

A generic revision of the Dorvilleidae (Polychaeta), with six new species from the deep North Pacific

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The Dorvilleidae are divided into eight genera: *Dorvillea*, *Schistomeringos* (new name), *Protodorvillea*, *Meiodorvillea* (new genus), *Exallopus* (new genus), *Ophryotrocha*, *Parophryotrocha*, and *Apophryotrocha* (new genus). Periodic maxillary replacement is found to occur in a manner which makes many often cited maxillary characters taxonomically unreliable. Therefore, the pharyngeal characters of all the type-species are redescribed or newly described. The discovery of new forms and the present interpretation of hard jaw parts permit construction of a phylogenetic scheme with *Dorvillea* as the most primitive genus containing living species. Suggestions are given for the advantageous use of the phenomenon of maxillary replacement in autecological investigation.

Evidence is presented against the cosmopolitan distribution of *Schistomeringos rudolphi*, a species often noted in nearshore pollution studies. Newly described species are *Dorvillea batia*, *Schistomeringos mediofurca*, *Meiodorvillea apalpata*, *Exallopus cropion*, *Ophryotrocha profunda*, and *Apophryotrocha mutabiliseta*, all from the deep North Pacific. A key to the genera is provided, as are listings of all the known species within each genus.

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INTRODUCTION

Collections by the Scripps Institution of Oceanography, University of California, in the Pacific Ocean from the San Diego Trough, the Aleutian Trench, and the abyss near the equator have revealed six new forms of dorvilleids. Some of these species exceed the range of morphologies heretofore observed in the family. Others provide clues to the relationships between known genera.

The present attempt is to incorporate the recognized species and the six new species of Dorvilleidae into a natural classification. Attention to detailed structure of the pharyngeal apparatus, as suggested by Fauchald (1970), permits such an arrangement for the first time. Use of these characters to distinguish between species requires an assessment of their variability within species. Attendant variability of external features is also appraised in some species to resolve those attributes which are most useful taxonomically.

New type material is deposited in the Allan Hancock Foundation of the University of Southern California, Los Angeles, California.

MATERIALS AND METHODS

All the new species were taken from samples obtained either in a 0.25 m², modified USNEL spade corer (Rosfelder & Marshall, 1967) or an epibenthic sled (Hessler & Sanders, 1967). All stations using these devices are designated herein with the prefix SIO (Scripps Institution of Oceanography, La Jolla, California). Complete SIO locality data are located in Table 1 for all these stations.

In the manner recommended by Fauchald (1970), whole small specimens were cleared for pharyngeal examination, while the jaws were removed by dissection from large individuals. To further expose jaw pieces in those species with opaque tissues, a mid-dorsal longitudinal incision was made before clearing.

The terminology of these parts is derived from Fauchald (1970), but differs sufficiently to warrant a brief redescription. All anatomical positions of the pieces refer to the completely retracted proboscis.

The carriers are the dorsalmost components of the chitinized apparatus whenever they are clearly present. In most species, they are fused posteriorly to produce a V-shaped structure (as in Fig. 5). Immediately below each carrier is a basal plate, defined as the posteriormost denticle or group of fused denticles in a given denticle row. These two basal plates are again most often posteriorly fused (as in Fig. 5). Anterior to each basal plate is a longitudinal series of denticles, free, toothed structures usually smaller in the longitudinal dimension than the basal plate. Another inferior and more medial series of denticles may also be present (as in Fig. 5) and is again terminated posteriorly by a basal plate.

The terminology of external morphology adheres to Pettibone (1961) and to Fauchald (1970). Some of the measurements referred to are illustrated in Fig. 2. Drawings and measurements were made with camera lucida attachments for Wild M5 and M20 microscopes. Body dimensions do not include parapodia.

Only the principal synonyms have been listed under the species discussed below.

SYSTEMATICS OF DORVILLEIDAE

Family Dorvilleidae Chamberlin, 1919

Description. The rounded prostomium nearly always bears a pair of dorsolateral antennae and a pair of lateral palps. Antennae and palps may be simple or may carry one or more articles. Rarely, either the antennae, palps, or even both may be absent. Up to four circular or reniform eyes may be present. Nuchal organs may occur as a pair of indistinct pouches at the postectal prostomial margin or may include a median papilla posterior to the antennae. Two apodous rings, not true segments (Åkesson, 1967), are present between the prostomium and the first setiger.

Parapodia are uniramous or subbiramous. Neuropodia are nearly always well developed and bear smooth or denticulate capillary setae above the principal acicula and heterogomph setae below. In addition, the supra-acicular bundle may contain furcate setae. When dorsal and ventral cirri occur, they are digitate, ellipsoid, or papilliform.

Dark, chitinized mandibles are always present. They are anteriorly flared and are most often denticulate. Maxillary structures consist of a pair of carriers and four rows of denticles with accompanying basal plates. These components are variously modified, lost, or fused, in age-specific and species-specific manners.

Remarks. As can be seen from a perusal of Pettibone's (1961) revision, the dorvilleids have suffered a plethora of nomenclatural difficulties. As she shows, most of these difficulties have been solved according to the International Code of Zoological Nomenclature (ICZN; Stoll & Melville, 1961), but one has been passed over. An historical review may be of some help in resolving the difficulty.

In 1855, Grube described *Staurocephalus rubrovittatus* (type-species by monotypy). This species lacks furcate setae. In 1866, Parfitt described *Dorvillea lobata*. In 1900, Verill realized *Staurocephalus* was preoccupied, and he proposed *Stauronereis* as a replacement name. At the same time, he proposed that *Nereis Rudolphi* delle Chiaje, 1828, a species with furcate setae, become the type-species of *Stauronereis*. Article 67(i) of the ICZN retroactively forbids changing of the type-species when a generic name is replaced. *Stauronereis* Verrill thus becomes invalid.

In 1910, McIntosh synonymized *Dorvillea lobata* and *Staurocephalus rubrovittatus*. *Dorvillea* thus became the valid name for the genus typified by *Staurocephalus rubrovittatus* Grube.

The group of dorvilleids typified by *Nereis Rudolphi* delle Chiaje is hence left without a name. *Schistomeringos*, Greek for "split bristle," is proposed. It is feminine in gender and refers to the characteristic furcate setae of the genus. The diagnosis very closely parallels that of *Stauronereis* sensu Pettibone (1961).

Genus *Schistomeringos* nom. nov.

Type-species. *Nereis Rudolphi* delle Chiaje, 1828.

Diagnosis. The prostomium diverges from a hemispherical shape by being slightly compressed dorsoventrally. Antennae and palps are well developed and are of approximately equal lengths. The latter are biarticulate and the former are multiarticulate. Dorsal and ventral cirri are present, the former being

biarticulate and enclosing an acicula. Three classes of setae are found in each species: (1) capillary, (2) furcate, and (3) compound heterogomph. Carriers may be fused with the basal plates of the superior rows of denticles, but four distinct rows of denticles are always apparent. The basal plates of the inferior rows of denticles are free and are over three times longer in longitudinal dimension than the longest denticles in their own rows.

Remarks. *Schistomeringos* includes the following species: *S. rudolphi* (delle Chiaje, 1828); *S. incerta* (Schmarda, 1861); *S. caeca* (Webster & Benedict, 1884); *S. longicornis* (Ehlers, 1901); *S. annulata* (Moore, 1906); *S. neglecta* (Fauvel, 1923); *S. japonica* (Annenkova, 1937); *S. furcata* (Hartman, 1953); and the new species described herein. The names of more poorly known subbiramous dorvilleids which may belong in the genus are listed in Appendix I.

Schistomeringos rudolphi (delle Chiaje, 1828)

(Fig. 1)

Nereis Rudolphi delle Chiaje, 1828: 176.

Staurocephalus Rudolphi: Fauvel, 1923: 446-7, fig. 178 a-p.

Dorvillea rudolphi: Hartman, 1944: 191.

Stauronereis rudolphi: Pettibone, 1963: 231-3, fig. 60 a-f, *partim*.

Dorvillea rudolphi: Fauchald, 1970: 156-9, pl. 27, figs a-j, *partim*.

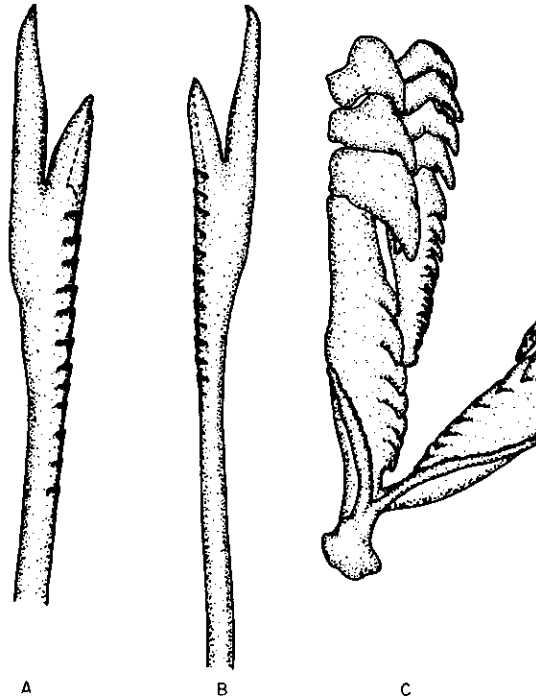


Figure 1. *Schistomeringos rudolphi* (delle Chiaje): A, furcate seta of parapodium 10; B, same; C, left posterior portion of maxillae in oblique view. A is from Dinard; B and C are from the Bay of Naples.

Material examined. Ten topotype specimens from the Bay of Naples (AHF 10950), five specimens from Concarneau, south-west Brittany (MNHN), and five specimens from Dinard, north-east Brittany (MNHN) were externally examined and then dissected for pharyngeal inspection.

Description. Both the external characters and pharyngeal parts of *S. rudolphi* have often been described, but their intrapopulation and intraspecific variabilities have never been objectively ascertained. Ten individuals were selected at random from the Bay of Naples sample. This sample of about 200 specimens was kindly provided by Fauchald and is the same one upon which his (1970) redescription is based. Table 2 lists those characters measured in the present study, their mean values, and their standard deviations. Figure 2a, b, d-g illustrates some of the measurements on the corresponding parts of *S. longicornis*.

Some of the variability in the cirrophore/cirrostyle ratio and in total number of compound setae per parapodium corresponds with the variability in overall size of the ten specimens (rank correlation, Tate & Clelland, 1957; 13-4). The number of free maxillary denticles is very strongly correlated ($P < 0.05$, rank correlation) with the size of the individual and cannot be used as a specific character without regard for the relative sizes of the specimens compared.

The present analysis of pharyngeal structure differs in part from that of Fauchald (1970). The basal plates of the superior rows of denticles are always fused posteriorly, albeit weakly. Eighty per cent of the specimens dissected lack what he describes as maxillae III and IV. The other two specimens roughly approximate his account but are interpreted to reveal the process of maxillary replacement, as summarized in the discussion section of this paper. Maxilla II *sensu* Fauchald is judged to be the replacement member for maxilla I, and maxilla IV is construed as the replacement for maxilla III. Maxilla I thus corresponds to the normal superior rows of denticles and basal plates, while maxilla III corresponds to the normal inferior rows. Close observation also reveals replacement carriers set immediately below and closely appressed to the older carriers.

