A new branchiate hesionid polychaete (Annelida, Hesionidae) from New Caledonia

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ABSTRACT
We describe *Hesiobranchia lifouensis* n. gen., n. sp. from coral reefs at Lifou, Loyalty Islands, New Caledonia in the south-west Pacific. It is distinguished from all other hesionids by the presence of two elongated lateral projections on the proboscis, by having both noto- and neurochaetae starting on segment 5, by the presence of parapodial branchiae, and by a unique pigmentation pattern. A morphology-based parsimony analysis of the phylogeny of hesionids indicates that *H. lifouensis* n. gen., n. sp. belongs within Gyptini and is the sister group of *Gyptis* Marion & Bobretzky *in* Marion, 1874.

KEY WORDS
Annelida,
Polychaeta,
Hesionidae,
Hesiobranchia n. gen.,
Hesiobranchia lifouensis n. sp.,
new genus,
new species.

RÉSUMÉ
Un nouveau Hesionidae (Polychaeta) de Nouvelle-Calédonie avec des branchies.
Nous décrivons *Hesiobranchia lifouensis* n. gen., n. sp., une nouvelle espèce ainsi qu'un nouveau genre d'Hesionidae, en provenance des récifs de corail de Lifou, Îles Loyauté, en Nouvelle-Calédonie au sud-ouest de l'océan Pacifique. Ce polychète se distingue des autres Hesionidae par la présence de deux projections allongées latéralement du proboscis, par la possession simultanée de noto- et neurochètes débutant au segment 5, par la présence de branchies sur les parapodes, et par un motif de pigmentation unique à ce jour. Une analyse de parcimonie de la phylogénie des Hesionidae, basée sur des caractères morphologiques, indique que *H. lifouensis* n. gen., n. sp. se place au sein des Gyptini comme groupe frère de *Gyptis* Marion & Bobretzky *in* Marion, 1874.

MOTS CLÉS
Annelida,
Polychaeta,
Hesionidae,
Hesiobranchia n. gen.,
Hesiobranchia lifouensis n. sp.,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The Hesionidae Grube, 1850 include 24 genera and about 135 species in current use (Pleijel & Rouse 2000; Westheide 2000; Pleijel 2001a, b, 2004). During the expedition LIFOU 2000 (Bouchet *et al.* 2000) to Loyalty Islands, New Caledonia, south-west Pacific, the second author collected four specimens of an undescribed hesionid among dead corals in shallow water. We here refer these specimens to a new genus and a new species, *Hesiobranchia lifouensis* n. gen., n. sp. Although *H. lifouensis* n. gen., n. sp. is clearly a member of Hesionidae, as seen by e.g., the presence of enlarged dorsal and ventral cirri on segment 3 (Pleijel 1998), its relationships within this taxon is much less straightforward. For this reason, we assess its relationships in a morphology-based phylogenetic analysis, together with 20 other hesionid representatives.

ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris;
LM	light microscopy;
SEM	scanning electron microscopy.

MATERIAL AND METHODS

Specimens were collected by scuba from dead *Acropora* Oken, 1815. They were relaxed in 10% magnesium chloride, studied and photographed alive, fixed in formaldehyde in sea water (10%) for about 24 hours, rinsed in fresh water, and subsequently transferred to 70% ethanol. Parapodia for LM were mounted in Gurr Aquamount™. For SEM studies, one specimen was critical point dried, sputter-coated with gold, and examined in a Hitachi S-4300. The SEM specimen is in FP's collection, the other specimens and slides are deposited at MNHN.

For the phylogenetic analysis the terminal taxa were selected to span the diversity of hesionids. The choice of members of Chrysopetalidae Ehlers, 1864 (*Dysponetus bulbosus* Hartmann-Schröder, 1982) and Nereididae Johnston, 1865 (*Alitta virens* (Sars, 1835)) as outgroups are based on previous studies by Glasby (1993) and Pleijel & Dahlgren (1998). Most characters are simple binary, either scored as absence/presence, or with both states specified. For linked characters we applied "C-coding" *sensu* Pleijel (1995), where the absence/presence of a composite feature is treated as one character, different expressions of this feature as separate characters, and taxa lacking the feature are scored as inapplicable (i.e. treated as question marks, "?", in the analysis) for the different expressions. The data set (character list in Appendix 1 and matrix in Appendix 3) includes 38 parsimony-informative characters and 84 character states. All characters were given equal weights and were treated as unordered except for characters 18, 19, 21 and 22, which were treated as ordered based on their additive degrees of similarities.

