4 (syntypes of *papillatus*).

DISTRIBUTION. Known only from the type locality (Fig. 2C).

Polytoreutus zimmeri Michaelsen, 1914
(Figs 8D & 9D)

Polytoreutus zimmeri Michaelsen, 1914 : 117.

DESCRIPTION. *External characters.* Length 28–32 mm, diameter 2 mm, segments 130–160. Prostomium prolobous. Clitellum annular (*xiii*)*xiv–xvi*(*xvii*). Setae at *xxx, aa* : *ab* : *bc* : *cd* = 2·3 : 2·0 : 2·6 : 1·0. Secondary (?) male pore small lateral slit 17/18 with perhaps the ectal ends of the prostatic ducts seen within (penis, ?absent); male pore carried on a low, circular porophore extending 16/17–18/19. Spermathecal pore inconspicuous, small lateral slit in 18/19. Genital papillae absent. Female pores $\frac{1}{2}$*xiv* in setal line *c.*

Internal characters. Prostates tubular, extending posteriorly to about *xxviii*; anteriorly each is bifid with a lateral subterminal cornu leading forwards into *xiv* where it receives the vas deferens of its side. Male pouch of moderate size. Spermathecal system comprises a slender, short median, adiverticulate duct passing backwards from the anterior furcation to *xvi* where it divides to form a massive ring around the male pouch then unites at the

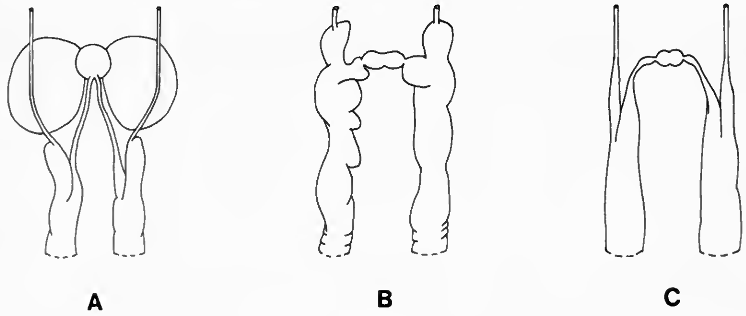

Fig. 10 *Polytoreutus kirimaensis* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *kirimaensis*; (B) *usambariensis*; (C) *usindjaensis.*

spermathecal pore and continues posteriorly as a blind sac for perhaps six or seven segments; the fertilization chambers are distal, terminally situated on the anterior furcae.

Type locality. Amani, Usambara, Tanzania.

Material examined. *Previous record.* 2C 3A Amani, Usambara, Tanzania (5° 09′ S, 38° 36′ E), 1000 m; Hamburg V 8345 (syntypes of *zimmeri*).

Distribution. Known only from the type locality (Fig. 2C).

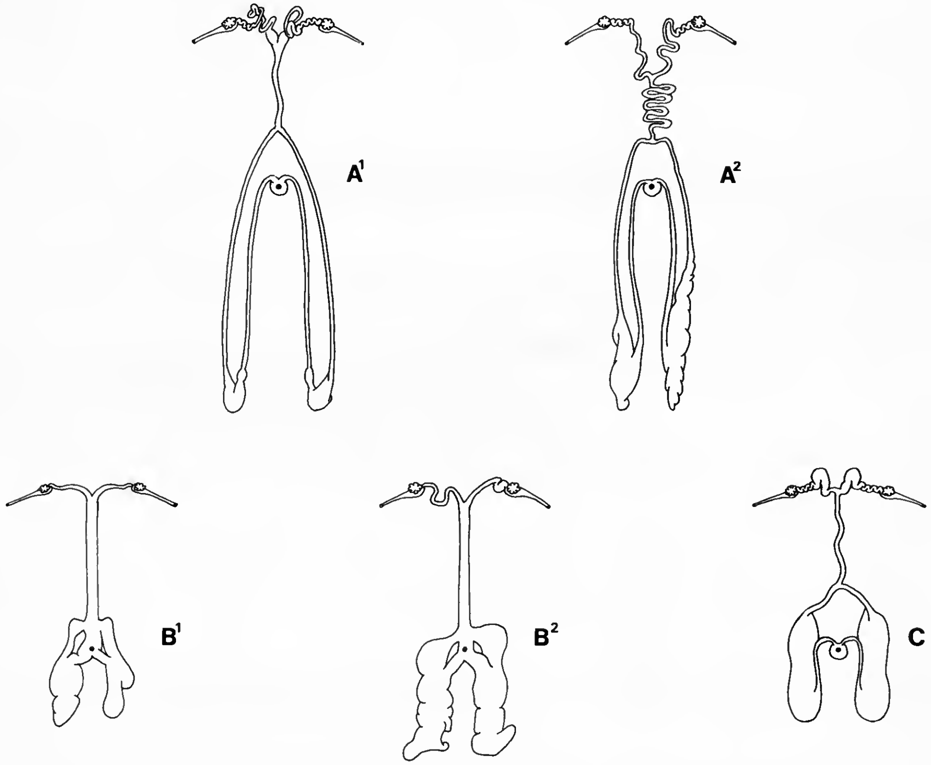

Fig. 11 *Polytoreutus kirimaensis* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *kirimaensis* (1 after Michaelsen, 1896 and after Beddard, 1907 syn. *ruwenzori*, 2 syn. *sylvestris* syntype and after Beddard, 1907 syn. *granti*); (B) *usambariensis* (1, 2 syntypes); (C) *usindjaensis* (syntype).

Polytoreutus kirimaensis species group

(Figs 10 & 11)

Diagnosis. Male and spermathecal pores separate. Receptaculum seminis with two pairs of posterior diverticula united distally to form a pair of lateral sacs, diverticula may be elongate to form a system of afferent and efferent ducts serving the paired lateral sacs, the median longitudinal element of the receptaculum seminis may be lacking between (*xvi*), *xvii* and *xviii*; anterior furcae mainly slender with terminal (distal) fertilization chambers.

Distinguishing characters. The species group consists of three species: *kirimaensis* Michaelsen, 1896; *usindjaensis* Michaelsen, 1896 and *usambariensis* Michaelsen, 1905. They are separable on several characters.

usambariensis. Externally a longitudinal, midventral seminal groove extends posteriorly from the genital field to near or behind *xxx* (resembling the shorter seminal groove present in members of the *kenyaensis* species group); receptaculum seminis with short diverticula in *xviii* and *xix* united distally and extending posteriorly for only a few segments, median longitudinal element of receptaculum present throughout; prostates tubular, ectally with paired lateral cornu receiving the vasa deferentia.

usindjaensis. External seminal groove absent; receptaculum seminis with median longitudinal element absent posteriorly, diverticula moderately long united at lateral pouch about the level of the spermathecal pore; prostates tubular, ectally deeply incised to form two long cornu with the lateral cornu receiving the vasa deferentia and the medial cornu forming the prostatic ducts; paired accessory glands absent from the male pouch.

kirimaensis. External seminal groove absent; receptaculum seminis with median longitudinal element absent posteriorly, diverticula very long and convoluted united at paired lateral sacs some distance behind the spermathecal pore; prostates often almond-shaped, the vasa deferentia pass terminally into the prostates but the prostatic ducts are subterminal; paired accessory glands present associated with the male pouch.

Polytoreutus kirimaensis Michaelsen, 1896

(Figs 10A & 11A)

Polytoreutus kirimaensis Michaelsen, 1896 : 16; Michaelsen, 1900 : 417.
Polytoreutus silvestris Michaelsen, 1896 : 18; Michaelsen, 1900 : 418; Michaelsen, 1910 : 80; Michaelsen, 1921 : 19.
Polytoreutus sylvestris (lapsus) Beddard, 1907 : 415.
Polytoreutus ruwenzorii Beddard, 1907 : 415.
Polytoreutus granti Beddard, 1907 : 420.

DESCRIPTION. *External characters.* Length 110–265 mm (77 mm holotype of *ruwenzorii,* not located, and 310, 430 mm excessively relaxed, macerating syntypes of *silvestris*), diameter 4·0–5·5 mm, segments 114–236 (*not* 300 as reported by Michaelsen, 1896 : 18). Prostomium epilobous. Clitellum *xiii–xvii,* annular, incomplete ventrally *xvii* around secondary male pore. Setae at *xxx, aa* : *ab* : *bc* : *cd* = 4 : 3 : 4 : 1. Secondary male pore *xvii* to 17/18, penis usually protruding to a length up to 1·5 segments (or more). Spermathecal pore 18/19, seen as a narrow slit. Genital field sometimes developed *xix–xl* with ventral setae enlarged and body wall between setal lines *bb* slightly raised and glandular. Female pores *xiv* by furrow 14/15 in line with the nephridiopores at ½*cd.*

Internal characters. Prostates flattened and 'almond-like' *xvii, xviii–xxii, xxiii, xxiv, xxv* or *xxvi,* muscular prostatic duct situated subterminally passing to a small male pouch, ectally each prostate is simple where it receives the vas deferens of its side; depending on individual variation, growth and/or preservation techniques, the ectal end of the prostate may appear to taper towards the prostatic duct with the vas deferens closely applied; alternatively the terminal portion receiving the vas deferens may be folded or diverging from the prostatic duct so causing the ectal end to have a bifid appearance. The spermathecal system is complex: two slender afferent ducts (left and right) pass posteriorly, rarely posterolaterally, from a small spermathecal atrium at the spermathecal pore, these dilate to form a small sac in the region of the prostates; an efferent duct passes forwards from each sac (the efferent ducts are often entwined with the afferent ducts) and the left and right efferent ducts unite mid-ventrally anteriad to the male pouch to form a single longitudinal duct; this median duct continues forwards to form the main body of the receptaculum seminis extending to near *xiv* where it bifurcates with the furcae passing laterally to distal (terminally situated) fertilization chambers. The median duct and the furcae are variably convoluted, often there is an abrupt transition between an enlarged ental and slender ectal region of the furcae but this disparity in size between the two ends of a furcae is variably present, even between the left and right furcae in a single individual. The spermathecal atrium is variable in appearance from globular to onion-shaped depending on methods of preservation; never large in size, often difficult to see. Paired 'accessory glands', or pouches, of uncertain function present in *xvi–xix,* situated laterally to both the small male pouch and the spermathecal atrium, communicating with the former.

