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A New Species of *Megalomma* Johansson, 1927 (Polychaeta: Sabellidae: Sabellinae) from Taiwan, with Comments on Sabellid Dorsal Lip Classification

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Kirk Fitzhugh (2003) A new species of *Megalomma* Johansson, 1927 (Polychaeta: Sabellidae: Sabellinae) from Taiwan, with comments on sabellid dorsal lip classification. *Zoological Studies* **42**(1): 106-134. A new species, *Megalomma cinctum*, is described from the intertidal zone of Hungtou Yu, also known as Orchid Island, located off the southeast coast of Taiwan. The species is most similar to *M. coloratum* (Chamberlin), *M. modestum* (Quatrefages), *M. quadrioculatum* Willey, *M. roulei* (Gravier), and *M. splendidum* (Moore), each of which has 1 pair of dorsalmost compound eyes on the radioles, sometimes with additional eyes on the 2nd and 3rd pairs of radioles, and the middorsal margins of the peristomial collar are fused to the lateral margins of the fecal groove, forming dorsolateral pockets. *Megalomma cinctum* is distinct from these species by the presence of a narrow, white, transverse band on setiger 2, and sometimes also on setiger 3. The number of pairs of radiolar eyes in *M. cinctum* is much more variable than has been reported in other species, and is strongly correlated with body size. Additional variability in the species is also reported for the number of pairs of radioles, peristomial collar shape, number of thoracic setigers, occurrence of the white transverse bands on setigers 2 and 3, and pigmentation patterns on the crown and thorax. The species is dioecious, but asexual reproduction also occurs by scissiparity. The description of *M. cinctum* also includes details on the internal construction of the dorsal lip radiolar appendages, necessitating an emendation of the definition of the genus. A brief survey is also presented of dorsal lip internal construction within the Sabellidae, and the implications of those findings for the determination of cladistic relationships among Sabellinae genera are discussed.
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Key words: Annelida, Fan worm, Sabellid, Systematics, Cladistics.

The genus *Megalomma* Johansson, 1927, has been the subject of several recent systematic studies (Perkins 1984, Fitzhugh 1989, Knight-Jones 1997). In her review of the genus, Knight-Jones (1997) lists 23 valid species names. Subsequently, Nishi (1998) described a species from the intertidal zone along Phuket Island, Thailand, and Fitzhugh (2002b) described a species from the continental shelf off Thailand, in the Andaman Sea. Of the species currently described, only 5 have type localities in the western Pacific Ocean: *M. acrophthalmos* (Grube 1878) from the Philippines, *M. pacificum* Johansson, 1927, from the Gilbert Islands, *M. trioculatum* Reish, 1968, from the Marshall Islands, and *M. suspiciens* (Ehlers 1904) and *M. kaikourense* Knight-Jones, 1997, both from New Zealand. The present paper describes a new species from the intertidal zone of Hungtou Yu, also known as Orchid Island, located off the southeast coast of Taiwan.

During the study of this new species of *Megalomma*, it was recognized that a feature of the branchial crown dorsal lips has not been fully considered in sabellid systematics. While the occurrence of radiolar appendages in the dorsal lips has recently become an integral part of sabellid taxonomy (Knight-Jones 1983, Perkins 1984, Fitzhugh 1989), the presence or absence of a branchial skeleton within the appendage has been infrequently reported (e.g., McIntosh 1918, Nicol 1931, Orrhage 1980, Fitzhugh 2002b). The presence or absence of the radiolar appendage skeleton among species in sabellid genera, and the necessity of including this and other associated characters in descriptions are discussed. As a result, an emended definition is also provided for *Megalomma*.

MATERIALS AND METHODS

Specimens of the new species of *Megalomma* described in the present paper were collected by hand, fixed in 10% seawater-formalin, then transferred to 70% ethanol. Specimens in the type series have been deposited in the following institutions: National Museum of Natural Science, Taichung, Taiwan (NMNS), and the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History, Los Angeles, California (LACM-AHF). Additional material examined in the course of this study came from the LACM-AHF collection and from the Florida Marine Research Institute, St. Petersburg, Florida (FSBC).

For examination of the internal structure of some dorsal lips, simple transverse sections were prepared by cutting an isolated lip at mid-length with a pair of ophthalmic micro-scissors, then cutting off this exposed surface from the remainder of the lip as thinly as possible. Sections were then placed in glycerol on a microscopic slide, and examined unstained using a compound microscope.

SYSTEMATIC ACCOUNT

Genus *Megalomma* Johansson, 1927, emended

Definition: Medium- to large-sized species with numerous radioles; radiolar skeleton with 4 or more rows of cells. Palmate membrane and radiolar flanges absent. One or more pairs of radioles each with a single, sessile, compound eye situated along inner radiole margin near distal end. Dorsal lips triangular, radiolar appendages present, indicated by longitudinal ridge or "midrib" along entire length; distinct blood vessel and radiolar sheath tissue ("surrounding sheath tissue" sensu Orrhage 1980, see below) extending through length of appendages, without a branchial skeleton extension; dorsal pinnular appendages present or absent. Ventral lips and parallel lamellae present. Posterior peristomial ring collar present. Inferior thoracic notosetae broadly hooded, arranged in 2 or more transverse rows. Abdominal neurosetal fascicles with 2 transverse rows of elongate, narrowly hooded setae. Thoracic uncini avicular; numerous, very small teeth above main fang; breast well developed; handles of medium length. Companion setae with very thin, tear-drop-shaped distal ends situated perpendicular to shaft. Abdominal uncini similar to thoracic ones, but with shorter handles.

Remarks: The present definition primarily follows that given by Perkins (1984) and Fitzhugh (1989). As was indicated by Fitzhugh (1989), monophyly of the genus is based on the presence of unpaired, distal, compound radiolar eyes. Compound eyes at the distal ends of radioles are also known in *Stylomma palmatum* Knight-Jones, 1997 (see also Knight-Jones and Perkins 1998). The arrangement of eyes differs, however, in the 2 genera in that they are sessile in *Megalomma* species and stalked in *S. palmatum*. The inclusion of *Stylomma* Knight-Jones in the cladistic analysis of Sabellinae genera by Fitzhugh and Rouse (1999) also showed that the eyes were independently derived in the 2 genera.

The emendation provided here is to point out (1) that the radiolar appendages of the dorsal lips do not have an associated branchial skeleton, and (2) that dorsal pinnular appendages can be present or absent. The new species described below lacks both the pinnular appendages and a radiolar appendage skeleton, which has prompted this modification of the definition of the genus. Although recent definitions of *Megalomma* (e.g., Perkins 1984, Fitzhugh 1989, Knight-Jones 1997) have taken into consideration the presence of radiolar appendages, this has only been to the extent of recognizing the general shape of the dorsal lips, indicating the presence of those appendages. The presence of radiolar appendages can readily be observed in species of *Megalomma* by the longitudinal ridge or "midrib" (Knight-Jones 1983 1997, Knight-Jones and Walker 1985, Knight-Jones et al. 1991, Knight-Jones and Perkins 1998) extending through the length of the lips.

In his investigations on the structural relations between sabellid dorsal lip radiolar appendages ("lip-associated radioles") and radioles, Orrhage (1980) described the internal components of both structures. At least 4 distinct features are common to the interior of radiolar appendages and radioles: (1) a coelomic space, (2) a blood vessel branching from the branchial vessel, (3) surrounding sheath tissue, referred to here as radiolar appendage surrounding sheath tissue, and (4) a pair of nerves. Orrhage also found that in at least 1 species he examined, *Sabella penicillus* Linnaeus (now *S. pavonina* Savigny, see Knight-Jones and Perkins 1998), a branchial skeleton, composed of thick-walled cells, was also present within the radiolar appendages. As a result of recent work by Fitzhugh (2002b) and Fitzhugh et al. (in prep.), it has become apparent that taxonomic studies of sabellids require consideration of the presence or absence of at least the radiolar appendage skeleton, and preferably both the skeleton and the surrounding sheath. The occurrence of radiolar appendage skeletons and the surrounding sheath in the Sabellidae is further discussed below in “Dorsal lip radiolar appendages in Sabellidae species.”

The inclusion of the presence of surrounding sheath tissue and the absence of a radiolar appendage skeleton in the definition of *Megalomma* is not based on an exhaustive survey of currently described species. Rather, the intent is to suggest that these conditions will be found in currently described species, as well as to promote the inclusion of these features in future descriptions. As will be discussed later, it appears that some degree of predictive ability as to the presence or absence of a skeleton in Sabellidae species can be based on the external morphology of the dorsal lips.

***Megalomma cinctum* sp. nov.**

(Figs. 1-10, 14C)

Megalomma sp. Yuan, 1992: 1-19, figs. 1-16.

Materials: Pacific Ocean, Taiwan, Hungtou Yu (Orchid Is.). Holotype: NMNS 3705-001 (specimen with 6 radiolar eyes), northern coastline, about 1 km east of Langtao Village, base of karst rock cliff, mid-intertidal zone, rock surfaces covered with dense, low-growing, coralline algae, depth 0-3 cm, 22°4’46"N, 121°32’13"E, coll. K. Fitzhugh and P.-J. Liu, 27 Apr. 1997. Paratypes: from same locality as holotype, NMNS 3705-002 (4 specimens, none with radiolar eyes), NMNS 3705-003 (9 specimens, each with 1-2 radiolar eyes), NMNS 3705-004 (4 specimens, each with 3-4 radiolar eyes), NMNS 3705-005 (2 specimens, each with 5 radiolar eyes), LACM-AHF 2085 (4 specimens, none with radiolar eyes), LACM-AHF 2086 (82 specimens, each with 1-2 radiolar eyes), LACM-AHF 2087 (23 specimens, each with 3-4 radiolar eyes), LACM-AHF 2088 (6 specimens, each with 5-6 radiolar eyes), and LACM-AHF 2089 (28 fragments, consisting of detached branchial crowns and specimens without crowns).

Etymology: The specific epithet refers to the transverse white bands present around setigers 2 and 3.

Description: Holotype complete, with 7 thoracic and 33 abdominal setigers. Total branchial crown length 2.5 mm; total thorax-abdomen length 7.0 mm; maximum width 0.6 mm throughout most of trunk, with slight tapering in posterior abdominal setigers; most of trunk cylindrical, except for slight dorsoventral flattening in posterior 1/3 of abdomen. Each half of branchial crown with 8 fully developed radioles; distal ends short, only extending slightly beyond distalmost pinnules (Fig. 1); ventral margins of branchial lobes with 3 to 4 very short, incompletely developed radioles without pinnules. Branchial lobes semicircular. Palmate membrane absent. Radiolar skeleton axis composed of 4 rows of cells; outer surfaces of radioles rounded, flanges absent. Sub-distal compound eyes present on dorsalmost 3 pairs of radioles; eyes on dorsalmost pair of radioles distinctly larger than other eyes, subspherical, not spirally arranged around radioles (Fig. 1A); eyes on 2nd radiole pair intermediate in size to 1st and 3rd pairs, with distal radiole ends slightly enlarged (Fig. 1B); distal ends of 3rd pair of radioles not enlarged (Fig. 1C). Distal ends of dorsalmost radioles with very short filaments, not extending beyond eyes; distal filaments on 2nd and 3rd pairs of radioles filiform, extending well beyond eyes, similar to distal ends of more-ventral radioles (Fig. 1D). Dorsal lips erect, triangular (Fig. 2A), about 1/4 length of branchial crown; radiolar appendages present but without branchial skeleton; surrounding sheath tissue present through length of appendages, oblong in transverse section (Fig. 14C), with greatest width nearly equivalent to width of adjacent blood vessel; pinnular appendages absent; proximalmost pinnule adjacent to each dorsal lip distinctly larger than other pinnules. Ventral lips about 1/2 length of dorsal lips, broadly rounded distally. Ventral parallel lamellae short, completely concealed by ventral collar margin; ventral sacs absent. Mid-dorsal collar margins attached to fecal groove, forming very narrow gap (Fig. 3A). Dorsolateral collar margins smooth, without incisions, even in height; branchial lobe bases and peristomium almost completely concealed by collar laterally and ventrally, only partially exposed mid-dorsally (Fig. 3). Lateral collar margins same height as dorsal margins (Fig. 3B). Collar completely incised midventrally, bounded by overlapping triangular lobes with rounded distal margins (Fig. 3C); ventral collar margin only slightly higher than lateral and dorsal margins. Notopodia on setiger 1 composed of superior and inferior rows of elongate narrowly hooded setae; superior group distinctly longer than inferior one. Notopodial fascicles on setigers 2-7 with superior group of elongate narrowly hooded setae and 2 inferior rows of broadly hooded setae (Fig. 2C). Neuropodial uncini on thoracic setigers with main fang surmounted by numerous rows of minute teeth, breast well developed, handles elongate (Fig. 2D). Companion setae with membranous, tear-drop-shaped distal end situated perpendicular to slender shaft (Fig. 2E); shafts slightly wider than uncini handles. Thoracic neuropodial tori longest on setiger 2, located laterally on segments, and not contacting ventral shields (Fig. 3B, C); tori successively shorter on remaining thoracic setigers, with setiger 7 tori about 1/2 length of tori on setiger 2. Abdominal neuropodia each with 2 transverse rows of elongate, narrowly hooded setae; setae in posterior row longer than those in anterior. Abdominal notopodia avicular uncini (Fig. 2F) with main fang surmounted by numerous rows of minute teeth; breast well developed; handles less than 1/2 length of handles of thoracic uncini; tori slightly shorter than those of setiger 7. Pygidium short, broadly rounded (Fig. 2B); 3 to 4 pairs of light red pygidial eyespots along lateral margins. No biannulate segments. Thoracic and abdominal ventral glandular shields well developed, rectangular (and bisected by fecal groove in abdominal setigers), present on all setigers (Fig. 3C). Radioles with 4 light brown, transverse pigment bands; 1st or proximalmost band widest, located at bases of radioles, slightly less than 1/4 total radiole length; 2nd pigment band about 1/2 as wide as 1st band; 3rd and 4th pigment bands equal in width, each about 1/2 as wide as 2nd band; 4th pigment band located about 3/4 distance

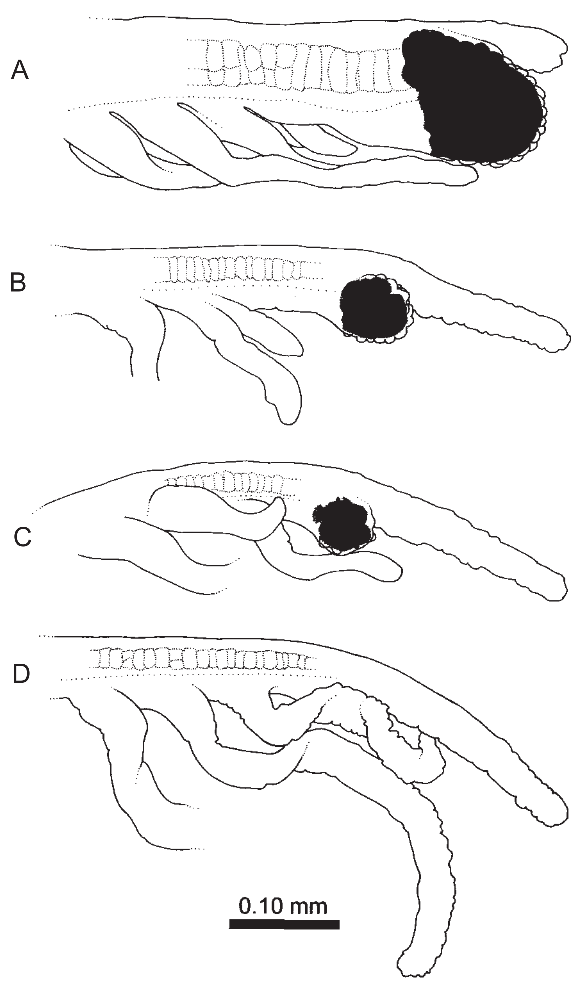

Fig. 1. *Megalomma cinctum* sp. nov. (A-C) Distal ends of 1st, 2nd, and 3rd dorsalmost radioles, respectively, showing variability in compound eye development; (D) distal end of the median radiole. A-D: LACM-AHF 2088, paratypes.