Matrices were entered in MacClade 4.0 (Maddison & Maddison 2003) and analysed in PAUP* 4.0b10 (Swofford 2001) with "default settings" for the heuristic searches, except for the addition sequence which was set to random with 1000 replicates. Bremer support was calculated in PAUP together with AutoDecay (Eriksson 1996).

SYSTEMATICS

Family HESIONIDAE Grube, 1850
Subfamily OPHIODROMINAE Pleijel, 1998
Tribe GYPTINI Pleijel, 1998

Hesiobranchia n. gen.

TYPE SPECIES. — *Hesiobranchia lifouensis* n. sp.

ETYMOLOGY. — Named formed from the combination of the stem of the taxon name "Hesionidae" and "branchiae", gender feminine.

DESCRIPTION

Monotypic; see *Hesiobranchia lifouensis* n. sp.

Hesiobranchia lifouensis n. sp.
(Figs 1-3)

"Undescribed hesionid from Lifou, Loyalty Islands" – Pleijel & Rouse 2004: fig. 2.

MATERIAL EXAMINED. — **Loyalty Islands.** Lifou, Santal Bay, Cape Aimé Martin, 20°46.7'S, 167°02.6'E, among dead *Acropora*, 20 m, scuba, 11.XI.2000, coll. F. Pleijel,

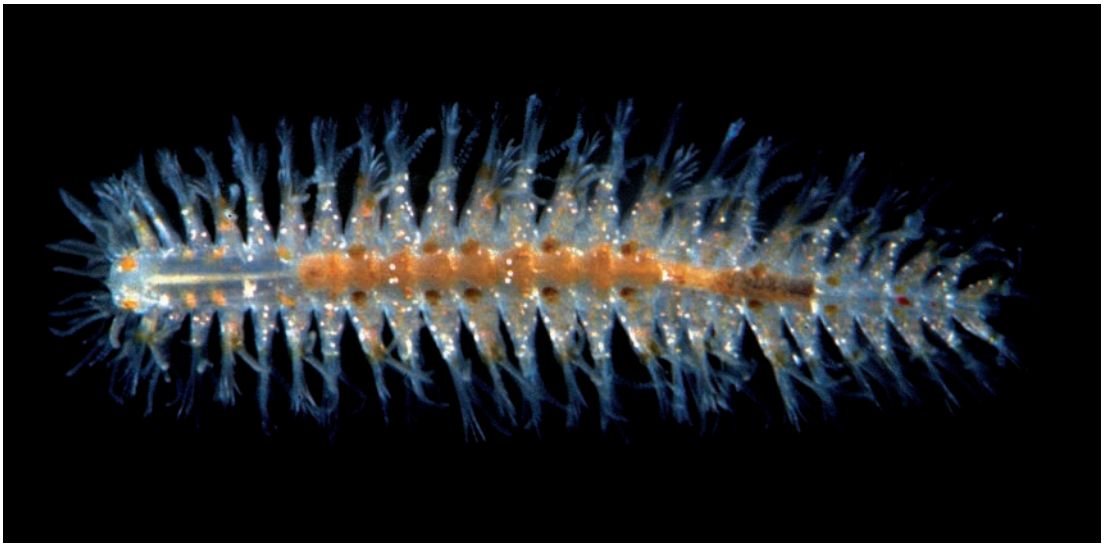

FIG. 1. — Live picture of *Hesiobranchia lifouensis* n. gen., n. sp., paratype (MNHN POLY TYPE 1449), dorsal view, *c.* 5 mm in length.

holotype (MNHN POLY TYPE 1446, and two slides with parapodia 1447, 1448); 1 paratype (MNHN POLY TYPE 1449, and four slides with parapodia 1450-1453). — Lifou, Santal Bay, Cape Aimé Martin, 20°45.51'S, 167°01.98'E, among dead corals, 25 m, scuba, 21.XI.2000, coll. F. Pleijel, 1 paratype (MNHN POLY TYPE 1454); 1 specimen (mounted for SEM, in F. Pleijel's collection).

ETYMOLOGY. — Named for the type locality, Lifou.

DISTRIBUTION. — Only known from Lifou, Loyalty Islands, New Caledonia.

