J. Mar. Biol. Ass. U.K. (2004), **84**, 701–710
Printed in the United Kingdom

Kirkia heterobranchiata, a new genus and species of extratubular brooding sabellid (Polychaeta: Sabellidae) from São Paulo, Brazil

João M. de M. Nogueira*, Eduardo López[†] and Maíra C.S. Rossi*

*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (IB–USP), Rua do Matão, travessa 14, n. 101, 05508-900, São Paulo, SP, Brazil, e-mail: nogueira@ib.usp.br. [†]Departamento de Biología, Unidad de Zoología, Universidad Autónoma de Madrid, Cantoblanco, 28049, Madrid, Spain, e-mail: eduardo.lopez@uam.es

A new genus and species of sabellid polychaete from an organically enriched beach in São Sebastião, State of São Paulo, is described. *Kirkia heterobranchiata* is unique among sabellids for brooding the embryos on the dorsalmost pair of radioles, which exhibits several modifications for this purpose, rather than on ventral radioles. Morphologically, *K. heterobranchiata* is most closely related to *Perkinsiana riwo*, here referred to as the new genus, as suggested by phylogenetic analysis. The new genus is characterized by the shape of the lips (dorsal lips roughly triangular, broader than long; ventral lips lower, ventrally fused and distally rounded), by the absence of both radiolar and pinnular appendages, by having uncini with very short handles in both the thorax and abdomen, and by the ability to brood embryos in cocoons attached to the branchial crown.

INTRODUCTION

The genus *Perkinsiana* Knight-Jones, 1983 was originally described to accommodate several species which did not fit well in the genera in which they were placed at that time. In describing this genus, Knight-Jones (1983) included 11 species, and three additional species were subsequently described (Rouse, 1996; Giangrande & Gambi, 1997). Among the latter, *P. riwo* Rouse, 1996, required modifications on the definition of the genus, allowing for the presence or absence of dorsal lip radiolar and pinnular appendages, radioles with two rows of skeletal cells in lateral view, collar dorsally fused to the faecal groove, uncini with very short handles throughout, and abdominal neurochaetae in two rows (Rouse, 1996). This alteration has been questioned by Knight-Jones (personal communication), mostly due to the absence of dorsal lip appendages.

Subsequent to the description of *Perkinsiana*, Fitzhugh (1989) performed a phylogenetic analysis of Sabellidae genera and found no apomorphies for the genus. Fitzhugh has been updating his analysis of sabellid relationships since that time, adding new taxa as they were described and reinterpreting some characters (Fitzhugh, 1992a,b, 1993, 1995, 1996, 1998, 1999, 2002a,b, 2003; Rouse & Fitzhugh, 1994; Fitzhugh & Simboura, 1995; Fitzhugh & Rouse, 1999). The phylogenetic analyses of Fitzhugh & Rouse (1999) and Fitzhugh (2003) included *P. riwo* in a clade separated from *Perkinsiana rubra* (Langerhans, 1880), the type species of the genus, chiefly due to the absence of dorsal lip radiolar appendages.

Further, Fitzhugh (2003) discussed the importance of the morphology of dorsal lips for recognizing three distinct conditions within Sabellinae: one without radiolar appendages, to which *P. riwo* belongs, another with radiolar appendages lacking skeletal cells, which includes *Perkinsiana sensu stricto*, and a third with radiolar appendages with an internal skeleton.

Many studies have been conducted on the reproductive strategies of polychaetes (see Wilson, 1991), and particularly on sabellids (Knight-Jones & Bowden, 1984; Rouse & Fitzhugh, 1994; Rouse, 1995; Gambi & Patti, 1999; Gambi et al., 2000). There are three main strategies for sexual reproduction in the family, broadcast spawning, intratubular brooding and extratubular brooding, which seem to be related to body size (Rouse & Fitzhugh, 1994) and/or habitat (Giangrande et al., 1994; Gambi & Patti, 1999). With regard to members of *Perkinsiana*, several reproductive strategies have been documented. While *P. antarctica* (Kinberg, 1867) and *P. riwo* are extratubular brooders (Knight-Jones & Bowden, 1984; Rouse & Fitzhugh, 1994; Rouse, 1996; Gambi & Patti, 1999; Gambi et al., 2000), *P. littoralis* (Hartman, 1967) and *P. borsibrunoi* Giangrande & Gambi, 1997 are broadcast spawners, and *P. milae* Giangrande & Gambi, 1997 primarily reproduces asexually by scissiparity (Giangrande & Gambi, 1997; Gambi & Patti, 1999; Gambi et al., 2000).

A new species of sabellid, very similar to *P. riwo* and sharing with it most of the differences in regard to *Perkinsiana sensu stricto*, was recently found in an organically enriched beach in the State of São Paulo, Brazil. We describe a new genus to accommodate both species, and the Brazilian species is described.