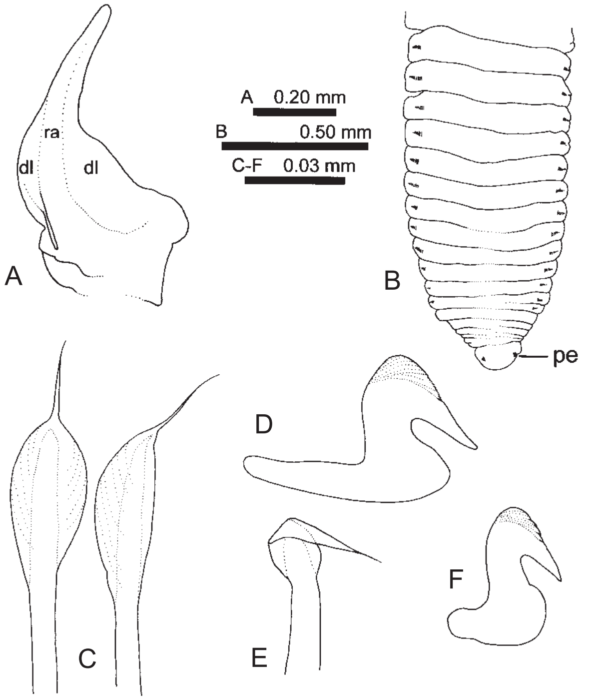

Fig. 2. *Megalomma cinctum* sp. nov. (A) Dorsal lip; (B) posterior end, dorsal view; (C) inferior thoracic broadly hooded notosetae from setiger 2; (D) thoracic uncinus from setiger 2; (E) companion seta from setiger 2; (F) abdominal uncinus from setiger 9. Abbreviations: *dl*, dorsal lip lateral lamellae; *pe*, pygidial eyespot; *ra*, radiolar appendage. A-F: LACM-AHF 2086, paratypes.

along crown; pigmentation in bands distributed over outer and lateral radiole margins and adjacent pinnules; dorsal and ventral lips with light brown pigment over surfaces; remainder of crown unpigmented, cream-colored or light pink. Peristomial collar and setiger 1 with small, light brown spots distributed evenly over surface except on ventral shield; one pair of triangular, dark brown pigment patches present dorsolaterally along anterior margin on setiger 2 (Fig. 3A); remainder of trunk without pigment patterns, cream-colored or light pink. Setigers 2 and 3 each with narrow, whitish, transverse band completely encircling each setiger (Fig. 3); bands on each setiger arranged in an M-shaped pattern dorsally and ventrally, with dorsomedian part of each band extending to posterior margin of setiger (Fig. 3A) and ventromedian part along posterior margin of ventral shield (Fig. 3C); bands extending laterally along posterior margins of neuro- and noto-podia (Fig. 3B); band on setiger 2 more prominent than that on setiger 3. Peristomial eyespots not observed. Dioecious; gametes abdominal (not observed in type specimens, see “Remarks”); asexual reproduction also occurs by scissiparity (see “Remarks”). Tubes mainly composed of sand grains, with some detrital material.

Specimen variation: Among the paratypes, the following 6 features were found to vary from what is described for the holotype.

Radiolar eyes. Among paratypes with a branchial crown (n = 134), the most common condition is the presence of only 1 pair of eyes on the dorsalmost radioles (n = 83, Fig. 4A). The next most-common patterns are either the presence of 2 pairs of eyes (n = 14), or one half of the crown with 1 eye and the other half with 2 eyes (n = 13). Only 2 specimens, among them the holotype, have 3 pairs of eyes. Five specimens have 2 and 3 eyes on each half of the crown, respectively. The greatest disparity between eyes on each half of the crown is in 1 specimen with 4 and 2 eyes, respectively. Six specimens lack eyes altogether. Seven specimens have only 1 eye on a dorsalmost radiole; in most of these instances, the dorsalmost radiole on the other half of the crown appears to be either malformed or in the process of regeneration. The relation between body size, as indicated by branchial crown length, and total number of

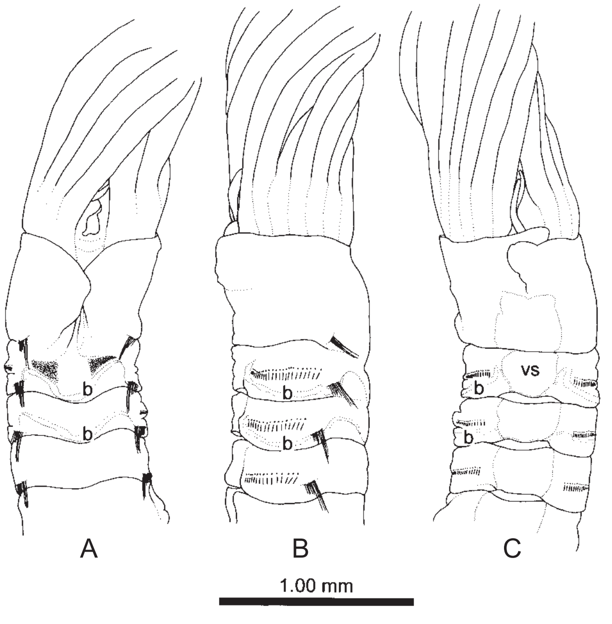

Fig. 3. *Megalomma cinctum* sp. nov. (A-C) Dorsal, lateral (left side), and ventral views, respectively, of the anterior end. Abbreviations: *b*, whitish, transverse bands on setigers 2 and 3 (cf. Fig. 7); *vs*, ventral shield. A-C: NMNS 3705-001, holotype.

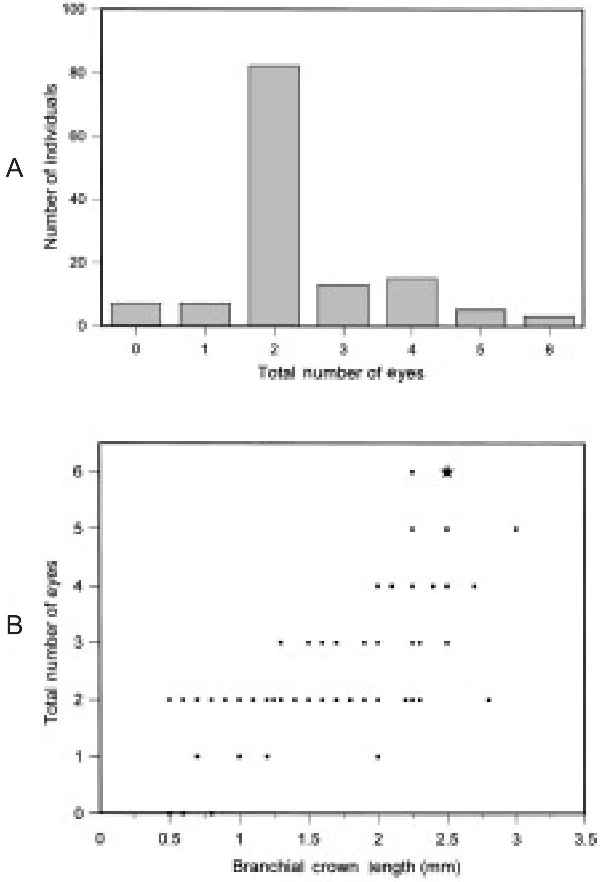

Fig. 4. Compound radiolar eyes in *Megalomma cinctum* sp. nov. (A) Total number of eyes among type specimens; (B) relationship between total number of eyes and body size as indicated by branchial crown length. The holotype is indicated by a star.

eyes shows a strong positive correlation (n = 134, r = 0.74, p < 0.001, Fig. 4B), suggesting that some of the variability in numbers of eyes is a function of age.

The dorsalmost pair of eyes is usually distinctly larger than those on adjacent radioles (Fig. 1A), and slightly wider than the radiole on which it occurs. Some specimens with only 1 pair of eyes do have dorsalmost eyes that are not as well developed and are more similar to the more-lateral eyes (Fig. 5B).

The distal ends of the dorsalmost radioles in the holotype do not extend beyond the eyes (Fig. 1A), which also occurs in many of the paratypes. There are, however, instances in which distal ends do extend beyond the eyes to varying degrees (Fig. 5). The occurrence of longer tips does not appear to have any relation to body size.

Radioles. The number of pairs of radioles ranges from 4 to 10 within the type series, with the largest number of specimens having 5 pairs (Fig. 6A). Using branchial crown length as a surrogate for relative age, there is a significant positive correlation with the number of radioles, indicating that new radioles are added as an individual grows (n = 134, r = 0.91, p < 0.001, Fig. 6B).

Collar margins. The mid-dorsal collar margins may form a very narrow gap, as in the holotype (Fig. 3A), or margins can be moderately to well separated (Fig. 7). Lateral collar margins range from even in height, as in the holotype (Fig. 3B) to distinctly oblique, depending on the degree to which the ventral collar lobes extend anteriorly. Ventral collar lobes overlap to some extent in some specimens (Fig. 3C), while in others the lobes lie adjacent to one other or they are separated by a narrow gap (Fig. 8).

Number of thoracic setigers. Within the type series, the number of thoracic setigers ranges from 5 to 8, with the majority of individuals having either 6 or 7 (Fig. 9A). Using branchial crown length as an indication of total body length, there is no relation between the number of thoracic setigers and age (n = 127, r = 0.039, p > 0.001, Fig. 9B).

White transverse bands. The occurrence of transverse bands on setigers 2 and 3, as seen in the holotype of *Megalomma cinctum* (Fig. 3), was observed in only 7 paratypes, with branchial crown lengths ranging from 1.2 to 2.5 mm. The most

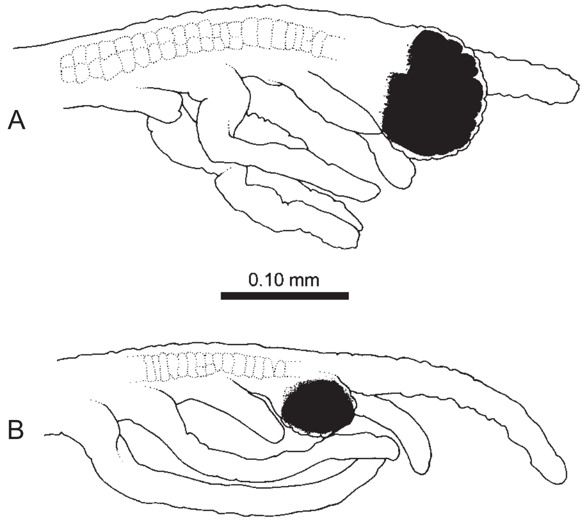

Fig. 5. Distal ends of dorsalmost radioles in *Megalomma cinctum* sp. nov. (A-B) Variability in the extension of distal radiolar filaments beyond compound eyes (cf. Fig. 1A). The specimen in (A) has branchial crown and trunk lengths of 1.6 and 3.4 mm, respectively, with only 1 pair of compound eyes. The specimen in (B) has branchial crown and trunk lengths of 1.3 and 3.0 mm, respectively, with only 1 pair of compound eyes. A-B: LACM-AHF 2086, paratypes.

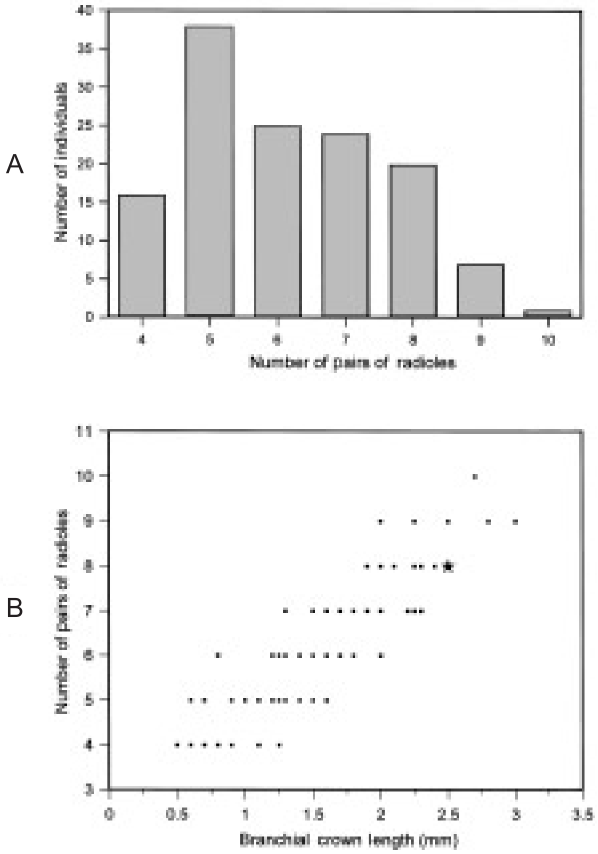

Fig. 6. Radioles in *Megalomma cinctum* sp. nov. (A) Distribution of pairs of radioles among type specimens; (B) relationship between the number of pairs of radioles and body size as indicated by branchial crown length. The holotype is indicated by a star.

common condition (n = 112) is that of a single band on setiger 2 (Fig. 10A). An additional 15 paratypes, most of which are small individuals with a branchial crown length of less than 1.0 mm, do not have bands on any setigers. Among the available specimens, there is a positive correlation between the number of bands and body size (n = 134, r = 0.51, p < 0.001, Fig. 10B).

Pigmentation. The extent of body wall pigmentation on the branchial crown and thorax varies with body size. Pigment patterns described for the holotype are typical of larger specimens, whereas pigmentation in medium- to small-sized specimens is more limited. The smallest specimens commonly show no pigment pattern, or else pigment is limited to the basal 1/4 of the branchial crown. The number of transverse pigment bands on radioles tends to increase in a proximal to distal direction with an increase in body size. Similarly, pigmentation on the anterior thorax is usually absent or very faint in small specimens, and variably developed in medium-size specimens.

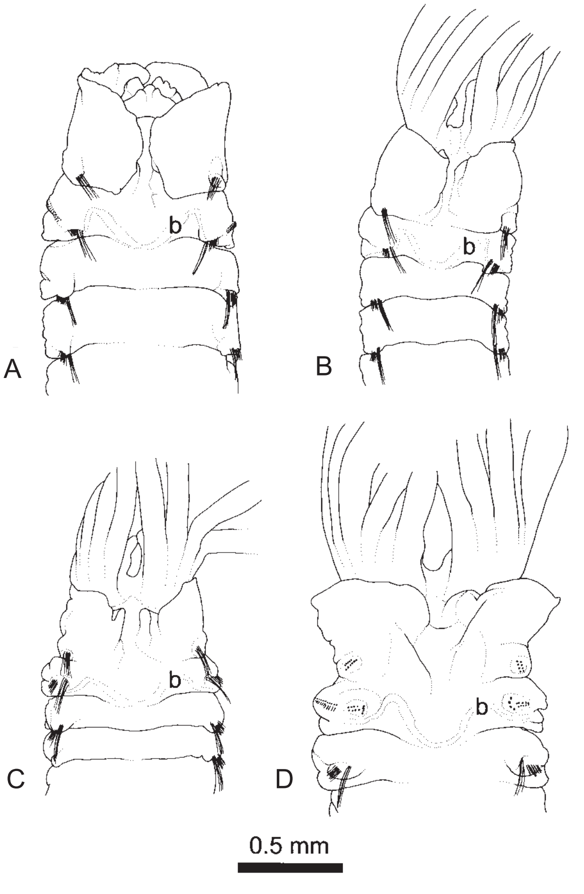

Fig. 7. Dorsal collar variation in *Megalomma cinctum* sp. nov. (A-D) Dorsal views of peristomial collar regions, showing variability in degree of separation between mid-dorsal collar margins (cf. Fig. 3A). Abbreviation: *b*, whitish, transverse band on setiger 2 (cf. Fig. 3). A-D: LACM-AHF 2086, paratypes.