TYPE LOCALITY. Kirima, northwestern Lake Albert, Zaire.

MATERIAL EXAMINED. *Previous records.* Uganda: 2C Primary forest, northwest of Mount ?Ruwenzori ('Runssoro') (0° 30′ N, 3° 10′ E), 800–1200 m; Hamburg V. 246 (syntypes of *silvestris*). 2C Entebbe (0° 04′ N, 32° 28′ E), 1000–1500 m; Stockholm 392 (*silvestris*: Michaelsen, 1921). 13C Pasture, banana plantation and bush, University farm, Makerere College, ?Kabanyolo ('Kabanyola'), near Kampala (0° 27′ N, 32° 37′ N), 1500 m; BM(NH) 1981.8.1–12 (*Polytoreutus* sp., Block and Banage, 1968). 3C Eucalyptus and Acacia woodland, Makerere Hill, near Kampala (0° 20′ N, 32° 34′ E), –1500 m; BM(NH) 1981.8.13–15 (*Polytoreutus* sp., Block and Banage, 1968).

New Records. Uganda (*Coll.* E. Oxtoby): 13C 4A Leaf litter under hedge in house garden in '25th January' Avenue, Kampala (0° 19′ N, 32° 35′ E), –1500 m, May 1974; BM(NH) 1981.6.1173–1189. 1C 6A Makerere University, Zoology Department Rest House, near Butiaba, Lake Albert (approx. 1° 49′ N, 31° 19′ E), –1000 m, May 1974; BM(NH) 1981.6.1191–1197. 1C Grassland beside road between Kampala (0° 19′ N, 32° 35′ E) and Entebbe (0° 04′ N, 32° 28′ E), +1000 m, 6 June 1974; BM(NH) 1981.6.1190.

Other new records. 3C Kampala, Uganda (0° 19′ N, 32° 35′ E), +1000 m; BM(NH) 1924.6.28.1 & BM(NH) 1932.5.418–19. 2 'lots' Kibale Forest, (0° 30′ N, 30° 25′ E), –2000 m; Harvard (*personal communication*).

OTHER RECORDS. 1C Kirima, northwest of Lake Edward, Zaire (0° 10′ S, 29° 39′ E), 500–1500 m; (holotype of *kirimaensis,* not located September 1978, Zoologisches Museum, Hamburg). 1C Mount Ruwenzori, Uganda (0° 23′ N, 29° 54′ E), +1500 m; (holotype of *ruwenzorii*, not located November 1976, British Museum (Natural History)). 10C Entebbe, Uganda (0° 04′ N, 32° 29′ E), –1500; Turin OL.199. 2C Mitiana, Mount Ruwenzori, Uganda (0° 23′ N, 29° 54′ E), +1000 m, Turin OL.282. 6C Ibanda, Mount Ruwenzori, Uganda (?0° 20′ N, 30° 06′ E), +1000 m; Turin OL.283. 4C Toto, Mount Ruwenzori, Uganda (0° 30′ N, 30° 30′ E), –2000 m; Turin OL.198. 1C Mount Ruwenzori, Uganda (0° 23′ N, 29° 54′ E), +1000 m; (holotype of *granti*, not located November 1976, British Museum (Natural History)). ?Primary forest, Avakubi, River Aruwimi, Zaire, 22 Apr. 1908; (Michaelsen, 1910 : 80).

DISTRIBUTION. Uganda and eastern Zaire, below 2000 m (Fig. 2D).

REMARKS. Variation was not understood when this species was first described so when variants were collected they were separated usually as distinct taxa. There was, too, a misconception about the morphological stability of the coelomic tissues forming the complex spermathecal systems. Now it is evident that while maintaining a basic pattern, the spermathecal systems can vary widely depending on growth and the volume of received sperm also the methods employed to preserve the specimens. Previously the result was that both Beddard and Michaelsen described species (three on single specimens) by giving undue significance to minor internal individual differences. When describing *ruwenzorii* and *granti,* Beddard remarked on the coincidence of this couplet occurring on Mount Ruwenzori in the same way that *kenyaensis* and *montiskenyae* are sympatric on Mount Kenya. Although these Mount Ruwenzori taxa are now considered to be synonymous, there is nevertheless a couplet in this area but comprising *kirimaensis* and *usindjaensis* from northwestern Tanzania and Rwanda.

Polytoreutus usambariensis Michaelsen, 1905
(Figs 10B & 11B)

Polytoreutus usambariensis Michaelsen, 1905 : 353; Michaelsen, 1910 : 81; Michaelsen, 1914 : 120.

DESCRIPTION. *External characters.* Length 140–280 mm, diameter 6–8 mm, segments

216–292. Prostomium prolobous. Clitellum annular $\frac{1}{2}$*xiii–xvii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 9 : 3 : 6 : 1. Secondary male pore small $\frac{2}{3}$*xvii*, carried on a low porophore; penis very small (seldom seen). Spermathecal pore 18/19, seen as a narrow slit (larger than the secondary male pore). Genital field comprises a median, longitudinal seminal groove with raised glandular walls passing from the male pore to *xxx, xxxii* between setal line *aa*; posteriorly the walls broaden to form a scutate area between $\frac{1}{2}$*ab* over *xxx–xxxv, xxxvi*. Female pores $\frac{1}{3}$*xiv* slightly below setal line *d*.

Internal characters. Prostates tubular, often massive, occasionally extending back to *xxx*; the ectal ends are bifid with the lateral cornu receiving the vas deferens. Male pouch small, almost double being transversely 'dumb-bell' shaped, receiving the prostates postero-laterally. Spermathecal system comprises a simple receptaculum seminis with paired diverticula in *xviii* and *xix* fused together entally on each side (occasionally ectally too, Michaelsen, 1914) with the posterior pair sometimes penetrating several segments back to *xxii, xxiii*; fertilization chambers distal (located terminally) on the anterior furcae.

TYPE LOCALITY. Amani, Usambara, Tanzania.

MATERIAL EXAMINED. *Previous records.* Tanzania: 2C 1A Amani, Usambara (5° 09′ S, 38° 36′ E), –1000 m; Hamburg V. 6666 (syntypes of *usambariensis*). 2C Coastal stream area, 'probably Amani in Usambara' Tanzania, 5° 09′ S, 38° 36′ E, –1000 m; Hamburg V. 6478 (syntypes of *usambariensis*). 2A in stream alluvium and foliage of 'Mogaweges', Amani, Usambara (5° 09′ S, 38° 36′ E), –1000 m; Hamburg V.6724 (*usambariensis*: Michaelsen, 1910).

New records. Amani, Usambara (5° 09′ S, 38° 36′ E) Tanzania, –1000 m, 22 Nov. 1962; Hamburg V. 12288, *Coll.* Loveridge.

OTHER RECORDS. Tanzania: Nguelo, Usambara (4° 45′ S, 38° 30′ E), 500 m; Berlin 3893 (syntypes of *usambariensis*). 1C Amani, Usambara, (5° 09′ S, 38° 36′ E), –1000 m; (*usambariensis*: Michaelsen, 1914).

DISTRIBUTION. Coastal region, northeastern Tanzania (Fig. 2D).

Polytoreutus usindjaensis Michaelsen, 1896
(Figs 10C & 11C)

Polytoreutus usindjaensis Michaelsen, 1896 : 14; Michaelsen, 1900 : 416.
Polytoreutus wittei Michaelsen, 1937*b* : 12.

DESCRIPTION. *External characters.* Length 125–255 mm, diameter 4·5–6·0 mm, segments 150–253. Prostomium prolobous, longitudinal striations may be seen on the peristomium giving the appearance of a tanylobic condition. Clitellum annular *xiii–xvii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore, small ovoid, 17/18, distal end of the small penis may be seen; small area around the male pore somewhat glandular and possibly raised slightly (male pore apparently not carried on a porophore). Spermathecal pore small, circular 18/19, vicinity of pore slightly glandular. Genital markings absent. Female pores $\frac{1}{2}$*xiv* in setal line *d*.

Internal characters. Prostates tubular extending back to *xxx–xxxii*; ectally strongly incised to form two cornu, the lateral cornu tapers gradually to receive the vas deferens while the mesial cornu develops into a short muscular prostatic duct that leads into the hinder dorso-lateral surface of a small, incipiently paired male pouch. Spermathecal system is composed of a pair of lateral sacs extending posteriorly *xvii–xxv* (less in juveniles and subadults) with paired afferent ducts passing from the equators of the sacs (posterior ends of the sacs in subadults) to a small spermathecal atrium and paired efferent ducts issuing anteriorly which unite mesially in *xvii* to form a single median, somewhat convoluted, duct that leads to the anterior furcation in *xiii*; fertilization chambers distal (located terminally) on the anterior furcae.

TYPE LOCALITY. Usindja (3° 30′ S, 31° 30′ E), northern Western Province, Tanzania.

MATERIAL EXAMINED. *Previous records.* 1C In hot springs, Mtagata, north of Bukoba, Lake Victoria, Tanzania (1° 15′ S, 31° 05′ E), –1500 m; Hamburg V. 248 (syntype of *usindjaensis*). 1C Amranda, southwestern Lake Victoria, Tanzania (2° 56′ S, 32° 10′ E), –1500 m; Hamburg V 247, (syntype of *usindjaensis*). 2C N'Gando Lake, north of Lake Kivu, Rwanda (1° 35′ S, 29° 35′ E), 2400 m; Brussels 1 G.14949 (syntypes of *wittei*).