Briefly, the maxilla consists of the following parts: a toothed pair of posteriorly fused carriers, two superior denticle rows with toothed and

Table 1. Station data for those samples collected from Scripps Institution of Oceanography vessels (SIO). The prefix H indicates the sample was collected by R. Hessler; J indicates collection by P. Jumars. Only H84 was collected with an epibenthic sled; all the other samples were taken with a box corer

No.	Date	Depth (m)	North latitude	West longitude	Locality
H22	13-XII-69	1224	32° 28.2'	117° 29.8'	San Diego Trough
J14	6-XII-71	1224	32° 28.2'	117° 29.8'	San Diego Trough
J15	6-XII-71	1229	32° 28.1'	117° 29.8'	San Diego Trough
J22	5-I-72	1223	32° 28.9'	117° 30.1'	San Diego Trough
H39	20-VII-70	7298	50° 58.0'	171° 37.5'	Aleutian Trench
H84	19-I-72	4435-4438	3° 1.9'	125° 0.8'	Equatorial Pacific

Table 2. Statistics from various characters of *Schistomeringos rudolphi* from the Bay of Naples, where \bar{x} is the mean, S.D. is the standard deviation, R is right, L is left, and the sample size is 10. (See also text and Fig. 2.)

Character and side of specimen		\bar{x}	S.D.
Number of groups of teeth on basal plate of superior denticle row of maxillae	R	8.1	1.4
	L	8.1	1.2
Number of groups of teeth on basal plate of inferior denticle row of maxillae	R	13.0	3.7
	L	17.5	5.0
Number of denticles in superior denticle row of maxillae	R	31.3	6.9
	L	31.0	7.3
Number of "free" teeth of mandible	R	4.0	1.6
	L	3.8	1.0
Number of antennal articles including basal one	R	6.8	2.2
	L	6.3	2.6
Length of palpostyle/length of palpophore	R	0.31	0.12
	L	0.35	0.12
Length of ventral cirrus/length of neuropodium, parapodium 10	R	0.45	0.04
	L	0.45	0.04
Distance to insertion of ventral cirrus/length of neuropodium, parapodium 10	R	0.45	0.06
	L	0.43	0.06
Length of neuropodium/length of dorsal cirrus, parapodium 10	R	0.59	0.05
	L	0.64	0.07
Length of cirrostyle/length of cirrophore, parapodium 10	R	0.45	0.12
	L	0.43	0.16
Length of shortest appendage/length of longest appendage of compound setae of parapodium 10	R	0.41	0.05
	L	0.44	0.07
Length of short tine/length of long tine, average for furcate setae of parapodium 10	R	0.50	0.04
	L	0.49	0.05
Number of capillary setae, parapodium 10	R	2.1	0.98
	L	2.1	0.50
Number of furcate setae, parapodium 10	R	1.8	0.79
	L	1.7	0.47
Number of compound setae, parapodium 10	R	10.6	2.7
	L	10.0	2.3

posteriorly fused basal plates, and two inferior denticle rows with free, toothed basal plates. The arrangement of these parts is shown in Fig. 1C.

Remarks. *S. rudolphi* was originally described from the Bay of Naples. In those characters measured, populations from Brittany agree with the topotypes. It is doubtful, however, that the specimens reported by Day (1967) from South Africa are conspecific. His illustration (p. 456, fig. 17.21d) shows denticulation of the medial edge of the long tine of the furcate seta. As can be seen in Fig. 1A, B, such denticulation is absent in specimens from the Bay of Naples and from Brittany. In view of these findings, it may prove worthwhile to re-examine the affinities of *S. rudolphi sensu* Pettibone (1963) from the eastern coast of North America.

Distribution. *S. rudolphi* is found in shallow water in the Mediterranean Sea and off Brittany. It may be ampho-Atlantic but does not appear to be cosmopolitan.

Schistomeringos longicornis (Ehlers, 1901)

(Fig. 2)

Stauronereis longicornis Ehlers, 1901: 150-1, pl. 19, figs 18-21, pl. 20, figs 4-6.

Stauronereis articulatus Hartman, 1938: 101-2, figs 39-44; Rioja, 1941: 724-7, pl. 6, figs 10-18.

Dorvillea articulata: Hartman, 1944, 189, 1968, 817, figs 1-5; Rioja, 1947: 205; Reish, 1963: 426.

Dorvillea rudolphi: Berkeley & Berkeley, 1948: 86-7, figs 127-129; Fauchald, 1970: 156-9, pl. 27, figs a-j, *partim*.

Stauronereis rudolphi: Pettibone, 1963: 231-3, fig. 60 a-f, *partim*.

Dorvillea atlantica: Hartman, 1963: 35; 1968: 819, figs 1-5.

Material examined. The specimens considered by Hartman in her original (1938) description of *Stauronereis articulatus* were externally examined as follows: the holotype from Dillon Beach, Marin County (USNM 20363); two individuals from Point Conception, Santa Barbara County (AHF 3617); and, three examples from San Pedro, Los Angeles County (AHF 3618). Five additional specimens from Point Vicente, Los Angeles County (AHF 4806-57, referred to *S. articulatus* by Hartman) were similarly treated, as were single specimens from each of the following localities in Washington and British Columbia (BCPM): Massacre Bay near Orcas Island, Harney Pass near Orcas Island, Strait of Juan de Fuca, and Blubber Bay. Six specimens taken from the Coronado Canyon and referred to *Dorvillea atlantica* by Hartman (1963, 1968) were externally inspected and then dissected for pharyngeal examination.

Remarks. Differences are observed in qualitative and quantitative characters among the populations of *S. longicornis*. For example, in the Coronado Canyon sample, two of the six specimens bear an aberrant type of seta among the normal compound ones (Fig. 2B, C). These unusual setae are longer than the normal compound sort but completely lack the basal shaft. Hence a fraction of this population bears simple setae below the neuroacicula. In addition, the eyes in this deep-water population are much less heavily pigmented than those of the shallow-water forms. As Hobson notes (*pers. comm.*), furcate setae may not appear in specimens from the Pacific Northwest anterior to the fourth, fifth, or even fifteenth setiger.

Although Pettibone (1963) and Fauchald (1970) include them under one name, confidence in the difference between the East Pacific and Mediterranean species stems from the fact that, despite the differences among populations within each of the species, they remain distinct on the basis of the tabled characters (Table 3). This list is by no means exhaustive. For example, the species also differ in the shapes, sizes, and numbers of teeth on the anterior denticles of the superior rows and in the numbers of groups of teeth in the basal plates, but these differences are far more difficult to quantify than are the tabled features. Variability due to the age or size of the specimens must be extracted from these maxillary characteristics before they can be reliably employed in species discriminations. Similarly, *S. rudolphi* appears to have fewer compound setae per parapodium than does *S. longicornis*, but the difference is again confounded with relative sizes of the individuals, large

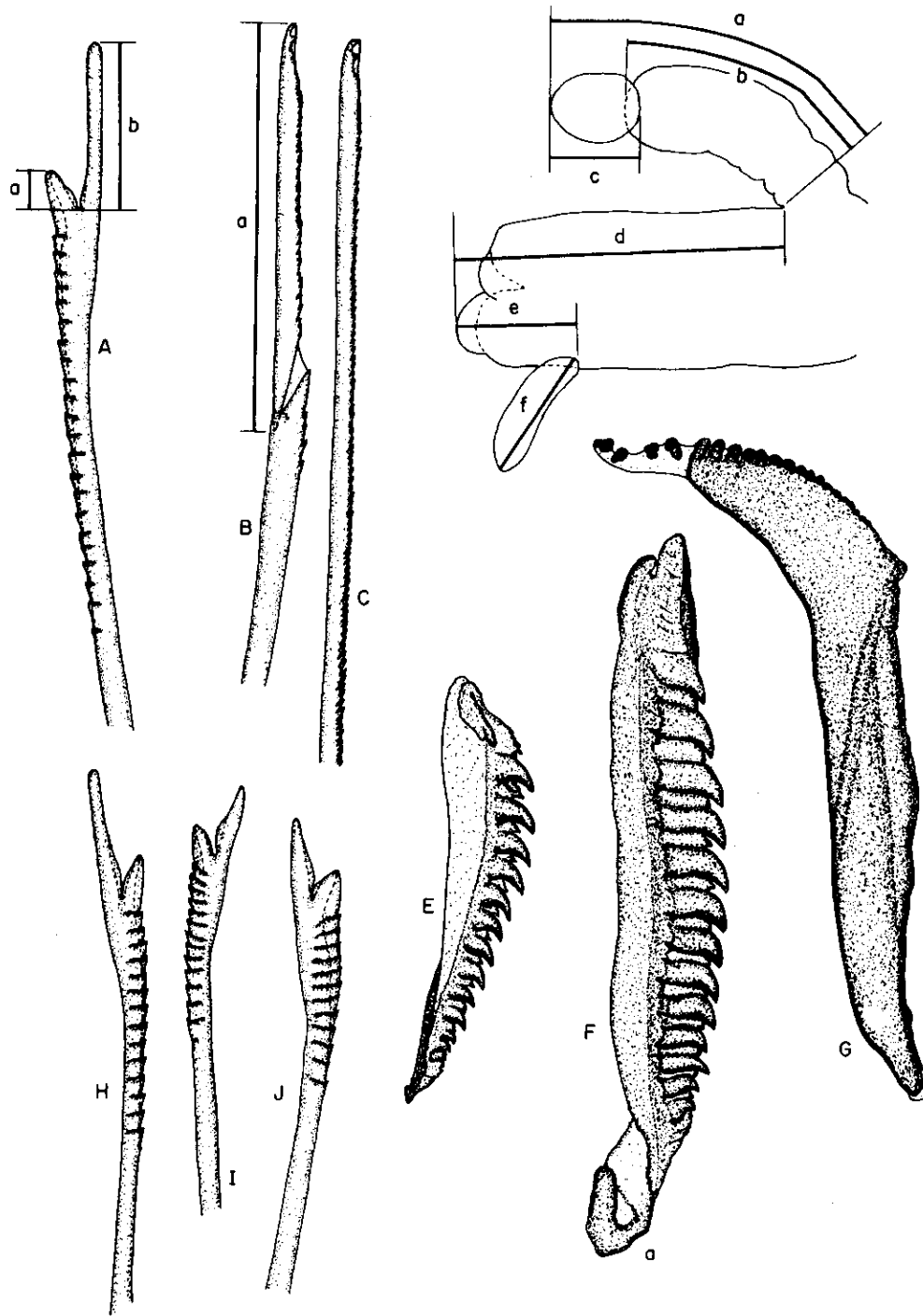


Figure 2. *Schistomeringos longicornis* (Ehlers): A, furcate seta, a, length of short tine, b, length of long tine; B, compound seta, a, length of appendage; C, unusual simple seta (see text.); D, parapodial outline, a, length of dorsal cirrus, b, length of cirrophore, c, length of cirrostyle, d, length of neuropodium, e, distance to insertion of ventral cirrus, f, length of ventral cirrus; E, right basal plate with 14 groups of teeth from the inferior denticle row, in side view; F, right basal plate with 14 groups of teeth from the superior denticle row, a, posterior end broken away from the left basal plate, in side view; G, left mandible with four "free" teeth; H-J, furcate setae. A-G are from the Coronado Canyon; H is from Harney Pass; I is from Point Conception; and, J is from Point Vicente. All parapodial parts are from parapodium 10.