DESCRIPTION

Holotype 4 mm long for 25 segments; paratype (MNHN POLY TYPE 1454) 4.5 mm long for 31 segments, paratype (MNHN POLY TYPE 1449) 5 mm long for 29 segments (posteriorly incomplete), specimen mounted for SEM 2 mm long for 20 segments (posteriorly incomplete). Body elliptical in outline with truncated anterior end and tapered posterior, venter flattened (Fig. 1). Prostomium rounded, slightly wider than long, with posterior incision (Fig. 2A). Palpophores cylindrical; palpostyles also cylindrical but much thinner, with rounded tips; palpophores and palpostyles of equal length (Fig. 2B). Paired antennae tapered, pointed, without ceratophores, shorter than palpostyles (Fig. 2A). Median antenna much shorter than paired antennae, pointed, inserted between anterior pair of eyes; median antennal furrows and ceratophore absents. Anterior pair of eyes rounded, larger than posterior pair and situated farther apart; posterior pair rounded to reniform, both pairs with lenses. Nuchal organs prominent, middorsally coalescing (Fig. 2A). Distinct facial tubercle absent. Proboscis smooth and unarmed, divided into proximal and distal parts by concentric groove, terminal ring with one long, flattened and pointed process each side. Proboscis extending backwards to segment 10 in non-everted condition. Lip glands absent. Anterior dorsal and ventral cirri and cirrophores on segments 1-4 elongated and stouter than on following segments, indistinctly annulated. Notopodial lobes and notochaetae, and neuropodial lobes and neurochaetae, absent on segments 1-4 (Fig. 2A, B). Segment 5 with both notopodial lobes and notochaetae and neuropodial lobes and neurochaetae (Fig. 3A), similar to following ones. Dorsal cirri rather short, cylindrical, indistinctly annulated. Elevated dorsal cirri on segment 8, 10, 12, 15, 17, 19, 21, 23, 25 and 27. Notopodia on segments 2 and 3 with single