OTHER RECORDS. Swampy stream, north Usindja, Tanzania (3° 30′ S, 30° 31′ E), 2000 m; Berlin 2434 (syntype of *usindjaensis*). Bukoba, Lake Victoria, Tanzania (1° 20′ S, 31° 58′ E), 1500 m; Berlin 2435 (syntype of *usindjaensis*). Kafuro, Karagwe, near Lake Burig, Tanzania (2° 20′ S, 31° 2′ E), 2000 m; Berlin 2455 (syntype of *usindjaensis*).

DISTRIBUTION. Rwanda and northwestern Tanzania (Fig. 2D).

Polytoreutus kilindinensis species group
(Figs 12 & 13)

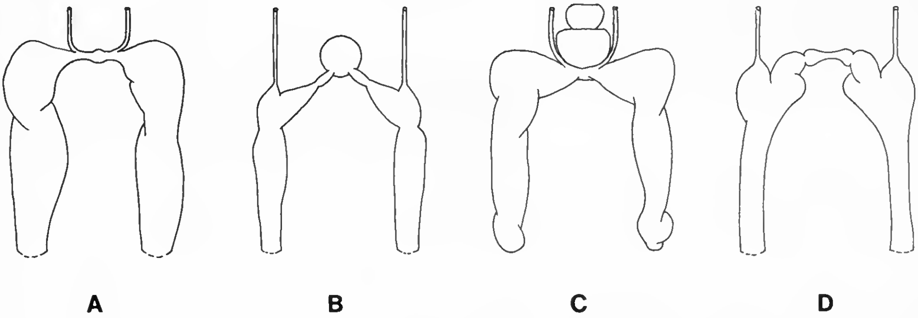

Fig. 12 *Polytoreutus kilindinensis* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *bettonianus*; (B) *finni*; (C) *hindei*; (D) *kilindinensis*.

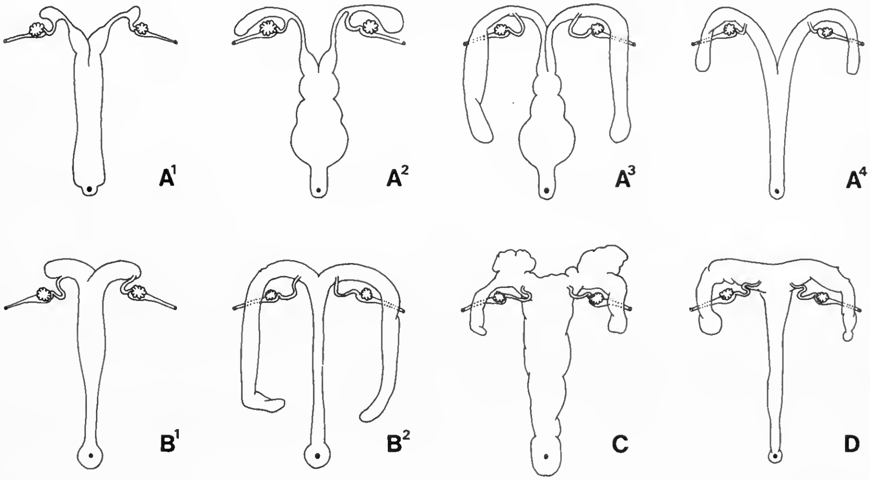

Fig. 13 *Polytoreutus kilindinensis* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *bettonianus* (1 holotype, 2 new record, 3 syn. *baralypton* holotype, 4 after Michaelsen, 1937 syn. *loveridgei*); (B) *finni* (1 after Stephenson, 1933 syn. *striatus*, 2 holotype and syn. *chaloneri* holotype); (C) *hindei* (paratype); (D) *kilindinensis* (syntype).

Diagnosis. Male and spermathecal pores separate, receptaculum seminis adiverticulate; anterior furcae often massive and flexed backwards for several segments, each furca with a proximal (basal) duct leading to a fertilization chamber.

Distinguishing characters. The species group is formed from four species: *kilindinensis* Beddard, 1894; *finni* Beddard, 1894; *hindei* Beddard, 1901 and *bettonianus* Beddard, 1902. They can be separated on the morphologies of the receptaculum seminis and the male pouch.

kilindinensis. Anterior bifurcation of the receptaculum seminis in *xiii*; male pouch small (secondary male and spermathecal pores small).

finni. Anterior bifurcation of the receptaculum seminis in *xiii*; male pouch large (secondary male and spermathecal pores large).

hindei. Anterior bifurcation of the receptaculum seminis in *xiii*; male pouch with anterior accessory pouch (secondary male pore large, spermathecal pore small).

bettonianus. Anterior bifurcation of the receptaculum seminis beginning *xiv–xvi*; male pouch small, transversely oval.

Polytoreutus bettonianus Beddard, 1902

(Figs 12A & 13A)

Polytoreutus bettonianus Beddard, 1902 : 199.
Polytoreutus baralypton Cognetti, 1911 : 507.
Polytoreutus loveridgei Michaelsen, 1937 : 454.

Description. *External characters.* Length 90–230 mm, diameter 2·5–5 mm, segments 175–314. Prostomium pro- proepilobous. Clitellum *xiii–xviii,* annular. Setae at *xxx,* *aa* : *ab* : *bc* : *cd* = 5 : 3 : 5 : 1. Secondary male pore 17/18 on a low, somewhat transversely oval porophore $\frac{1}{2}$*xvii*–$\frac{1}{2}$*xviii* usually with the papilliform penis protruding. Spermathecal pore 18/19, surrounded by raised tumid lips; in contracted specimens the spermathecal pore is a narrow slit and the lips seen as a transverse pad, in relaxed specimens both the pore and the lips are circular. Female pores at $\frac{3}{4}$*xiv* at the same level as the nephridiopores in $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular extending back to *xxii–xxvi,* somewhat constricted intersegmentally. Ectally they taper sharply to form a short muscular duct which enters a small, transverse male pouch; the vasa deferentia enter simply into the lateral surfaces of the prostates at the region of taper. (Infrequently the ectal end of a prostate may coil causing it to appear as a bulla.) The spermathecal system comprises a simple median adiverticulate receptaculum seminis, frequently with slight segmental pouching. The receptaculum passes forwards from the spermathecal pore to the anterior bifurcation sited between *xiv–xvi* (the greater the volume of sperm products, the more anteriorly the bifurcation occurs). The lateral furcae continue anteriorly to *xiii* where they flex laterally. In subadults the furcae may be slender and the fertilization chambers terminally located, in older worms a diverticulum develops on each furca which in fully adult individuals becomes the massive distal end of the furca while the fertilization chambers and their ducts become apparently non-terminal and proximal on these massive secondary furcae.

Type locality. Lugari, Kenya.

Material examined. *Previous records.* Kenya: 1C Lugari (0° 39′ N, 34° 53′ E); BM(NH) 1902.11.26–21–25 (holotype of *bettonianus*). 1C Nairobi (0° 17′ S, 36° 50′ E), –2500 m; BM(NH) 1911.4.21.1. (holotype of *baralypton*).

New records. (*Coll.* E. Oxtoby): 3C Wet grass, Sirimon Track, Mount Kenya, Kenya (0° 03′ S, 37° 17′ E), 4000 m, 19 Nov. 1974; BM(NH) 1981.6.434–436.

Other records. 2C Golbanti, on the Tana River, Kenya (2° 27′ S, 40° 07′ E), –200 m; (syntypes of *loveridgei* not located April 1980, Museum of Comparative Zoology, Harvard).

Distribution. Kenya (Fig. 2E).

Polytoreutus finni Beddard, 1894
(Figs 12B & 13B)

Polytoreutus finni Beddard, 1894 : 241; Beddard, 1895 : 611; Michaelsen, 1900 : 415.
Polytoreutus elongatus (lapsus) Beddard, 1894 : 242.
Polytoreutus chaloneri Smith & Green, 1919 : 156; Michaelsen, 1937 : 473.
?*Polytoreutus striatus* Stephenson, 1933 : 241.

DESCRIPTION. *External characters.* Length 90–188 mm, diameter 2–5 mm, segments 147–501. Prostomium prolobous. Clitellum $\frac{1}{3}$*xiii*–$\frac{1}{3}$*xviii,* annular, sometimes incomplete ventrally by the secondary male pore. Setae at *xxx*, *aa* : *ab* : *bc* : *cd*=4 : 2 : 3 : 1. Secondary male pore located in the posterior half of *xvii,* carried on a large glandular porophore extending 16/17 to 17/18 sometimes with indistinct radiating grooves, tip of the penis protruding (in excessively relaxed specimens, the penis may be seen within the secondary male pore together with a pair of lateral pads situated more posterolaterally). Spermathecal pore usually large 18/19 possibly with tumid lips surmounting a glandular pad (extending $\frac{1}{2}$*xviii*–$\frac{1}{3}$*xx*) which may unite anteriorly with the glandular porophore carrying the secondary male pore. (When the genital field is fully developed, the precise locations of the secondary male and spermathecal pores are difficult to determine.) Female pores $\frac{1}{2}$–$\frac{2}{3}$*xiv* at the same level as the nephridiopores in $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular but tend to be somewhat moniliform due to intersegmental constrictions, often flexed anteriorly (depending on relaxation of specimen) leading back possibly to *xxvii*; ectally each has a small lateral, subterminal cornu receiving the vas deferens of its side (when the prostates are strongly moniliform, the vasa deferentia enter into the penultimate ectal chambers); the main body of each prostate passes into the posterolateral surfaces of the large male pouch. Spermathecal system comprises a simple, adiverticulate median receptaculum seminis leading from the spermathecal pore (where in fully adult specimens the adjacent portion of the receptaculum is thickened as if to form a 'bursa copulatrix') to the anterior bifurcation in *xiii*; the lateral furcae are massive and flexed ventrally and/or posteriorly with their distal extremities located near the flexures of the prostates; fertilization chambers served by ducts arising proximally (basally) from the furcae.