MATERIALS AND METHODS

Collections were made at low tide (−0.2, 0.1, and −0.2 m, respectively) at Praia do Araçá, São Sebastião, on 24 July 2002, 3 December 2002, and 15 July 2003. The area is an organically enriched beach, with very poor water circulation. Specimens were obtained by

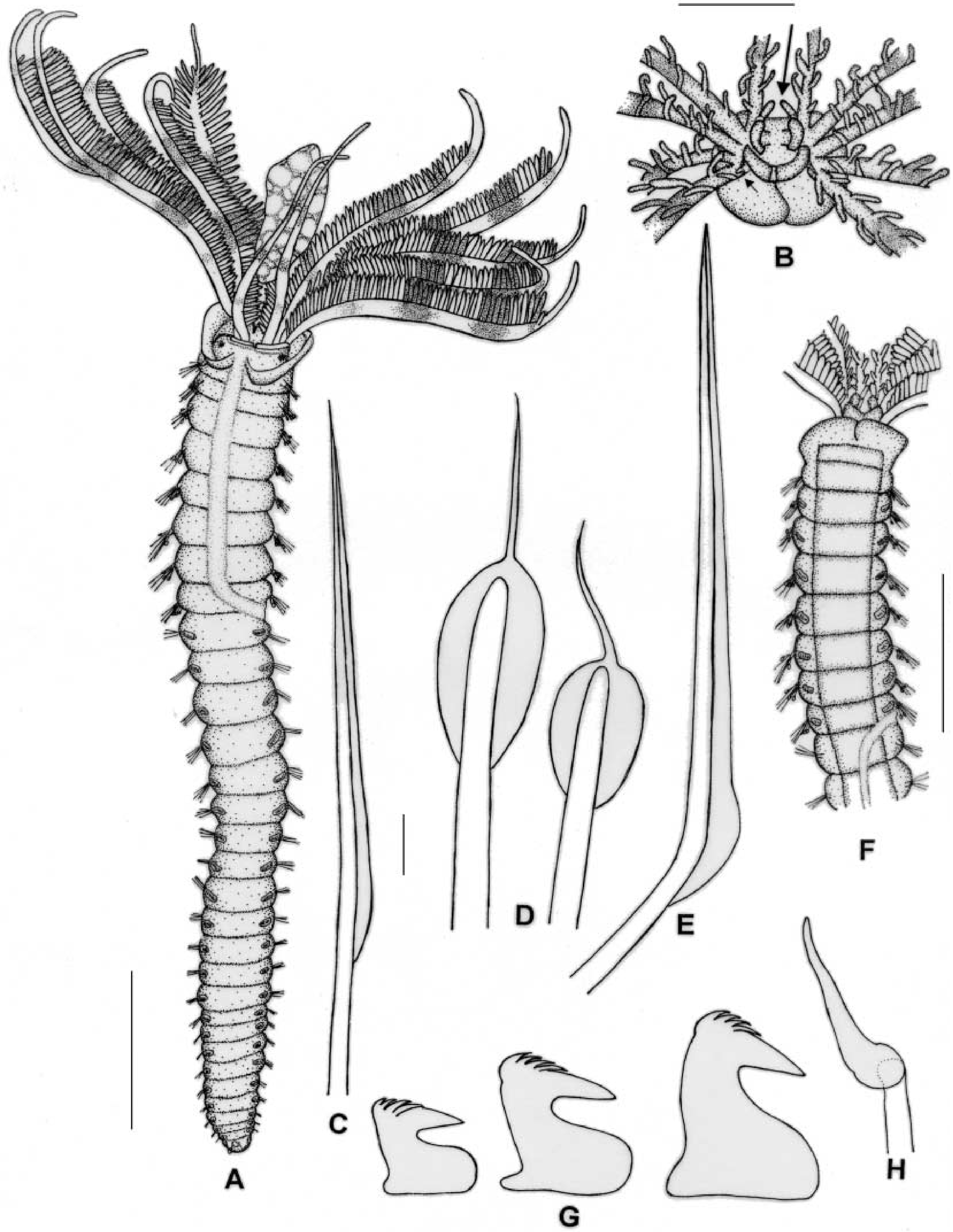

Figure 1. *Kirkia heterobranchiata* gen. nov., sp. nov. (A, F, holotype, MHN-BPO 14/0; B, paratype 12, MHN-BPO 14/3; C–E, G,H, paratype 6, MNCNM 16.01/9247). (A) Entire animal, dorsal view; (B) oral area, superior view (large arrow=lowest pinnule, dorsalmost radiole; short arrow=lowest pinnule, ventralmost radiole); (C) narrowly hooded superior thoracic notochaeta; (D) paleate inferior thoracic notochaetae; (E) broadly hooded abdominal neurochaeta; (F) thorax, ventral view; (G) thoracic uncini, chaetiger 7 (from left to right: ventralmost, intermediate and dorsalmost uncini); (H) companion chaeta. Scale bars: A, F, 1 mm; B, 0.5 mm; C–E & G,H, 10 μm.