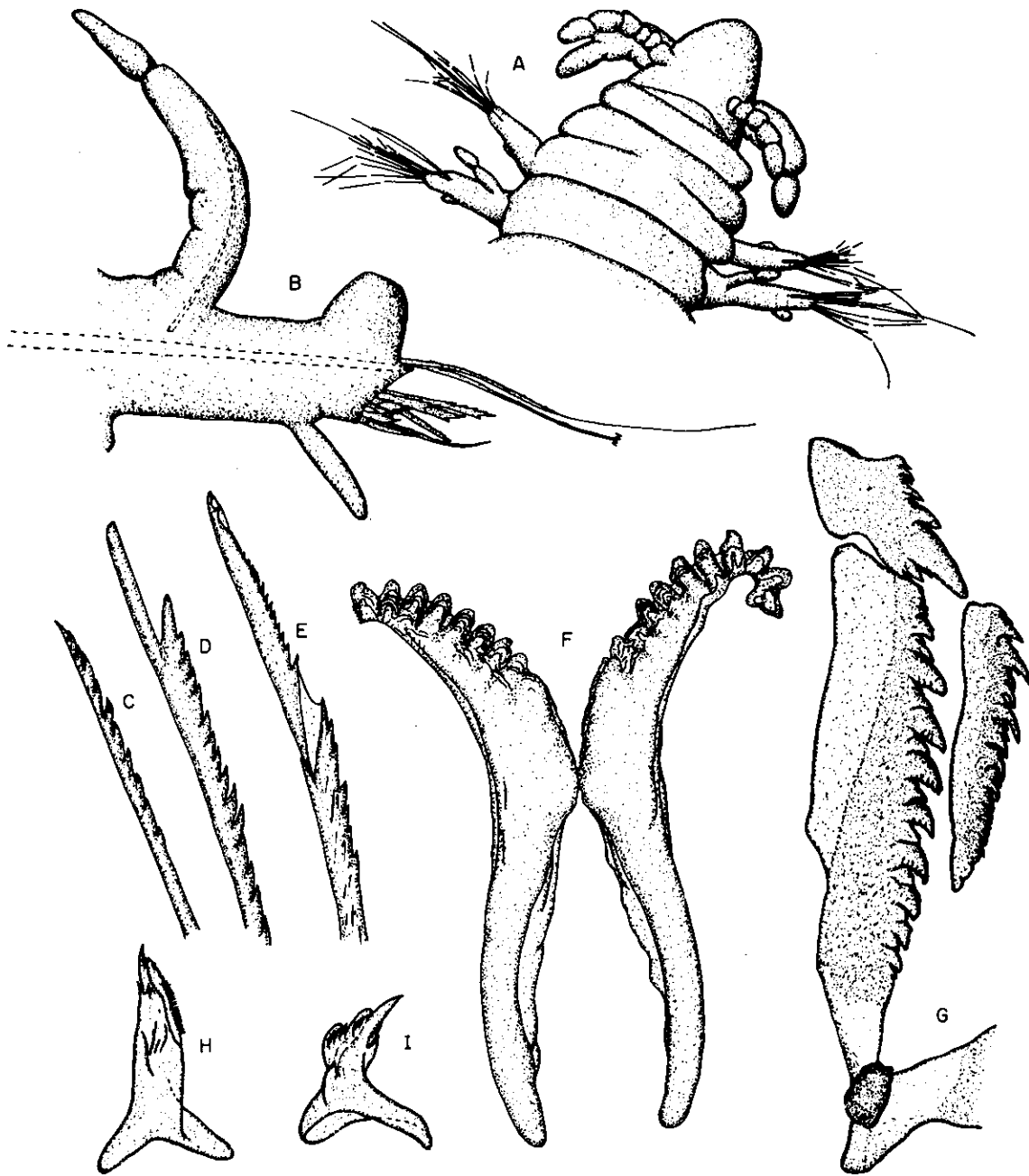


Figure 3. *Schistomeringos mediofurca* sp. nov.: A, anterior in dorsal view; B, parapodium 10 with distal swelling, sawtoothed line indicating a broken seta; C-E, the three types of setae in parapodium 33; F, mandibles in dorsal view; G, posterior left portion of maxillae in oblique view; H, far anterior denticle of inferior row; I, far anterior denticle of superior row. All drawings are from the paratype.

the latter are biarticulate or simple. Dorsal and ventral cirri are present, the former being biarticulate or simple and enclosing an acicula. Two classes of setae are found in each species: (1) capillary and (2) compound heterogomph. Furcate setae are absent. Carriers and four rows of denticles are always apparent, although the carriers may be fused with the basal plates of the superior rows of denticles. The basal plates of the inferior denticle rows may be fused with the basal plates of the superior rows. When they are not so joined, the inferior basal plates are shorter in the longitudinal dimensions than three times the length of the longest teeth in their own rows.

Remarks. *Dorvillea* includes the following species: *D. rubrovittata* (Grube, 1855); *D. rubra* (Grube, 1856); *D. vittata* (Grube, 1856); *D. socialis* (Webster, 1879); *D. australiensis* (McIntosh, 1885); *D. cerasina* (Ehlers, 1901); *D. moniloceras* (Moore, 1909); *D. romeri* (Augener, 1912); *D. angolana* (Augener, 1918); *D. crassa* Chamberlin, 1919; *D. gardineri* (Crossland, 1924); *D. similis* (Crossland, 1924); *D. pseudorubrovittata* Berkeley, 1927; and, the new species described herein. Some subbiramous dorvilleids which may belong to this genus are listed in Appendix I.

Dorvillea rubrovittata (Grube, 1855)

(Fig. 4)

Staurocephalus rubrovittatus Grube, 1855: 97; Ehlers, 1868: 424, pl. 18, figs 1-16; McIntosh, 1910: 353-7, pl. 55, fig. 1, pl. 61, fig. 7, pl. 73, fig. 4, pl. 81, fig. 9; Fauvel, 1923: 445-6, fig. 177, a-l.

Staurocephalus erucaeformis Malmgren, 1865: 184; 1867: 177, pl. 9, fig. 50.

Dorvillea lobata Parfitt, 1866: 113, figs 1-5.

Teleonereis rubrovittatus: Verrill, 1900: 648.

Dorvillea rubrovittata: Hartman, 1944: 187-9; Day, 1967: 457-8, fig. 17.21 k-m; Hartmann-Schröder, 1971: 261.

Material examined. Four specimens from Dinard, France, and six from Algiers (MNHN) were examined by dissection. These specimens agree in external detail with a specimen from Nice, France, identified by Grube (ZMUH V-884). An additional example with its jaws everted (LL, locality unknown) required no dissection.

Description. The carriers of this species have not previously been described. Specimens from Brittany and from Algeria have in common denticulate carriers which are fused posteriorly but are free from the basal plates of the superior denticle rows (Fig. 4C). These basal plates are themselves fused posteriorly. The basal plates of the inferior rows are free and appear to be little more than slightly modified, single denticles.

The specimens from Brittany have denticles in the middle of the superior rows with main fangs well over five times the lengths of the corresponding teeth in Mediterranean examples (Fig. 4A, B). This disturbing find suggests that close comparisons of even more widely separated populations of *D. rubrovittata* might reveal the lumping of several subspecies or even species under the same binomial. The observed differences in denticle type could permit considerable divergence in food preferences.

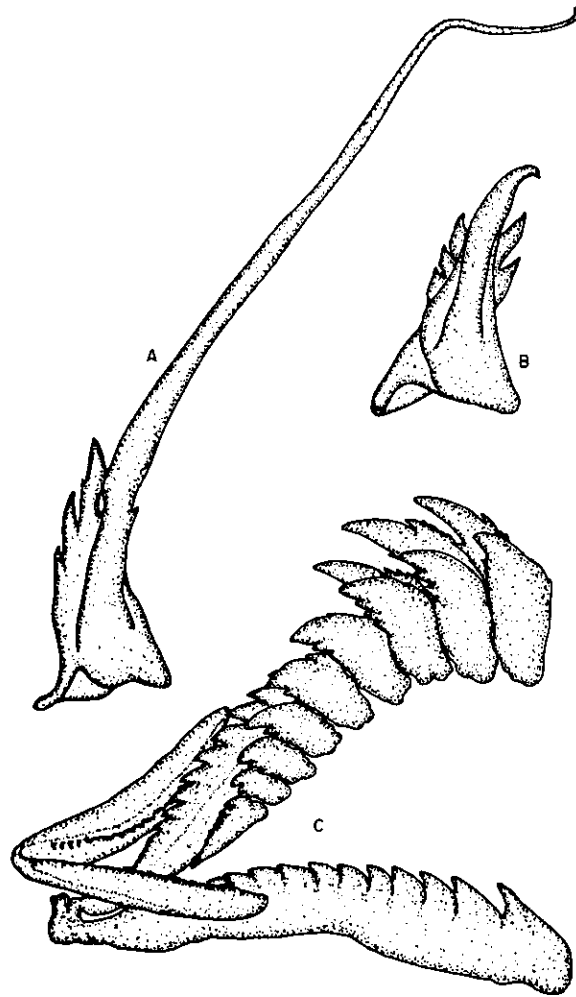


Figure 4. *Dorvillea rubrovittata* (Grube). Maxillae: A, median tooth of superior denticle row from Brittany; B, median tooth of superior denticle row from Algiers; C, left posterior portion from Algiers in oblique view.

One of the specimens from Algiers has partially doubled maxillary parts. As in *S. rudolphi*, the more ventral, unworn parts are thought to be replacements.

Distribution. The type locality is the Adriatic, but the species has been reported from northern European latitudes to tropical West Africa in the Atlantic, as well as from several localities in the Mediterranean. It has been found only in shallow water.

Dorvillea gardineri (Crossland, 1924)

(Fig. 5)

Staurocephalus (Dorvillea) gardineri Crossland, 1924: 93-9, figs 112-118.

Staurocephalus gardineri: Fauvel, 1953: 280, fig. 143, d-f.

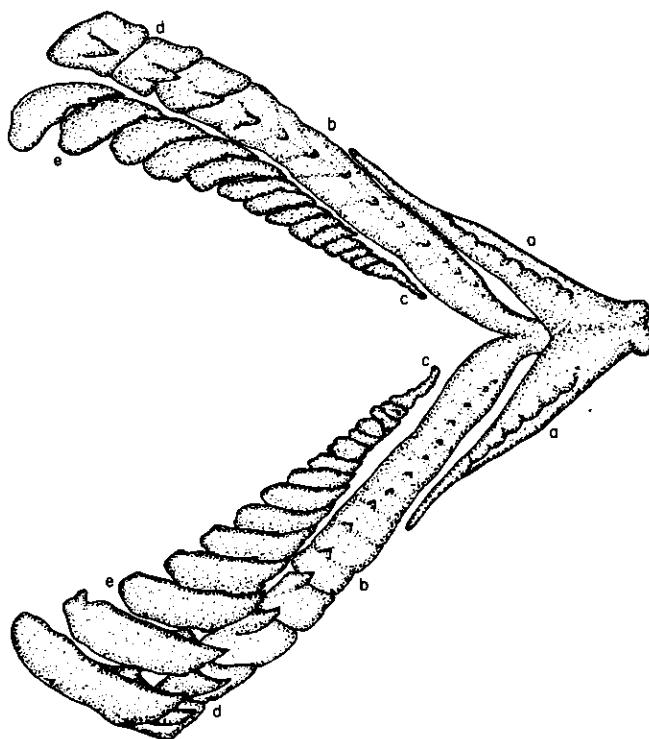


Figure 5. *Dorvillea gardineri* (Crossland). Maxillary apparatus in oblique view: a, carrier; b, basal plate of superior row; c, basal plate of inferior row; d, denticle of superior row; e, denticle of inferior row. The specimen is from Bikini Atoll.

Papilliodorvillea gardineri: Pettibone, 1961: 181-2.

Dorvillea gardineri: Day, 1967: 455, fig. 17.21, a-c.

Material examined. One specimen from East Africa (syntype, BM 1923-11-5-13) and one from Kuwait, Arabian Gulf (BM 1969: 224) were examined externally. A longitudinal, dorsomedial incision was made in a third specimen from Hulule, Male Atoll, Maldives (BM 1924-3-1-61) for pharyngeal examination. The jaw parts of two specimens from Bikini Atoll (AHF 5910 and 5911) were removed and examined.

Description. Crossland (1924) has admirably described the external morphology and denticles of *D. gardineri*. The posterior portion of the maxillary apparatus is more poorly known.

The carriers are very weakly denticulate and are fused posteriorly (Fig. 5). They are free from the basal plates of the superior rows of denticles. These basal plates are joined posteriorly and are in turn free from the basal plates of the inferior rows of denticles. These inferior basal plates are very short, roughly twice the length of the longest denticle of the inferior row.