TYPE LOCALITY. Zanzibar, Tanzania.

MATERIAL EXAMINED. *Previous records.* 1C Garden soil; Kilindini, Mombasa Island, Kenya (4° 04′ S, 39° 39′ E), 0–200 m; BM(NH) 1904.10.5.439 (holotype of *finni*). 1C Mkonumbi, near Lamu, Kenya (2° 18′ S, 40° 42′ E), −200 m; USNM 16834 (holotype of *chaloneri*). 1A Mombosasa near Witu, Kenya (2° 20′ S, 40° 30′ E), −200 m; Hamburg V. 12283 (*chaloneri*: Michaelsen, 1937). 1C Fragments Madehani, Ukinga Mountains, 'at north end of Lake Nyasa', Tanzania (9° 21′ S, 34° 02′ E), +1000 m; Harvard 2101 (holotype of *striatus*).

New records. Kenya (*Coll.* E. Oxtoby): 2C 5A Sandy soil in forest road, Roka Forest, off the Malindi-Kilifi road, Kilifi District (3° 26′ S, 39° 54′ E), 100 m, 29 June 1974; BM(NH) 1981.6.484–490. 5C 2A Sandy soil, sisal plantation, inland of Kilifi, 20 miles north of Mombasa (3° 38′ S, 39° 51′ E), 100 m, 18 Oct. 1970; BM(NH) 1981.6.491–498. 3C 4A Beside sandy road, near Shimo-la-Tewa school, Mombasa (3° 58′ S, 39° 44′ E), 100 m, 29 June 1974; BM(NH) 1981.6.477–483.

OTHER RECORDS. Kenya: 1C Rabai, near Mombasa (3° 56′ S, 39° 34′ E), 65 m ('200 ft'); BM(NH) 1909.8.12.4. 1A Mkonumbi, near Lamu (2° 16′ S, 40° 42′ E), 16 m ('50 ft'); (*chaloneri*: Michaelsen, 1937; not located, Museum of Comparative Zoology, Harvard, April, 1980).

DISTRIBUTION. Apart from the single record of (?) *striatus* Stephenson from western Tanzania, sandy soils near sea level in the coastal regions of Kenya and Tanzania (Fig. 2E).

Polytoreutus hindei Beddard, 1901
(Figs 12C & 13C)

Polytoreutus hindei Beddard, 1901 : 336.

DESCRIPTION. *External characters.* Length 92–157 mm, diameter 3–4 mm, segments 239–342. Prostomium pro-epilobous. Clitellum annular *xiii–xviii.* Setae at *xxx, aa* : *ab* : *bc* : *cd*= 4 : 2 : 3 : 1. Male pore large, superficially rectangular occupying the entire midventral area of *xvii* between setal lines *aa*; bounded laterally by a pair of raised longitudinal pads each filling the intersetal area *ab* between 16/17 and 17/18 and limited anteriorly and posteriorly on *xvi* and *xviii* by a raised, transverse pad formed from the ventral surfaces of these segments between setal lines *bb*: within the male pore, the floor is glandular and slopes up to 16/17 where a slit-like transverse orifice to the internal accessory pouch may be seen. Penis absent. Spermathecal pore 18/19, seen as a lateral slit. (Additionally, a pore-like pit often present midventrally in 19/20.) Genital field present consisting of a raised, pigmented area, somewhat scutate in appearance, on *xix–xxii* between setal lines *bb.* Female pores on the posterior region of *xiv,* near furrow 14/15, in setal line *d.*

Internal characters. Prostates tubular, short extending only to about *xxv*; ectally they are flexed mesially to pass into the posterior surface of a large male pouch; the vasa deferentia lie over the lateral parts of the male pouch to pass simply into the dorsal surfaces of the ectal ends of the prostates. The spermathecal system comprises a massive adiverticulate median sac passing from the anterior bifurcation to the spermathecal pore; the anterior furcae are massive and flexed with their distal ends lying above the male pouch, they are connected basally (proximally) to the fertilization chambers by ducts arising from the posterior surfaces of the posterior part of the furcae. Accessory pouch present lying immediately before (almost overlaid by) the large male pouch, the accessory pouch tapers posteriorly to discharge midventrally into the male pouch.

TYPE LOCALITY. Kitui, Kitui District, Kamba Province, Kenya.

MATERIAL EXAMINED. *Previous records.* 2C 1A ?Kitui ('Titui'), Kamba Province, Kenya (° 21′ S, 38° 01′ E), 900–1200 m ('3000–4000 ft'); BM(NH) 1902.1.21.1 & 1964.4.1 (holotype and paratype of *hindei*).

New records. Kenya (*Coll.* E. Oxtoby): 1C 15A Ngangao ('Ngangau') Forest, Taita Hills (3° 22′ S, 38° 20′ E), 1500 m, 10 Aug. 1978; BM(NH) 1981.6.650–665. 3C 1A 'Bushwackers' camp, 20 km northeast of Kibwesi (2° 25′ S, 38° 00′ E), –1000 m, Apr. 1977; BM(NH) 1981.6.666.669.

DISTRIBUTION. Southeastern Kenya, above 1000 m (Fig. 2E).

Polytoreutus kilindinensis Beddard, 1894
(Figs 12D, 13D & 14)

Polytoreutus kilindinensis Beddard, 1894 : 236; Beddard, 1895 : 611; Michaelsen, 1900 : 415.

DESCRIPTION. *External characters.* Length 118–352 mm, diameter 2·5–6·0 mm, segments 220–652. Prostomium prolobous. Clitellum annular *xiii–xviii* ($\frac{1}{3}$*xix*), incomplete ventrally and saddle-shaped $\frac{1}{3}$*xvii*–$\frac{1}{3}$*xix.* Setae at *xxx, aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore small on a low porophore 17/18, sometimes with the penis everted (penis long and bifid distally, Fig. 14). Spermathecal pore small transverse slit in 18/19. Genital field forming a somewhat trapezoidal glandular area 17/18–21/22, occasionally extending anteriorly around the male porophore. Female pores paired at $\frac{3}{4}$*xiv* at the same level as the nephridiopores at $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular but tending to become moniliform ectally due to intersegmental constrictions, extending posteriorly to *xxxv*; ectally subterminally bifid with each lateral cornu receiving the vas deferens of its side and each mesial cornu leading into a small male pouch (or seemingly directly into the ventral parietes depending on the preservation techniques employed). The spermathecal system comprises a slender median adiverticulate receptaculum seminis passing anteriorly from the spermathecal pore to the anterior bifurcation located usually in *xiii* but in more mature individual sometimes in *xiv*; the lateral furcae are massive being flexed posteriorly with their distal extremities reaching to the region of the male pouch. The ducts to the paired fertilization chambers arise basally from the proximal ends of the furcae.

Type locality. Kilindini, Mombasa Island, Kenya.

Material examined. *Previous records.* 2C 2A Garden soil (dampened by regular deposits of household slops), Kilindini, Mombasa Island, Kenya (4° 04′ S, 39° 39′ E), –200 m; BM(NH) 1904.10.5.440–441 (syntypes of *kilindinenses* [label data 'Zanzibar District', 2A *not* noted in original description]).

New records. Kenya (*Coll.* E. Oxtoby): 3C 7A Damp soil, not flooded, in rice cultivation area, off the old Mombasa road, inland of ?Shanzu ('Shansu') (3° 58′ S, 39° 45′ E), 100 m, 5 May 1972; BM(NH) 1981.6.1149–1158. 5C 5A Sandy loam, temporary flood area, paddy field, Magazoni village, Tiwi Location (4° 15′ S, 39° 32′ E), – 100 m, 28 June 1974; BM(NH) 1981.6.1163–1172. 1C Sandy soil, under Neem trees, Shimo-la-Tewa school, Mombasa (3° 58′ S, 39° 44′ E), – 100 m, 29 Jun. 1974; BM(NH) 1981.6.1162. 3C Origin uncertain; probably from, flooded sandy soil, Kenya-Somali border, Northern Territories (approx. 2° 00′ S, 42° 00′ E), 100 m, ?1973; BM(NH) 1981.6.1159–1161. 17C 5A Grassland, Bargoni School, Lamu District (2° 03′ S, 400° 47′ E), – 100 m, 12 Jul. 1978; BM(NH) 1981.6.1120–1142. 2C Kiunga road, near Milimani (approx. 1° 46′ S, 40° 50′ E), 100 m, 14 Jul. 1978; BM(NH) 1981.6.1143–1144. 3C 1A Cultivation, near pipe-line office, road between Kinango (4° 09′ S, 39° 19′ E) and Kwale (4° 10′ S, 39° 28′ E), Shimba Hills, – 500 m, 12 Aug. 1978; BM(NH) 1981.6.1145–1148.

Other record. 1C (fragment) Mombasa, Kenya (4° 03′ S, 39° 40′ E), 0–100 m; Stockholm 390.

Distribution. Sandy soils, frequently in wet situations especially in coastal areas, eastern Kenya (Fig. 2E).

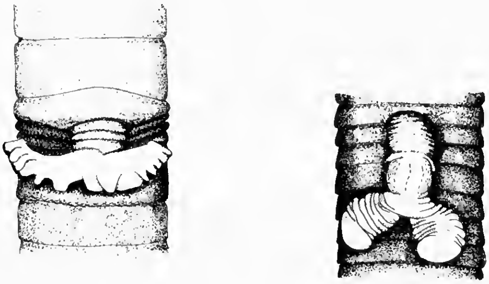

Fig. 14 *Polytoreutus kilindinensis.* External ventral view, penes of two individuals subjected to different techniques of preservation.