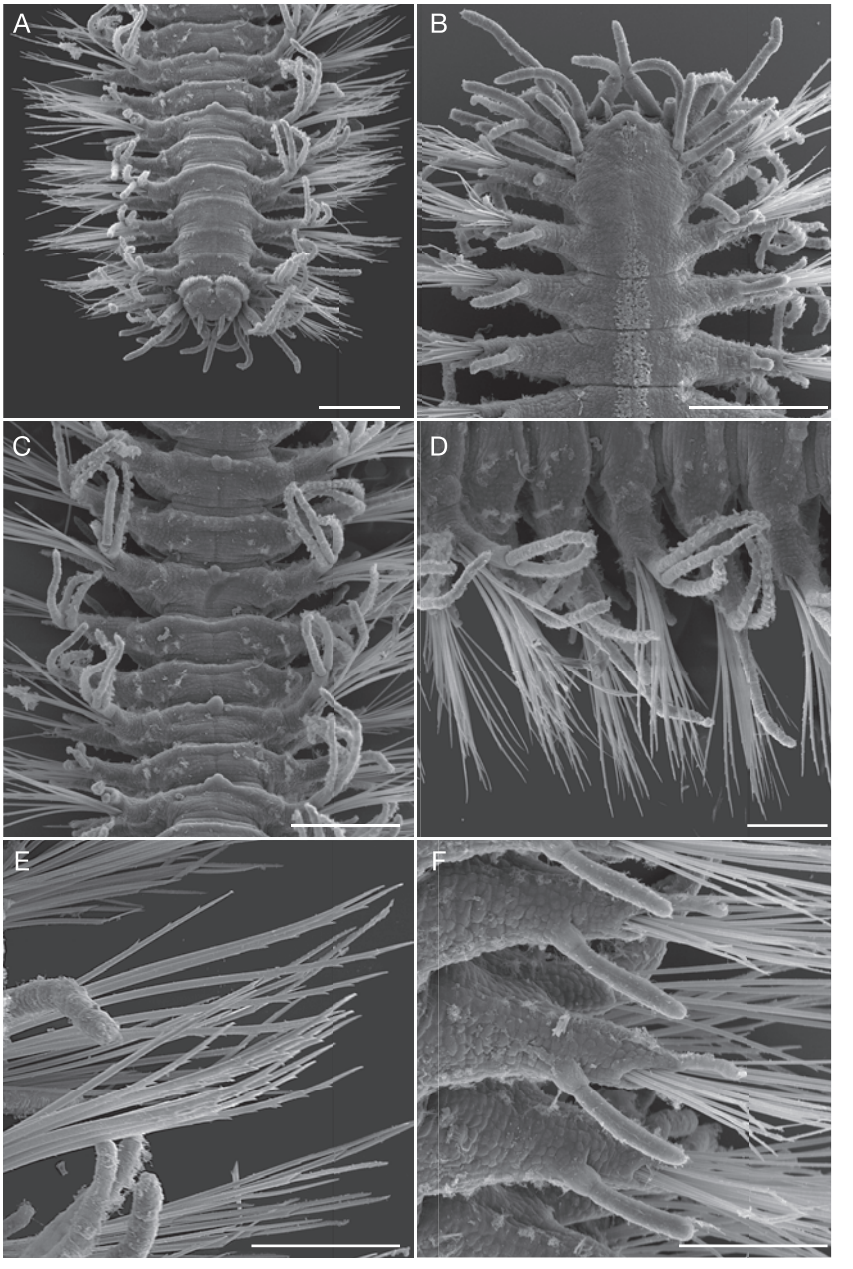

FIG. 2. — SEM pictures of *Hesiobranchia lifouensis* n. gen., n. sp.: **A**, anterior end, dorsal view; **B**, anterior end, ventral view; **C**, median segments, dorsal view; **D**, median parapodia, left side; **E**, chaetae from median segments, antero-dorsal view; **F**, median parapodia, left side, antero-ventral view. Scale bars: A-C, 0.3 mm; D, 150 µm; E, F, 60 µm.

branchial filaments, notopodia on segment 4 and following segments with two branchial filaments, inserted just above and below dorsal cirri (Figs 2C, D; 3B). Branchiae shorter than dorsal cirri on all segments. Notopodial lobes small, conical, with single notoacicula. Notochaetae of single

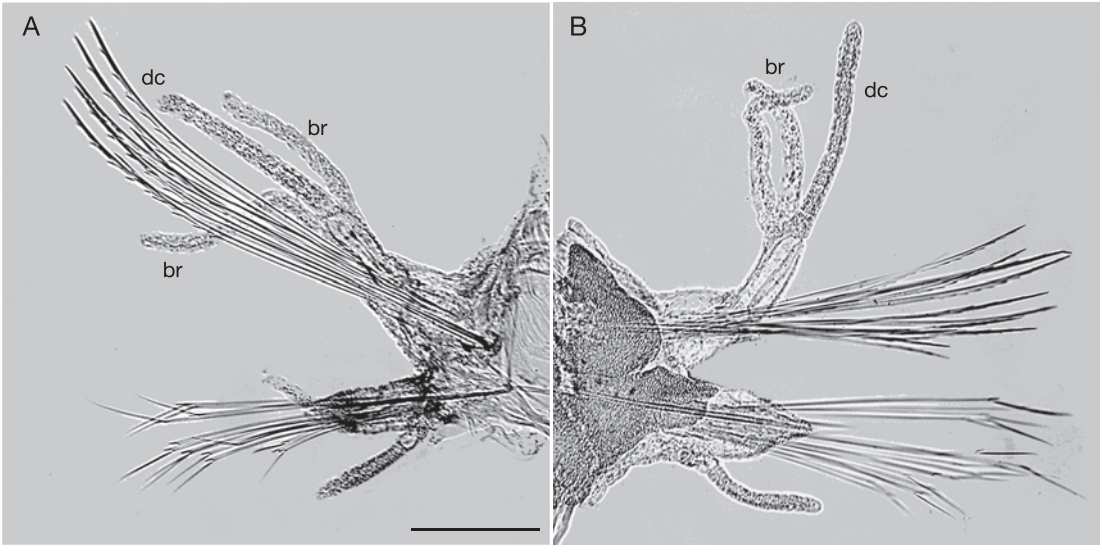

FIG. 3. — LM pictures of of *Hesiobranchia lifouensis* n. gen., n. sp.: **A**, paratype (MNHN POLY TYPE 1449), parapodium segment 5, left side; **B**, holotype (MNHN POLY TYPE 1446), parapodium segment 12, right side. Abbreviations: **br**, branchia; **dc**, dorsal cirrus. Scale bar: 2 mm.

kind, 5-13 simple capillaries, internally camerated, with two longitudinal rows with alternating teeth (Fig. 2E). Neuropodial lobes conical, neuroacicula single. Neurochaetae all compound, about 10; shafts internally camerated; blades unidentate, dorsal and median ones much longer than ventral ones. Small middorsal tubercles on segment 10, 12, 15, 17 and 19 (visible only on SEM mounted specimen) (Fig. 1A, C). Ventral cirri cylindrical with rounded tips, without distinct annulations, inserted subdistally on neuropodium, with distinct cirrophores (Figs 2F; 3B). Pygidium rounded, with median papilliform projection, pygidial cirri not observed.

Colour

Body of live specimens transparent with large number of small white spots; paired larger dorsolateral orange marks and at tips of noto- and neuropodia, notably on segment 5, 8, 12, 15, 17, 19, 23, 25 and 27 (largely coinciding with elevated dorsal cirri and middorsal tubercles); gut brown to orange; eyes orange (Fig. 1), with poorly delineated pigmentation. Preserved specimens opaque, orange pigmentation no longer visible.