Remarks. This species was investigated for pharyngeal characters which might bear upon Pettibone's (1961) argument for separate generic status for those dorvilleids possessing a nuchal papilla (*Papilliodorvillea* Pettibone, 1961, with *Staurocephalus* (*Dorvillea*) *gardineri* Crossland, 1924, as its type-species).

The hard pharyngeal parts of *D. gardineri* differ very little from those of *D. rubrovittata* in their arrangement. Denticulations of the carriers are very much weaker in *D. gardineri*, and denticle shapes differ somewhat in the two species, but this difference is not as great as that between some pairs of species in the group of subbiramous dorvilleids without furcate setae and without a nuchal papilla, e.g., *D. cerasina* and *D. rubrovittata*. (See Fauchald, 1970, for a description of the jaws in *D. cerasina*.) Therefore, the inclusion of *Staurocephalus* (*Dorvillea*) *gardineri* in *Dorvillea* is favoured here.

Distribution. The species is recorded from East Africa at Kuwait and Wasin, from the Maldive Islands, and from Bikini Atoll. It is thus a tropical, shallow-water Indian Ocean species.

Dorvillea batia sp. nov.

(Fig. 6)

Material examined. Five specimens were obtained in three samples from the San Diego Trough as follows: one in SIO J22 (holotype, AHF Poly. 1074), three in SIO J15 (paratypes, AHF Poly. 1075), and one in SIO H22 (paratype, AHF Poly. 1076). Two of the examples from SIO J15 and one from SIO H22 were cleared in xylol and mounted whole after being dorsally incised.

Description. The holotype is 3.3 mm long and 0.34 mm wide. It is complete and bears 44 setigers. The prostomium is depressed hemispherical (Fig. 6A, C). Near its posterior margin are a pair of well developed, subulate palps laterally and a pair of slightly longer antennae dorsolaterally. The latter are basically cirriform but carry rapidly tapering tips. Eyes are absent. Lappet-like ventral cirri are present from the first parapodium. From the second parapodium, a digitiform dorsal cirrus with an enclosed acicula is present, with or without a slight distal swelling, but without a true cirrostyle. Neuropodia are biacicular (Fig. 6E); the larger upper acicula divides the setal fan into two fascicles. The dorsal fascicle consists of an approximately elliptical array of smooth capillaries, while the ventral fascicle consists of a linear array of smooth, heterogomph spinigers (Fig. 6A, D). Setae decrease in abundance in far posterior setigers. The pygidium (Fig. 6B) bears numerous supra-anal papillae and a pair of multiarticulate, cirriform appendages ventrolateral to the anal opening.

The maxillary carriers are fused together with both pairs of basal plates (Fig. 6F). All denticles are bird-wing shaped with a main fang distally and fine denticulations along the medial edge. Each half of the mandible (Fig. 6G) bears a thin, transparent area surrounded by thicker, darker material and is bifurcate anteriorly and denticulate anteromedially.

The gut is filled with fine, particulate, orange matter. The distinctive color corresponds to that of a sympatric species of astrorhizid foraminiferan which bears abundant epifauna. Both this circumstantial evidence and the shape of *D. batia* denticles suggests that it may graze this epifauna.

Remarks. *Dorvillea batia* differs from other known members of the genus in the lack of denticulations along any of its setae, in the shape of its denticles, in the presence of spinigers rather than falcigers, and in the shape of its mandibles. It is named for the bushy appearance its numerous setae give.

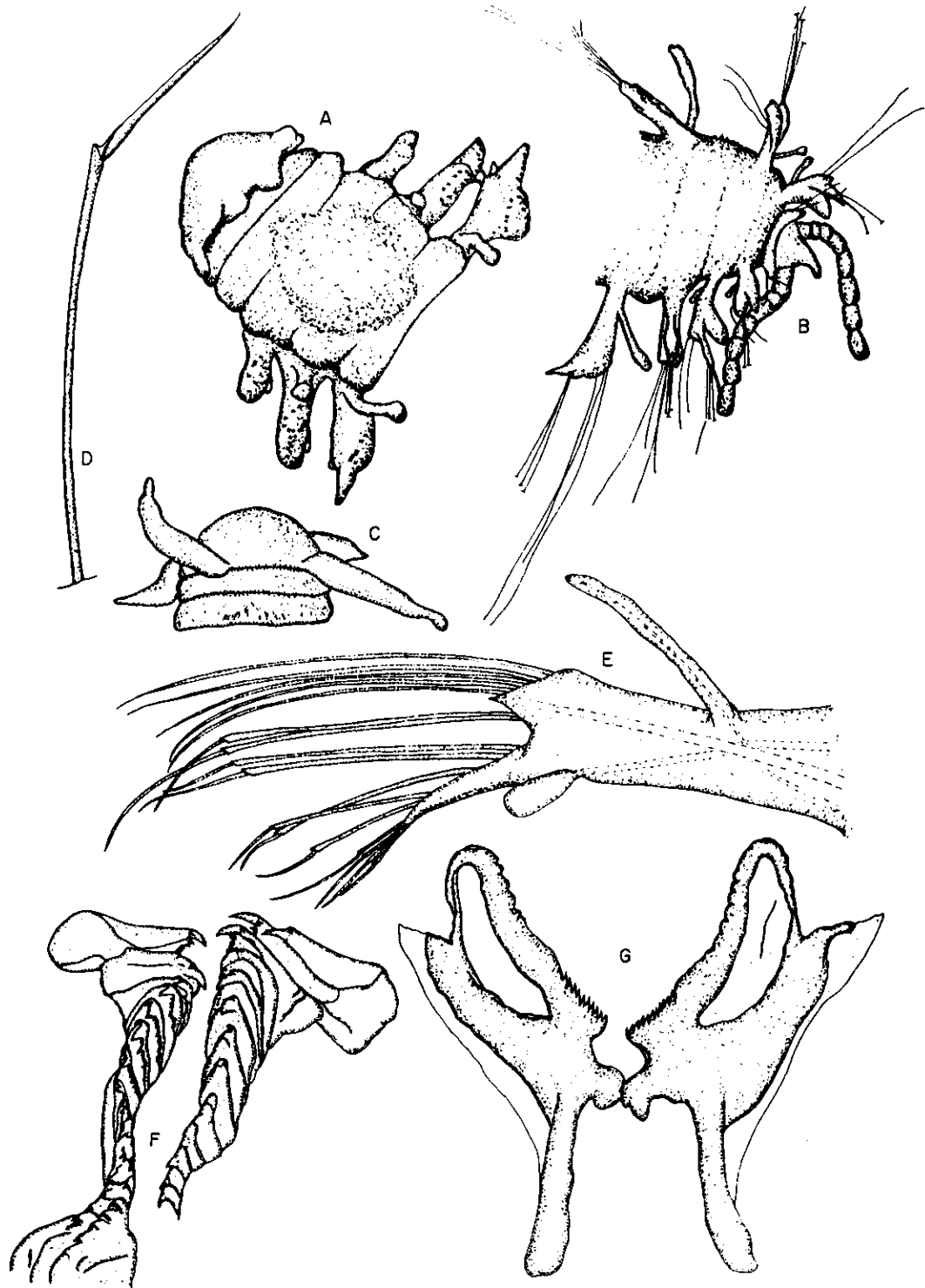


Figure 6. *Dorvillea batia* sp. nov: A, anterior in dorsal view, setae not shown but insertions marked, antennae missing; B, posterior of same specimen in ventral view, one parapodium missing and broken setae marked by a short, perpendicular line; C, head in dorsal view; D, compound seta of parapodium 36; E, parapodium 36; F, maxillae in oblique view, broken apart at posterior end to reveal inferior denticle row, the denticles of which are hidden by the superior row; G, mandibles in dorsal view. A-B and D-G are drawn from paratypes; C is from the holotype.

Distribution. The species is known only from the Coronado Sea Fan region of the San Diego Trough in a silty mud at depths of 1223-1229 m.

Genus *Protodorvillea* Pettibone, 1961

Type-species. *Staurocephalus kefersteini* McIntosh, 1869.

Diagnosis. The prostomium is roughly pear shaped but is slightly compressed dorsoventrally. Palps are well developed, bearing at least one article. Antennae are small or absent entirely. Dorsal cirri lack aciculae. Three classes of setae are found in each species: (1) capillary, (2) furcate, and (3) compound heterogomph. Carriers and (four rows) of denticles are always present. Carriers may be fused with the basal plates of the superior denticle rows, and these basal plates may, in turn, be fused with those of the inferior denticle rows.

Remarks. *Protodorvillea* includes the following species: *P. kefersteini* (McIntosh, 1869); *P. atlantica* (McIntosh, 1885); *P. egena* (Ehlers, 1913); *P. gracilis* (Hartman, 1938); *P. gaspeensis* Pettibone, 1961; and, *P. biarticulata* Day, 1963.

Protodorvillea kefersteini (McIntosh, 1869)

(Fig. 7)

Staurocephalus kefersteini McIntosh, 1869: 417, fig. 11; 1910: 358, pl. 55, fig. 2, pl. 66, fig. 8, p. 73, fig. 5, pl. 81, fig. 10; Southern, 1914: 84; Fauvel, 1923: 444-5, fig. 177, m-u.

Protodorvillea kefersteini: Pettibone, 1961: 178, 180; Hartmann-Schröder, 1971: 262, fig. 87, *partim*; Hobson, 1971a: 542-3, fig. 8.



Figure 7. *Protodorvillea kefersteini* (McIntosh). Oblique view of right side of posterior portion of maxillae, syntype from Lochmaddy, Scotland.

Material examined. Single specimens from Blacksod Bay, Ireland, (BM 1914: 12: 12: 24), and St. Nazaire, France, (BM 1928-4-26-157), were examined externally. Two additional examples from Lochmaddy, North Uist, Scotland (syntypes, BM 1921: 5: 1: 1547), were similarly treated, and one of these animals was dorsally incised to reveal the maxillary details.

Description. The external morphology of *P. kefersteini* has been recently redescribed (Hartmann-Schröder, 1971; Hobson, 1971a), but, except for the shape of the anterior denticles and mandibles, (Hartmann-Schröder, 1971), the pharyngeal apparatus remains poorly known. The posteriorly fused, denticulate carriers are free from the basal plates of the superior denticle rows (Fig. 7). These basal plates are posteriorly fused, while those of the inferior rows are free both from the dorsal pair and from each other. Both inferior and superior

basal plates are denticulate and about three times as long in the longitudinal dimensions as the longest denticles in their respective rows.

Distribution. The species is known from the European Atlantic Coast and from Massachusetts in shallow water to 44 m. Hobson (1971a) refers the North Pacific records cited by Hartmann-Schröder to *P. gracilis*. Hobson's view is favoured here.

Protodorvillea gaspeensis Pettibone, 1961

(Fig. 8)

Protodorvillea gaspeensis Pettibone, 1961: 178-80, fig. 6; Hobson, 1971b: 247, fig. 1A, B.

Material examined. One specimen from the Gulf of St. Lawrence (holotype, USNM 30008) and two specimens from Buzzards Bay (USNM 43516) were examined externally. The pharyngeal apparatus was removed from one of the Buzzards Bay specimens and mounted.