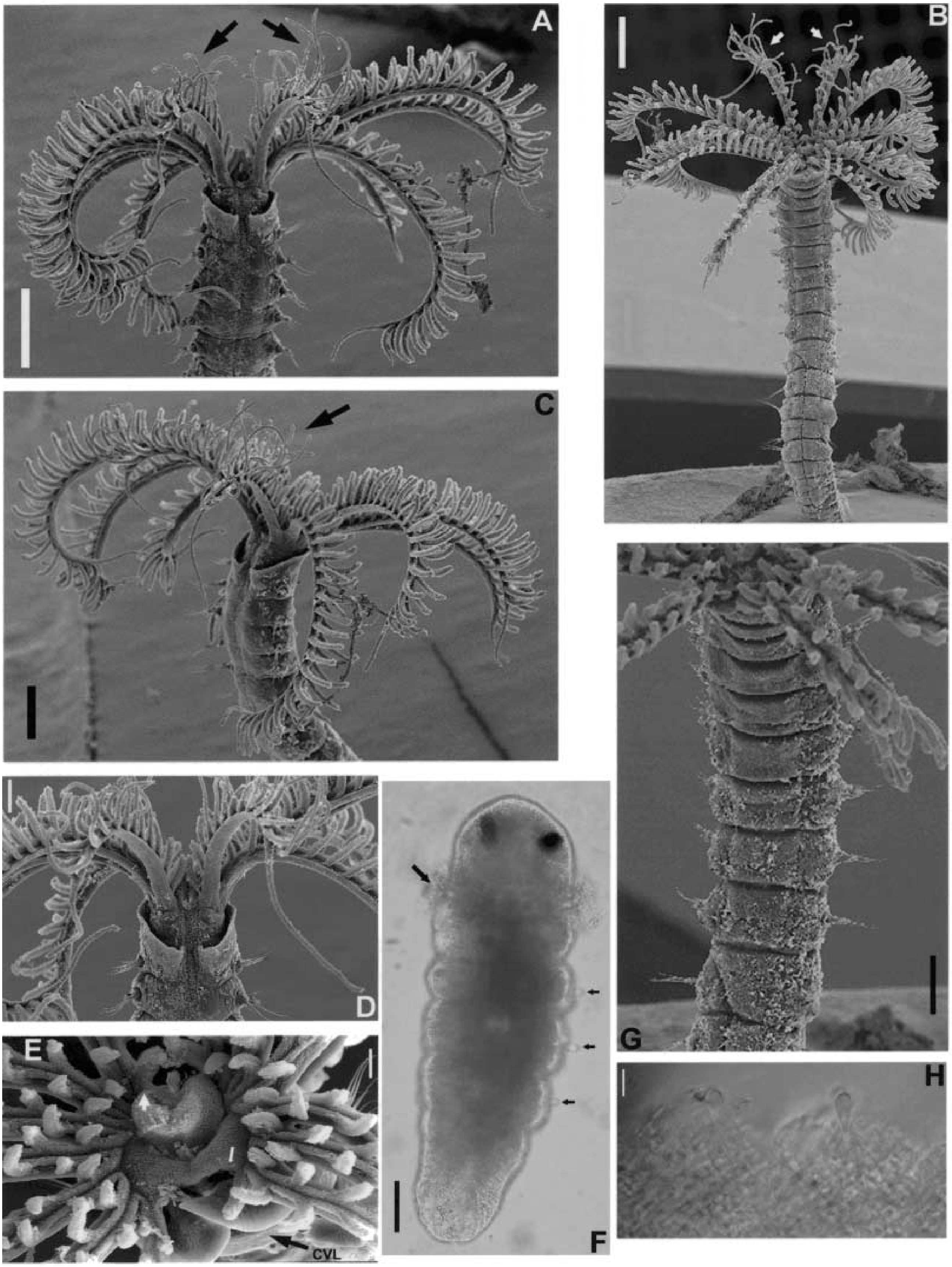

Figure 2. *Kirkia heterobranchiata* gen. nov., sp. nov. (A–C) Anterior end, dorsal, ventral and lateral views, respectively (arrows point to modified pinnules of dorsalmost pair of radioles); (D) collar, dorsal view; (E) oral area (broad arrow points to the membrane between dorsal lips and the proximalmost pinnule of dorsalmost pair of radioles; thin arrow points to the membrane between ventral lips and the proximalmost pinnule of ventralmost pair of radioles; cvl=collar ventral lappets); (F) larva (MHN-BPO 14/5), dorsal view (long arrow points to prototroch; short arrows point to larval paleate notochaetae); (G) thorax, ventral view; (H) larval chaetae. Scale bars: A, 600 μm; B,C, 400 μm; D,G, 200 μm; E,F, 40 μm; H, 10 μm.

scraping the rocks with a chisel; they dwelled among algal tufts and dense aggregations of spionid tubes embedded in a mucous matrix.

Living specimens were examined with a stereomicroscope, extracted from their tubes, relaxed with menthol (a few crystals in a Petri dish with seawater), and fixed in 4% seawater formalin. Four specimens were critical-point dried, covered with 25 nm of gold and examined under scanning electron microscope (SEM). Five specimens were mounted in glycerine-jelly permanent slides, five specimens were mounted in Hoyer's medium on permanent slides, and the remaining were washed and preserved in 70% ethanol.

Line drawings were made from the holotype and from slide-mounted paratypes, with a drawing tube attached to stereo- and light microscopes, respectively.

Type material has been deposited at MHN (Museu de História Natural), MNCN (Museo Nacional de Ciencias Naturales de Madrid), ZMUC (Zoological Museum of the University of Copenhagen), LACM (Allan Hancock Polychaete Collection at the Natural History Museum of Los Angeles County), and NMW (National Museum and Galleries of Wales, Cardiff).

The recent, unpublished phylogenetic analysis presented here was performed by Kirk Fitzhugh (LACM) and kindly made available for inclusion in the present paper. The basis for Dr Fitzhugh's analyses will be published elsewhere.

SYSTEMATICS

Family SABELLIDAE Latreille, 1825
Subfamily SABELLINAE Latreille, 1825
Genus *Kirkia* gen. nov.

Type species

Kirkia heterobranchiata sp. nov.

Etymology

The new genus is dedicated to Kirk Fitzhugh, not only for the great help he gave us in improving the present manuscript, but also as a well-deserved homage to an author who has been contributing to a better knowledge of Sabellidae during the last years, clarifying the relationships within the group and providing modern descriptions of many new and older taxa.