REMARKS

The dorsal tubercles could be observed on the SEM mounted specimen only, and further studies are required to assess that they do not represent fixation or critical point drying artifacts. They are absent from all other hesionids studied to date.

The accessory extensions on the notopodia are here interpreted as branchiae, which seems likely from their position and in that they, in contrast to the dorsal cirri, are heavily ciliated.

PHYLOGENETIC RELATIONSHIPS OF *HESIOBRANCHIA LIFOUENSIS* N. GEN., N. SP.

The morphological characters and examined material are detailed in Pleijel (1998), with the addition of *Hesiobranchia lifouensis* n. gen., n. sp., "*capricornia*" Pleijel & Rouse, 2000, *Parahesione* sp. for which we could add new information to that in Pleijel (1998) based on a specimen collected at Lifou, and one of the outgroups, *Dysponetus bulbosus*, which was based on newly collected topotypes. There are some further differences to the previous analyses of Pleijel (1998)

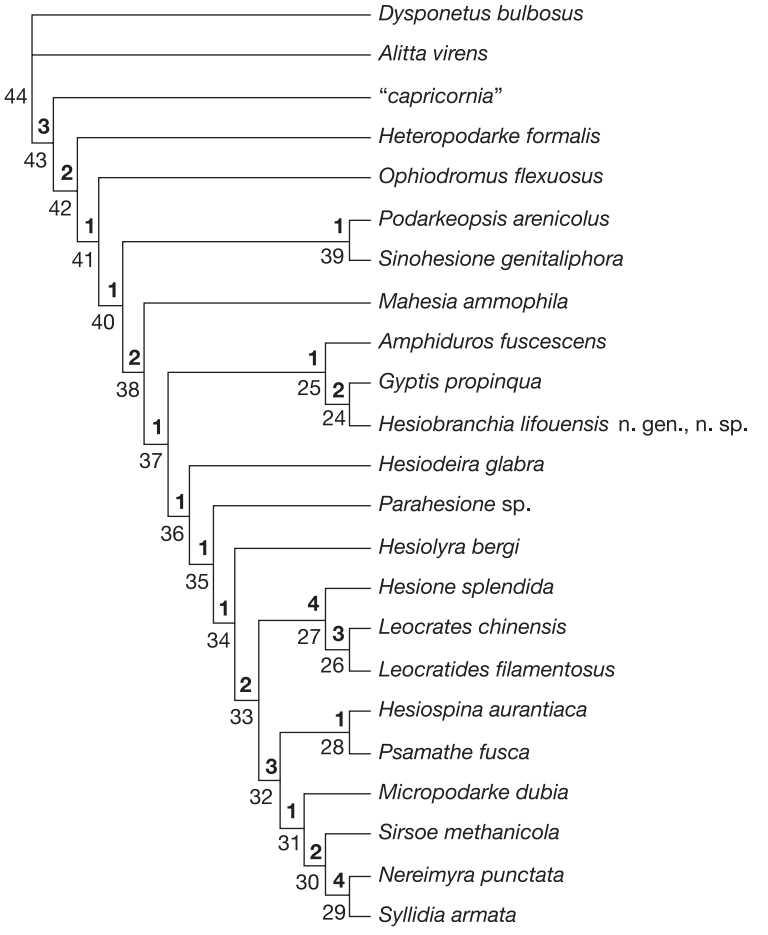

FIG. 4. — The single most parsimonious tree. Numerals above lines represent Bremer support values, numerals below lines represent node numbers.

and Pleijel & Rouse (2000), due to the fact that we here applied another coding strategy and avoided the previously used "absence-presence" coding for linked characters. The table showing the alternation pattern of dorsal cirri in Pleijel (1998: table III) was unfortunately altered in the type-setting process in that study, and we here provide a corrected version for the terminals included in the present analysis (Appendix 2). The taxon sampling differs also from the previous analysis. Here we use a more restricted set, with only a single representative of each genus. Also several poorly known taxa, including *Bonuania parva* Pillai, 1965 and *Wesenbergia problematica* (Wesenberg-Lund, 1950), are removed. The more restricted set of terminals also affected the characters in that many then became autapomorphic and were removed before our present analysis.

The analysis yielded a single equally parsimonious tree, with a length of 108 steps, a CI of 0.43, and a RI of 0.60 (Fig. 4; Appendix 4).