Description. Pettibone (1961) and Hobson (1971b) have thoroughly described the external characters of *P. gaspeensis*. The dissected individual bears eight rows of denticles (Fig. 8B, C, D). The superior four rows of denticles are very similar except in numbers of denticles. The same is true of the four inferior rows. The second and fourth rows from the top are thus interpreted as replacement parts. The numbers of denticles in each row, proceeding from top to bottom, are: 5, 11, 9, 12. Four or five of those in the second (replacement) row appear fused together into a basal plate. All the denticles bear minute teeth distributed uniformly over their dorsal surfaces. In addition, denticles of the superior rows have a larger main fang posterodorsally. The carriers appear fused with each other and with the basal plates of the superior rows of denticles. The nature of the basal plates of the inferior rows of

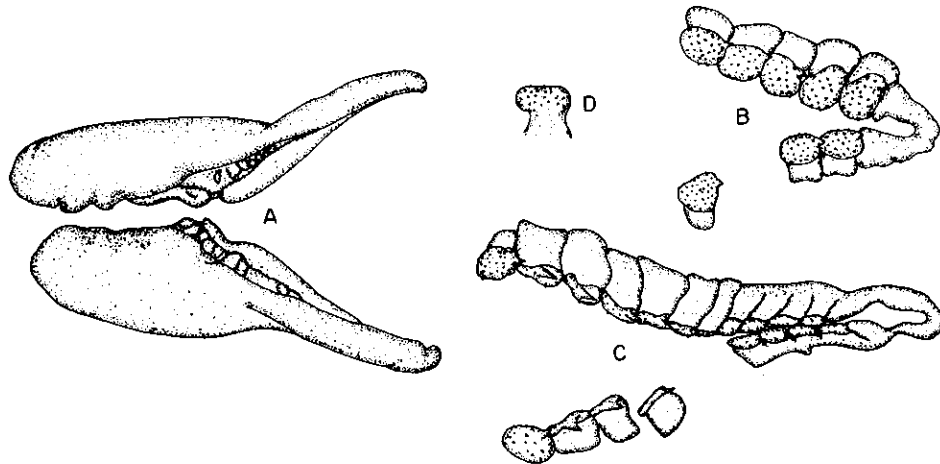


Figure 8. *Protodorvillea gaspeensis* Pettibone: A, mandibles in dorsal view; B, superior denticle rows in dorsal view, left side damaged; C, replacement parts for superior denticle rows in dorsal view, left side damaged; D, denticle from inferior row in oblique view. A-D are from a specimen from Buzzards Bay.

denticles is not discernible in the preparation. The mandibles (Fig. 8A) are anteriorly rounded and medially denticulate. They are not flared anteriorly if the illustrated position is the normal retracted one.

Remarks. Because of the small size of *P. gaspeensis* and its external similarity to species of the following genus, it was considered desirable to examine the pharyngeal apparatus. Only one specimen was available for dissection; hence, no indication is given of the potential variability of the characters described.

Distribution. The species is known from low water to 20 m in the northwestern Atlantic (Gulf of St. Lawrence, Quebec, and Buzzards Bay, Massachusetts).

Genus *Meiodorvillea* gen. nov.

Type-species. *Protodorvillea minuta* Hartman, 1965.

Diagnosis. The prostomium is roughly pear shaped. The palps are very small or absent. When they are present, they may be either simple or biarticulate. Antennae are small and clavate and are longer than the palps when both pairs of appendages are found. Dorsal cirri are small or lacking and never contain an acicula. Three classes of setae are found in each species: (1) capillary, (2) furcate or geniculate, and (3) compound heterogomph. Carriers and two rows of denticles are always present, although the rows of denticles may be represented by only their basal plates.

Remarks. *Meiodorvillea* includes the following species: *M. chilensis* (Hartmann-Schröder, 1962); *M. minuta* (Hartman, 1965); and, the new species described herein.

Meiodorvillea differs from *Protodorvillea* in the extreme reduction of its palps and of its maxillary apparatus. Most notably, *Meiodorvillea* bears only two rows of denticles. The name is indicative of the meiofaunal size of the contained species and suggestive of a close affinity with *Protodorvillea*. Inclusion of the following three species in *Protodorvillea* would, however, make that genus more heterogeneous in prostomical and maxillary characters than any other genus in the family.

M. minuta is considered first. It was chosen as the type-species because of the abundant material available for study.

Meiodorvillea minuta (Hartman, 1965)

(Fig. 9)

Protodorvillea minuta Hartman, 1965: 125-7, pl. 23; Hartman & Fauchald, 1971: 10, 195, 216.

Material examined. The holotype (AHF Poly. 0691) and a dozen additional specimens were examined externally. The holotype is from station S13, and the other examples, from station 105B of the Gay Head-Bermuda transect (Sanders *et al.*, 1965). Three of the latter specimens were dissected for pharyngeal examination.

Description. The individuals examined agree in all respects with Hartman's (1965) description except that two apodous peristomial rings are present.

Hartman's dorsal view (pl. 23, fig. a) is accurate, but the first peristomial ring is evident in ventral view. Dorsally, the second peristomial ring completely overlaps and obscures the first.

The maxillary apparatus (Fig. 9B) contains two rows of denticles continuous with a pair of posteriorly fused basal plates. A pair of relatively large, smooth carriers is found more dorsally. The mandibles (Fig. 9A) bear weak denticulations medially, are flared anteriorly, and are tapered to a point laterally.

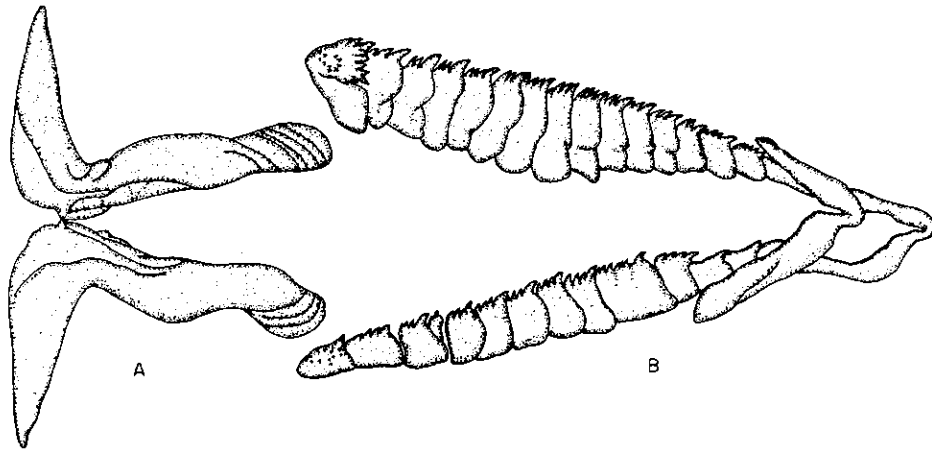


Figure 9. *Meiodorvillea minuta* (Hartman): A, dorsal view of mandibles; B, oblique view of entire maxillae. The specimen is from the continental slope off New England.

Distribution. The species is known only from 97-1102 m off New England and from 1135 m off Bermuda. See Hartman (1965) and Hartman & Fauchald (1971) for further locality data.

Meiodorvillea chilensis (Hartmann-Schröder, 1962b)

Protodorvillea gaspeensis chilensis Hartmann-Schröder, 1962b: 190-3, figs 173-5.

Material examined. None.

Remarks. This subspecies is elevated to specific rank because it is distinct from *P. gaspeensis* in many respects. The prostomium is more pointed and more pear shaped than that of *P. gaspeensis*; the palps are relatively shorter. *M. chilensis* bears no denticulations on the appendages of its compound setae and differs also in the placement of the denticulations on its furcate setae. In the latter respect, it most closely approximates *M. minuta*. The pygidial appendages of *M. chilensis* are clavate as in the remainder of the genus, while those of *P. gaspeensis* are cirriform. It is hoped that future material will bear out this classification by revealing only two rows of denticles.

Distribution. The species is known from a single representative taken off the coast of Chile in 250-264 m.

Meiodorvillea apalpata sp. nov.

(Fig. 10)

Material examined. The holotype and one posterior fragment from SIO J14 (AHF Poly. 1086-7) were externally examined, as was an individual from SIO J22 (paratypes, AHF Poly. 1089). One complete and two halved specimens from SIO H22 (paratypes, AHF Poly. 1088) were similarly treated before the jaws from one of the halved specimens were dissected out and lost in mounting. The other anterior half was mounted whole after clearing.

Description. The holotype measures 2.8 mm long and 0.14 mm wide for 41 setigers plus prostomium, peristomium, and pygidium. A pair of short, clavate antennae insert dorsally on the pear-shaped prostomium (Fig. 10A) such that transverse and longitudinal lines drawn through their insertions would divide the wider posterior half of the prostomium into sixths. Palps are lacking. Of the two peristomial rings, the second is the longer and the wider. Dorsal cirri are absent; ventral cirri are lappet like and transparent. They are present on setigers 2-14 and are reduced or absent thereafter. Neuropodia (Fig. 10E) consist of two apparent parts, a dorsal, conical, opaque portion and a ventral, flattened transparent portion. The neuropodia are biacicular, one acicula being found in each of the two parts. Setae above the dorsal aciculae include gradually tapering capillaries and geniculate setae, though one or the other of these setal types may be absent in a particular parapodium. Geniculate setae (Fig. 10D) have smooth bases of constant diameter and a flattened, basally denticulate, distal portion. The first, largest tooth on this "pennant" appears to be the only vestige of the short tine of a furcate seta. Setae below the dorsal acicula are compound heterogomph (Fig. 10C) with a smooth, rounded, mitten-like, distal end of the shaft. The appendage is lanceolate or elongate lanceolate and lacks denticulation. The pygidium is crown shaped (Fig. 10B). Below the anus is a low, conical projection. Above the anus are numerous small papillae and two clavate appendages. Laterally, two additional, smaller, clavate appendages are evident.

The mandibles (Fig. 10F) are butterfly shaped and lack obvious denticulation. The maxillae (Fig. 10G) consist of a relatively large pair of posteriorly fused carriers free from the two basal plates, which are also posteriorly fused. No free denticles remain.

The gut is apparently empty in all available specimens.

Distribution. The species is known only from the Coronado Sea Fan region of the San Diego Trough in silty mud under 1223-1224 m of water.

Genus *Exallopus* gen. nov.

Type-species. Exallopus cropion sp. nov.

Diagnosis. The prostomium is depressed hemispherical. Antennae and palps are well developed and of approximately equal lengths. The palps are biarticulate, and the constriction near the bases of the antennae suggests articulation also. Dorsal cirri are absent. Capillary and compound, heterogomph setae are present after the first setiger. Setae in the first parapodium are thicker by a factor of about two and one half than any of those following and are