Distribution: In addition to the type locality, *Megalomma cinctum* is also known from the intertidal zone of Hsiao Liuchiu, off the southwestern coast of Taiwan, where the reproductive biology of the species (as *Megalomma* sp.) was studied by Yuan (1992, see "Remarks").

Remarks: In her revision of *Megalomma*, Knight-Jones (1997) segregated species into 5 artificial groupings based on (1) whether the mid-dorsal collar margins are fused to the fecal groove or are unattached, (2) whether the dorsolateral collar margins form pockets or not, and (3) the extent to which eyes occur on radioles (Table 1). These groupings have had general utility for the comparison of species (Nishi 1998, Fitzhugh 2002b), especially since no cladistic studies of the group have been conducted thus far. *Megalomma cinctum* belongs in Knight-Jones' (1997) group 1B, which is defined by the fusion of the middorsal collar margins to the fecal groove, the presence of dorsolateral collar pockets, and eyes occurring only on the dorsalmost radioles or sometimes the 4 to 6 most-dorsal radioles. The other species in this group

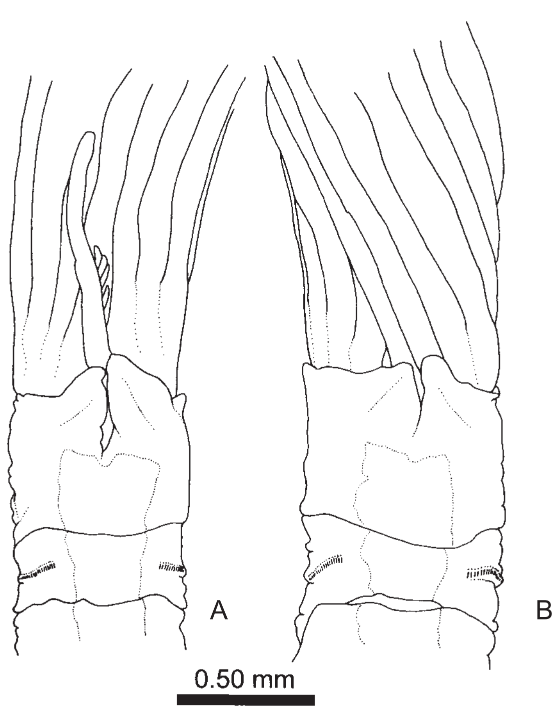

Fig. 8. Ventral collar variation in *Megalomma cinctum* sp. nov. (A-B) Ventral views of anterior ends, showing variability in ventral collar lobes (cf. Fig. 3C). A-B: LACM-AHF 2086, paratypes.

include *M. modestum* (Quatrefages 1866), *M. quadrioculatum* (Willey 1905), *M. splendidum* (Moore 1905), *M. roulei* (Gravier 1908a), and *M. coloratum* (Chamberlin 1919a). *Megalomma modestum* differs from *M. cinctum* in that the middorsal collar margins are shorter (Knight-Jones 1997: fig. 1G) and the ventrolateral collar margins are lower than the dorsal margins (Knight-Jones 1997: fig. 1J). Based on Knight-Jones' (1997: fig. 1G, H, J) illustrations, *M. modestum* also has a larger number of radioles, and the anterior thoracic neuropodial tori are considerably longer. *Megalomma modestum* is only known to have 1 pair of eyes (Knight-Jones 1997). *Megalomma coloratum* differs from *M. cinctum* in having 16-17 pairs of radioles (Chamberlin 1919a), a more prominent gap between the middorsal collar margins (Knight-Jones 1997: fig. 2P, Q) than is seen in *M. cinctum*, and the ventral margins of the neuropodial tori in posterior thoracic setigers being in contact with the ventral shields (Knight-Jones 1997: fig. 2R). The species is only known to have 1 pair of radiolar eyes. *Megalomma splendidum* has 2 to 3 pairs of spirally arranged eyes (Berkeley 1930: fig. 1A-C, as *Branchiomma burrardum*, Hartman 1938 1969), 20-23 pairs of radioles, and dorsolateral incisions in the collar. *Megalomma roulei* has 12 pairs of radioles and no body wall pigment pattern on the thorax (Gravier 1908a 1909). The species is known to have only 1 pair of radiolar eyes. In addition to the above distinctions, *M. cinctum* differs from other species in group 1B by the presence of the white band on setiger 2 (and setiger 3 when present).

Megalomma cinctum appears to be most similar to *M. quadrioculatum*. In the original description, based on a single specimen, Willey (1905) states that there are 14 pairs of radioles, with 2 pairs of eyes. Willey (1905: 307) describes the collar as having a "median incisura ventralis, a deep median dorsal notch and a still deeper submedian dorsal notch on each side." He does not

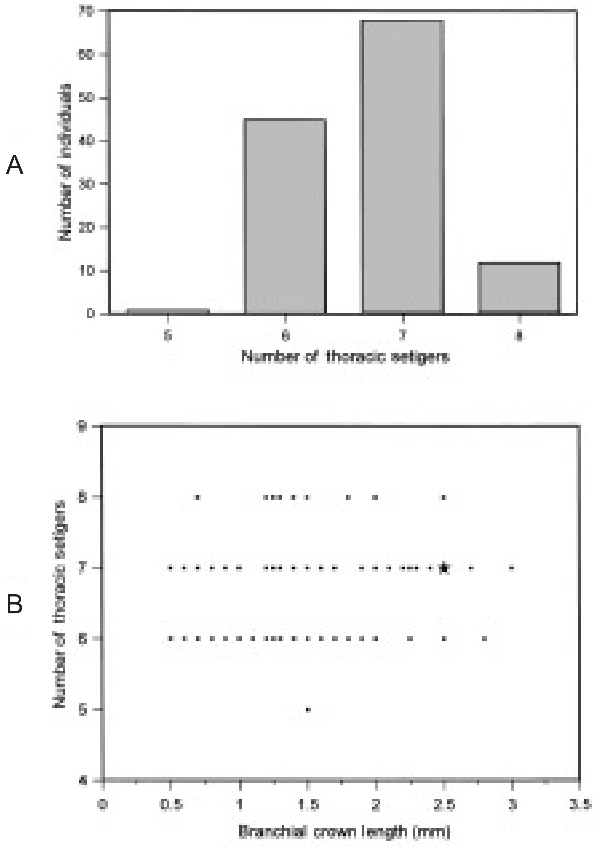

Fig. 9. Number of thoracic setigers in *Megalomma cinctum* sp. nov. (A) Total number of thoracic setigers from among type specimens; (B) relationship between the number of thoracic setigers and body size as indicated by branchial crown length. The holotype is indicated by a star.

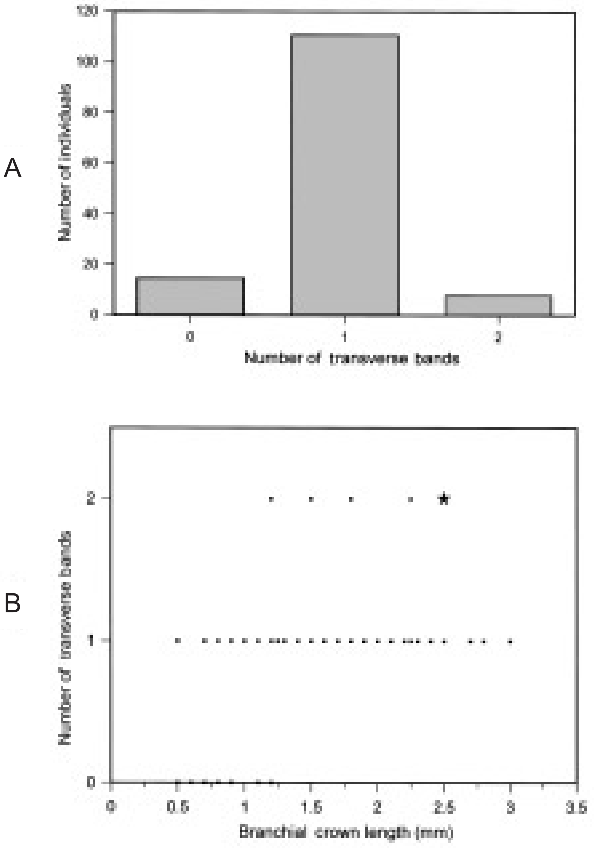

Fig. 10. White, transverse bands in *Megalomma cinctum* sp. nov. (A) Occurrence of bands in anterior thoracic setigers among type specimens; (B) relationship between the number of transverse bands and body size as indicated by branchial crown length. The holotype is indicated by a star.

mention the presence of ventral collar lobes, and his illustration of the ventral side of the anterior end does not clearly show the shape of the collar. Day's (1967: fig. 37.1m) illustration of the collar in a South African specimen shows the presence of what appear to be dorsolateral notches, but it is also possible that this actually represents the presence of prominent pouches on either side of the fecal groove. Day (1951) stated that the number of eyes for South African specimens can vary from 1 pair in juveniles to 3 pairs in larger individuals. Day (1967: 758, fig. 37.1m) later stated that there are "two or more" eyes on the radioles, and his illustration shows a specimen with about 6 pairs of eyes. Monro (1933) described a specimen from South Africa as having dorsolateral folds in the collar but no notches, and a prominent pair of ventral lobes. Monro also noted that the left half of the crown has 2 eyes and the right half has 3. *Megalomma cinctum* does not have dorsolateral pockets as pronounced as those in *M. quadrioculatum*. The white band on setiger 2 (and setiger 3 when present) that is typical in *M. cinctum* has never been reported in *M. quadrioculatum*. It seems unlikely that such a distinctive feature would have been overlooked by either Willey (1905), Monro (1933), or Day (1951 1967).

Megalomma cinctum is one of the most variable of species in the genus with respect to the occurrence of eyes. The majority of species of *Megalomma* have eyes present on most radioles (Table 1: groups 1A, 2A, 2C), such that variability is not really a phenomenon that requires consideration. Those species in which variability might be

Table 1. Species groups in *Megalomma* arranged according to criteria used by Knight-Jones (1997, see also Nishi 1998, Fitzhugh 2002b)

Group	Dorsal collar margins	Occurrence of subterminal eyes	Species	Type locality
1A	Fused to fecal groove, pockets present	On most radioles	*M. acrophthalmos* (Grube, 1878)	Philippines
			M. circumspectum (Moore, 1923)	California
			M. claparedii (Gravier, 1908b)	Red Sea
			M. lobiferum (Ehlers, 1887)	Florida
			M. multioculatum Fitzhugh, 2002b	Thailand, Indian Ocean
			M. pacifici (Grube, 1859)	Costa Rica
			M. pacificum Johansson, 1927	Gilbert Islands
			M. suspiciens (Ehlers, 1904)	New Zealand
			M. trioculatum Reish, 1968	Marshall Islands
			M. vesiculosum (Montagu, 1815)	England
			M. vigilans (Claparède, 1870)	Italy
1B	Fused to fecal groove, pockets present	Dorsalmost pair of radioles, sometimes also 2nd and 3rd pairs	*M. coloratum* (Chamberlin, 1919a)	California
			***M. cinctum* n.sp.**	**Taiwan**
			M. modestum (Quatrefages, 1866)	Peru
			M. quadrioculatum (Willey, 1905)	Ceylon
			M. roulei (Gravier, 1908a)	Peru
			M. splendidum (Moore, 1905)	Alaska
2A	Not fused to fecal groove, pockets present	On most radioles	*M. heterops* Perkins, 1984	Florida
			M. neapolitanum (Claparède, 1868)	Italy
2B	Not fused to fecal groove, pockets absent	Dorsalmost pair of radioles	*M. bioculatum* (Ehlers, 1887)	Florida
			M. gesae Knight-Jones, 1997	El Salvador
			M. kaikourense Knight-Jones, 1997	New Zealand
			M. pigmentum Reish, 1963	California
2C	Not fused to fecal groove, pockets absent	On most radioles	*M. mushaense* (Gravier, 1908b)	Red Sea
			M. nechamae Knight-Jones, 1997	Red Sea
2D	Not fused to fecal groove, pockets absent	First to 5th dorsalmost pairs of radioles	*M. miyukiae* Nishi, 1998	Thailand, Indian Ocean

a factor in discerning taxonomic relations include members of group 1B, mentioned above, where the number of eyes is known to exhibit variation at least in *M. quadrioculatum* (see above) and *M. cinctum*. Since some species in group 1B, i.e., *M. modestum*, *M. coloratum*, and *M. roulei*, are only known, based on very small sample sizes, to have 1 pair of subspherical eyes, whereas at least *M. quadrioculatum* and *M. cinctum* are known to have 1 or more pairs, decisions as to the identification of species should be based as much as possible on samples which are sufficiently large to consider the occurrence of variation in eye distribution. *Megalomma cinctum* appears to be the only known species in which the extension of the tips of the dorsalmost radioles beyond the eyes is known to exhibit substantial variation.

In addition to the known variability in the number of eyes in *Megalomma quadrioculatum* and *M. cinctum*, Nishi (1998) described limited variability in *M. miyukiae*. Among the 3 type specimens of *M. miyukiae*, Nishi stated that the holotype has 1 pair of eyes, and the paratypes have 3 and 5 pairs, respectively. The species has up to 10 pairs of radioles. Interestingly, the total body length of these specimens is inversely related to the number of eyes, with respective lengths of 45, 25, and 15 mm. Nishi (1998: table 1) placed *M. miyukiae* into Knight-Jones' (1997) group 2, in which mid-dorsal collar margins are free and pockets are absent, but assigned the species to a tentative subgroup, “2?”. Fitzhugh (2002b) designated this subgroup 2D (Table 1). Nishi distinguished his subgroup 2? by the presence of eyes on the 1st to 3rd dorsal pairs of radioles, but this is not consistent with the distribution between the 1st and 5th pairs he describes among the paratypes.

The reproductive biology of *Megalomma cinctum* (as *Megalomma* sp.) from the intertidal zone of Hsiao Liuchiu, off the southwestern coast of Taiwan, was studied by Yuan (1992) during 1991-1992. The species is dioecious, with abdominal gametes, and broadcast spawning was recorded in Dec. Yuan also found within the population that 4%-13% of individuals exhibited the results of scissiparity, which occurs throughout the year. Evidence of scissiparity exists among the type series, where there are adult specimens with regenerated posterior ends. Likewise, some very small individuals have a wide, somewhat truncate anterior end, and a very short branchial crown, suggesting that the anterior end had recently formed subsequent to scissiparity. Among the type specimens, no instances of recent, asexually derived specimens were found still occupying the same tube.

As part of his study, Yuan (1992: fig. 5) included illustrations of thoracic and abdominal hooded setae and uncini. These are consistent with what are described from among the types (Fig. 2C-F). In an illustration of the ventral side of the thorax, Yuan (1992: fig. 4A) shows the white, transverse band (“glandular ridge”) on setigers 2 and 3 as limited to the region of the ventral shields and bisecting each. As is noted in the description of the holotype (Fig. 3C), the bands do not extend through the ventral shields, but rather along their posterior margins. The degree of variability in the number of thoracic setigers observed in the type specimens, ranging from 5 to 8 , was also reported by Yuan for specimens from Hsiao Liuchiu.