The resulting tree topology disagrees in several respects with the previous ones by Pleijel (1998) and Pleijel & Rouse (2000). Hesionini Grube, 1850, as previously delineated, is well supported, and remains the sister group to Psamathini Pleijel, 1998. The differences involve the taxa Ophiodrominae Pleijel,

1998, Ophiodromini Pleijel, 1998, Gyptini, and Hesiolyrinae Pleijel, 1998 (monotypic for *Hesiolyra bergi* Blake, 1985). Ophiodrominae previously included both Gyptini and Ophiodromini (Pleijel 1998: table VII), whereas here it constitutes a grade, Gyptini no longer includes *Hesiodeira* Blake, 1985 and *Parahesione* Pettibone, 1956, and, Hesiolyrinae no longer has a basal position among hesionids, but instead is the sister to Hesionini. A further difference compared to the phylogeny in Pleijel & Rouse (2000) involves the position of "*capricornia*". In that study it was situated within Gyptini as sister to *Amphiduros* Hartman, 1959; here it is sister to the remaining Hesionidae. This instability may be related to the presence in this taxon of many general hesionid features, e.g., dorsally inserted median antenna, few cephalised segments, and ten proboscis papillae. Considering these features in combination with the small size of the animals suggest the possibility that their evolution involves progenesis or neoteny and, in that case, that their indicated basal positions may be spurious. However, since our aim here is to assess the position of our new taxon, and not to revise the whole of Hesionidae, we will not provide a reclassification. The different topologies are the outcome of slightly different taxon sampling and coding strategies, and serve to illustrate that the deeper relationships among hesionids are not well understood at present. These issues will be addressed in forthcoming studies, including also molecular data that should be neutral vis-à-vis ontogenies that are truncated by paedomorphic evolution (Ruta *et al.* in press).

As seen from the present analysis, *Hesiobranchia lifouensis* n. gen., n. sp. is a member of Gyptini and sister to *Gyptis* Marion & Bobretzky *in* Marion, 1874. The Gyptini affinity is evidenced by the presence of a posterior prostomial incision and the absence of a bent notochaetae, both features, however, which are homoplastic and appear elsewhere in hesionids. *Hesiobranchia lifouensis* n. gen., n. sp. furthermore is sister to *Gyptis propinqua* Marion & Bobretzky, 1875, as evidenced by having palpostyles and paired antennae of different shapes (homoplastic occurrence also in *Podarkeopsis arenicolus* (La Greca, 1946), "*capricornia*", within Hesioninae and outgroups), by the ventral cirri subdistally inserted on the neuropodium, and by the presence of a median pygidial papillae. Also these characters, however, have homoplastic occurences elsewhere in the hesionid tree, and given the rather low Bremer support (e.g., Bremer 1994) values (1 for a membership in Gyptini and 2 for a sister group relationship with *Gyptis*), we cannot place high confidence in the current placement of the new taxon. Its uniqueness, to the contrary, has strong support in a series of non-homoplastic autapomorphies, including a terminal proboscis ring with two long lateral processes, segment 5 with both notopodial lobes and notochaetae and neuropodial lobes and neurochaetae, the presence of middorsal tubercles, and the presence of branchiae.

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APPENDIX 1

Characters and character states.

1. Segment number: variable (0), fixed to 21 (1).
2. Body shape: slender (0), stout (1).
3. Metallic cuticle: absent (0), present (1).
4. Facial tubercle: absent (0), present (1).
5. Palpostyle shape: tapered (0), ovoid (1), inflated (2), spheroid (3).
6. Palpostyles similar to paired antennae: absent (0), present (1).
7. Median antenna: absent (0), present (1).
8. Position of median antenna: median (0), anterior (1).
9. Migration scars of median antenna: absent (0), present (1).
10. Eyes: absent (0), present (1).
11. Posterior prostomial incision: absent (0), present (1).
12. Lip glands: absent (0), present (1).
13. Papillae in terminal ring of proboscis: absent (0), 10 (1), more than 10 (2).
14. Proboscis ventral incision: absent (0), present (1).
15. Lateral jaws: absent (0), present (1).
16. Dorsal tooth or plates: absent (0), present (1).
17. Ventral tooth: absent (0), present (1).
18. Anterior enlarged dorsal cirri: segment 1-2 (0), segment 1-4 (1), segment 1-5 (2). Treated as additive.
19. Anterior enlarged ventral cirri: segment 1-2 (0), segment 1-3 (1), segment 1-4 (2). Treated as additive.
20. Notochaetae: absent (0), present (1).
21. Reduced notochaetae anterior segment: segment 1-3 (0), segment 1-4 (1), segment 1-5 (2), segment 1-8 (3). Treated as additive.
22. Reduced neurochaetae anterior segment: segment 1-2 (0), segment 1-3 (1), segment 1-4 (2). Treated as additive.
23. Dorsal cirri alternation group 2: absent (0), present (1).
24. Dorsal cirri alternation group 2.1: absent (0), present (1).
25. Dorsal cirri alternation group 2.2: absent (0), present (1).
26. Dorsal cirri alternation group 2.2.1: absent (0), present (1).
27. Dorsal cirri alternation group 2.2.2: absent (0), present (1).
28. Dorsal cirri alternation group 2.2.1.2: absent (0), present (1).
29. Notopodial capillaries with two rows of alternating teeth: absent (0), present (1).
30. Notopodial aciculary chaetae: absent (0), present (1).
31. Notopodial furcate chaetae: absent (0), present (1).
32. Notopodial bent chaetae with single distal row of teeth: absent (0), present (1).
33. Dark aciculae: absent (0), present (1).
34. Bidentate tips of blades of neurochaetae: absent (0), present (1).
35. Prolonged teeth of blades of neurochaetae: absent (0), present (1).
36. Neuropodial insertion of ventral cirri: subdistal (0), distal (1).
37. Adhesive glands: absent (0), present (1).
38. Median pygidial papillae: absent (0), present (1).