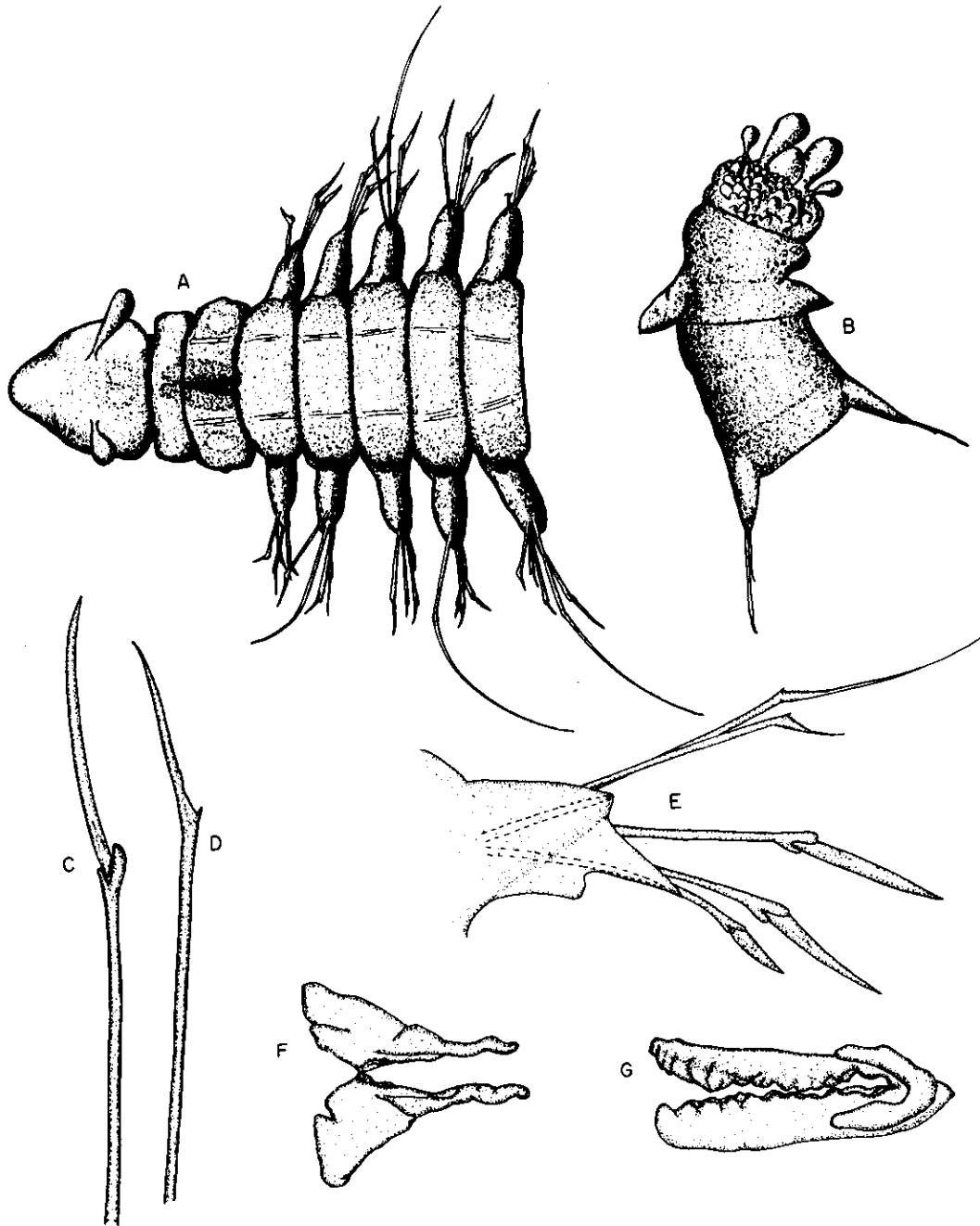


Figure 10. *Meiodorvillea apalpata* sp. nov: A, anterior end in dorsal view; B, posterior end in dorsal view; C, compound seta; D, geniculate seta; E, parapodium; F, mandibles in dorsal view; G, entire maxillae in oblique view. C-E are from parapodium 6. All drawings are from the paratypes.

markedly different in shape. Only one pair of carriers and two rows of denticles are present, the carriers being fused with basal plates.

Remarks. *Exallopus* is monotypic and is named for the "very different foot" it bears in front of all the others. The setae and maxillae clearly fall outside the range of variation for any other genus of Dorvilleidae.

Exallopus cropion sp. nov.

(Fig. 11)

Material examined. Two specimens from SIO J14 (AHF Poly. 1077-8) were examined. The holotype remains in alcohol, while the paratype was mounted whole after being cleared in xylol.

Description. The holotype is an ovigerous female in two pieces. It is 5.1 mm long and 0.21 mm wide and has 47 setigers. The pygidium and an unknown number of posterior setigers are missing. The rounded prostomium (Fig. 11A) bears two digitiform antennae arising at the posterior ends of a pair of shallow, longitudinal grooves. A constriction near the base may indicate the antennae are biarticulate. The palps each consist of a globose basal article with a digitate palpostyle. Parapodia (Fig. 11B) lack dorsal cirri. A ventral cirrus is absent on the first parapodium, weakly developed on the second, and fully formed and obovate on the third. Above the acicula of the first parapodium are a pair of slightly recurved, apparently smooth spines (Fig. 11E). Below are about four strongly curved, extremely thick, smooth falcigers (Fig. 11F). The shaft is bent in the opposite direction from the appendage, giving an overall recurved appearance. In the second and subsequent parapodia, these setae are replaced by denticulate capillaries (Fig. 11C) and spinigers with distally rounded but denticulate shafts and smooth appendages (Fig. 11D).

The mandibles (Fig. 11H) are anteriorly flared both laterally and dorso-ventrally in a trumpet shape, but denticulation is not apparent. The maxillae (Fig. 11G) contain only two rows of denticles, their basal plates fused posteriorly and also fused with the carriers.

The gut in both specimens is empty.

Remarks. The shape of the falcigers in the first setiger suggests a holding function. *E. cropion* may thus be commensal with some other species in the sample. It is named for the scythe-like appearance of these modified falcigers.

Distribution. The species is known only from the Coronado Sea Fan region of the San Diego Trough in silty mud at a depth of 1224 m.

Genus *Ophryotrocha* Claparède & Mecznikow, 1869

Type-species. *Ophryotrocha puerilis* Claparède & Mecznikow, 1869.

Diagnosis. The prostomium is roughly hemispherical. Antennae and palps are reduced to papilliform appendages. Dorsal cirri lack notoacaculae and may be absent altogether. Only two classes of setae are found in each species: (1) capillary and (2) compound heterogomph. Carriers and all four basal plates are fused in a characteristic ice-tong shape. Denticles of the inferior rows may be partly or completely fused with denticles of the superior rows, producing either four or two apparent rows of denticles.

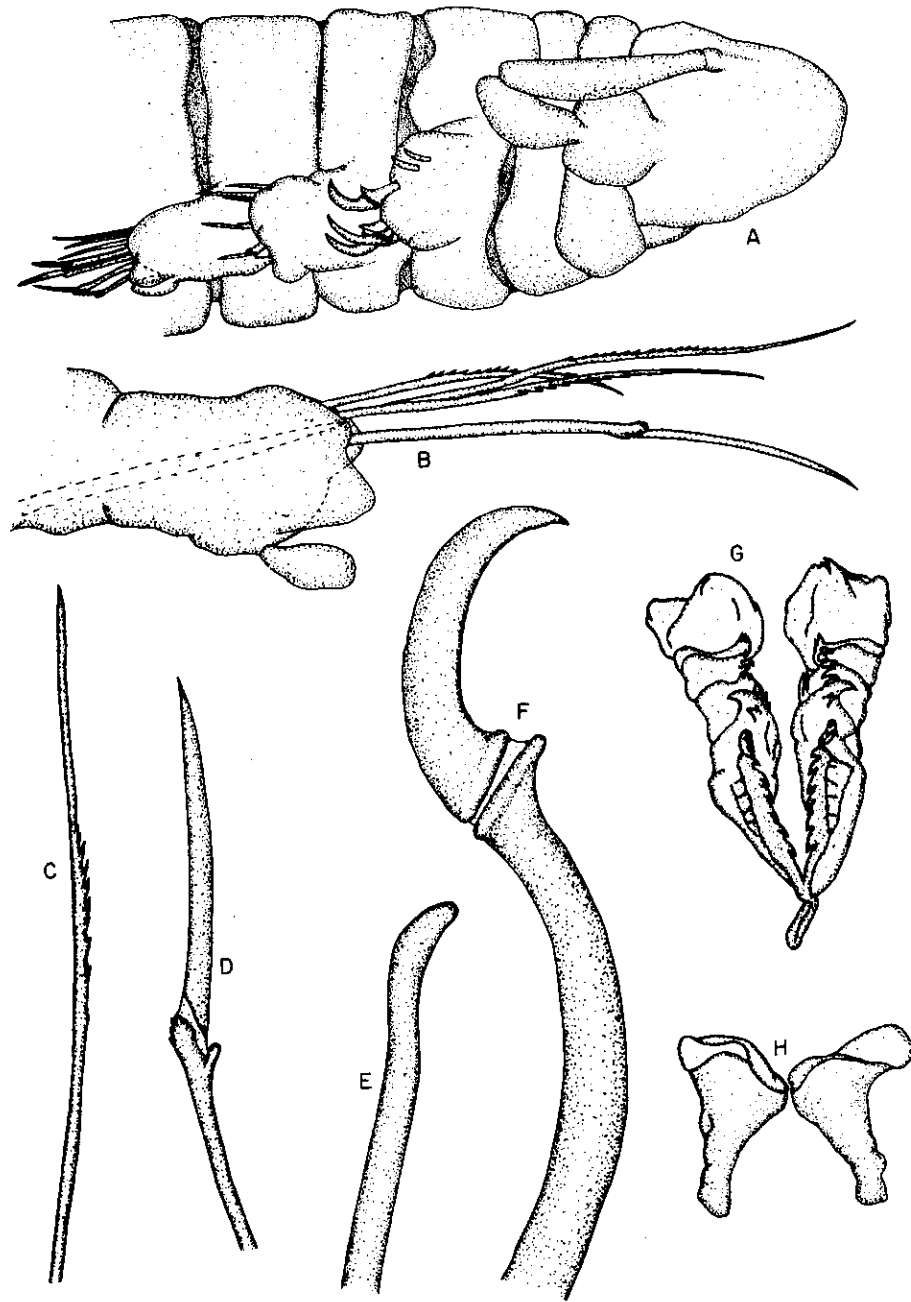


Figure 11. *Exallopus cropion* sp. nov: A, anterior end in side view; B, parapodium 22; C, simple seta from parapodium 23; D, compound seta from parapodium 23; E, simple seta from parapodium 1; F, compound seta from parapodium 1; G, entire maxillae in dorsal view; H, mandibles in dorsal view. A-F are from the holotype; G and H are from the paratype.

Remarks. *Ophryotrocha* includes the following species: *O. puerilis* Claparède & Mecznirow, 1869; *O. geryoncola* (Esmark, 1878); *O. claparedii* Studer, 1878; *O. littoralis* (Levinsen, 1879); *O. hartmanni* Huth, 1933; *O. minuta* Levi, 1954; *O. bacci* Parenti, 1961; *O. labronica* La Grecca & Bacci, 1962; *O. vivipara* Banse, 1963; *O. notoglandulata* Pfannenstiel, 1972; and, the new species described herein.

Ophryotrocha puerilis Claparède & Mecznirow, 1869

Ophryotrocha puerilis Claparède & Mecznirow, 1869: 184; Fauvel, 1923: 450, fig. 180 a-h; Hartman, 1944: 191, pl. 15, figs 325-330; Day, 1967: 452, fig. 17.20 a-f.

Material examined. Three specimens from Naples (MNHN) and one example without locality data (MNHN) were dissected for pharyngeal examination.

Description. Fauvel (1923), Hartman (1944), and Parenti (1961) all illustrate the denticles of *O. puerilis* as being of two distinct types. Those denticles with a distinct main fang are interpreted as the products of fusion of falcate superior denticles and plate-like inferior denticles; those without a main fang are thought to belong to the inferior row. In the following, newly described species, two free, falcate denticles remain in each albeit short superior row (Fig. 12F). The ice-tong-shaped forceps in *O. puerilis* is believed to be the product of the fusion of carriers and all four basal plates. (For a description of a similar process of fusion, see Sudzuki & Sekiguchi, 1972, who discuss the ontogeny of the maxillary apparatus in *O. notoglandulata*.) As Parenti (1961) illustrates, all that is apparent in the adult maxillae is one forceps continuous with two rows of diversely shaped denticles; the fusions in *O. puerilis* are all inferred.

Remarks. One of the specimens from Naples reveals maxillary replacement in *Ophryotrocha* to be like that in *Dorvillea*, *Schistomeringos*, and *Protodorvillea*. The worn parts are underlain by their still forming replacements.

Distribution. The species has been considered cosmopolitan in tropical and temperate intertidal regimes (Day, 1967). In light of the experimental evidence by Bacci & La Grecca (1953) demonstrating the lack of successful interbreeding in populations from as close as Naples and Plymouth, it is considered unlikely that even more distantly separated populations are conspecific. Furthermore, Banse (1963) has noted radical differences in the mating behaviours in populations from western North America and Europe.

Ophryotrocha hadalis sp. nov.

(Fig. 12)

Material examined. Four specimens from SIO H39 (AHF Poly. 1079-80) were externally examined. The holotype remains in alcohol, while the three paratypes were cleared and mounted whole.