Definition

Small-bodied sabellines, total body length less than 10 mm. Crown with 4–6 pairs of radioles, with two rows of skeletal cells in side view; eyes or ocelli, radiolar flanges, and palmate membrane absent. Dorsal lips triangular to squared, wider than long, distally rounded, without radiolar appendages; ventral lips lower, ventrally fused; dorsal and ventral pinnular appendages absent. Collar dorsally fused to faecal groove, laterally oblique, with two rounded, slightly overlapping ventral lappets. Anterior peristomial ring with one pair of lateral ocelli. Thorax with eight chaetigers, abdomen with up to 25 chaetigers in larger specimens. Collar chaetae narrowly hooded, subsequent notopodia with 1–2 rows of inferior paleate chaetae and one superior arc of very narrowly hooded chaetae; abdominal neuropodia with two rows of elongate, broadly hooded chaetae. Thoracic uncini avicular; breast well developed, with very short handle, shorter than the distance between breast and crest; companion chaetae with denticulate hood and elongate tips; ventral margins of neuropodial thoracic tori not contacting ventral shields; abdominal uncini similar to thoracic. Pygidium with or without ocelli.

Remarks

In the description of *Perkinsiana riwo*, Rouse (1996) emended the definition of the genus to accommodate this species. The placement of this species in *Perkinsiana* was not, however, supported by subsequent phylogenetic analyses (Fitzhugh & Rouse, 1999; Fitzhugh, 2003; K. Fitzhugh, personal communication), on which it appeared closer to *Potamilla* and *Laonome* Malmgren, 1866 than to *Perkinsiana rubra*, the type species of *Perkinsiana*, especially due to the absence of dorsal lips radiolar appendages (Fitzhugh & Rouse, 1999; Fitzhugh, 2003).

The cladogram presented here (Figure 4), demonstrates that *Kirkia heterobranchiata* gen. nov., sp. nov. and *P. riwo* are sister taxa, forming a monophyletic clade defined by the absence of dorsal lip appendages and the presence of uncini with short handles throughout. Therefore, we describe here this new taxon, the genus *Kirkia*, and transfer *P. riwo* to it.

Biology

Both species of *Kirkia* gen. nov. are brooders, although the homology between the strategies employed may be questionable (see *Remarks* for *Kirkia heterobranchiata*).

Kirkia heterobranchiata sp. nov.

Figures 1–3

Material examined

Fifty-seven specimens, all from Praia do Araçá (23°48′55.9″S 45°24′28.8″W), city of São Sebastião, State of São Paulo, Brazil. Thirty-three specimens collected on 24 July 2002 (including holotype and paratypes 1–18 and 20), 1 specimen collected on 3 December 2002 (paratype 19), and 23 specimens collected on 15 July 2003. All material collected at the intertidal zone, in rocks, living among algal tufts and dense aggregations of tubes of spionid polychaetes. Holotype and paratypes 1, 7, 12 and 13 deposited at the MHN (MHN-BPO 14/0 and MHN-BPO 14/1–4, respectively); paratypes 2, 6, 14 and 19 deposited at the MNCN (MNCN 16.01/9246–9249); paratypes 3, 8, 11 and 15 deposited at the ZMUC (ZMUC-POL 1656–1659); paratypes 4, 9, 16 and 18 at the LACM (LACM-AHF 2122–2125); and paratypes 5, 10, 17 and 20 at the NMW (NMWZ 2003.042.001–004). Larva released from paratype 19 deposited at MHN (MHN-BPO 14/5).

Etymology

The epithet, *heterobranchiata*, refers to the shape of the first pair of radioles in sexually mature specimens, which differs from the other radioles in that it is modified to hold the cocoon.

Description

Holotype: complete specimen, in good condition, 5.5 mm long, from collar to pygidium, with additional ~2.5 mm of tentacular crown; 0.5 mm wide at the level of the thorax. Thorax consisting of eight chaetigers,