APPENDIX 2

Alternation in orientation of dorsal cirri, illustrating the hierarchial degrees of similarity among the hesionids included in the phylogenetic analysis (*Mahesia ammophila* is excluded due to lack of information). **+**, elevated; **-**, horizontally oriented dorsal cirri. Modified after Pleijel (1998) (table III in Pleijel 1998 was unfortunately changed in the type-setting process, and many of the entries are therefore incorrectly aligned). Group 1 and 2 are distinct already from the first segments, group 2.1 and 2.2 differs from segment 19 and backwards, group 2.2.1 and 2.2.2 from segment 22 and backwards, and group 2.2.1.1 and 2.2.1.2 from segment 28 and backwards. The anterior segment are not included since their different morphology makes comparison difficult. It is also usually difficult to assess the variation on more posterior segments, and for *Hesiodeira glabra* it was only possible to assess on a few, anterior segments. Note: **1**, based on a newly collected specimen from Lifou.

Segment no.	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
GROUP 1																																				
Hesiolyra bergi	?	?	?	?	+	-	+	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+									
GROUP 2																																				
Hesiodeira glabra	?	?	-	+	-	+	-	+																												
"*capricornia*"	+	-	-	+	-	+	-	+	-	-	+																									
GROUP 2.1																																				
Amphiduros fuscescens	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-						
Gyptis propinqua	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-																
Hesiobranchia lifouensis n. gen., n. sp.	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-														
Hesione splendida	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+																					
Heteropodarke formalis	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-						
Leocrates chinensis	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+																					
Leocratides filamentosus	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+																					
Ophiodromus flexuosus	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-								
Parahesione sp.[1]	+	-	-	+	-	?	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	?	-	+											
Podarkeopsis arenicolus	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-						
Sinohesione genitaliphora	+	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-																		
GROUP 2.2																																				
GROUP 2.2.1																																				
GROUP 2.2.1.1																																				
Sirsoe methanicola	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+	-							
GROUP 2.2.1.2																																				
Hesiospina aurantiaca	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+	-	+	-	+	-	+	-	+	-					
Micropodarke dubia	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+	-	+	-	+	-	+	-							
Psamathe fusca	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
GROUP 2.2.2																																				
Nereimyra punctata	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+			
Syllidia armata	+	-	-	+	-	+	-	+	-	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+									

APPENDIX 3

Character matrix for the parsimony analysis. **?**, unknown state; **–**, unapplicable states; **U**, in *Dysponetus bulbosus*, character 5 refers to uncertainty for either 0 or 2.