Description. The holotype measures 1.3 mm long by 0.14 mm wide and has 22 setigers; the largest paratype is 3.7 mm long and 0.33 mm wide but is so battered that the number of setigers is indeterminable. An arcuate ridge is

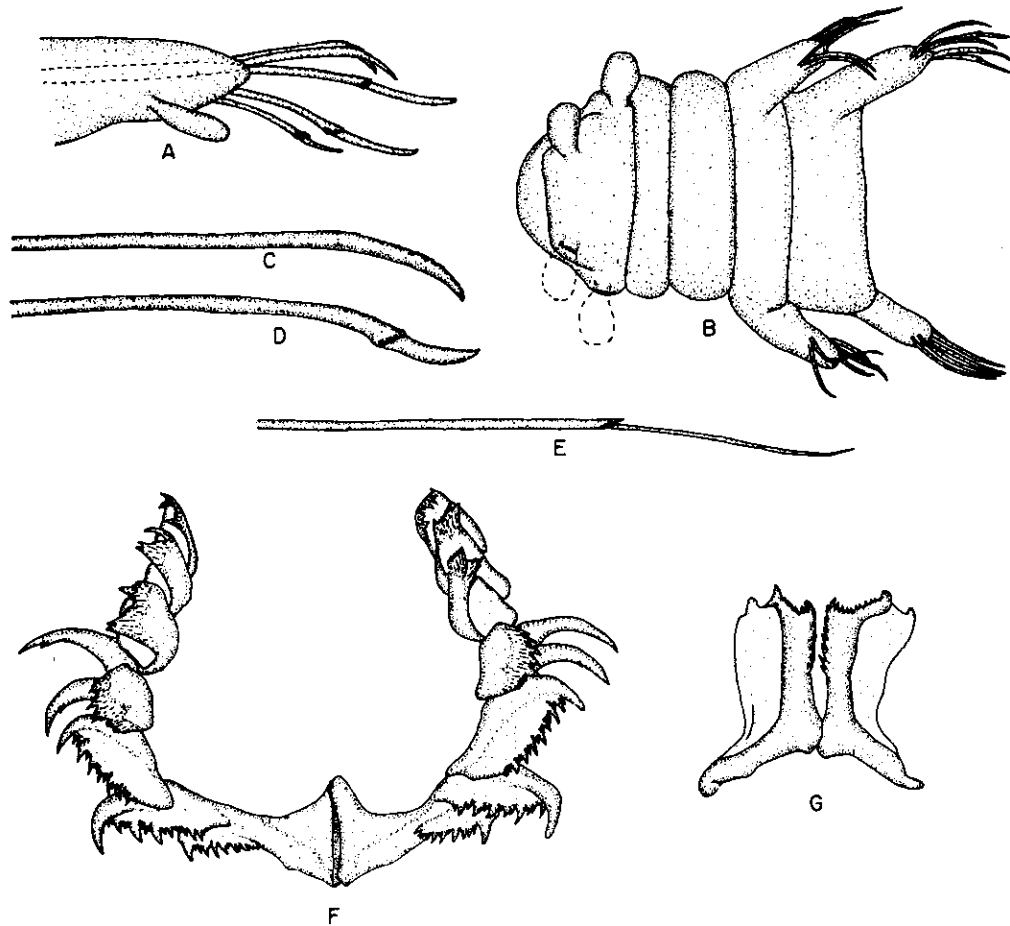


Figure 12. *Ophryotrocha hadalis* sp. nov: A, parapodium 10; B, anterior in dorsal view, left palp and antenna missing; C, simple seta of parapodium 10; D, compound seta of parapodium 10; E, compound seta of parapodium 20; F, entire maxillae in dorsal view with denticle rows spread apart; G, mandibles in dorsal view. A-E are from the holotype; F and G are from the paratypes.

present on the prostomium (Fig. 12B) below the level of the antennae. The palps are inserted laterally just anterior to the first peristomial ring. Eyes are absent. Parapodia (Fig. 12A) lack dorsal cirri; ventral cirri are short and digitate from the first parapodium. Setae become progressively thinner, longer, and smoother in proceeding from anterior to posterior setigers. Capillaries are always present dorsally on the neuropodium. Those in the anterior few setigers are denticulate as are the distal ends of the shafts of the compound falcigers (Fig. 12C,D). The decrease in thickness of more posterior setae is associated with the loss of all denticulation and a gradual change from short-appendaged falcigers to long-appendaged spinigers (Fig. 12E). The pygidium is unknown.

Carriers and basal plates all appear fused (Fig. 12F). In each of the two denticle series, four denticles are plate like and two are falcate. The former clearly belong to the inferior row and the latter clearly belong to the superior row. One additional denticle in each series appears to be the result of fusion of

a falcate and plate-like denticle pair. This denticle is the farthest posterior of the seven in each series. The mandible pieces (Fig. 12G) are each weakly bifurcate anteriorly and are denticulate both anteriorly and medially.

The gut is filled with dark, particulate matter.

Remarks. *O. hadalis* differs from the other species of the genus in its ridged, eyeless prostomium, its placement of antennae and palps, and its lack of dorsal cirri. It is the only species of *Ophryotrocha* in which some denticles can be distinctly assigned to the superior and inferior rows.

Distribution. The species is known from a single sample at 7298 m in the Aleutian Trench. It is named for this hadal distribution.

Genus *Parophryotrocha* Hartmann-Schröder, 1971

Type-species. *Ophryotrocha* (?) *isochaeta* Eliason, 1962.

Diagnosis. The prostomium is roughly hemispherical. Antennae and palps are entirely lacking. Dorsal and ventral cirri are absent. Only simple, acicular setae are present. Both pairs of carriers and all four basal plates are fused in an ice-tong shape. Four rows of denticles remain.

Remarks. *Parophryotrocha* is monotypic.

Parophryotrocha isochaeta (Eliason, 1962)

Ophryotrocha (?) *isochaeta* Eliason, 1962: 260, fig. 16.

Parophryotrocha isochaeta: Hartmann-Schröder, 1971: 260.

Material examined. None.

Description. Eliason's (1962) and Hartmann-Schröder's (1971) descriptions of the jaw parts of this species reveal a pattern homologous with that in *Ophryotrocha*—fused carriers and basal plates with falcate denticles in the short, dorsolateral row and plate-like denticles in the more medioventral row.

Distribution. *P. isochaeta* is known only from the Skagerrak in 637-650 m.

Genus *Apophryotrocha* gen. nov.

Type-species. *Apophryotrocha mutabiliseta* sp. nov.

Diagnosis. The prostomium is roughly hemispherical. Antennae are very long and cirriform; palps are well developed but are shorter and subulate. Dorsal cirri are without aciculae. Setae are of two types: (1) capillary and (2) compound heterogomph. Both pairs of carriers and all four basal plates are fused in an ice-tong shape. No free denticles are found.

Remarks. The genus is monotypic and is named for its presumed close affinities with *Ophryotrocha*. It is distinguished from *Ophryotrocha* because the long antennae and palps and simple jaws of *Apophryotrocha* imply a mode of life different from that of *Ophryotrocha* (Westhede, 1971; Akesson, 1967). The reduced jaws would be incompatible with a surface-scraping existence. The intricate structure of the compound setae and the paucity of capillary setae is also unlike the condition in *Ophryotrocha*.

Apophryotrocha mutabiliseta sp. nov.

(Fig. 13)

Material examined. Three specimens were obtained from SIO H84 (AHF Poly. 1081-3). The holotype (Fig. 13A) and a battered specimen remain in alcohol. The other paratype was cleared and mounted whole.

Description. The holotype is complete, measures 1.9 by 0.33 mm, and has seven setigers. One paratype (Fig. 13B) is ovigerous and complete, measuring 0.80 mm long by 0.21 mm wide and bearing six setigers. The other paratype has seven setigers. The prostomium is depressed hemispherical and bears a pair of subulate, lateral palps. The antennae are very much longer than the palps, nearly reaching the third setiger; they are cirriform. Digitiform dorsal and ventral cirri are located near the distal ends of the parapodia of the first setiger. Where the dorsal surface of the parapodium meets the body wall is another, low protuberance which is absent in other setigers. In the second through sixth parapodia (Fig. 13C), the dorsal cirrus is found more medially and is digitiform, while the ventral cirrus is papilliform. A single, fine capillary seta is found just ventral and distal to the insertion of the dorsal cirrus. Three or four heterogomph falcigers are present in each neuropodium; all are hooded and bidentate, but the shapes of their appendages are extremely variable (Fig. 13D-H). The blades of the posteriormost compound setae have a thinner portion which gives the impression of a keyhole. Although the seventh setiger may be lacking, may bear only a single capillary seta on each side, or may display both capillary and compound setae, it apparently never exhibits well developed parapodia. The pygidium is rounded, with two papilliform, posterolateral projections.

The mandibles (Fig. 13I) are anteriorly flared and bifurcate and are laterally weakly denticulate. Maxillae (Fig. 13J) consist only of an ice-tong shaped forceps more blunt than that of *Ophryotrocha*. No free denticles remain, but the left half of the forceps is denticulate on its ventral surface and both halves are denticulate on their dorsal surfaces. The ventral surface of the right half of the forceps is rough but not clearly denticulate. This partly asymmetric denticulation is present in all three specimens.

The gut appears empty.

Remarks. Except for Crossland's (1924) mention of asymmetric mandibles (not observed in the two specimens dissected for the present pharyngeal analysis) in *D. gardineri*, *A. mutabiliseta* is the only known case of asymmetry of pharyngeal parts in the Dorvilleidae. It is named for the variability in form of its compound setae.

Distribution. The species is known only from the equatorial Pacific in 4320-4323 m.

DISCUSSION

Day (1967) gives a convincing argument for combining *Dorvillea* and *Schistomeringos* (*Stauronereis* sensu Pettibone, 1961). They are separated here because the presence of furcate setae appears to be a very conservative feature and because the structure of the basal plates of the inferior denticle rows appears to differ in the two genera. Although the latter difference seems trivial