Remarks. Sometimes when the curious bifid penis is relaxed and (?)fully everted, it extends externally up to five segments in length. The size suggests that during copulation when, presumably, the penis is dilated, it would fill the posterior longitudinal region of the receptaculum seminis and the bifid distal ends could be accommodated within the proximal ends of the anterior furcae of the receptaculum seminis. (The primary male pore was not seen, possibly it lies between the bifid ends of the penis.)

Polytoreutus coeruleus species group
(Figs 15 & 16)

Diagnosis. Male and spermathecal pores separate; receptaculum seminis diverticulate anterior furcae often massive and flexed backwards for several segments, each furca with a proximal (basal) duct leading to a fertilization chamber.

DISTINGUISHING CHARACTERS. The species group comprises four species: *coeruleus* Michaelsen, 1890; *violaceus* Beddard, 1894; *gregorianus* Beddard, 1895 and *multiporus* Smith & Green, 1919. They are readily separable on the number and arrangement of the diverticula on the receptaculum seminis.

gregorianus. Receptaculum seminis extending *xiii–xix* with a single pair of diverticula in *xix*.

coeruleus. Receptaculum seminis extending *xiii–xix*, diverticulate throughout.

violaceus. Receptaculum seminis extending *xiii–xxi*, *xxii* or *xxiii*, diverticulate throughout.

multiporus. Receptaculum seminis extending *xiii–xxiv*, *xxv* or *xxvi*, diverticulate posteriorly, behind (?)*xviii* or *xix*.

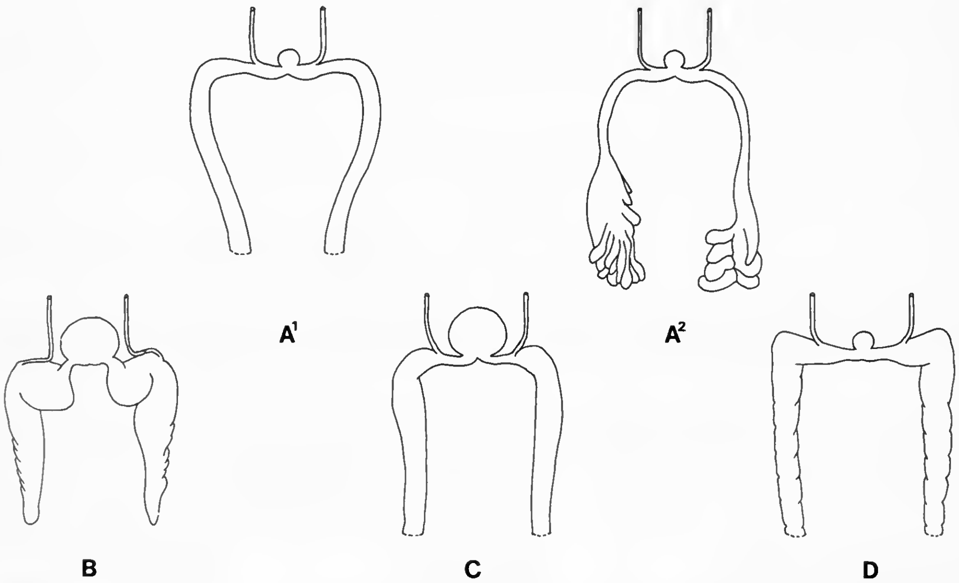

Fig. 15 *Polytoreutus coeruleus* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *coeruleus* (1 moderate development, 2 massive development); (B) *gregorianus*; (C) *multiporus*; (D) *violaceus*.

Polytoreutus coeruleus Michaelsen, 1890
(Figs 15A & 16A)

Polytoreutus coeruleus Michaelsen, 1890 : 24; Michaelsen, 1891 : 34; Beddard, 1895 : 609; Michaelsen, 1900 : 414.

Polytoreutus coeruleus affinis Michaelsen, 1890 : 24; Michaelsen, 1891 : 36; Beddard, 1895 : 610; Michaelsen, 1900 : 414.

Polytoreutus coeruleus korogweensis Michaelsen, 1890 : 24; Michaelsen, 1891 : 36; Beddard, 1895 : 610; Michaelsen, 1900 : 414; Michaelsen, 1905 : 351.

Polytoreutus coeruleus makakallensis Michaelsen, 1890 : 24; Michaelsen, 1891 : 35; Beddard, 1895 : 610; Michaelsen, 1900 : 414.

Polytoreutus coeruleus mhondaensis Michaelsen, 1890 : 24; Michaelsen, 1891 : 36; Beddard, 1895 : 610; Michaelsen, 1900 : 414.

Polytoreutus hexathecus Beddard, 1925 : 60.

Polytoreutus askarorum Michaelsen, 1937 : 464.

Polytoreutus bagiloanus Michaelsen, 1937 : 468.

DESCRIPTION. *External characters.* Length 52–118 mm, diameter 2–4 mm, segments 150–202 (72 *bagiloanus*). Prostomium prolobous. Clitellum *xiii–xviii* annular, in *xviii* incomplete ventrally and saddle-shaped. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 3 : 1. Secondary male pore 17/18 to posterior third of *xvii*, seen as a low porophore spreading from $\frac{1}{2}$*xvii*–$\frac{1}{2}$*xviii*, mostly circular, often with the tip of the penis protruding. Spermathecal pore 18/19 with narrow lips seen either as a narrow transverse slit or partly opened forming a somewhat oval aperture surrounding the papilliform ectal end of the receptaculum seminis. Genital papillae absent (other papillae, *see* Remarks). Female pores $\frac{1}{2}$*xiv* in or slightly above setal line *c*.

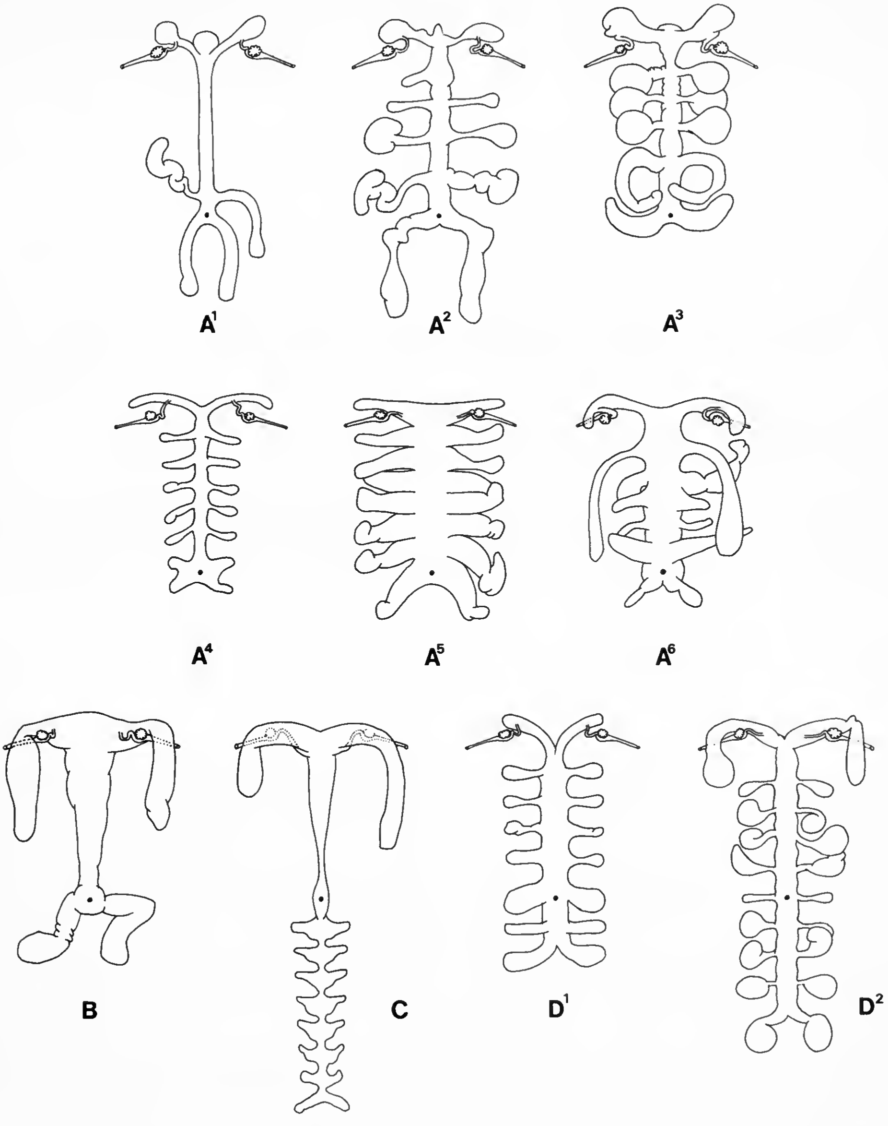

Fig. 16 *Polytoreutus coeruleus* species group. Female and spermathecal systems (schematic dorsal views, not to scale): (A) *coeruleus* (1 syn. *affinis* syntype and syn. *korogweensis* syntype, 2 syn. *makakallensis* syntype, 3 syn *hexathecus* syntype, 4 after Michaelsen, 1937 syn. *bagiloanus*, 5 after Michaelsen, 1937 syn. *askarorum*, 6 new record); (B) *gregorianus* (holotype); (C) *multiporus* (holotype); (D) *violaceus* (1 holotype and after Michaelsen, 1937 syn. *malindus*, 2 syn, *variabilis*: Michaelsen, 1905).