While the white, transverse bands on setigers

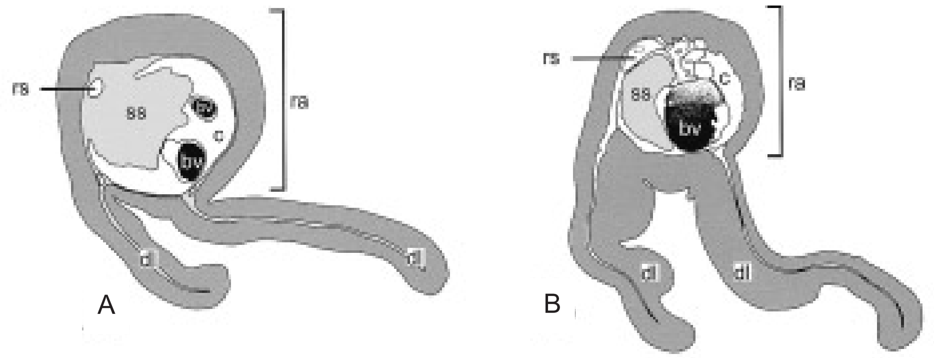

Fig. 11. Transverse sections through radiolar appendages in *Sabella pavonina*. (A) Slightly modified from Nicol (1931: fig. 3); note the surrounding sheath tissue completely surrounding the radiolar appendage skeleton; (B) drawn from a micrograph in Orrhage (1980: fig. 5); note the surrounding sheath tissue forming a discrete mass that is separate from the skeleton. Abbreviations: *bv*, blood vessel; *c*, coelom; *dl*, dorsal lip lateral lamellae; *ra*, radiolar appendage; *rs*, radiolar appendage skeleton; *ss*, supporting sheath tissue. A-B not drawn to scale; locations of sections along each dorsal lip unknown.

2 and 3 of *Megalomma cinctum* are reminiscent of the post-setal “glandular ridge” on setiger 2 in species of many plesiomorphic Sabellinae genera, e.g., *Amphicorina* Claparède, *Chone* Krøyer, *Euchone* Malmgren, *Jasmineira* Langerhans, and *Potamethus* Chamberlin. I am unaware of any evidence to suggest that the ridge in these latter taxa is homologous to that in *M. cinctum*. Such a relationship seems doubtful given that most species in *Megalomma* appear not to have such bands and the fact that the genus is not closely related to these plesiomorphic genera (Fitzhugh and Rouse 1999, see also “Dorsal lips and cladistic relationships” below).

Dorsal Lip Radiolar Appendages in Sabellidae Species

The definition of *Megalomma* was emended above to take into consideration the absence of branchial skeleton components and the presence of surrounding sheath tissue in dorsal lip radiolar appendages; these conditions were also included in the description of *M. cinctum*. As a result of these changes, it is necessary to consider the presence or absence of radiolar appendage skeletons and the surrounding sheath in individuals in the subfamily Fabriciinae and in genera of the Sabellinae, and the possible consequences these observations have for the systematics of fan worms.

A significant advance in the study of sabellid taxonomy and systematics occurred with the inclusion of detailed descriptions by Knight-Jones (1983) and Perkins (1984) of the branchial crown, including dorsal lips, in sabellid species. Subsequently, Fitzhugh (1989) included dorsal lip characters in the definitions of all Sabellidae genera, forming part of the basis for a cladistic analysis of relationships among genera, which has been continued through a number of subsequent analyses of relationships within the Fabriciinae (e.g., Fitzhugh 1991a b 1992a 1993 1998 1999 2002a) and Sabellidae (e.g., Fitzhugh 1991a 2002b, Rouse and Fitzhugh 1994, Rouse and Gambi 1997, Fitzhugh and Rouse 1999). Similarly, the inclusion of dorsal lip morphologies has become a standard part of sabellid descriptions (Knight-Jones and Walker 1985, Fitzhugh 1990a b c d 1991b 1992a b 1993 1998 1999 2002a b, Knight-Jones et al. 1991, Perkins 1991, Giangrande 1992 1994, Rouse 1993a b 1994 1996a b, Hsieh 1995, Rouse and Gambi 1997, Knight-Jones and Perkins 1998, Nishi 1998, Fitzhugh and Rouse 1999).

The taxonomic and systematic interest in dorsal lip morphologies was prompted by the histological work of Orrhage (1980), who found that among the species he examined in the genera *Chone*, *Euchone*, *Sabella* Linnaeus, and *Pseudopotamilla*

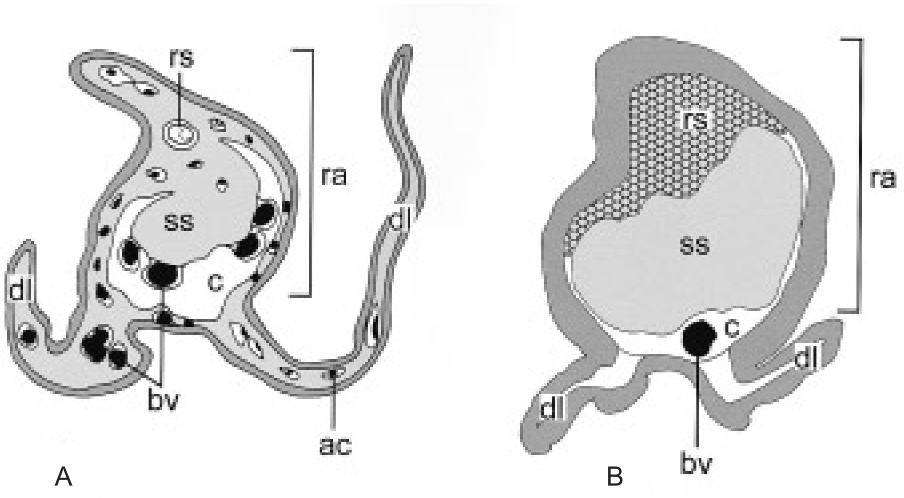

Fig. 12. Transverse sections through radiolar appendages in *Sabellastarte magnifica*. (A) Redrawn from Fitzsimons (1965: fig. 8); note the surrounding sheath tissue extending into the dorsal lip lamellae and completely surrounding the radiolar appendage skeleton; the section is probably from near the base of the lip, where the lateral lamellae are widest; (B) mid-region of lip from preserved specimen from the British Virgin Islands; note the surrounding sheath tissue does not extend into the short lateral lamellae and is separate from the skeleton, which is composed of numerous cells. Abbreviations: *ac*, anastomosing cells in skeletal sheath tissue; *bv*, blood vessel; *c*, coelom; *dl*, dorsal lip lateral lamellae; *ra*, radiolar appendage; *rs*, radiolar appendage skeleton; *ss*, supporting sheath tissue. A-B not drawn to scale. B: LACM-AHF.

Bush, a "lip-associated radiole" forms part of the dorsal lip (Orrhage1980: figs. 5, 9-11). This radiole was later referred to as a "radiolar appendage" by Perkins (1984), and this term was used by Fitzhugh (1989). Prior to Orrhage's study, the terms "palps" (e.g., Nicol 1931, Fitzsimons 1965) and "tentacles" (e.g., McIntosh 1918, see Orrhage 1980 for a summary of some earlier terminology) were most often used to denote the elongate lips. Orrhage (1980) determined that radiolar appendages and radioles of the branchial crown are homologous by the presence in both types of structures of (1) a coelomic space, (2) a blood vessel derived from the branchial blood vessel, (3) a pair of nerves, and (4) the surrounding sheath tissue, which is associated with the branchial skeleton in radioles (Figs. 11-14). In his examination of the dorsal lips of *S. pavonina*, Orrhage (1980: fig 5, see also McIntosh 1918: pl. 1, fig. 7, Nicol 1931: fig. 3, and Fitzsimons 1965: fig. 8) (Figs. 11-13) also noted the presence of an extension of the branchial skeleton into the dorsal lips, further establishing the homologous relationship between radiolar appendages and radioles. While Orrhage (1980: figs. 4, 9, 10) showed an association between the branchial skeleton and surrounding sheath tissue in the radioles, he appeared to make a further distinction between what he called the "surrounding sheath" (Orrhage 1980: fig. 5) and "supporting tissue" (Orrhage 1980: figs. 9, 10) in the radiolar appendages of *S. pavonina* and *P. reniformis* (Bruguière), respectively. Unfortunately, Orrhage did not discuss how these types of tissue might be distinguished or whether they should be considered distinct from one another. The only discernable difference based on his sections is that the surrounding sheath tissue tends to be very thick (Figs. 11-13, 14A-C), whereas supporting tissue only forms a relatively narrow layer (Fig. 14D). Both types of tissue are situated along the margin of the appendage between the blood vessel and appendage epithelium, and opposite the lip lamellae and coelomic space (e.g., Fig. 14). Based on my own observations of what Orrhage (1980) called supporting tissue in *Pseudopotamilla* (see below, Fig. 14D), this tissue appears to have essentially the same consistency and placement as the surrounding sheath tissue he described in *S. pavonina*. Since both types of tissue are also located in the same position in radiolar appendages, I assume that they can be considered identical. In my own hand-cut transverse sections of appendages, the surrounding sheath is usually arranged like a support rod, and can be about the same diameter as the adjacent blood vessel (Fig. 14B) or considerably larger (Fig. 14A, see below). Orrhage (1980) stated that the surrounding sheath tissue is composed of an opaque material, while Perkins (1984: 292) described it as "an extracelluar cartilaginous sheath containing some anastomosing cells", and Fitzsimons (1965: 650) described the tissue as a "clear hyaline mate-

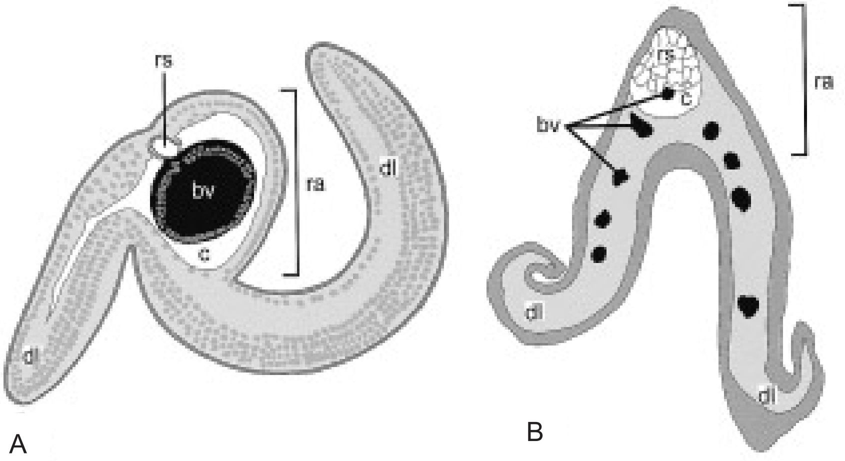

Fig. 13. Transverse sections through radiolar appendages in *Bispira* and *Branchiomma*. (A) *Bispira volutacornis*, redrawn from McIntosh (1918: pl. 1, fig. 7); note the absence of surrounding sheath tissue, the radiolar appendage skeleton composed of a single row of cells, and the connective tissue in the dorsal lip lamellae; (B) preserved specimen of *Branchiomma* sp. from the British Virgin Islands; section from mid-region of appendage; note the absence of surrounding sheath tissue, the skeleton composed of numerous cells, and the connective tissue in the dorsal lip lamellae. Abbreviations: *bv*, blood vessel; *c*, coelom; *dl*, dorsal lip lateral lamellae; *ra*, radiolar appendage; *rs*, radiolar appendage skeleton; *ss*, supporting sheath tissue. A-B not drawn to scale. B: LACM-AHF.

rial" with interspersed cells. From my own observations, the surrounding sheath appears to consist of a translucent to slightly opaque, gelatinous material that can have a slightly to moderately fibrous consistency.

In those instances in which dorsal lip radiolar appendages also have a branchial skeleton extension, the surrounding sheath tissue appears to have a variable distribution. For example, Nicol (1931: fig. 3) (Fig. 11A) showed the extension of the branchial skeleton completely encased by the surrounding sheath tissue in *Sabella pavonina*. Similarly, Fitzsimons (1965: fig. 8) (Fig. 12A) illustrated a transverse section through a dorsal lip of *Sabellastarte magnifica* (Shaw) in which she identified surrounding sheath tissue completely enveloping the branchial skeleton extension, as well as extending into the dorsal lip lamellae. For *S. pavonina*, Orrhage (1980: 126) stated that the single row of skeletal cells is "enveloped" by the surrounding sheath. But, based on his micrograph (Orrhage 1980: fig. 5) (Fig. 11B), the spatial relation between the skeleton and surrounding sheath appears to greatly differ in that the 2 tissues are discretely separate from one another. A third pattern was described by McIntosh (1918: pl. I, fig. 7) (Fig. 13A) for *Bispira volutacornis* (Montagu), where the radiolar appendages have a skeleton, but no surrounding sheath. A similar phenomenon has been observed in species of *Branchiomma* Kölliker (Fig. 13B, see below). In the survey of dorsal lip structures presented below, I have where possible made distinctions between surrounding sheath tissue organized in a cylindrical or rod-like form (Figs. 11B, 12B, 14A-C), and that which is more laminate (Fig. 14D) or putatively absent (Fig. 13).

Studies by McIntosh (1918: pl. I, fig. 7) (Fig. 13A), Nicol (1931: fig. 3) (Fig. 11A), Fitzsimons (1965: fig. 8) (Fig. 12A), and Orrhage (1980: fig. 5) (Fig. 11B) show the radiolar appendage branchial skeleton as composed of a single row of cells in *Bispira volutacornis*, *Sabellastarte magnifica*, and *Sabella pavonina*. Among individuals of *S. magnifica* (cf. Fig. 12), *S. pavonina*, and *Bispira* species (Fig. 13A) I have examined, the branchial skeleton extension is composed of multiple rows of cells. The degree to which the skeleton form varies might be of taxonomic value and should be considered in the future. The only species in which I have observed radiolar appendage skeletons with a single row of cells have been 2 species of *Laonome* Malmgren (see below).