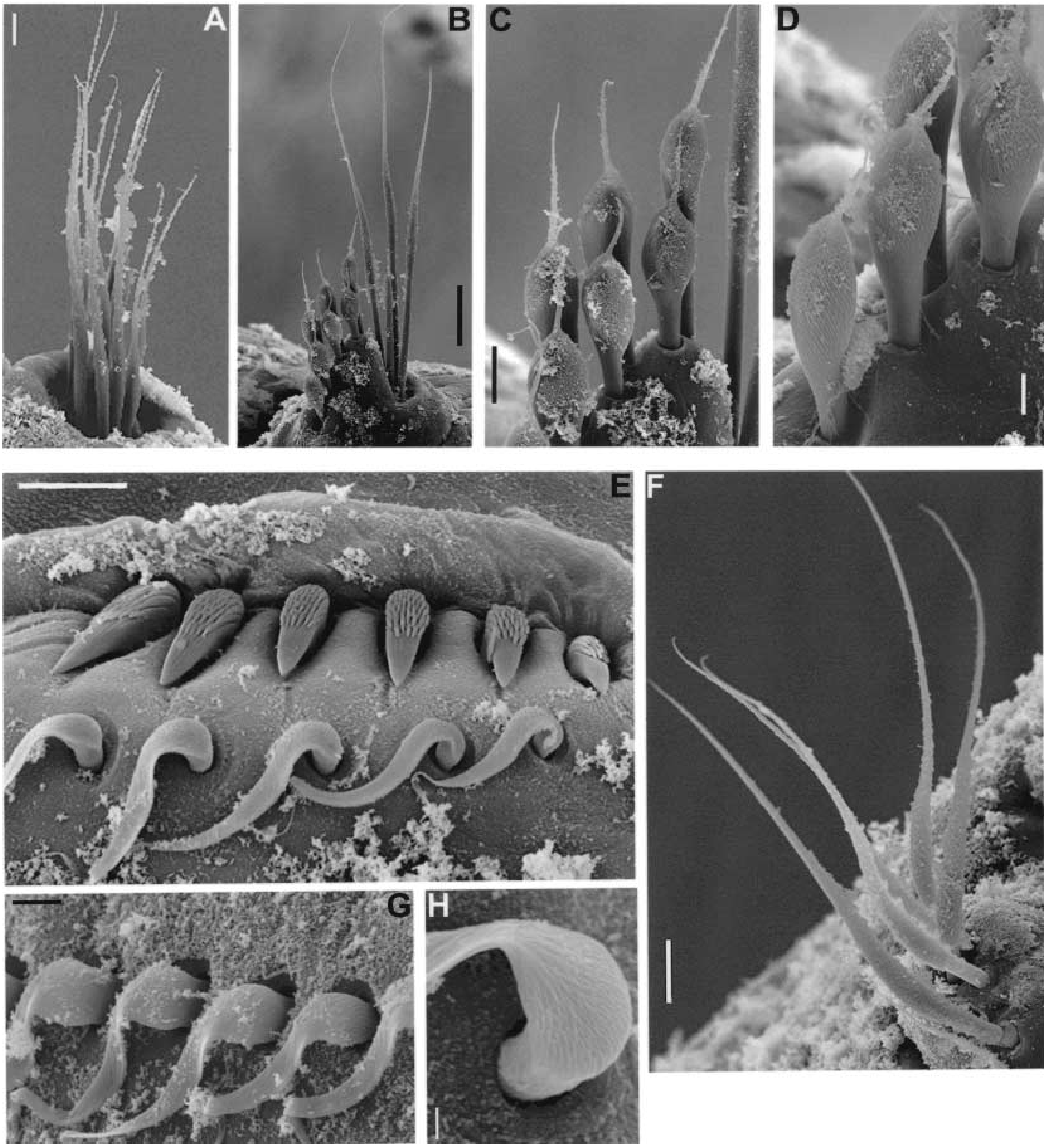

Figure 3. *Kirkia heterobranchiata* gen. nov., sp. nov. (A) Collar chaetae; (B) thoracic notopodium, with superior and inferior notochaetae; (C,D) inferior thoracic notochaetae; (E) thoracic neuropodium, with uncini and companion chaetae; (F) abdominal neuropodium; (G,H) companion chaetae. Scale bars: A, C, E, F, 10 μm; B, 30 μm; D, 5 μm; G, 4 μm; H, 1 μm.

abdominal chaetigers numbering 22. Crown with six pairs of radioles slender and proportionally elongate, ending by thin pinnule-less tip which measures up to 2–3 times the length of distal pinnules (Figure 1A); radioles without eyes or ocelli, but with four dark brown to black (in live material; yellowish to brown after fixation) patches along their length, each extending between three consecutive pinnules and continuing along those pinnules; proximal- and distalmost patches fainter than intermediate ones (Figure 1A). Dorsalmost pair of radioles shorter than the remaining ones in fertile specimens, measuring 1.8 mm, bearing pinnules only along proximal half, distal pinnules thinner and 2–3 times as long as those of other radioles; both radioles of dorsalmost pair close to each other and holding together one cocoon with embryos (Figure 1A; cocoon accidentally removed during manipulation, but preserved together with the holotype). Dorsal lips short, roughly squared, distally truncate, lacking radiolar and pinnular appendages; ventral lips lower, distally rounded, obliquely disposed and fused to each