Internal characters. Prostatic glands tubular, extending posteriorly to *xxvii–xxx*, occasionally the distal portions with segmental diverticula; ectally undifferentiated with the vasa deferentia entering simply near the union with the male pouch. The spermathecal system comprises a single median, diverticulate receptaculum seminis passing from the spermathecal pore to the anterior bifurcation in *xiii*. The diverticula are paired segmentally between *xiv–xix* although some may fail to develop while others may become greatly enlarged and pass through several segments. The anterior furcae are often poorly developed with short proximal ducts leading into the fertilization chambers.

TYPE LOCALITY. Korogwe, Usambara, Tanzania.

MATERIAL EXAMINED. *Previous records.* Tanzania: 3C 7A Near Korogwe, at or on the Rufu, Usambara (?5° 09′ S, 38° 29′ E), – 500 m; Hamburg V. 249 (holotype of *affinis*), Hamburg V. 252 & BM(NH) 1904.10.5.451 (syntypes of *korogweensis* Michaelsen, 1891). 2C 2A Msiri Stream, Makakalla Valley ('Thal'), East Unguru (5° 43′ S, 37° 44′ E), – 1000 m; Hamburg V. 250 (syntypes of *makakallensis*). 2C 6A Watering place near Mhonda, Pangani (6° 01′ S, 37° 55′ E), – 1000 m; Hamburg V. 251 & BM(NH) 1904.10.5.452 (syntypes of *mhondaensis*). 1C Tanga (5° 00′ S, 39° 06′ E), – 200 m; Hamburg V. 6659 (*korogweensis*: Michaelsen, 1905). 3C (fragments) River-bed soil, ?Wanga, near Kidele (6° 45′ S, 36° 45′ E), – 1000 m; BM(NH) 1924.10.20.2–5 (syntypes of *hexathecus*). 1C Bagilo, Ulunguru Mountains (6° 50′ S, 37° 50′ E), 2000 m ('6000 ft'); Hamburg V. 12284 (syntype of *bagiloanus*).

New records. (*Coll.* E. Oxtoby): 2C 1A Sandy soil, grassland, at 'Klosser's', Mafia Island, Tanzania (7° 50′ S, 39° 50′ E), 0–100 m, Apr. 1974; BM(NH) 1981.6.437–439.

OTHER RECORDS. Bagilo, Ulunguru Mountains, Tanzania (6° 50′ S, 37° 50′ E), 2000 m ('6000 ft'); (unique holotype of *askarorum* and syntype of *bagiloanus,* not located April 1980, Museum of Comparative Zoology, Harvard).

DISTRIBUTION. Northeastern Tanzania (Fig. 2F).

REMARKS. In the past the characters defining this species have been obscured due to the original type series comprising pathological specimens affected by (?) parasitization. Externally these specimens have one to four pit-like invaginations in the body wall in or near the mid-ventral line in the vicinity of the male and spermathecal pores, internally these structures are seen to be cyst-like within the circular and longitudinal muscles. In the specimens examined, most of the pits were empty but a few had a blackened, amorphous contents. Michaelsen regarded these apertures as genital pits, 'pubertätsgruben', and provided an illustration of a section of one (1890 : fig. 29). Then believing that they formed discrete patterns, Michaelsen went on to describe a separate *forma* for each arrangement of his 'pubertätsgruben'. Later when Beddard received specimens from Wanga which he named *hexatheca,* the large pits were confused with the male and spermathecal pores in one specimen and the locations of these pores were recorded incorrectly, while internally one cyst near the spermathecal duct was reported as a bursa copulatrix although there is no communication between the cyst and the spermathecal system. Additionally in one syntype of *hexatheca,* a cyst has developed near the male pore causing it to atrophy so as to be scarcely visible while internally the cyst has enveloped most of the male terminalia causing the region to appear superficially as a large bursa propulsoria. There are no signs of cyst development in the new records from Mafia Island.

The cyst-like structures by their large mass frequently affect nearby organs. The partial suppression of the male pore in *hexatheca* is exceeded in other specimens where the emission of sperm is prevented. When the latter condition prevails, there is a massive store of sperm in segment *xii,* the distal portions of the seminal vesicles are grossly dilated while the distal valves of the prostates may be expanded with segmentally arranged digitate diverticula. In other specimens the ectal region of the receptaculum seminis, also possibly the spermathecal pore, may be affected so preventing an interchange of sperm while the anterior pairs of diverticula on the receptaculum fail to develop.

The effects of the cyst-like structures on the morphologies of the worms are variable and prevent any two specimens within a series from sharing the degree of resemblance usually encountered among conspecific individuals. As a result the morphology of the species is poorly understood. This report provides the only account of deformation, probably due to parasitization, in a species of *Polytoreutus*. It is curious that since the incidence is seemingly widespread in *coeruleus* that comparable teratological changes have not been detected in other species of the genus. (See also below, *Remarks* under *P. violaceus.)*

Polytoreutus gregorianus Beddard, 1895
(Figs 15B & 16B)

Polytoreutus gregorianus Beddard 1895 : 612; Michaelsen, 1900 : 415; Beddard, 1901 : 187.

DESCRIPTION. *External characters.* Length (11 adults) 205–338 mm, diameter 6–8 mm, segments 350–569. Prostomium prolobous. Clitellum annular *xiii–xviii.* Setae at *xl,* $aa : ab : bc : cd = 6 : 3 : 4 : 1$. Secondary male pore 17/18 small lateral slit with glandular, crenulated lips through which the distal end of the small penis may protrude. Spermathecal pore small, circular 18/19. A genital pit, or depression, present on *xviii* in fully mature individuals, transversely oval lying between setal lines *bb*. Pad-like, transversely rectangular genital pads or papillae present *(xix) xxiv–xxxiv (xxxvi)* each completely occupying the ventral surface of its segment between lines *bb*; the tissue forming the pads is more deeply pigmented and obliterates setae *a* always and setae *b* sometimes; each pad is somewhat concave or at least (especially the more anteriorly located pads) incised with a lateral groove. Female pores $\frac{3}{4}$*xiv* in line with the nephridiopores at $\frac{1}{2}$*cd.*

Internal characters. Prostates tubular, each clearly formed of two parts, with a short, stout anteriorly directed proximal portion separated by a flexure from a long, more slender posteriorly directed distal portion extending back to *xxvi–xxviii* (the whole resembling the hind limb of a tetrapod); the vas deferens passes entally along the antero-lateral surface of the proximal portion of the prostate of its side which it enters at the flexure. Male pouch large, receiving the prostates latero-posteriorly. The spermathecal system comprises a massive, single, adiverticulate receptaculum seminis passing from the spermathecal pore to the anterior bifurcation; posteriorly there is a pair of short, lateral diverticula extending backwards for four to six segments, anteriorly the furcae are massive and flexed posteriorly with their distal ends extending to the level of the male pouch: proximal ducts lead to the fertilization chambers issuing basally from the posterior surfaces of the proximal ends of the furcae.

TYPE LOCALITY. Fuladoya, Giriama District, Seyidie Province, Kenya.

MATERIAL EXAMINED. *Previous records.* 1C Near Fuladoya Giriama, Seyidie Province, Kenya (3° 48′ S, 39° 35′ E), –200 m; BM(NH) 1904.10.5.438 (holotype of *gregorianus*).

New records. Kenya (*Coll.* E. Oxtoby): 4C Sandy soil, sisal plantation, inland of Kilifi, 20 miles north of Mombasa, Giriama District, Seyidie Province (3° 38′ S, 39° 51′ E), –200 m, Aug. 1970; BM(NH) 1981.6.644–647. 1C Mwea or Sukari Ranch (opposite Kenyatta College), Nairobi; BM(NH) 1981.6.648. 10C 125A Cultivated sandy soil, field near Gede, Malindi, Seyidie Province, (3° 18′ S, 40° 01′ E), –100 m, 29 June 1974; BM(NH) 1981.6.507–643. 6 Juveniles ?Ngangao ('Ngangau'), Taita Hills, (3° 22′ S, 38° 20′ E), –1500 m, 10 Aug. 1978; BM(NH) 1981.6.499–504. 1C Mombasa-Malindi road, near radio station, –100 m, Aug. 1974, BM(NH) 1981.6.649. 1C 1A Sandy soil at edge of Roka Forest, off Kilifi-Malindi road (3° 26′ S, 39° 54′ E), –100 m, 29 June 1974; BM(NH) 1981.6.505–506.

DISTRIBUTION. Coastal lowlands, southeastern Kenya (Fig. 2F).

Polytoreutus multiporus Smith & Green, 1919
(Figs 15C & 16C)

Polytoreutus multiporus Smith & Green, 1919 : 161; Michaelsen, 1937 : 475.

Description. *External characters.* Length 100–370 mm, diameter 3–5·5 mm, segments 264–670. Prostomium prolobous. Clitellum (*xiii*) *xiv–xvii, xviii* (*xix*), saddle-shaped. Setae at *xxx, aa* : *ab* : *bc* : *cd* = 8 : 4 : 6 : 1; genital setae (mature adults) borne on papillae *xiii–xvi, xix–xxvi* with *ab* enlarged to about twice the size of *cd* (in adults, setae absent *xvii, xviii* and more anteriorly or posteriorly situated genital setae and papillae may fail to develop too). Secondary male pore *xvii,* seen as a low crenulated tumid porophore, usually with the tip of the penis protruding through the aperture; in one paratype the penis is fully everted. Spermathecal pore 18/19, seen mostly as a narrow transverse slit bordered by raised, tumid lips, clearly seen as a circular aperture in excessively relaxed specimens. Intersegmental accessory pores located midventrally in 19/20–23/24, small 24/25 or 25/26 (the pores lead into a diverticulate posterior prolongation of the receptaculum seminis). Female pores $\frac{3}{4}$*xiv* at the same level as the nephridiopores in $\frac{1}{2}$*cd.*

Internal characters. Prostates long, reaching back nearly to *vl*; ectally each tapers sharply into a short muscular duct which leads into the posterior surface of a large male pouch, each vas deferens enters simply into the sharply tapering ectal end of the prostate of its side. The spermathecal system comprises a median receptaculum seminis adiverticulate anteriorly but with a posterior prolongation with paired segmental diverticula extending from the spermathecal pore to *xxvi, xxv* or *xxvi* (communicating with the exterior through the midventral intersegmental accessory pores).