Within some genera I have examined in which species lack a skeleton in the radiolar appendages, yet have a very thick surrounding sheath, e.g., *Hypsicomus* Grube (Fig. 14A), *Anamobaea* Krøyer, and *Notaulax* Tauber, the sheath is probably the functional equivalent of a skeleton. A similar function was dramatically illustrated by Fitzsimons (1965: fig. 4), where the

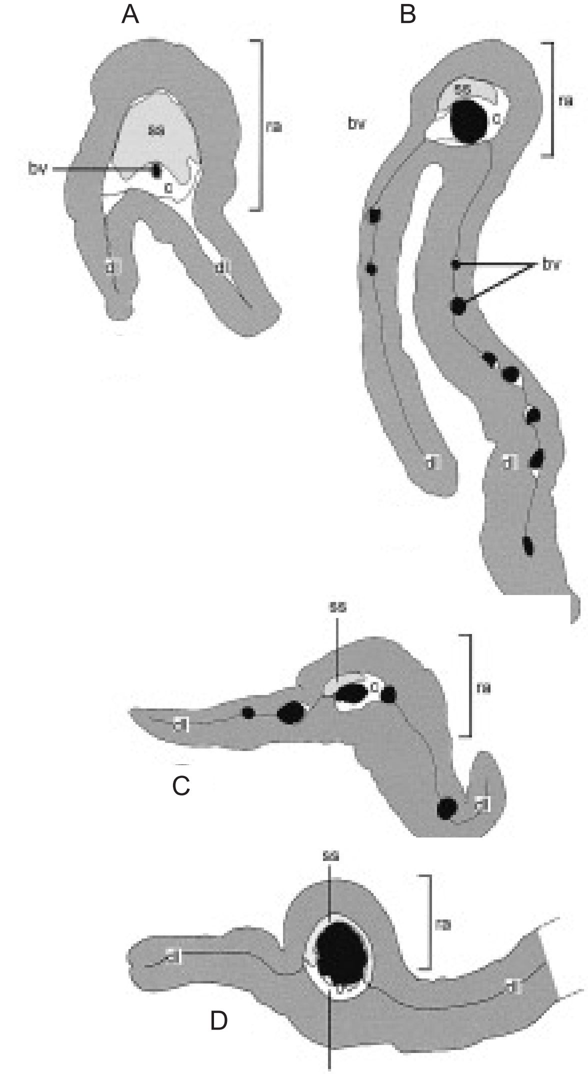

Fig. 14. Transverse sections through radiolar appendages in *Hypsicomus*, *Megalomma*, and *Pseudopotamilla*. (A) *Hypsicomus* sp. from Belize, mid-region of appendage; (B) *Megalomma splendidum* from California, mid-region of appendage; (C) *Megalomma cinctum* sp. nov., mid-region of appendage; (D) *Pseudopotamilla reniformis*, redrawn from Orrhage (1980: fig. 10), near base of appendage. Note the absence of a radiolar appendage skeleton in all species. A-D not drawn to scale. Abbreviations: *bv*, blood vessel; *c*, coelom; *dl*, dorsal lip lateral lamellae; *ra*, radiolar appendage, *ss*, supporting sheath tissue. A: FSBC I 44140; B: LACM-AHF; C: LACM-AHF 2086, paratype.

epithelial tissue was removed from the branchial lobes and dorsal lips, with remaining tissue of the radiolar appendages represented by the very prominent surrounding sheath tissue overlying the branchial skeleton.

Cochrane (2000: 9) suggested that the recognition of radiolar appendages, especially in small specimens of *Amphicorina* and *Amphiglena*, should be based on the presence of a branchial skeleton extension: "Because the radioles and pinnules contain skeletal cells, correct usage of the terminology would demand that a dorsal radiolar appendage should be equipped with internal skeletal elements. If these are lacking, an elongate continuation of a dorsal lip may very well merely be a long dorsal lip." Similar reasoning was used by Fitzhugh and Rouse (1999: 376) regarding *Amphiglena* and *Terebrasabella* Fitzhugh and Rouse (see below). To the contrary, however, Orrhage's (1990) study has shown that the presence of the skeleton is not a definitive criterion for indicating the presence of appendages. Rather, the critical structures to be considered are the presence of a coelomic space, a blood vessel derived from the branchial vessel, the paired radiolar nerves, and surrounding sheath tissue (e.g., Fig. 14).

Observing dorsal lips in transverse section (Figs. 11-14) shows the presence of the radiolar appendage as a longitudinal axis, with the lip itself forming a pair of lamellae on either side of the appendage. External examination of a dorsal lip can usually indicate the presence of a radiolar appendage by the overall shape and surface of the longitudinal axis of the lip. Dorsal lips with radiolar appendages are usually triangular in shape, often distinctly longer than wide. Shape is variable, however, depending on the width and height of the dorsal lip lamellae on either side of the radiolar appendage, as well as on the length of the appendage relative to the lamellae. It is often the case in large to moderately sized specimens that the presence of the radiolar appendage is indicated by a distinct longitudinal ridge, or "mid-rib" (Knight-Jones 1983), which forms the axis of the dorsal lip (e.g., Fig. 2A). In smaller species, such as in *Amphicorina* (e.g., Rouse 1994: figs. 10, 28, 37) or *Amphiglena* (e.g., Rouse 1993a: fig. 5, 1994: fig. 56), this ridge might not be apparent. Especially in those instances in which a ridge is not visible and the lips are not very elongate, it would be advisable to carefully inspect the lips for the presence of supporting sheath tissue and/or a branchial skeleton. In contrast, dorsal lips without radiolar appendages tend to be distally rounded, with length and width more comparable (Knight-Jones 1983: figs. 1A, 2D, Perkins 1984: fig. 2B), and more closely resembling the ventral lips.

Consistent with Orrhage's (1980) findings, I have pointed out that in those instances in which a branchial skeleton extension is not present in the dorsal lip radiolar appendages, the appendages can be characterized by the general elongate shape of the lips and distally tapered ends, and the presence of surrounding sheath tissue. It should be noted that none of the sabellid species examined by Orrhage (1980) lacked radiolar appendages. This limitation in his observations still leaves open the question of whether blood vessels in dorsal lips that are broadly rounded and putatively do not have radiolar appendages are homologous with the large vessel associated with radiolar appendages. Of the species in genera I have observed (see below) that appear to lack radiolar appendages based on dorsal lip shape, such as in some species of *Laonome* Malmgren, *Fabrisabella* Hartman, *Chone*, and *Jasmineira*, the dorsal lips are not vascularized by a single blood vessel, but by a plexus of vessels. A matter which has not yet been resolved is whether the derivation of dorsal lip vascularization in broadly rounded dorsal lips is in any way homologous to the vascularization in radiolar appendages, which could call into question the distinction between the presence or absence of radiolar appendages in variously shaped lips based only on vascularization. While the transverse sections provided by Orrhage (1980: figs. 5, 9-11, see also McIntosh 1918: pl. 1 fig. 7) (Figs. 11B, 13A, 14D) only show a single large blood vessel in the appendages, Nicol (1931: fig. 3) (Fig. 11A) and Fitzsimons (1965: fig. 8) (Fig. 12A) showed several distinct vessels in the coelom of the appendages of *Sabella pavonina* and *Sabellastarte magnifica*, respectively. It is also not uncommon to observe vessels in the lateral lamellae (Figs. 12A, 13B, 14B-C). For the present discussion, I am assuming that the derivation of blood supplies in broadly rounded and more elongate dorsal lips is the same. A related issue which deserves investigation is the origin of blood vessels in the lip lamellae on either side of the radiolar appendages.

The need for more-careful systematic examinations of the structural components of dorsal lips is exemplified by what has been reported in species of *Chone*. For example, Fitzhugh (1989) stated that radiolar appendages are either absent or present in individuals in the genus. In her review of *Chone* species from the Mediterranean, Giangrande (1992) provided very good documentation of the various shapes of dorsal lips among species from the region. She also noted that among specimens identified as *C. infundibuliformis* Krøyer, dorsal lips can be distinctly elongate (Giangrande 1992: fig. 1e), suggesting the presence of radiolar appendages, or distally rounded (Giangrande 1992: fig. 1c), suggesting their absence. Giangrande (1992: 519) commented, however, that none of the specimens of *C. infundibuliformis* examined showed the "radiolar support indicated by Orrhage (1980)." I would interpret this conclusion to indicate that the longitudinal ridge or "mid-rib" in the lips is either not visible or not present. In those instances in which I have examined elongate lips in species of *Chone* without a discernable ridge, there is a blood vessel extending the length of the lip which I would interpret to be the vessel of the radiolar appendage described by Orrhage (1980). Especially in those instances in which lips do not exhibit a longitudinal ridge, the only gross morphological criteria, other than general shape, that can be used to identify radiolar appendages is the presence of the radiolar skeleton (when present), or the combined presence of supporting sheath tissue, a blood vessel, and the coelom.

Table 2. Occurrence of dorsal lip radiolar appendages and associated skeletons in sabellin genera. Predicted features for currently unknown lip conditions are indicated by the superscript (a). The genus *Candela* is not included since the status of the dorsal lips is unknown. See text for discussion

		Radiolar appendages	Branchial skeleton extension
Group I	*Calcisabella*	absent	----
	Caobangia	absent	----
	Chone (in part)	absent	----
	Fabrisabella	absent	----
	Jasmineira (in part)	absent	----
	Laonome (in part)	absent	----
	Perkinsiana riwo	absent	----
	Potamilla	absent	----
Group II	*Amphicorina*	present	absent
	Amphiglena	present	absent
	Anamobaea	present	absent
	Chone (in part)	present	absent
	Demonax	present	absent
	Desdemona	present[a]	absent[a]
	Euchone	present	absent
	Eudistylia	present	absent
	Hypsicomus	present	absent
	Jasmineira (in part)	present	absent
	Laonome (in part)	present	absent
	Megalomma	present	absent
	Myxicola	present	absent
	Notaulax	present	absent
	Panoumethus	present	absent
	Perkinsiana s.s.	present	absent[a]
	Potamethus	present	absent
	Potaspina	present	absent[a]
	Pseudopotamilla	present	absent
	Schizobranchia	present	absent
	Terebrasabella	present	absent
Group III	*Bispira*	present	present
	Branchiomma	present	present
	Laonome (in part)	present	present
	Pseudobranchiomma	present	present[a]
	Sabella	present	present
	Sabellastarte	present	present
	Stylomma	present	present[a]

Subsequent to Orrhage's (1980) description of radiolar appendages, the further distinction between radiolar appendages with and without a branchial skeleton has only recently been applied taxonomically. In the description of *Laonome andamanensis*, Fitzhugh (2002b: fig. 29A) described the presence of a radiolar appendage skeleton consisting of a single row of cells extending through the length of the dorsal lip. The same condition was found in *L. triangularis* Hutchings and Murray, 1984, by Fitzhugh et al. (in prep.). The differential occurrence of a skeleton in radiolar appendages among species in the same genus therefore requires further taxonomic attention. Just as the description of radiolar appendages has become standard practice in sabellid taxonomy, so should the presence or absence of the branchial skeleton in these appendages, as well as the occurrence and shape of surrounding sheath tissue when it can be observed. A revised summary of the occurrence of radiolar appendages in individuals in the Sabellidae, as well as the occurrence of associated skeletons, is presented in table 2. This is a very cursory survey, but appears to show interesting results. The overall distribution of radiolar appendages within Sabellidae genera remains fairly consistent with what was reported by Fitzhugh (1989), but there are some notable emendations that require comment. What follows is a brief overview of dorsal lip morphologies within the Sabellidae.

Subfamily Fabriciinae Rioja, 1923

Dorsal lips in Fabriciinae species are quite uniform in that radiolar appendages are not present. The lips are usually triangular in shape and distally rounded (Banse 1956 1957, Fitzhugh 1989 1992a 1998, Rouse 1993b 1996b). There are, however, species in *Pseudofabriciola* Fitzhugh which have dorsal lips reduced to low ridges (e.g., Fitzhugh 1991b 1998), and all species in *Novafabricia* Fitzhugh exhibit this condition (e.g., Fitzhugh 1990b 1993 1998). Among my own studies, I have never observed blood vessels or other structures extending into the lips that might suggest the presence of radiolar appendages. Rouse (1993b) did describe the presence of a "branchial skeleton" in the branchial lobes and radioles of some species of *Fabriciola* Friedrich, but there are no extensions of this "skeleton" into the dorsal lips. Similar skeletal structures have not been reported in any other species in the subfamily. Fitzhugh (1989 1991a) did not include dorsal lip conditions in the definition of the subfamily, since, based on cladistic analyses in those respective studies, dorsal lips without radiolar appendages was considered plesiomorphic for the Sabellidae as well as the Fabriciinae.

Subfamily Sabellinae Latreille, 1825

Dorsal lips in species of this subfamily exhibit much greater diversity than that seen in the Fabriciinae, especially because of the absence or presence of radiolar appendages. General discussions of sabellin dorsal lip morphology can be found in Knight-Jones (1983), Perkins (1984), and Fitzhugh (1989). As was the case for the Fabriciinae, the definition for the Sabellinae given by Fitzhugh (1989 1991a) did not make reference to dorsal lips since it was assumed that lips without radiolar appendages was the plesiomorphic condition. With the recognition that branchial skeletons can be present or absent in sabellin radiolar appendages, it will be useful to examine current data on dorsal lip morphology within genera of the subfamily.

***Amphicorina* Claparède, 1864.** The dorsal lips in species of this genus are elongate, and either triangular (Banse 1957: fig. 3b, Rouse 1994: fig. 37) or filiform (Rouse 1994: figs. 10, 28, pers. obs.). Lateral lamellae are not present. In their definitions of the genus, Fitzhugh (1989) and Rouse (1994) stated that radiolar appendages are absent. For the present study, I examined the dorsal lips of several unidentified specimens of *Amphicorina* from the Caribbean Sea, and there is a large blood vessel present through the length of the lip, but there is no evidence of a branchial skeleton extension. I have not been able to determine if surrounding sheath tissue is present. Taking into consideration the elongate form of the dorsal lips, it would appear that radiolar appendages are actually present in *Amphicorina*. At this time, I would not consider the presence of a distinct blood vessel in the lip as conclusive evidence of appendages. Herein, however, is the difficulty I alluded to earlier with regard to what criteria can be used to determine the presence of radiolar appendages. In the case of *Amphicorina* species, dorsal lips are so narrow that without being able to determine the presence of supporting sheath tissue, and in the absence of lateral lamellae and a median longitudinal ridge, the only basis at this time for claiming that appendages are present is the elongate condition of the lips. Settling this question will probably have to rely on the presence or absence of supporting sheath tissue. In the meantime, however, if we consider that in those instances in which appendages are known to be absent, the dorsal lips are low and broadly rounded, then the general shape in *Amphicorina* species suggests the presence of an appendage.

***Amphiglena* Claparède, 1864.** The dorsal lips in species of *Amphiglena* are somewhat similar to those in *Amphicorina* species in that they are narrow, elongate, and distinctly longer than wide (Rouse 1993: fig. 5, 1994: figs. 44, 56, Rzhavsky 1995: fig. 1D, Rouse and Gambi 1997: figs. 12, 18). At least in some species, such as *A. pacifica* Annenkova, there is a narrow, proximal lamella along the margin adjacent to the dorsalmost radioles, but no indication of a longitudinal ridge (Rzhavsky 1995, pers. obs.). Previous definitions of *Amphiglena* by Fitzhugh (1989), Rouse (1993 1994), and Rouse and Gambi (1997) state that radiolar appendages are present based on the general shape of the dorsal lips. Fitzhugh and Rouse (1999) mistakenly used the criterion of branchial skeleton absence in the dorsal lips to suggest that appendages are absent. In my examination of *A. pacifica* for this study, I did find a blood vessel extending through the length of the lips and adjacent surrounding sheath tissue, indicating the presence of radiolar appendages. The surrounding sheath in this instance was cylindrical and about the same width as the blood vessel.

***Anamobaea* Krøyer, 1856.** In the definition of this genus, Fitzhugh (1989) stated that radiolar appendages are present. For the present study, I have examined unidentified specimens from the Caribbean, in which radiolar appendages have a very thick, cylindrical surrounding sheath that is considerably larger than the adjacent blood vessel (cf. Fig. 14A). There is no extension of the branchial skeleton. The appendages are very long and slender, with the remainder of the lips forming short basal lamellae. As I noted above, the well-developed surrounding sheath probably functions as the main skeletal support for the appendages. The overall shape of the dorsal lips is nearly identical to what Perkins (1984: figs. 23B, 27C, respectively) illustrated for species of *Hypsicomus* and *Notaulax* (see below).