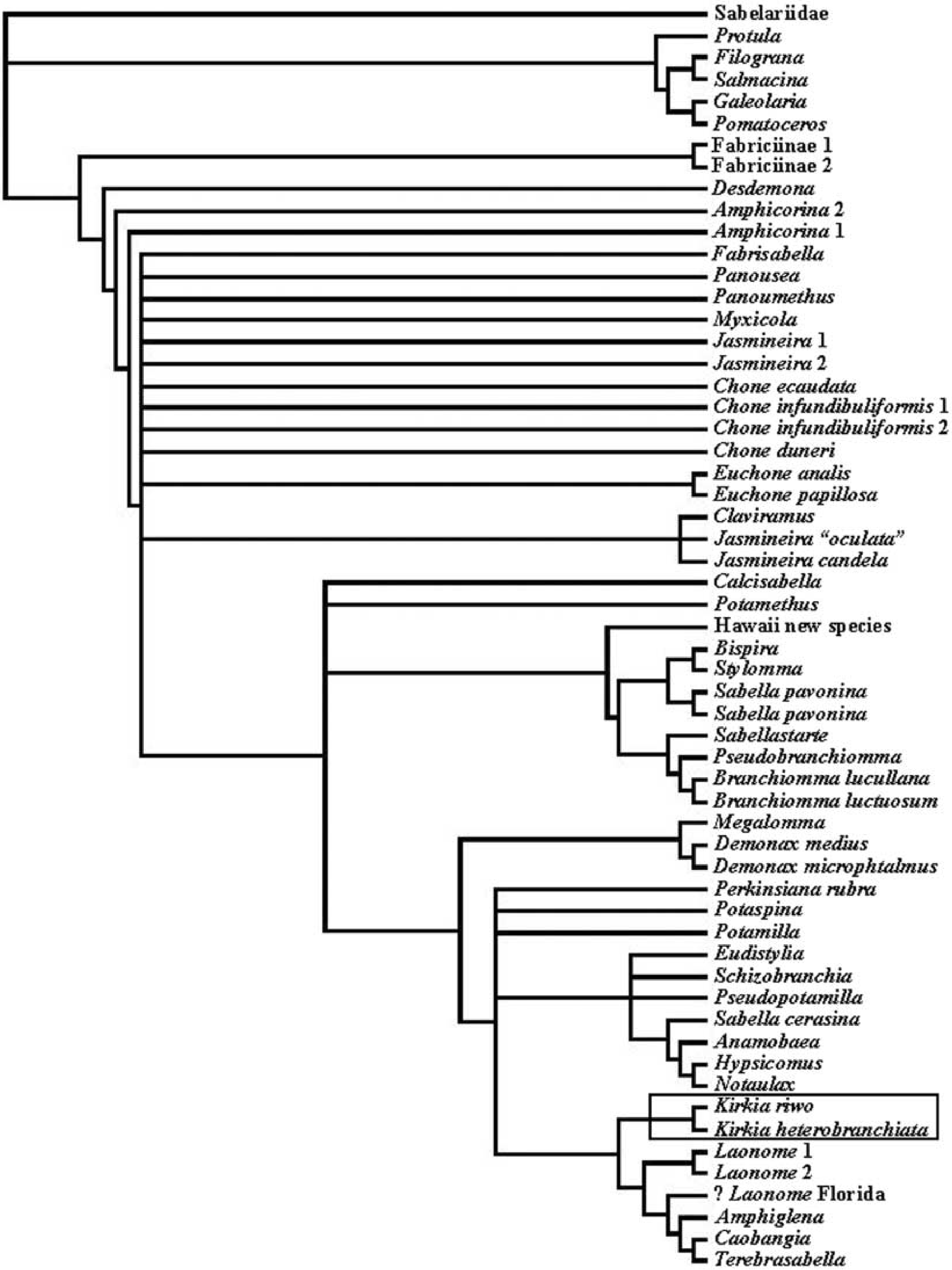

Figure 4. Phylogeny of Sabellinae, including *Kirkia* gen. nov. Methods and characters/states list after Fitzhugh. Rectangular area refers to the new genus *Kirkia*.

Table 1. *Main similarities and differences between* Kirkia heterobranchiata *sp. nov. and* Kirkia riwo *(data for* K. riwo *based on Rouse, 1996).*

Character	*K. heterobranchiata*	*K. riwo*
Radiolar tips	Short, ∼2–3 times length of distal pinnules	Longer, up to half length of radioles
Radiolar skeleton	Two cells wide, in lateral view	Same
Dorsal lips	Short, broader than long, without radiolar appendages and pinnular appendages	Same
Ventral lips	Low, fused to each other, without radiolar appendages	Same
Collar	Low, dorsally fused to faecal groove, laterally oblique, with one pair of overlapping ventral lappets	Same, but ventral lappets do not overlap
Thoracic notochaetae	Superior chaetae narrowly hooded, in an arc. Inferior chaetae paleate, in two rows	Chaetae with the same shape, but inferior chaetae in single rows
Abdominal neurochaetae	Elongate, broadly hooded, in two rows	Same
Uncini	Avicular, with breast well developed and short manubrium	Same
Companion chaetae	With broader denticulate area and long mucro	Same
Pygidial ocelli	Absent (in adults and larvae)	Present (in adults and larvae)
Brooding	Cocoon attached to dorsalmost pair of radioles, which is modified	Cocoon attached to ventral unmodified radioles
Larvae	Released with four chaetigers, each with one single chaeta, similar to inferior thoracic notochaetae in adults, but without mucro	Released with three chaetigers, with chaetae similar to both types of thoracic notochaetae in adults
Habitat	Rocky shores, among polydorid spionids, in São Paulo, Brazil	Mangrove roots, in Papua New Guinea

other mid-ventrally; lips connected to the adjacent radioles by thin membranes. Collar low, dorsally reaching the same level as first pair of notopodia and fused to lateral edges of faecal-groove, laterally oblique and forming one pair of short and slightly overlapping ventral lappets, separated by cleft longer than first ventral shield (Figure 1F); anterior peristomial ring well exposed dorsal and laterally, with one pair of black, dorso-lateral ocelli (Figure 1A). Ventral shields uniformly wide along thorax, not indented by tori. Thorax with eight chaetigers, the first chaetiger with two rows of narrowly hooded notochaetae (collar chaetae), those of superior row longer; all other thoracic notopodia with two types of chaetae: superior group with 3–4 very narrowly hooded chaetae, arranged in arc, inferior group with two oblique rows of paleate chaetae, with 3–4 chaetae each; paleate chaetae with oval hood and with tip at least as long as hooded area, those on anterior row longer. Thoracic neuropodia with tori with 6–13 uncini each; frequently, uncini increasing in size from ventral to dorsal edge of torus, smaller uncini the oldest. Uncini avicular, with very short manubrium and well developed breast, extending to about distal end of main fang, which is surmounted by a crest of 4–5 rows of short teeth. Companion chaetae with denticulate hood and long and thin membrane. Abdominal notopodial tori with up to 12 uncini, similar to those in thorax; abdominal neuropodia with 3–7 broadly hooded chaetae, similar to superior thoracic notochaetae but slightly bulbous at knee, arranged in two rows, and in some chaetigers, apparently randomly, one short and thin spine-like chaeta (possibly, just the tip of one chaeta in formation); chaetae narrower in posterior chaetigers. Body tapered distally. Pygidium trilobed, eyespots absent.