The lateral furcae are massive and flexed posteriorly, possibly extending to the anterior (ectal) ends of the prostates, communicating with the fertilization chambers by proximal, basally arising ducts.

Type locality. Mkonumbi, near Lamu, Kenya.

Material examined. *Previous record.* 5C Mkonumbi, near Lamu, Kenya (2° 16′ S, 40° 42′ E), 16 m USNM 16835, (holotype and paratypes of *multiporous*).

New records. Kenya (*Coll.* E. Oxtoby): 1C Sandy soil on road between staff housing, Shimo-la-Tewa school, Mombasa (3° 58′ S, 39° 44′ E), –200 m, 29 Jun. 1974; BM(NH) 1981.6.1365. 2C Cultivated sandy soil, field near Gede, Malindi (3° 18′ S, 40° 01′ E), –200 m, 29 Jun. 1974; BM(NH) 1981.6.1349–1350. 11C 3A Bushland by the road between Majenjo (approx. 1° 45′ S, 40° 20′ E) and Kiunga (1° 44′ S, 41° 30′ E), –200 m, 12 Jul. 1978; BM(NH) 1981.6.1351–1364.

Other records. Kenya: Michaelsen, 1937 : 475 (not located April 1980. Comparative Zoology, Harvard): 2? Mkonumbi, near Lamu, (2° 16′ S, 40° 42′ E), 16 m ('50 ft'); 4? Gongoni, 10 miles north of Malindi (3° 05′ S, 40° 10′ E), 25 m ('75 ft'); 1? Malindi, 65 miles north of Mombasa (3° 13′ S, 40° 08′ E), 33 m ('100 ft'); 1? Changamwe, 3 miles west of Mombasa (4° 01′ S, 39° 37′ E), 63 m ('192 ft').

Distribution. Eastern Kenya (Fig. 2F).

Polytoreutus violaceus Beddard, 1894
(Figs 15D & 16D)

Polytoreutus violaceus Beddard, 1894 : 230; Beddard, 1895 : 610; Michaelsen, 1897 : 51; Michaelsen, 1900 : 413; Michaelsen, 1905 : 352.
Polytoreutus violaceus variabilis Michaelsen, 1897 : 52; Michaelsen, 1900 : 413; Michaelsen, 1905 : 352; Michaelsen, 1913 : 55.
Polytoreutus malindus Michaelsen, 1937 : 460.

Description. *External characters.* Length 80–140 mm, diameter 2·5 mm, segments 83–209. Prostomium prolobous but in contracted (preserved) specimens seemingly epilobous or when longitudinal striations present on segment *i*, possibly tanylobous. Clitellum saddle-shaped ½*xiii–xviii*. Setae at *xxx*, $aa : ab : bc : cd = 3 : 2 : 3 : 1$. Secondary male pore *xvii*, variable in appearance according to the degree of eversion of the penis: when the penis is retracted, the secondary male pore is seen as a lateral slit with crenulated lips; when the penis is partly everted, the secondary male pore seen as a low circular ridge around the distal part of the penis; when the penis is fully everted, the tissues previously forming the lips of the secondary male pore are now drawn out to form the basal portion of the penis. Penis small, onion-shaped when turgid. Spermathecal pore inconspicuous, lateral slit 18/19. Flattened, pad-like genital papillae present, single, median ventral: characteristically present on a single segment *xxi–xxxiii*, commonly *xxii–xxiv* with the papilla frequently impinging on the adjacent segments; other single midventral papillae may be present *xiv*, *xv*, *xvi* and/or *xviii*, frequently imperfectly developed but may cause the clitellum superficially to appear to be annular. Female pores paired ½*xiv* above setal line *c*.

Internal characters. Prostates tubular, variable in length extending back usually to c. *xxx* exceptionally only to *xxiii*, constricted intersegmentally. Ectally the prostates commonly pass laterally before curving posteriorly, the anterior surface of the lateral flexure receives the vas deferens of its side. Male pouch small, usually not seen as it is contained within the body wall, the prostates discharge into its posterior surface. Spermathecal system comprises a single, diverticulate longitudinal receptaculum seminis extending forwards from *xxi* (occasionally *xxiii*) to the anterior bifurcation in *xiii*. In addition to the anterior furcae, there are commonly seven pairs of diverticula occurring more or less segmentally, occasionally only six pairs of diverticula develop, exceptionally more (nine pairs are present in one individual from Mchinga so increasing the number of pairs posteriad to the prostates from the typical 3 to 5 pairs). The fertilization chambers are sub-terminal on the massive anterior furcae, their ducts arise from the posterior surfaces of the basal (proximal) portions of the furcae.

TYPE LOCALITY. Zanzibar, Tanzania.

MATERIAL EXAMINED. *Previous records.* 1C Zanzibar, Tanzania (6° 06′ S, 39° 13′ E), –200 m; BM(NH) 1904.10.5.437 (syntype of *violaceus*). 5C 2A Dar-es-Salaam, Tanzania (6° 48′ S, 39° 18′ E), –200 m; Hamburg V. 4516 (surviving syntypes of *variabilis*). 8C 2A Mtschinga, Wanga, north of Lindi, Tanzania (9° 40′ S, 39° 40′ E), 3–5 m; Hamburg V. 6207 & V. 6216 (Michaelsen, 1905 : 352). 4C 1A Damp soil, close by a water course, Bububu, Zanzibar (6° 06′ S, 39° 13′ E), –200 m; Hamburg V. 7512 (Michaelsen, 1913 : 55).

Other records. Malindi, Kenya (3° 13′ S, 40° 08′ E), 15 m ('50 ft'); (unique holotype of *malindus*; not located April, 1980 in the Museum of Comparative Zoology, Harvard). Mombasa, Kenya (4° 03′ S, 39° 40′ E), –200 m; (Michaelsen, 1897 : 51). Danda, near Kingani River, Tanzania (6° 23′ S, 38° 52′ E), 200 m; (Michaelsen, 1896 : 51). Mrogoro, Tanzania (?6° 49′ S, 37° 40′ E), –1000 m; (Michaelsen, 1897 : 51). ?Mbanja ('Banja'), Wanga, north of Lindi, Tanzania (?9° 45′ S, 39° 40′ E), –200 m; (Michaelsen, 1897 : 52).

DISTRIBUTION. Eastern districts of Kenya and Tanzania at low altitudes (Fig. 2F).

REMARKS. Preserved material of this species exhibits a range of variations most of which are natural, that is biological, but some are due to the differing techniques employed by collectors. Unfortunately undue taxonomic significance has been attributed to both categories of differences with the result that several new taxa have been recognized to accommodate variants. Externally the genital papillae vary in number, location and size, presumably according to the age and degree of sexual development of the individual. Michaelsen seemingly considered that the position and development of the papillae were taxonomically important but re-examination of his material reveals that these differences are individual although sometimes constant in the members of a single series. Other external variations in preserved material are seen in the presence and size of the penis, i.e. the extent to which the penis protrudes through the secondary male pore and its shape, whether flattened or rounded. But these differences appear to be directly attributable to collecting techniques and subsequent preservation. Extremes may be seen in contracted, well-preserved specimens having the penis retracted to excessively relaxed, often almost macerating, specimens in which the penis is well-formed and onion-shaped with no sign remaining of the secondary male pore. (Intermediately relaxed, moderately well preserved specimens usually have only the distal portion of the penis protruding.) The extent to which the penis protrudes can be correlated with internal variations in the size of the male pouch, this structure is usually evident when the penis is retracted but not seen when the penis is everted.

Also internally, the receptaculum seminis may vary in detail both in the numbers of diverticula and in the size and shape of these sacs. Comparable variations are present in most species of this family since the spermathecal systems are composed of delicate, coelomic tissues whose morphologies within the limits of the species, are largely determined in detail by the volume and main sites of aggregation of the sperm carried and to some extent, the disposition and development of adjacent organs. The prostates can vary too. In subadult specimens the prostates are short and regular but in older individuals these glands may be long, occasionally convoluted and constricted intersegmentally when large. The differences between this species and *coeruleus* are slender. The two species can be separated on the characters of the receptaculum seminis, *coeruleus* possesses only a single pair of diverticula behind the spermathecal pore whereas there are three or more pairs in *violaceus.*

Polytoreutus arningi species group
(Figs 17 & 18)

Diagnosis. Male and spermathecal ducts (in mature adults) open externally into a common pore or concavity. Anterior furcae of the receptaculum seminis often poorly developed with proximal (basal) or distal (terminal) ducts leading to the fertilization chambers.

Distinguishing characters. The group comprises three species: *arningi* Michaelsen, 1897 from Tanzania, *stierlingi* Michaelsen, 1899 from Kenya and Tanzania, *monoporus* sp. nov. from Kenya. They are separable mainly on the occurrence of 'copulatory sacs' and the size of the male pouch also the morphology of the spermathecal system.

arningi. Male pouch large with paired posterolateral 'copulatory sacs'. Receptaculum seminis simple passing directly from the anterior bifurcation to the spermathecal pore; anterior furcae poorly developed and may be overlooked.