***Bispira* Krøyer, 1856.** The presence of radiolar appendages in specimens of *Bispira* was reported by Fitzhugh (1989) and Knight-Jones and Perkins (1998). As can be seen in other closely related genera, e.g., *Branchiomma*, *Sabella*, and *Sabellastarte* Krøyer (see below), dorsal lips in *Bispira* commonly appear very long and slender (e.g., Knight-Jones and Perkins 1998: figs. 13B, 18F, 19C, 26A). I have examined several unidentified specimens of *Bispira* from the Philippines and the Caribbean, as well as *B. monroi* (Hartman), and all have a prominent branchial skeleton with multiple rows of cells and a thick, cylindrical surrounding sheath extending through the long radiolar appendages. It appears that the surrounding sheath and skeleton are separate from one another. In contrast, however, McIntosh (1918: pl. 1, fig. 7) (Fig. 13A) clearly illustrated a radiolar appendage from what he called *B. volutacornis*, which has a skeleton composed of a single row of cells and no surrounding sheath. I have not examined specimens in this species to confirm McIntosh's observation. Interestingly, a similar arrangement was observed in a species of *Branchiomma* (see below).

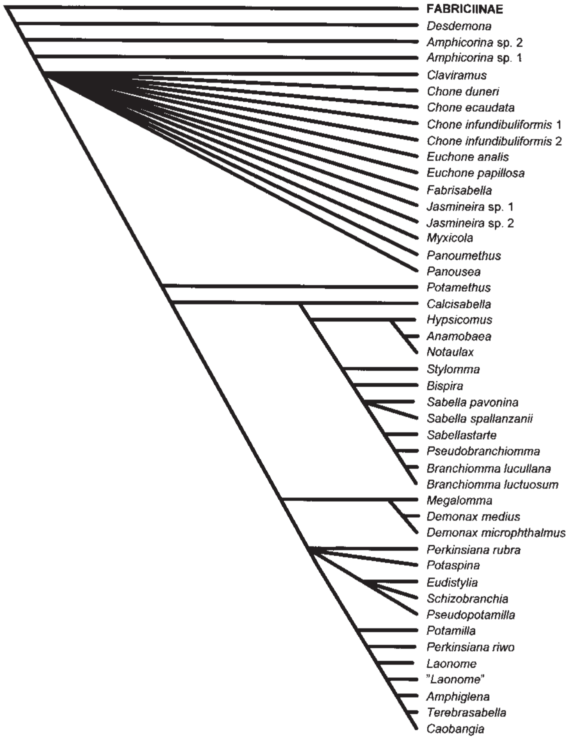

Fig. 15. Consensus tree derived from 9270 cladograms, showing the relationships among Sabellinae genera. See text for explanation.

Knight-Jones and Perkins (1998) describe at least 2 species which have very short radiolar appendages: *Bispira guinensis* (Augener) and *B. turneri* Hartman (Knight-Jones and Perkins 1998: figs. 21E, 28C, respectively). I have examined specimens of *B. turneri*, and the internal components are the same as those in species with more-elongate lips. The co-occurrence of short radiolar appendages and extensions of the branchial skeleton in *B. turneri* is especially significant in that most sabellin species examined in the present survey have appendages that are short (e.g., Fig. 2A) but do not have an associated skeleton. This suggests that at this time, one should use caution when inferring the presence or absence of a skeleton from the radiolar appendage length. On the other hand, it is worthwhile noting that *Bispira* has consistently been part of the exclusive clade including *Branchiomma*, *Pseudobranchiomma* Jones, *Sabella*, *Sabellastarte*, and *Stylomma* (Fitzhugh 1989: fig. 28, 1991a: figs. 5, 7, Rouse and Fitzhugh 1994: fig. 43, Fitzhugh and Rouse 1999: fig. 12) (Figs. 15-16). From the present survey, species examined in *Bispira*, *Branchiomma*, *Sabella*, and *Sabellastarte* have radiolar appendage skeletons, and it is predicted that skeletons also exist in *Pseudobranchiomma* and *Stylomma* (see below). It is conceivable that our understanding of cladistic relationships among sabellin genera might provide insights into to what might be concluded about radiolar appendage construction. For instance, if the presence of a radiolar appendage skeleton is a synapomorphy for the above-mentioned clade, then there might be a greater likelihood that appendage length is independent of skeleton presence since species in the clade are phylogenetically constrained to have a skeleton (see "Dorsal lips and cladistic relationships" below). On the other hand, in genera in which known skeleton presence is sporadic, as in *Laonome* (see below), this independence between appendage shape and skeleton occurrence might not be so readily assumed.

Branchiomma **Kölliker, 1858.** The presence of radiolar appendages in this genus was reported by Fitzhugh (1989), Knight-Jones (1994), and Knight-Jones et al. (1991). Of several unidentified specimens of *Branchiomma* from the Caribbean Sea I have examined, a distinct skeleton with multiple rows of cells is present in the radiolar appendages (Fig. 13B). In these instances, the appendages are very elongate and tapered, with narrow lateral lamellae (cf. Knight-Jones et al. 1991: fig. 6B). The co-occurrence of a skeleton with appendages of this shape is consistent with what is seen in species of *Bispira* and *Sabella*. Surrounding sheath tissue appears to be absent, which is similar to the condition illustrated for *Bispira volutacornis* by McIntosh (1918, cf. Fig. 13). The lateral lamellae contain thick, fibrous, connective tissue and blood vessels (Fig. 13B), but the consistency of this connective tissue is not the same as the supporting sheath tissue seen in species in other genera. This difference in texture would seem to preclude interpreting this tissue in *Branchiomma* as being supporting sheath as appears to have been done in *Sabellastarte magnifica* by Fitzsimons (1965, Fig. 12A, see below).

Knight-Jones et al. (1991: 847, fig. 6E) noted that the dorsal lips in *Branchiomma lucullanum* (Delle Chiaje) are "short and blunt, length about 2 times breadth and 0.1 times length of crown." Dorsal lips with these dimensions might suggest that this species does not have a radiolar appendage skeleton given that species in other genera I have examined with this condition consistently lack an associated skeleton. A notable exception to this observation was discussed in the previous section for *Bispira*, where in the case of *B. turneri*, a skeleton is present in short radiolar appendages. I predict that an examination of radiolar appendages in *B. lucullanum* will reveal the presence of a skeleton as well. The basis for this prediction follows in part from what was discussed above for *Bispira*, as well as from the discussion of radiolar appendage skeletons and cladistic relationships among sabellid genera presented below under "Dorsal lips and cladistic relationships".

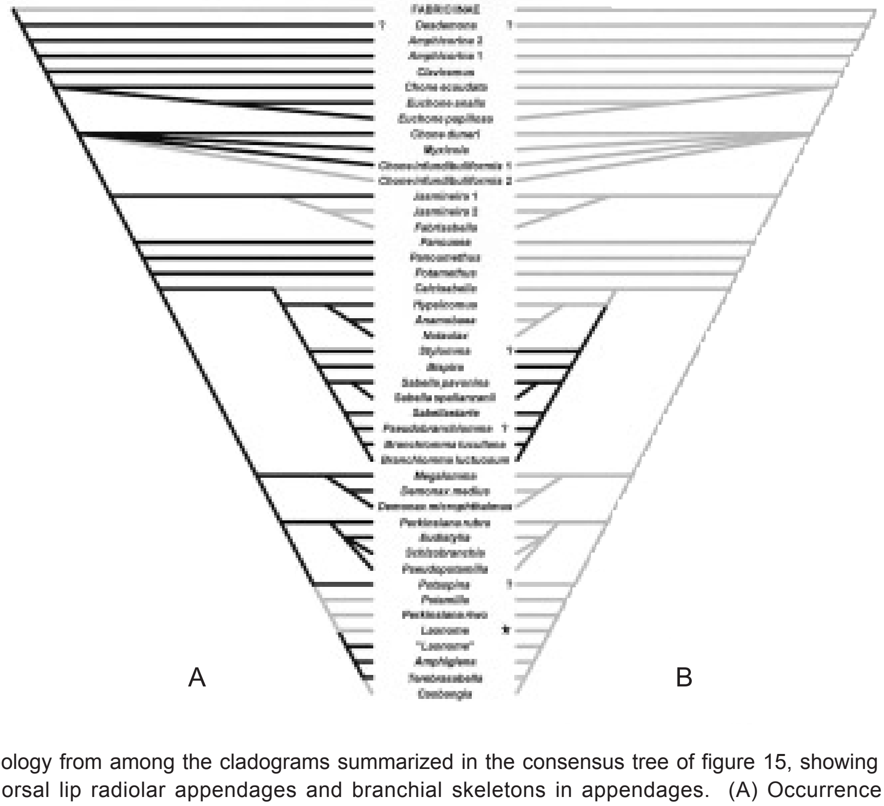

Fig. 16. Single topology from among the cladograms summarized in the consensus tree of figure 15, showing comparisons between optimizations for dorsal lip radiolar appendages and branchial skeletons in appendages. (A) Occurrence of dorsal lip radiolar appendages within the Sabellidae, indicated by black branches; (B) occurrence of radiolar appendage branchial skeletons within the Sabellidae, indicated by black branches. The star (★) adjacent to *Laonome* indicates the apomorphic occurrence of an appendage branchial skeleton in the genus. A question mark "?" to the left of a taxon indicates that the presence or absence of radiolar appendages is unknown; a question mark "?" to the right of a taxon indicates that the presence or absence of a radiolar appendage skeleton is unknown.

***Calcisabella* Perkins, 1991.** The dorsal lips in the only species in this genus, *C. piloseta* Perkins, are low, triangular, and distally rounded (Perkins 1991: fig. 1C), suggesting that radiolar appendages are absent. I have not examined the lips in this species.

***Caobangia* Giard, 1893.** Among species in this genus, the inner margins of the branchial lobes were first described by Fitzhugh (1989) as not having dorsal lips. This conclusion was based on the poorly preserved material of *C. brandti* described by Jones (1974). Subsequently, I have been able to examine well-preserved specimens of *C. brandti* recently collected by Dr. Greg Rouse from northern Thailand and *C. billeti* Giard I collected from northern Vietnam. Contrary to what was reported by Fitzhugh (1989), dorsal lips appear to be present as very low, triangular lobes. There is no evidence of a well-developed blood vessel or skeleton extending into the lips that would indicate the presence of radiolar appendages.

***Chone* Krøyer, 1856.** Fitzhugh (1989) defined *Chone* as having dorsal lips with or without radiolar appendages. These alternative conditions were based on observations of specimens identified as *C. duneri* Malmgren, *C. aurantiaca* (Johnson), and *C. infundibuliformis* Krøyer. It was in the case of *C. infundibuliformis* that Fitzhugh (1989) found the dorsal lips to be either low and broadly rounded, indicating the absence of radiolar appendages, or elongate and distally tapering, typical of the presence of appendages. Orrhage (1980) also found radiolar appendages present in specimens of *C. infundibuliformis* he examined, stating that they have the same form as those in *Pseudopotamilla reniformis*, but he did not specifically describe their shape relative to the lip lamellae. Among large and small specimens identified as *C. infundibuliformis*, Giangrande (1992) found dorsal lips to be either distally rounded or distinctly elongate, respectively (Giangrande, 1992: fig. 1c, e). With regard to elongate dorsal lips in *C. infundibuliformis*, Giangrande (1992: 519) stated, however, that "in no specimens the radiolar support indicated by Orrhage (1980) was seen." Based on Giangrande's illustrations of dorsal lips in *C. infundibuliformis*, *C. longiseta* Giangrande, *C. acustica* (Claparède), *C. arenicola* Langerhans, *C. collaris* Langerhans, *C. duneri* Malmgren, *C. filicaudata* Southern, and *Chone* sp., I would interpret her conclusion to mean that there is no longitudinal ridge or midrib along the length of the lips. The absence of a ridge is not a sufficient criterion for deciding the presence or absence of radiolar appendages, as was shown above in the case of *Amphicorina* and *Amphiglena*. I consider the more pertinent criterion to be the elongate shape of the lips as indicating the presence of radiolar appendages. Except in the case of large specimens of *C. infundibuliformis*, all of the dorsal lips illustrated by Giangrande (1992: figs. 1e, 3c, 6d, 8c, 11b, 13b, 15e, 17d) have dorsal lips with basal lamellae and tapered distal ends.

For the present study, I examined the lips in *Chone ecaudata* (Moore), *C. mollis* (Bush), and a new species from the British Virgin Islands (Fitzhugh in prep.). The lips in these species are wide basally, tapering distally to slender tips, but with no discernable longitudinal ridge. A distinct median blood vessel is present, but there is no branchial skeleton extension, which is consistent with Orrhage's (1980) description of the lips as being like those in *Pseudopotamilla reniformis*. A cylindrical surrounding sheath is present, which was not specifically reported by Orrhage, and it is about the same diameter as the blood vessel. The shapes of the lips are similar to those illustrated by Giangrande (1992), indicating the presence of radiolar appendages in the species she examined, except in the case of large individuals identified as *C. infundibuliformis*. I have also examined a large specimen, i.e., total trunk length 70 mm, from Tomales Bay, northern California, that was identified by Dr. Olga Hartman as *C. infundibuliformis* (for the purposes of the present survey, I will not address the validity of the identification). The dorsal lips of this specimen are thick, broadly rounded, and enervated by a network of large blood vessels, very similar in appearance to what was described by Giangrande (1992: fig. 1c) for large members of this species from Europe.

***Claviramus* Fitzhugh, 2002b.** This genus is represented by at least 3 species, *C. candelus* (Grube) from the Adriatic Sea, *C. oculatus* (Langerhans) from Madeira, and *C. grubei* Fitzhugh from the Andaman Sea off Thailand. In her description of specimens tentatively identified as *C. oculatus* from the northern Atlantic, Cochrane (2000: fig. 2.5.5d) noted that the dorsal lips are elongate, about 5 times longer than wide, and slightly tapered; internal features of the lips were not described. The overall shape of the dorsal lips is similar to that seen in some species of *Amphicorina*, *Amphiglena*, and *Terebrasabella heterouncinata* Fitzhugh and Rouse (see below) in that neither lateral lamellae nor a median ridge are evident. Fitzhugh (2002b) described similar dorsal lips in *C. grubei*. Cochrane (2000) redescribed the holotype of *Sabella candela* (now *C. candelus*), but was unable to examine the lips. Based on general lip shape, it would appear that radiolar appendages could be interpreted as being present in *C. oculatus* and *C. grubei*.

Demonax **Kinberg, 1867.** Significant revisions of this genus were provided by Knight-Jones (1983) and Perkins (1984), both of whom noted the presence of dorsal lip radiolar appendages. Subsequent studies by Knight-Jones and Walker (1985), Fitzhugh (1989), and Giangrande (1994) also included the presence of radiolar appendages in the definition of the genus.

The internal structures of radiolar appendages were examined in *Demonax medius* (Bush) and unidentified specimens for the present survey. The overall slender, triangular shape of the lips, with lamellae on either side of the appendages, is similar to what was shown by Knight-Jones (1983: figs. 4H, 5E, 6C, D, 7E, 8E, 9A), Perkins (1984: figs. 3A, 7C, 9, 11, 15F, 19A, B), and Giangrande (1994: figs. 1c, 3d). The radiolar surrounding sheath is cylindrical, with a diameter ranging from about 2.5 times greater than that of the adjacent blood vessel to only slightly larger. A radiolar appendage skeleton is absent.

Desdemona **Banse, 1957.** Fitzhugh (1989) stated that the dorsal lips of *D. ornata* Banse, and *D. aniara* Hutchings and Murray do not have radiolar appendages. I have not reexamined these species for the present study. However, given the close similarities between *Desdemona* and *Amphicorina*, the proximity of the 2 genera cladistically, and the questionable monophyly of each, I predict that the dorsal lips in species of *Desdemona* are similar to those in species of *Amphicorina*, in which radiolar appendages are present. Banse's (1957: fig. 7a) illustration of the anterior end of *D. ornata* suggests that the dorsal lips are somewhat elongate, as is the case in species of *Amphicorina* (see above). A similar condition was also clearly indicated in *D. aniara* by Hutchings and Murray (1984: fig. 31.1).