Other material

The material examined varies in regard to size, pigmentation of the crown, number of pairs of radioles, development of the modifications of the dorsalmost pair of radioles, length of radiolar tips and number of thoracic and abdominal chaetigers.

Specimens varied between 2.5–5.5 mm in length, from collar to pygidium, with additional 0.8–3 mm of tentacular crown. The tentacular crown may have 4–6 pairs of radioles and, although all specimens have the four pigmented patches described for the holotype, they are fainter and less evident in some of them. The bare, pinnule-less tips vary in length, tending to be longer in larger individuals. On the other hand, the modifications of the first pair of radioles are present only in sexually mature specimens, showing a gradient on the length of those radioles and of their pinnules, from the same size as on other radioles to the highly modified condition described for the holotype (Figure 2A–C). Dorsal and ventral lips have the same shape as in the holotype, dorsal lips distally truncated, ventral lips rounded and medially fused, both lips connected to the adjacent radioles by thin membranes (Figures 1B & 2E).

Collar with the same shape in all specimens, low, ending at the level of first notopodia and fused to the edges of faecal-groove, laterally oblique, and with short, slightly overlapping ventral lappets (Figures 1B, 2A–E,G). Anterior peristomial ring always well exposed, but peristomial ocelli tend to be fainter in larger individuals, sometimes only visible under light microscope.

Among the 57 specimens studied, five have seven thoracic chaetigers, two have six, two have five, and the other two have only four; all of the remainder have eight thoracic chaetigers. As most of the specimens with fewer than eight thoracic chaetigers are not complete posteriorly, it is not possible to determine their actual size in order to investigate whether this character is size-dependent or not. The number of abdominal chaetigers ranges from 12 to 23. In all specimens, chaetae are as in holotype: collar with two rows of narrowly hooded notochaetae (Figure 3A); from chaetiger 2 to the end of thorax, superior notochaetae in an arc of 3–4 long, thin, and very narrowly hooded chaetae, inferior chaetae in two oblique rows of paleate chaetae with tip at least as long as the hooded area (Figures 1C–D, 3B–D). Thoracic neuropodial tori not indenting ventral shields, each torus with up to 13 uncini with very short manubrium, well developed breast and 4–5 rows of short teeth above main fang, and companion chaetae with denticulate hood, and long and thin membrane (Figures 1G,H, 3E,G,H). Abdominal neuropodia with two rows of broadly hooded chaetae (Figures 1E & 3F), and in some chaetigers, one short and thin spine-like chaeta.

Green blood. Dorsal and ventral vessels evident in live material, the former much larger and contractile; one dorsal vessel around each of the cartilaginous bases of the crown, with one ramification for each radiole and penetrating ventralwards between the bases of the crown. Dorsal lip vessels not observed.

In sexually mature specimens, anterior 1–5 abdominal segments containing coelomic-maturating oocytes in different stages of development within the same segment, varying from ~30–90 μm in diameter. Sperm not observed.

Biology

The new species was found in an organically enriched beach, among dense aggregations of brown, polydorid sand grain tubes embedded in a mucous matrix. Other polychaetes found among those tubes were *Pseudobranchiomma emersoni* Jones, 1962, and unidentified species of *Notaulax* and *Pseudopotamilla*. The tubes of *K. heterobranchiata* sp. nov. are distinguished from those of the spionids by being slightly shorter and broader.

Kirkia heterobranchiata sp. nov. seems to be a seasonal species. It was first collected on 24 July 2002, when most rocks were covered by dense mat of *Polydora* sp. tubes within which tubes of *K. heterobranchiata* were particularly abundant. Samplings at Praia do Araçá were repeated several times since that first collection, as well as in other organically enriched areas, such as Ilha Porchat, Praia das Vacas, and Ilha das Palmas. Several additional collections in presumed unpolluted beaches with stronger water circulation were also made. Sabellids were particularly abundant in all those samples, especially in organically enriched areas, but *K. heterobranchiata* was found only twice again, always at Praia do Araçá, represented by a single specimen obtained on 3 December 2002 and 23 specimens on 15 July 2003. Since in all those three occasions brooding specimens were obtained and collections were made in winter and late spring, the species appears to reproduce sexually throughout the year.

The single specimen (paratype 19) collected on 3 December 2002 was brooding four embryos. While extracting it from the tube, a swimming larva was released from the cocoon. That larva had four chaetigers, each with a single chaeta, similar to the inferior thoracic notochaetae of adults, but distally rounded, without a mucro (Figure 2F,H).

Finally, asexual reproduction by scissiparity is also likely to occur in *K. heterobranchiata*, being the possible explanation for the variability observed on the number of thoracic chaetigers (Knight-Jones & Bowden, 1994; Nogueira & Knight-Jones, 2003).

Remarks

Kirkia heterobranchiata sp. nov. differs from all species of *Perkinsiana* in having uncini with very short manubria, collar dorsally fused to the faecal groove, and dorsal lips without radiolar appendages.