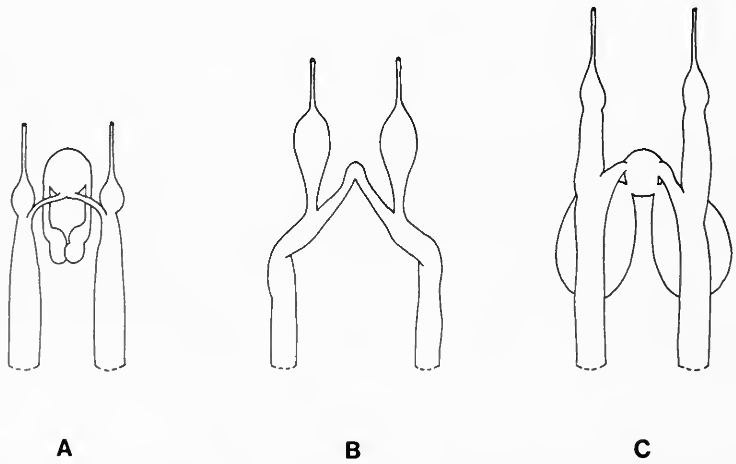

Fig. 17 *Polytoreutus arningi* species group. Prostates, anterior regions (schematic dorsal views, not to scale): (A) *arningi*; (B) *monoporus*; (C) *stierlingi.*

stierlingi. Male pouch small with paired posterolateral 'copulatory sacs'. Receptaculum seminis simple extending posteriorly as a blind sac behind the spermathecal pore to about *xxv*; anterior furcae swollen but truncate.

monoporus. Male pouch inconspicuous, parietal 'copulatory sacs' absent. Receptaculum seminis simple but extending posteriorly as a blind sac to about *xxv*; anterior furcae well developed but not massive as in members of the *kilindinensis* species group.

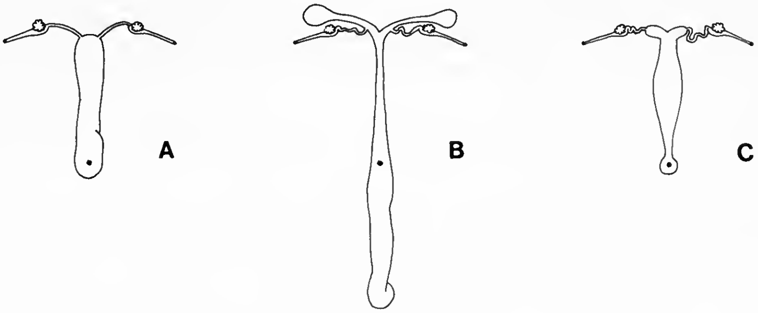

Fig. 18 *Polytoreutus arningi* species group. (A) *arningi* (syn. *fuellerborni* syntype); (B) *monoporus* (syntype); (C) *stierlingi* (syntype).

Polytoreutus arningi Michaelsen, 1897
(Figs 17A & 18A)

Polytoreutus arningi Michaelsen, 1897 : 53; 1900 : 417.
Polytoreutus fuelleborni Michaelsen, 1905 : 360.

Description. *External characters.* Length 150–230 mm, diameter 4–6 mm (up to 11 mm at clitellum), segments circa 270. Prostomium prolobous. Clitellum *xiii–xvii* annular, incomplete ventrally in subadults and seemingly saddle-shaped. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 2 : 4 : 1. Male and spermathecal pores concealed within a common copulatory pouch with a large circular to scutate orifice *xviii* bordered by an elevated glandular ridge; within the pouch the spermathecal pore may be seen surrounded by raised lips and immediately posteriorly, paired copulatory appendages (the copulatory appendages may appear as papillae or in excessively relaxed individuals, may even extend outside of the pouch). The perigenital ridge is horseshoe-shaped latero-posteriorly and limited anteriorly (in mature specimens) by a transverse bow-shaped ridge in *xvi* and *xvii* raised into a median papilla. Female pores paired $\frac{3}{4}$*xiv* in setal line *c*. Pore-like, median papillae occasionally in 19/20.

Internal characters. Prostatic glands tubular, somewhat clavate being more slender ectally, extending back perhaps to *xxxii* but possibly only to *xxii* when strongly flexed; subterminal ectal cornu present receiving the vas deferens of its side. Male pouch large, penis not seen. The spermathecal system comprises a simple, adiverticulate receptaculum seminis passing forwards from the spermathecal pore to the anterior bifurcation in *xiii*, the fertilization chambers are located distally (terminally) on the lateral furcae. A pair of raised pads are present in the parietal wall posterolaterally to the spermathecal pore (termed 'copulatory sacs' by Michaelsen); these contain the copulatory appendages which when everted, protrude externally through the orifice of the copulatory pouch (their size depending on the preservation techniques employed).

Type locality. Kirombero (Ulanga valley) and Ruaha valley, Tanzania.

Material examined. *Previous records.* 2C 6A (fragments) Kiromberu, Ulanga valley (approx. 8° 10′ S, 37° 30′ E) and Ruaha valley (approx. 7° 40′ S, 37° 30′ E), Uhehe Territory, Tanzania, –200 m; Hamburg V. 4484 (syntypes of *arningi*). 2C Langenburg north of Lake

Malawi ('Njassa') (9° 30′ S, 34° 10′ E), Tanzania; Hamburg V. 6669 (holotype of *fuelleborni*) and Hamburg V. 7643 (paratype of *fuelleborni*).

DISTRIBUTION. Central and western Tanzania (Fig. 2G).

Polytoreutus stierlingi Michaelsen, 1899
(Figs 17B & 18B)

Polytoreutus stierlingi Michaelsen, 1899 : 134; 1900 : 416.

DESCRIPTION. *External characters.* Length 60, 102 mm, diameter 3, 4 mm, segments 104, 247, posterior half of the body slender about half the diameter of the anterior region (2 clitellate specimens). Prostomium pro(epi)lobous. Clitellum annular, $\frac{2}{3}$*xiii–xvii*. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 4 : 3 : 4 : 1. Male and spermathecal pores (of adults) contained within a single 'copulatory' pore or concavity extending $\frac{1}{2}$*xvi*, *xvii*–$\frac{1}{3}$*xix*, in subadults the male pore opens into a shallow concavity extending between $\frac{1}{2}$*xvi* or *xvii* to $\frac{2}{3}$*xviii* with the spermathecal pore slit-like and inconspicuous in 18/19; 'copulatory' pore with a stout penis protruding anteriorly and the distal ends of paired copulatory appendages seen posteriorly, the body wall around the 'copulatory' pore or concavity is raised and highly glandular. Genital papillae and markings absent. Female pores paired $\frac{3}{4}$*xiv* in setal line *c*.

Internal characters. Prostates tubular extending back to *xxx–xxxii*, anteriorly each has a long anterior cornu reaching forward from *xvii* to *xv* where it receives the vas deferens of its side; male pouch inconspicuous with large, paired posterolateral accessory pouches (containing the copulatory appendages) lying ventrally *xviii–xx*. The spermathecal system comprises a single, median adiverticulate receptaculum seminis extending from the anterior bifurcation in *xiii* to beyond the spermathecal pore, perhaps to *xxv*; the anterior furcae are swollen but short (possibly longer in mature adults), proximally paired (basal) ducts lead to the fertilization chambers.

TYPE LOCALITY. 'Iringa' (?Kuirenga), Tanzania.

MATERIAL EXAMINED. *Previous record.* 1C fragment ?Kuirenga ('Iringa'), Ruaha Valley Uhehe Territory, Tanzania (7° 46′ S, 37° 42′ E), −200 m; Hamburg V. 5040 (holotype of *stierlingi*).

New records. Kenya (*Coll.* E. Oxtoby): 2C(subadults) 31A(juveniles) ?Ngangao ('Ngangau', Forest, Taita Hills, (3° 22′ S, 38° 20′ E), −1500 m, 10 Aug. 1978; BM(NH) 1981.6.1369–1404. 5A (juveniles) Roadside mud, Vuria radio station, Taita Hills, (?3° 25′ S, 38° 18′ E), −1500 m, 13 Aug. 1978; BM(NH) 1981.6.1405–1409.

DISTRIBUTION. Central Kenya to central Tanzania (Fig. 2G).

Polytoreutus monoporus sp. nov.
(Figs 17C & 18C)

DESCRIPTION. *External characters.* Length 67, 102 mm, diameter 2·0, 2·5 mm, segments 121, 225. Prostomium epilobous, open posteriorly. Clitellum $\frac{1}{2}$*xiii–xvii* annular. Setae at *xxx*, *aa* : *ab* : *bc* : *cd* = 3 : 2 : 3 : 1. Male and spermathecal pores contained within a single elongate; 'copulatory pore' or concavity, 17/18–$\frac{1}{2}$*xviii* long and *aa* wide; a prominent male porophore (? penis present) occupies the anterior part of the 'copulatory pore' while the posterior part is deeply sunken with a glandular floor and a pair of lateral and a pair of posterior pads surrounding a medial spermathecal pore. Female pores paired $\frac{3}{4}$*xiv* midway between setal lines *c* and *d*.

Internal characters. Prostates tubular, long and slender, reaching back to about *xxx*; anteriorly each has a long subterminal anterior cornu extending to 15/16 where it receives the vas deferens of its side. Male pouch not seen. Spermathecal system single, adiverticulate with a simple receptaculum seminis extending posteriorly far behind the spermathecal pore to about *xxv*; the furcae of the anterior bifurcation are massive with proximal (basal) ducts leading to the fertilization chambers.

TYPE LOCALITY. Vuria, Taita Hills, Kenya.

MATERIAL EXAMINED. (*Coll.* E. Oxtoby): 2C Roadside mud, Vuria radio station, Taita Hills, Kenya (3° 25′ S, 38° 18′ E), –1500 m, 13 Aug. 1978; BM(NH) 1981.6.1209–1210 (syntypes of *monoporous*).

DISTRIBUTION. Known only from the type locality (Fig. 2G).

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