A 3rd species, *Desdemona antarctica* Hartmann-Schröder and Rosenfeldt, does not belong in this genus. The presence of a posterior peristomial ring collar (Hartmann-Schröder and Rosenfeldt 1989: figs. 81-83) suggests that the species should be in *Amphicorina*. Hartmann-Schröder and Rosenfeldt (1989) did not describe the dorsal lips.

Euchone **Malmgren, 1866.** The definition of this genus by Fitzhugh (1989) includes the presence of radiolar appendages, which was based on observations of *E. analis* (Krøyer), as well as on findings reported by Orrhage (1980) for this species and *E. papillosa* (Sars). Orrhage (1980) did not find a radiolar appendage skeleton and did not specifically report the occurrence of surrounding sheath tissue.

For the present survey, I have examined specimens of *Euchone limnicola* Reish, *E. arenae* Hartman, *E. incolor* Hartman, and several unidentified specimens, all of which confirm the findings of Orrhage (1980) and Fitzhugh (1989) regarding the presence of radiolar appendages. The dorsal lips consist of basal lamellae, then taper distally, with much the same appearance as that illustrated by Giangrande (1992, see above) for species of *Chone*. A distinct blood vessel extends through the length of the radiolar appendages, and there is no associated branchial skeleton. I have observed surrounding sheath tissue that is about the same diameter as the adjacent blood vessel in *E. limnicola*. Orrhage (1980) did state that the radiolar appendages in the species of *Euchone* he examined are similar to those in *Pseudopotamilla reniformis*, which would suggest that the surrounding sheath he observed is more laminate rather than cylindrical. Cochrane (2000: fig. 2.4.5a) illustrated a detached crown of an undescribed species, *Euchone x*, showing the triangular dorsal lips. Cochrane (2000: fig. 2.4.5b) also provided a micrograph of a transverse section through the base of the crown, clearly showing the dorsal lips. Unfortunately, resolution of details within the lips is not sufficient to clearly discern the internal structures.

Eudistylia **Bush, 1905.** The presence of dorsal lips with radiolar appendages in species in this genus was included in the definition provided by Fitzhugh (1989). *Eudistylia vancouveri* (Kinberg) was examined for the present study. The dorsal lips are broadly triangular, with well-developed lamellae on either side of the radiolar appendages, the latter only extending slightly higher than the lamellae. The internal structure of the appendages closely resembles what Orrhage (1980: figs. 9, 10, cf. Fig. 14D) described in *Pseudopotamilla reniformis*, with a distinct blood vessel located between the coelomic space and a narrow layer of supporting sheath tissue. A branchial skeleton extension is absent. The arrangement of the supporting sheath tissue is the same as that seen in *P. occelata* Moore and *Schizobranchia insignis* Bush (see below), which were also examined for the present study.

***Fabrisabella* Hartman, 1969.** The dorsal lips in *F. vasculosa* Hartman were first described by Fitzhugh (1989) insofar as to indicate that radiolar appendages were absent. A reexamination of several paratypes (LACM-AHF) confirms this condition. Consistent with the absence of radiolar appendages, the dorsal lips are low and broadly rounded, and have a network of blood vessels.

***Hypsicomus* Grube, 1870.** In his definition of this genus, Perkins (1984) stated that the dorsal lips have radiolar appendages that are long and slender, with short basal lamellae. Perkins (1984: fig. 23B) illustrated a dorsal lip in *H. stichophthalmos* (Grube) in which the total lip length is about 7 times longer than the greatest width. Based on Perkins' illustration, the dorsal lips closely resemble those in species of *Anamobaea* (see above) and *Notaulax* (see below). I have examined an unidentified species of *Hypsicomus* for the present study. The radiolar appendages lack a branchial skeleton extension but have a surrounding sheath with a diameter distinctly greater than the adjacent blood vessel (Fig. 14A). This construction is similar to that observed in species of *Anamobaea* and *Notaulax*. Such uniformity might be expected given that in all cladistic analyses involving Sabellinae genera, *Hypsicomus* is part of an exclusive clade with these 2 genera (Fitzhugh 1989: fig. 28, 1991a: figs. 5, 7, Rouse and Fitzhugh 1994: fig. 43, Fitzhugh and Rouse 1999: fig. 12) (Figs. 15, 16).

***Jasmineira* Langerhans, 1880.** The presence of radiolar appendages in this genus was reported by Fitzhugh (1989), based on the examination of *J. caeca* Ehlers, *J. filiformis* Hartman, *J.* sp. cf. *J. pacifica* Annenkova, and *J. regularis* Hartman. Based on information from 3 species examined in the present study, *Jasmineira* actually exhibits 2 conditions. *Jasmineira labrofusca* Fitzhugh, has low, distally rounded dorsal lips without radiolar appendages (Fitzhugh 2002b: fig. 22A), while *J. filiformis* Hartman has long, slender radiolar appendages without a skeletal extension. Hartman (1965: 233, pl. 52, fig. a) noted the presence of the lips, referring to them as "long, slender palpi". *Jasmineira lobata* Fitzhugh also has long, slender radiolar appendages that lack a skeleton (Fitzhugh 2002b: fig. 25A). I have not determined the presence or absence of a surrounding sheath or supporting tissue in any of the species examined.

***Laonome* Malmgren, 1866.** The definition of *Laonome* provided by Fitzhugh (1989) stated that dorsal lips do not have radiolar appendages. This conclusion was based on observations limited to the type species, *L. kroyeri* Malmgren. Subsequently, Hsieh (1995) described *L. albicingillum* from Taiwan, which also lacks radiolar appendages. In both species, the dorsal lips are relatively short and distally rounded (Hsieh 1995: fig. 6, pers. obs.). There is no distinct single blood vessel extending through the length of the lips, but rather a network of vessels, and there is no branchial skeleton extension. Fitzhugh (2002b: fig. 29A) described *L. andamanensis* from Thailand, which has very long, tapering radiolar appendages, within which a radiolar appendage skeleton is present.

A revision of *Laonome* is being prepared by Fitzhugh et al. These authors have examined all species in the genus except *L. indica* Southern. Among these, *L. triangularis* Hutchings and Murray, from Australia also has very long, tapering radiolar appendages and a branchial skeleton extension, neither of which was originally described by Hutchings and Murray (1984). A possible additional species in which a skeleton might be present in radiolar appendages is *L. elegans* Gravier, from the Red Sea. Gravier (1908b: 103) referred to the appendages as "grande palpes", and accurately illustrated them as very long and slender (Gravier 1906: pl. 7, fig. 279). It is the pronounced elongation of the appendages, as seen in *L. andamanensis*, *L. triangularis*, and species in several other genera (i.e., *Sabella*, *Branchiomma*) that appears to be most typical in those instances in which an associated skeleton is present. The absence of radiolar appendages in *L. kroyeri* and *L. albicingillum* is also the condition in 2 new species from California and China (Fitzhugh et al. in prep.).

Laonome is especially interesting in regards to the disparity between dorsal lip morphologies. Based on the present survey of genera, there are 3 general patterns that seem to characterize dorsal lips: (1) radiolar appendages absent, (2) radiolar appendages without an associated extension of the branchial skeleton, and (3) radiolar appendages with a skeleton. The most common condition observed thus far in the Sabellinae is that species in a given genus all have 1 type of dorsal lip construction. Only 3 genera are known to have a combination of 2 morphologies: *Chone*, *Jasmineira*, and *Laonome*. *Chone* and *Jasmineira* exhibit conditions (1) and (2), whereas *Laonome* shows conditions (1) and (3).

"*Laonome*" sensu Fitzhugh (2002b). This currently unnamed genus is known from 2 species. One of these species, "*Laonome*" sp. 1, was informally described by Fitzhugh (2002b: figs. 31-32) from the Andaman Sea, Thailand. The other species, which will be described by Fitzhugh and Rouse (in prep.), is from estuarine waters along the east coast of Florida, in the Atlantic Ocean. Fitzhugh (2002b) provides an overview of the features which justify recognizing these species in a separate genus.

Dorsal lip morphology is only known from the Florida species. The lips are erect, longer than wide, distally tapered, with no obvious lateral lamellae. Overall, the lips closely resemble what has been described in some species of *Amphiglena* (e.g., Rouse 1993: fig. 5, Rouse and Gambi 1997: figs. 12, 18) and in *Terebrasabella heterouncinata* (Fitzhugh and Rouse 1999: fig. 3B). Because of the very small size of the Florida species of "*Laonome*", nothing is currently known regarding vascularization of the lips or if surrounding sheath tissue is present. A skeleton is, however, absent. Given the general shape of the lips, I conclude that radiolar appendages are present, but this will need to be confirmed by a careful histological examination of the lips.

***Megalomma* Johansson, 1927.** The dorsal lips among members of this genus were well documented by Perkins (1984), who included the presence of radiolar appendages in his definition, which was followed by Fitzhugh (1989) and Knight-Jones (1997). The lateral lamellae are well developed, and the radiolar appendages are readily discernable by the presence of a longitudinal ridge or midrib (Fig. 2A) (Perkins 1984: figs. 38B, 39B, 42D, 43A, Nishi 1998: fig. 2A, B).

The emended definition for *Megalomma* presented earlier, which points out the absence of a skeleton in radiolar appendages, is based on my examination of *M. cinctum*, sp. nov. (Fig. 14C), *M. circumspectum* (Moore), *M. splendidum* (Moore) (Fig. 14B), *M. pigmentum* Reish, and *M. acrophthalmos* (Grube). In addition to the features described by Perkins (1984), radiolar appendages have a distinct blood vessel and a surrounding sheath that is about the same diameter as the blood vessel.

***Myxicola* Koch, 1847.** Fitzhugh (1989: 70) stated that species of *Myxicola* have an unusual arrangement of the dorsal lips and radiolar appendages: "Dorsal radiolar appendages not fused with [dorsal] lips but emerging medially from lip base on margin opposite branchial lobes (surrounded in part by dorsal lips)". Ventral lips were reported as being absent. As part of his histological work, Orrhage (1980: 129) noted that the dorsal lips in *M. infundibulum* (Renier) are "equipped with two appendages". Unfortunately, he was unable to further interpret his findings as to the derivation of those appendages, i.e., whether they are radiolar or pinnular. It is likely that Orrhage was referring to the same structures at the bases of the lips that Fitzhugh (1989) called radiolar appendages.

The arrangement of structures reported by Fitzhugh (1989) was also seen in specimens identified as *Myxicola infundibulum* from the eastern Pacific Ocean examined for the present study. A pair of short, grooved, digitiform processes arises from the bases of a pair of low, well-developed lips. These lips extend from the dorsalmost edges of the inner branchial lobe margins to the ventralmost edges, with the digitiform processes located along the inner margin of each lip, adjacent to the mouth. The interior of the digitiform processes contains a network of blood vessels and a narrow surrounding sheath, and there is no evidence of a skeleton.

Given the general construction of the digitiform processes, it would appear to follow that a different interpretation can be given to the appendages reported by Fitzhugh (1989). Consistent with what has been seen in other Sabellinae species, the digitiform processes should be interpreted as a combination of dorsal lips and radiolar appendages. The overall shape of the structures that essentially surround the dorsal lips can therefore be considered to be the ventral lips. Compared with other Sabellinae species, however, the ventral lips in *Myxicola* are unique in that they extend dorsoventrally along the entire interior margins of the branchial lobes, as opposed to only adjacent to the ventral half of the lobes.

***Notaulax* Tauber, 1879.** In his definition of the genus, Perkins (1984) stated that the dorsal lips have radiolar appendages that are long and slender, with short basal lamellae. Based on Perkins' (1984: fig. 27C) illustration of a dorsal lip in *N. nudicollis* (Krøyer), the total lip length is about 8 times longer than the greatest width. I have examined specimens of several unidentified species of *Notaulax* from the Caribbean, and the radiolar appendages are very similar to those seen in *Anamobaea* and *Hypsicomus* (see above, cf. Fig. 14A), with a surrounding sheath distinctly wider than the blood vessel and no branchial skeleton extension.

***Panoumethus* Fitzhugh, 2002b.** This genus contains 1 species, *P. dubius* Fitzhugh, from the Andaman Sea, Thailand. The dorsal lips are relatively short, about 1/6 the length of the crown, but taper distally, with short lateral lamellae, and have a distinct median blood vessel (Fitzhugh 2002b). I examined paratypes (LACM-AHF) for the present study and could find no evidence of a skeleton. There appears to be a roughly cylindrical surrounding sheath extending through the appendages, which is slightly smaller in diameter than the blood vessel. As the dorsal lips are very small, a more-thorough histological examination is necessary to confirm the present findings.

***Perkinsiana* Knight-Jones, 1983, sensu stricto.** The presence of dorsal lip radiolar appendages was included in the original definition of this genus by Knight-Jones (1983), which was followed by Fitzhugh (1989). Fitzhugh (1989) did note, however, that there are no synapomorphies to establish the monophyly of the genus. Rouse (1996a) emended the definition of the genus to include species with or without radiolar appendages in order to accommodate *P. riwo* Rouse. The very questionable placement of *P. riwo* in this genus was indicated in the cladistic analyses of Sabellinae genera performed by Rouse and Fitzhugh (1994: fig. 44) and Fitzhugh and Rouse (1999: fig. 12), where *P. riwo* and *P. rubra* (Langerhans) were included, yet did not occur as an exclusive clade. As a result, *P. riwo* will be treated separately here from those *Perkinsiana* species with radiolar appendages.

For the present study, I have not examined any of the species Knight-Jones (1983) included in this genus. There are, however, two lines of evidence to suggest that these species have radiolar appendages that lack a skeleton. First, all previous cladistic analyses involving *Perkinsiana* (Fitzhugh 1989: fig. 31, 1991a: fig. 5, Rouse and Fitzhugh 1994: fig. 43, Fitzhugh and Rouse 1999: fig. 12) place the genus within a clade that is well removed from genera with species having a radiolar appendage skeleton, i.e., the clade comprising *Bispira*, *Branchiomma*, *Sabella*, *Sabellastarte*, *Stylomma*, and *Pseudobranchiomma*, as well as some species of *Laonome*. Second, the illustrations of dorsal lips from among the species included in the genus by Knight-Jones (1983: figs. 12B, 14A, 16D, 17B, 18B, 19C, 20E) show radiolar appendages that are usually shorter than those seen in species in which a skeleton is present.

***Perkinsiana riwo* Rouse, 1996a.** This species is considered separate from *Perkinsiana* sensu stricto in that the radiolar appendages are absent. Rouse's (1996a) description of the dorsal lips is limited in that he only stated that appendages are absent, without giving any particulars as to the shape of the lips. Rouse (1996a: fig. 21) does provide a schematic diagram of the inner branchial lobe margin, showing the dorsal lip to be roughly triangular. I have examined some paratypes and the dorsal lips are broadly rounded, as is typical in species where radiolar appendages are absent.

***Potamethus* Chamberlin, 1919b.** The definition of this genus by Fitzhugh (1989) stated that radiolar appendages are present. Knight-Jones (1983) did not consider dorsal lips in her revision. For the present study, I have only examined specimens of *P. singularis* Hartman. The dorsal lips in this species are elongate and roughly triangular. A blood vessel extends through the length of the lips, indicating the presence of a radiolar appendage, but a skeleton is absent. I observed no surrounding sheath tissue.