Among the species currently included in *Perkinsiana*, *P. minuta* (Treadwell, 1941) was described from Ilha de São Sebastião, an island situated in front of the beach where *K. heterobranchiata* sp. nov. was found, and separated from the shore by a channel 2–6 km wide. Besides the characters discussed above, *P. minuta* differs from *K. heterobranchiata* in being twice as long as the latter, with thorax characteristically short, composed of four chaetigers according to the original description (Treadwell, 1941), or five, based on the redescriptions of type material by Hartman (1956) and Knight-Jones (1983). Furthermore, the paleate chaetae of *P. minuta* are very slender, with hood gradually tapering towards the tip, while those of *K. heterobranchiata* have oval hood, clearly separated from the tip by a marked constriction. Finally, the tori indent the ventral shields in the former, but not in the latter.

The ability to incubate embryos on the radioles has been documented for several sabellids (McEuen et al., 1983; Giangrande et al., 1994; Knight-Jones & Bowden, 1984; Rouse & Fitzhugh, 1994; Rouse, 1996; Gambi & Patti, 1999; Gambi et al., 2000). In the particular case of *Perkinsiana*, *P. antarctica* (Kinberg, 1867) also does it, however this species attach the cocoon to ventral radioles, which are not modified.

Knight-Jones (personal communication) has suggested that the modifications of the dorsalmost radioles could be due to stretching of the pinnules and contraction of the radioles, both caused by the presence of the cocoon. We believe the shapes of these radioles are not due to changes in elasticity, however, because sexually mature specimens without a cocoon also exhibit varying degrees of modification, even before they produce a cocoon, and specimens which had their cocoons accidentally removed during extraction from tubes maintained the same modified radiolar shape while still alive for 1–2 hours after cocoon loss. Furthermore, the dorsalmost pair of radioles has a different distribution of pinnules, with much longer distal bare tips compared with other radioles.

Kirkia riwo and *K. heterobranchiata* differ because *K. riwo* has radioles with pinnule-less tips extending for about half of their length, paleate chaetae in single rows and pygidium with a pair of ocelli. The main similarities and differences between both species are summarized in Table 1.

Kirkia riwo and *K. heterobranchiata* lack dorsal and ventral pinnular appendages, however *K. heterobranchiata* sp. nov. has thin membranes connecting the lips to the basal pinnules of the adjacent, dorsal or ventral radioles (Figures 1B & 2E). According to Fitzhugh (personal communication), those pinnules, although slightly enlarged, are not true pinnular appendages as they are much closer to the radioles than to the lips, while pinnular appendages are distinctly fused to the lateral margins of the dorsal lips.

In regard to reproduction, these species differ from each other in that *K. riwo* broods the embryos on ventral unmodified radioles, while *K. heterobranchiata* sp. nov. holds them with the dorsalmost pair of radioles, which is adapted for that function in fertile specimens. Since the structures which hold the cocoons in the two species are not strictly homologous (dorsalmost pair of radioles versus ventral radioles), it might be speculated whether they have independent origins or are just alternate conditions of being an embryo-brooder character. Due to all affinities discussed above, it seems more likely to consider the second hypothesis as the correct, and the embryo-brooding ability is just one more similarity joining both species.

Finally, larvae of *K. riwo* are released from eggs in a three chaetigers state and have chaetae similar to both types of thoracic notopodial chaetae in adults (Rouse, 1996), while in *K. heterobranchiata* sp. nov. the larva observed had four chaetigers and only spatulate chaetae (Table 1).

DISCUSSION

Prior to the description of *Kirkia riwo*, Rouse & Fitzhugh (1994) performed a phylogenetic analysis of Sabellidae, considering also reproductive characters and including that species as *Perkinsiana* 'New Guinea' (PNG). In that analysis, *K. riwo* appeared as the sister taxon to *Potaspina*, both close to *P. rubra*.

Perhaps encouraged by that fact, Rouse (1996) preferred to enlarge the diagnosis of *Perkinsiana* to accommodate his species, instead of describing a new genus. However, the author pointed out the necessity of a review of all species included in the genus at that time (Rouse, 1996: 103).

The analysis presented here was performed by Kirk Fitzhugh and kindly made available to us. The consensus tree of 11518 most parsimonious trees is presented in Figure 4. It supports the description of a new genus to accommodate *K. heterobranchiata* and *K. riwo*; this taxon is characterized mostly by the shape of the lips, absence of radiolar and pinnular appendages, uncini with very short handles, and the ability to brood embryos in the crown.

This work was supported by the State of São Paulo Research Foundation (FAPESP) within the BIOTA/FAPESP—The Biodiversity Virtual Institute Program (www.biotasp.org.br); M.C.S.R. is also supported by another FAPESP project (02/08950-3). We are very grateful to the two referees who revised the present manuscript, for the comments and suggestions; to Cecília Amaral, coordinator of BIOTA/FAPESP/Bentos Marinho project, for all the support; to the staff of Departamento de Zoologia, IB–USP, and the technicians Enio Mattos and Marcelo Cardagi; to the Laboratório de Microscopia Eletrônica, IB–UNICAMP (Instituto de Biologia–Universidade Estadual de Campinas), namely the technicians Adriane Sprogis and Antônia Lima, for the help with SEM; to Ronaldo Francine Filho, for our Figure 2F; to Erica V. Pardo for information about the type locality; and to CEBIMar-USP, Centro de Biologia Marinha da Universidade de São Paulo, for hosting two of us (J.M.M.N. and M.C.S.R.) and providing all support for two collections.

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Submitted 4 February 2003. Accepted 24 May 2004.