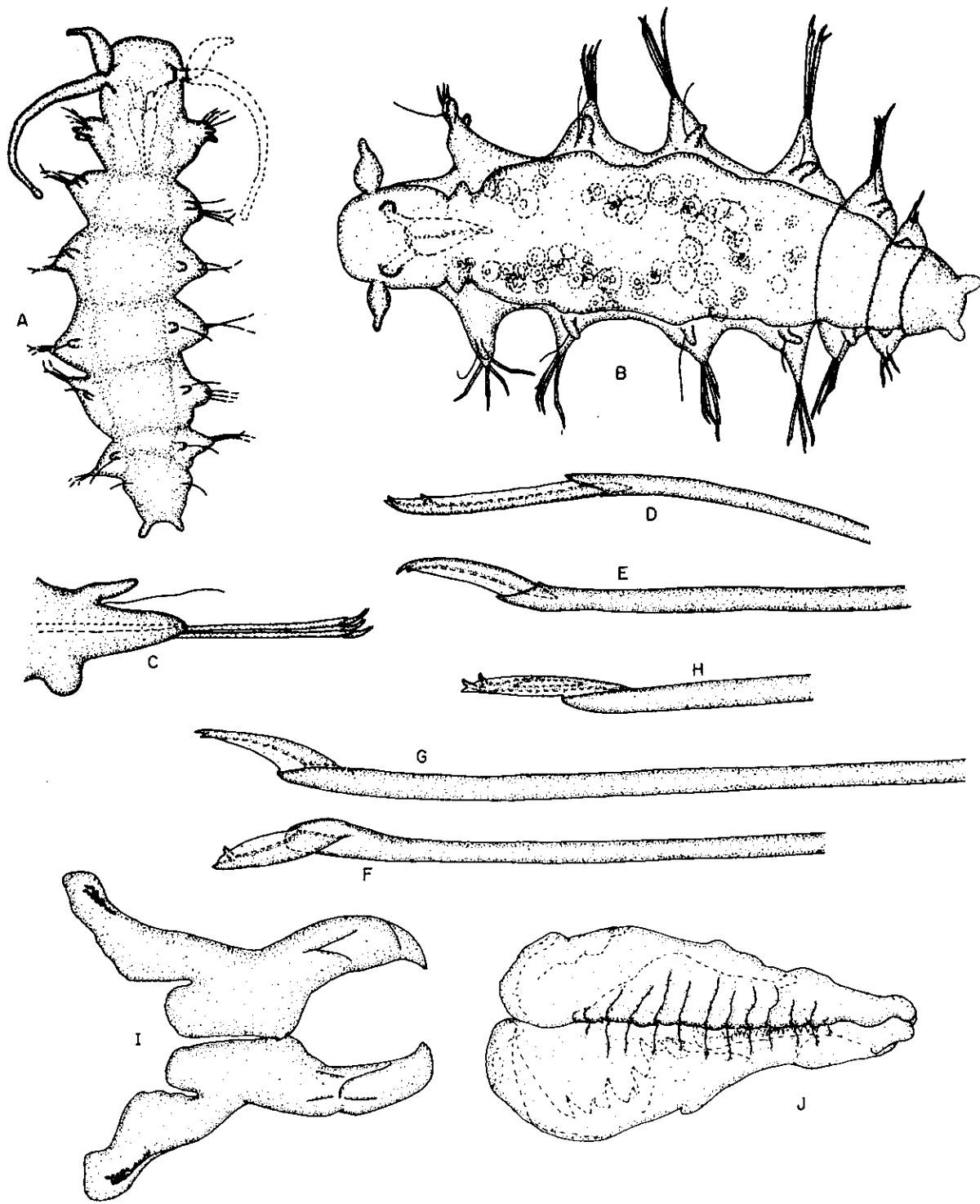


Figure 13. *Apophryotrocha mutabiliseta* sp. nov: A, dorsal view, right palp and antenna missing; B, dorsal view, antennae missing, all ova figured; C, parapodium 3; D-H compound seta of, respectively, parapodia 1, 2, 4, 5, 6; I, mandibles in dorsal view; J, entire maxillae in dorsal view. A is from the holotype; B-J are from the ovigerous paratype.

in regard to the operation of the jaws, it may be the beginning of the divergence of maxillary morphologies in the two main branches of the following proposed phylogenetic scheme.

Meiodorvillea apalpata may appear to differ from *M. minuta* as much as *Apophryotrocha* differs from *Ophryotrocha*. Its complete lack of palps, however, does not represent a functional dissimilarity from the palps of *M. minuta* which are so small and so positioned that they are probably of no use in food manipulation. Both *M. minuta* and *M. apalpata* are bathyal and are found in soft sediments.

Dorvillea batia is intermediate between *Dorvillea* and *Ophryotrocha* in many respects—size, maxillary morphology, mandibular morphology, and degree of development of a dorsal cirrophore. Its palps are also somewhat reduced with respect to other species of the genus *Dorvillea*. However, the absence of neotenic characters, the presence of well-developed antennae, and, especially, the presence of notoacaculae place it in *Dorvillea*.

Hartmann-Schröder (1971) has placed *Parapodrilus* Westheide, 1965, in *Dorvilleidae*. It may have evolved by reduction from a *Parophryotrocha*-like ancestor as she suggests (1971 and pers. comm.), but the present point of view is that the evidence is too scanty for the placement of *Parapodrilus* in *Dorvilleidae*. Ontogenic comparison with *Ophryotrocha puerilis* (Åkesson, 1967) and investigation of the musculature of the peristomial region of *Parapodrilus* would be useful in this regard. Complete lack of prostomial appendages and jaws, however, indicates separate familial status might be advisable for *Parapodrilus* even if *Ophryotrocha* or *Parophryotrocha* contains its nearest living relative.

The taxonomic value of quantitative maxillary characters must be seriously re-examined in light of present evidence. In the sample of *Schistomeringos rudolphi* from the Bay of Naples (AHF 10950), the number of free maxillary denticles is strongly correlated ($P < 0.05$) with overall body size. In addition, doubled or partially doubled numbers of maxillary parts are found in some individuals of *Dorvillea rubrovittata*, *S. rudolphi*, *Protodorvillea gaspeensis*, and *Ophryotrocha puerilis*. These doubled sets are restricted to individuals with broken or worn teeth, and unworn teeth are always found immediately beneath their worn homologues. The unworn teeth are found within the soft tissues of the pharynx, while only the bases of the worn denticles, carriers, and basal plates are anchored in these tissues. When denticles in the lower, unworn sets are fully formed, they always exceed or equal in number the denticles of the worn rows. The simplest explanation of all these observations is that maxillae are occasionally replaced in many, if not all, the species of *Dorvilleidae*. It is not known whether this phenomenon extends to other Euniceroidea.

Before quantitative characters are used in species discriminations, it must be shown that interspecific variability can be distinguished from intraspecific variability. Although the observed size-correlated variability is a taxonomic complication, it may prove valuable ecologically. Perhaps numbers of denticles can be used as an indication of age of the individual. It remains to be shown, however, whether replacement is a function of size, of age, of wear, or of some combination of factors. Ontogeny of the maxillary parts may well reveal a phylogeny more detailed and more accurate than the one presented here in Fig. 14.

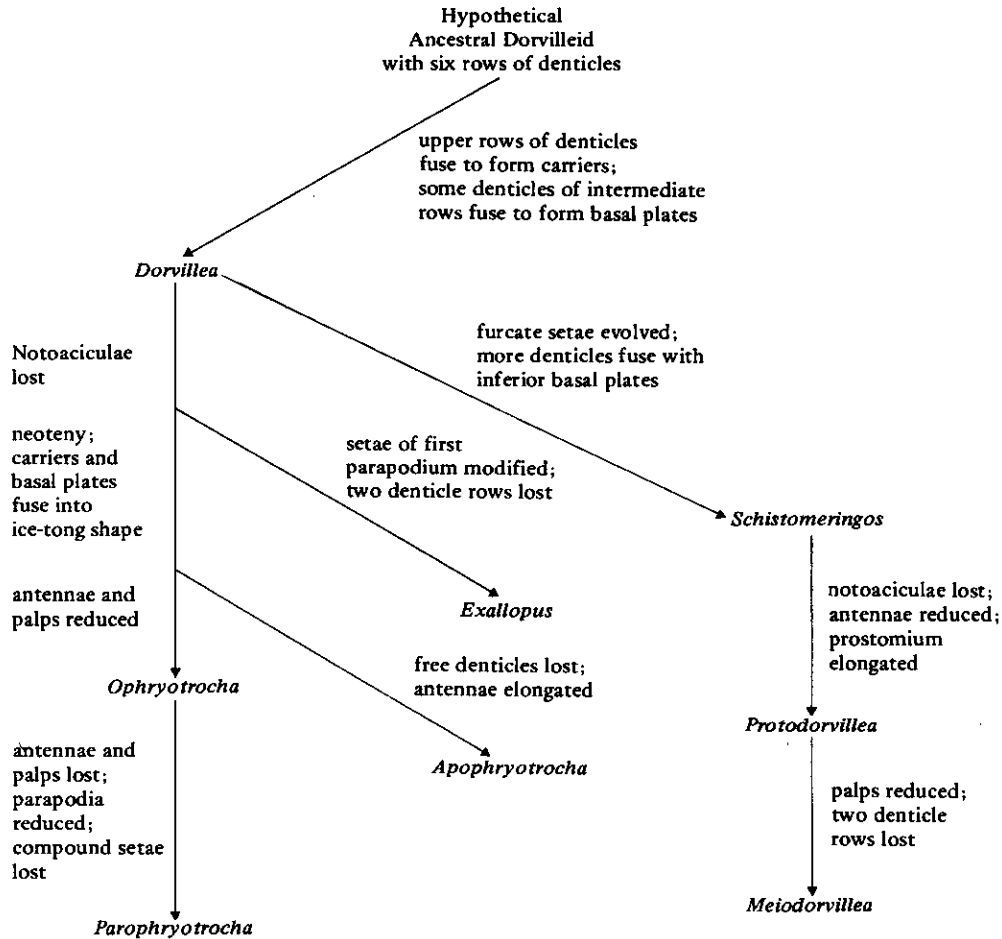


Figure 14. A tentative phylogeny of the genera of Dorvilleidae based on the external characters and hard jaw parts of those species discussed in the text.

Both major branches result from the process of reduction, but two divergent modes are seen. The *Schistomeringos-Protodorvillea-Meiodorvillea* branch undergoes reduction of body size, jaw structures, and prostomial appendages in the adult, all the while conserving the furcate seta. The *Dorvillea-Ophryotrocha-Parophryotrocha-Apophryotrocha* branch has apparently been produced by neotenic reduction with an associated reduction in maxillae and mandibles. If the ancestral dorvilleid were provided with branchiae, seven pairs of antennae, and one pair of tentacular cirri, reduction of these parts and fusion and reduction of jaw parts could produce any of the families of the superfamily Euniceoidea.

Close attention to maxillary and other characters also bears upon the question of cosmopolitanism of polychaete species. The consistent differences found between *Schistomeringos rudolphi* and *S. longicornis* and between allopatric populations of *Dorvillea rubrovittata* underscore the abundant need in polychaete systematics for close and quantitative comparisons of widely separated populations of supposedly cosmopolitan species. The high incidence

of cosmopolitanism in polychaetes reported by Ekman (1953), coupled with findings of unsuccessful interbreeding of allopatric populations (Bacci & La Grecca, 1953), leads to the uneasy realization that many different species of polychaetes may be grouped under the same binomial. As Fauchald (1969) has pointed out, the degree of difference employed by polychaete systematists for specific and generic distinction is often considerably greater than that used by systematists in other taxa. Recent findings, such as those of Bellan & Lagardère (1971) for *Nerine cirratulus* and *N. mesnili*, indicate that there need not be much morphological distinction even between sympatric species of polychaetes.

Additional material may prove the distinctions employed here to be too coarse, but, at present, the genera of Dorvilleidae may be distinguished according to the following key.

KEY TO THE GENERA OF DORVILLEIDAE

1. Notoacicula present 2
Notoacicula absent 3
2. Furcate setae present *Schistomeringos*
Furcate setae absent *Dorvillea*
3. Furcate or geniculate setae present 4
Furcate and geniculate setae absent 5
4. Palps well developed *Protodorvillea*
Palps reduced or absent *Meiodorvillea*
5. Only simple acicular setae present *Parophryotrocha*
Both capillary and compound setae present 6
6. Setae of first setiger markedly different from others . *Exallopus*
Setae of first setiger similar to others 7
7. Antennae long and cirriform *Apophryotrocha*
Antennae reduced and papilliform *Ophryotrocha*

APPENDIX I

Poorly known subbiramous dorvilleids

The following four species are indeterminable on the basis of their original descriptions: *Anisoceras bioculata* Grube, 1856; *Staurocephalus Grubei* Kinberg, 1865; *Priognathus Boeckii* Malmgren, 1867; and, *Staurocephalus microphthalmus* Grube, 1880.

The following three species remain poorly known; they were described before attention focused on the presence or absence of furcate setae and so can not be definitely assigned to either *Dorvillea* or *Schistomeringos*: *Staurocephalus brachyceros* Grube, 1878b; *Staurocephalus brevipinnis* Grube, 1878a; and, *Staurocephalus filicornis* Grube, 1878a.

Staurocephalus australis Haswell, 1886, and *Staurocephalus Loveni* Kinberg, 1865, clearly belong to *Schistomeringos*. Insufficient information is available, however, to evaluate Augener's (1922) synonymy of these two nominal species.

Staurocephalus matsushimaensis Okuda & Yamada, 1954, is described

without mention of furcate setae. Imajima & Hartman (1964) redescribe it as having furcate setae but do not list the material they examined.

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