***Potamilla* Malmgren, 1866.** The dorsal lips in species of this genus lack radiolar appendages and are distally rounded (Knight-Jones 1983: figs. 1A, D, 2D, see also Perkins 1984: fig. 2B). Knight-Jones (1983) and Fitzhugh (1989) included dorsal lip construction in their respective definitions of the genus. Based on his cladistic analysis of genera, Fitzhugh (1989: 77, fig. 28) concluded that the putative loss of radiolar appendages and the presence of a branchial crown palmate membrane are synapomorphies for the genus. A subsequent analysis by Fitzhugh and Rouse (1999: figs. 12, 13A, 15), however, placed *Potamilla* in a clade with *Perkinsiana riwo*, *Laonome*, *Amphiglena*, and *Terebrasabella*, defined by the putative loss of radiolar appendages. As a result, the only synapomorphy remaining for *Potamilla* is the presence of a palmate membrane. Although the present study shows that radiolar appendages are present in *Amphiglena*, *Terebrasabella* (see below), and some species of *Laonome*, the symplesiomorphic condition of appendage absence in *Potamilla* appears to still hold (Fig. 16A).

***Potaspina* Hartman, 1969.** The dorsal lips in the only species in the genus, *P. pacifica* Hartman, were first described by Fitzhugh (1989) as having radiolar appendages. The dorsal lips are elongate and relatively slender, indicating that appendages are present. Hartman (1969: 723) described the lips as "long, foliose palpi, each about 4 times as long as wide...". Unfortunately, since the species is known from a single specimen, I have not removed any portion of a lip to determine whether a branchial skeleton extension is present.

***Pseudobranchiomma* Jones, 1962.** Jones

(1962: 200) noted that the dorsal lips (“oral tentacles”) in the types species of the genus, *P. emersoni* Jones, are about 1/4 the length of the branchial crown. The definition of *Pseudobranchiomma* provided by Fitzhugh (1989) was based on this species (but see Knight-Jones 1994 for other species that should be assigned to this genus). Radiolar appendages are present based on the elongate nature of the dorsal lips. I did not examine *P. emersoni* for the present study, but predict that the radiolar appendages do contain skeletons. This prediction is based on the fact that in previous cladistic analyses (Fitzhugh 1989: fig. 28, 1991a: figs. 5, 7, Rouse and Fitzhugh 1994: fig. 43, Fitzhugh and Rouse 1999: fig. 12), *Pseudobranchiomma* has consistently occurred in a clade with *Bispira*, *Branchiomma*, *Sabella*, *Sabellastarte*, and *Stylomma*. It will be interesting to see if the putative absence of the surrounding sheath in *Branchiomma* (see above) is also the case in species of *Pseudobranchiomma*.

***Pseudopotamilla* Bush, 1905.** The presence of radiolar appendages in *P. reniformis* was first described histologically by Orrhage (1980: figs. 9, 10) (Fig. 14D), followed by the inclusion of the feature in the definition of the genus by Knight-Jones (1983: fig. 3C), and then Fitzhugh (1989). *Pseudopotamilla occelata* was examined for the present study. The dorsal lips are broadly triangular, with well-developed lamellae on either side of the radiolar appendages, the latter only extending slightly higher than the lamellae. The internal structure of the appendages closely resembles that shown by Orrhage (1980, Fig. 14D), with a distinct blood vessel located between the coelomic space and a narrow band of supporting sheath tissue, and the absence of a skeleton. The arrangement of the supporting sheath is the same as that seen in *Eudistylia vancouveri* (see above) and *Schizobranchia insignis* Bush (see below).

***Sabella* Linnaeus, 1767.** The presence of radiolar appendages in species of *Sabella* have been reported by Nicol (1931: fig. 3) (Fig. 11A), Orrhage (1980: fig. 5) (Fig. 11B), Perkins (1984: fig. 2A), Fitzhugh (1989), and Knight-Jones and Perkins (1998). Orrhage (1980, see also Nicol 1931) noted the presence of a skeleton and surrounding sheath tissue in the dorsal lips of *S. pavonina*. These structures are also present in specimens of *S. pavonina* examined for the present study. The surrounding sheath is cylindrical and very well developed, as is also seen in species of *Bispira*. I noted earlier that there is a discrepancy between the relations of surrounding sheath tissue and branchial skeleton extension (cf. Fig. 11) described by Nicol (1931) and Orrhage (1980).

***Sabellastarte* Krøyer, 1856.** The dorsal lips in species of *Sabellastarte* have radiolar appendages (Fitzhugh 1989) which are slender and very long (Fitzsimons 1965: fig. 1A, pers. obs.), similar to those in *Sabella pavonina* illustrated by Perkins (1984: fig. 2A). I have examined the radiolar appendages in *Sabellastarte indica* Savigny and *S. magnifica*. There is a prominent skeleton composed of many rows of cells and a thick surrounding sheath (Fig. 12B), both of which appear to be distinct from one another and very similar to what are found in *Bispira* and *Sabella*. The relation between the surrounding sheath tissue and the skeleton observed in the present study is not consistent with what was reported by Fitzsimons (1965, Fig. 12A) in *S. magnifica*. She showed the skeleton in the dorsal lips, which consisted of a single row of cells, as completely enclosed by the surrounding sheath. The transverse section illustrated by Fitzsimons appears to be from near the base of the lip, where lateral lamellae are most prominent, while the section I examined is from the middle of the lip. It seems unlikely, however, that these different locations could account for these discrepancies. A more-systematic histological examination of the lips in other species might be necessary to resolve this issue.

***Schizobranchia* Bush, 1905.** Fitzhugh (1989) included the presence of radiolar appendages in the definition of this genus. *Schizobranchia insignis* was examined for the present study. The dorsal lips are broadly triangular, with well-developed lamellae on either side of the radiolar appendages, the latter only extending slightly beyond the lamellae. A blood vessel is clearly visible in the appendages, but a skeleton is absent. The surrounding sheath is limited to a narrow band, rather than the more-cylindrical arrangement seen in species of most other genera, lying along the margin of the appendage opposite the blood vessel and coelomic space. This is the same pattern seen in *Eudistylia* and *Pseudopotamilla* (see above, cf. Fig. 14D). Interestingly, these 3 genera have consistently been grouped as an exclusive clade in previous cladistic analyses (Fitzhugh 1989: fig. 28, Rouse and Fitzhugh 1994: fig. 43, Fitzhugh and Rouse 1999: fig. 12).

***Stylomma* Knight-Jones, 1997.** The dorsal lips in the only species in this genus, *S. palmatum* (Quatrefages), are described by Knight-Jones and Perkins (1998) as long (about 1/3 the length of the branchial crown) and tapered, with radiolar appendages present. I have not examined this species, but predict that the radiolar appendages do have a skeleton. As with the prediction made above that a skeleton occurs in species of *Pseudobranchiomma*, the prediction here for *Stylomma* is based on previous cladistic analyses (Fitzhugh and Rouse 1999: fig. 12) (Figs. 15-16, pers. obs.) which place *Stylomma* in an exclusive clade with *Bispira*, *Branchiomma*, *Pseudobranchiomma*, *Sabella*, and *Sabellastarte*.

Terebrasabella **Fitzhugh and Rouse, 1999.** Fitzhugh and Rouse (1999) stated that the only species in this genus, *T. heterouncinata* Fitzhugh and Rouse, lacks radiolar appendages. The dorsal lips in *T. heterouncinata* are unusual in that they are about 6 times longer than wide, with only slight distal tapering, and do not have lateral, basal lamellae (Fitzhugh and Rouse 1999: fig. 3B). I now consider Fitzhugh and Rouse's statement that radiolar appendages are absent to be in error. There are 2 reasons for this conclusion: (1) the general elongate shape of the lips is consistent with the interpretation of appendage presence in other genera, and (2) there is a very narrow blood vessel running through the length of the lip along the margin adjacent to the dorsalmost radioles, the presence of which is consistent with the presence of similar vessels in those species with appendages. Close examination of the lips does not indicate the presence of a skeleton, which is consistent with what was reported by Fitzhugh and Rouse (1999). I have not been able to discern the presence of a surrounding sheath.

Dorsal Lips and Cladistic Relationships

The present observations suggest that there are 3 general groups, or patterns, that can be recognized among sabellin taxa regarding relationships between dorsal lips and the occurrence of radiolar appendages, and skeletons in those appendages. These groups are summarized in table 2 as groups I, II, and III. Group I includes taxa in which dorsal lips do not have radiolar appendages, and hence no associated skeleton. Taxa in group II have radiolar appendages without an associated skeleton, and group III contains taxa in which a skeleton is present in the radiolar appendages. The majority of Sabellinae genera belong to group II, while group I consists of a mixture of taxa that have not previously shown any particularly close relationships. The composition of group III is especially interesting in that all of the genera except *Laonome* have consistently formed a clade in earlier cladistic analyses (Fitzhugh 1989 1991a, Rouse and Fitzhugh 1994, Fitzhugh and Rouse 1999). Similarly, with the more-refined interpretation of dorsal lip structure that has been attempted in the present survey, it will be essential to reassess cladistic relationships among Sabellinae genera.

The presence of 4 structural components was described above and may enable one to identify radiolar appendages: (1) the elongate, triangular shape of the lips, (2) a large blood vessel extending through the length of a putative radiolar appendage, (3) surrounding sheath tissue, and (4) an extension of the branchial base skeleton. Since in some instances the identification of radiolar appendages in the present study has only been based on conditions (1) and (2), there are limits as to what data on the occurrence of radiolar appendages can be introduced into a cladistic analysis. At the least, conditions (1) and (2) appear to covary, such that together they denote the presence of appendages. What still requires investigation is whether or not surrounding sheath tissue is always present in appendages, especially among small species in genera such as *Amphicorina*. It is clear from the above survey that the branchial skeleton extension is variable in its occurrence. For the purposes of integrating the present data into a cladistic analysis among Sabellinae genera, this would be limited to considering the following 4 characters that describe alternate conditions for the dorsal lips and the interiors of radiolar appendages, respectively:

(A) Construction of dorsal lips:
    (0) triangular or broadly rounded (i.e., radiolar appendages absent); (1) elongate and tapered (i.e., radiolar appendages present).
(B) Interior of radiolar appendages:
    (0) with a coelomic space, appendage blood vessel, and sometimes surrounding sheath tissue (i.e., skeleton absent); (1) with a coelomic space, appendage blood vessel, sometimes surrounding sheath tissue, and skeleton present.

The characters in (A) are essentially unchanged from what has been included in recent studies (Fitzhugh 1989 1991a, Rouse and Fitzhugh 1994, Fitzhugh and Rouse 1999). It is the inclusion of (B), as well as the reinterpretation of dorsal lips among some Sabellinae genera that needs to be assessed relative to other characters that have been used in previous analyses.

Using data from an ongoing reassessment of sabellin characters, which will be presented in revisions of *Laonome* by Fitzhugh et al. (in prep.) and *Caobangia* by Rouse and Fitzhugh (in prep.), a preliminary cladistic analysis involving the characters in (A) and (B) was performed for the present study. The data matrix consists of 129 properties distributed among 56 subjects – the more typical, though epistemologically incorrect (cf. Mahner and Bunge 1997, Fitzhugh in prep.), phraseology would be 129 "character states" and 56 "characters". The majority of taxa included are the same as those used by Fitzhugh and Rouse (1999), with the exception that a distinction is made between species of *Amphicorina* with and without a posterior peristomial ring collar, and alternate forms of *Chone infundibuliformis* are included based on the presence or absence of radiolar appendages, with a similar differentiation having been made for *Jasmineira*.

These data were analyzed using PAUP* 4.0b5 (Swofford 1998), with the heuristic tree search option, with all characters given equal weight, with multi-character complexes ("multistate characters") treated as non-additive, and with the Fabriciinae acting as the outgroup. This analysis produced 9270 trees, each with length of 169, consistency index of 0.426, and retention index of 0.802. The strict consensus tree is shown in figure 15. The overall patterns of relationships summarized by the consensus tree are essentially the same as have been found in previous analyses. There are, however, some distinct changes, such as the sister-group relation between the clade containing *Hypsicomus*, *Notaulax*, and *Anamobaea* and the clade comprising *Bispira*, *Branchiomma*, *Pseudobranchiomma*, *Sabella*, *Sabellastarte*, and *Stylomma*, as well as the relation of *Caobangia* to other Sabellinae genera. Specific details as to properties supporting these relationships will be discussed by Fitzhugh et al. (in prep.) and Rouse and Fitzhugh (in prep.).

With regard to the occurrence of radiolar appendages in sabellin taxa, the present data now show this feature to be plesiomorphic for the subfamily (Fig. 16A). This interpretation is, however, contingent on the assumption that the elongate shape of lips in species of *Desdemona* and *Amphicorina* represents the presence of radiolar appendages. It was noted above in reference to the occurrence of radiolar appendages that this structure is present in the majority of sabellin taxa (Table 2: group II). As a result, the absence of radiolar appendages is interpreted as 5 instances of putative loss: (1) in large-sized specimens of *Chone infundibuliformis*, (2) the clade consisting of *Fabrisabella vasculosa* and some species of *Jasmineira*, (3) *Calcisabella piloseta*, (4) the clade comprising *Potamilla*, *Perkinsiana riwo*, *Laonome*, "*Laonome*", *Amphiglena*, *Terebrasabella*, and *Caobangia*, and (5) within this latter clade, the reacquisition of appendages in the clade of "*Laonome*", *Amphiglena*, *Terebrasabella*, and *Caobangia*, then with the subsequent loss of appendages in *Caobangia*. While results are consistent with previous analyses that have raised questions regarding the monophyly of *Chone* (Fitzhugh 1989 1991a, Rouse and Fitzhugh 1994, Fitzhugh and Rouse 1999), there also is the matter of the monophyly of *Jasmineira*, which like *Chone* has species with and without radiolar appendages. Similar concerns were raised by Cochrane (2000). The questionable monophyly of *Amphicorina*, which was raised by Rouse (1992a b 1994) and is evident in the present results, is also a matter that needs to be addressed at some point.

It was noted earlier in reference to table 2 that taxa forming group III, which have a skeleton in the radiolar appendages, with the exception of *Laonome*, have consistently formed a clade in previous cladistic analyses. This clade is maintained in the present study, and the presence of the skeleton in appendages is an additional synapomorphy (Fig. 16B). While the presence of skeletons has not yet been determined in species of *Pseudobranchiomma* and *Stylomma*, present results suggest that this feature will be found in these taxa. The homoplasious occurrence of skeletons in *Laonome triangularis* and *L. andamanensis* appears to have been a derivation within the genus.

Future Prospects

The present survey of sabellid dorsal lip morphologies is very cursory, and raises far more questions into the systematics of the group than it provides insight for. At least 5 areas require further consideration from both taxonomic and systematic standpoints: (1) confirmation of the presence of radiolar appendages among species in genera such as *Desdemona*, *Amphicorina*, *Potamethus*, *Potaspina*, *Stylomma*, and *Pseudobranchiomma*; (2) determination of the extent to which surrounding sheath tissue is present among species and genera; (3) characterization of the shapes of surrounding sheath tissue, i.e., cylindrical, oblong, laminate, and enveloping the skeleton or distinctly separate; (4) determination of the relations between the vascularization of lips with and without appendages; and (5) more-thorough examinations within genera for the presence of a branchial skeleton associated with dorsal lips. These points of concern will especially be critical within genera with species that vary greatly in size, as in *Chone* and *Euchone*, and for the determination of whether or not elongate dorsal lips in small individuals consistently have appendages. Acquiring greater clarification of these issues will necessitate a systematic histological survey of lip morphologies within genera, preferably with the inclusion of these data in taxonomic applications. Gaining a better understanding of dorsal lip morphologies will not only enhance data for taxonomic purposes but also provide additional information for the inference of phylogenetic relationships.

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