	5	10	15	20	25	30	35	
Dysponetus bulbosus	0000U	?1001	00??1	00?01	-0---	---10	0000?	001
Alitta virens	00003	00--1	00001	00001	00---	---00	0010?	000
Amphiduros fuscescens	00000	11001	10000	00221	22110	00010	01000	100
"*capricornia*"	00000	01001	00100	00111	111??	???10	01000	000
Gyptis propinqua	00001	01001	11200	00221	22110	00011	01000	001
Hesiobranchia lifouensis n. gen., n. sp.	00000	01001	10?00	00221	12110	00010	00000	001
Hesiodeira glabra	00010	?1000	?020?	00211	221??	???10	00000	10?
Hesiolyra bergi	00010	10--0	00200	11221	22000	00001	11000	000
Hesione splendida	11110	00--1	10000	00220	–2110	00000	00110	000
Hesiospina aurantiaca	00000	00--1	00200	00220	–2111	10100	00011	000
Heteropodarke formalis	00000	11111	00100	00?11	?1110	00000	00000	000
Leocrates chinensis	11110	01001	10100	11221	32110	00010	00110	000
Leocratides filamentosus	11110	01001	10200	11220	–2110	000??	00110	000
Mahesia ammophila	00002	111?1	00200	00121	22???	???10	00000	100
Micropodarke dubia	000?0	00--1	00200	00210	–1111	10100	00001	011
Nereimyra punctata	00010	00--1	11111	00211	31101	01000	00000	001
Ophiodromus flexuosus	000?2	11111	00000	00211	21110	00010	10000	100
Parahesione sp.	000?0	10-01	00000	00221	02010	00010	00000	100
Podarkeopsis arenicolus	00001	01111	00100	00121	32110	00011	10000	100
Psamathe fusca	00001	00--1	00200	00220	–2111	10100	00001	000
Sirsoe methanicola	00010	?1000	0011?	??210	-0?11	10000	00000	001
Sinohesione genitaliphora	000?0	11111	00?00	00?21	22110	00001	00001	111
Syllidia armata	00010	00--1	01111	00210	–1101	01000	00000	001

APPENDIX 4

Apomorphy list for the parsimony analysis. Node numbers refer to cladogram in Figure 4. **CI**, consistency index; ⇒, unambiguous optimizations; →, several equally parsimonious optimizations exist.

Node	Character number	CI	Transformation
node 44 → *Dysponetus bulbosus*	38	0.250	0 ⇒ 1
node 44 → *Alitta virens*	5	0.500	0 ⇒ 3
	7	0.250	1 ⇒ 0
	29	0.200	1 ⇒ 0
	33	0.500	0 ⇒ 1
node 44 → node 43	13	0.250	0 → 1
	15	0.500	1 ⇒ 0
	18	0.667	0 → 1
	19	0.500	0 ⇒ 1
	21	0.429	0 → 1
	22	0.500	0 ⇒ 1
node 43 → node 42	6	0.250	0 ⇒ 1
	8	0.500	0 ⇒ 1
	9	0.500	0 ⇒ 1
	21	0.429	1 → 2
node 42 → node 41	36	0.333	0 ⇒ 1
node 41 → node 40	19	0.500	1 ⇒ 2
	22	0.500	1 ⇒ 2
node 40 → node 38	9	0.500	1 → 0
	13	0.250	1 ⇒ 2
node 38 → node 37	8	0.500	1 ⇒ 0
	18	0.667	1 ⇒ 2
node 37 → node 25	11	0.333	0 ⇒ 1
	32	0.250	0 → 1
node 25 → *Amphiduros fuscescens*	13	0.250	2 ⇒ 0
node 25 → node 24	6	0.250	1 ⇒ 0
	36	0.333	1 ⇒ 0
	38	0.250	0 ⇒ 1
node 24 → *Gyptis propinqua*	5	0.500	0 ⇒ 1
	12	0.500	0 ⇒ 1
	30	0.333	0 ⇒ 1
node 24 → *Hesiobranchia lifouensis* n. gen., n. sp.	21	0.429	2 ⇒ 1
	32	0.250	1 → 0
node 37 → node 36	4	0.500	0 ⇒ 1
node 36 → *Hesiodeira glabra*	10	0.333	1 ⇒ 0
	19	0.500	2 ⇒ 1
node 36 → node 35	7	0.250	1 ⇒ 0
	23	0.500	1 → 0
node 35 → node 34	29	0.200	1 ⇒ 0
	36	0.333	1 ⇒ 0
node 34 → *Hesiolyra bergi*	10	0.333	1 ⇒ 0
	16	0.500	0 ⇒ 1
	17	0.500	0 ⇒ 1
	24	0.500	1 ⇒ 0
	30	0.333	0 ⇒ 1
	31	0.333	0 ⇒ 1
	32	0.250	0 ⇒ 1
node 34 → node 33	6	0.250	1 ⇒ 0
	20	0.333	1 ⇒ 0
	21	0.429	2 ⇒ 3
	23	0.500	0 → 1
node 33 → node 27	1	1.000	0 ⇒ 1
	2	1.000	0 ⇒ 1
	3	1.000	0 ⇒ 1

Node	Character number	CI	Transformation
	11	0.333	0 ⇒ 1
	33	0.500	0 ⇒ 1
	34	0.500	0 ⇒ 1
node 27 → *Hesione splendida*	13	0.250	2 ⇒ 0
node 27 → node 26	7	0.250	0 ⇒ 1
	16	0.500	0 ⇒ 1
	17	0.500	0 ⇒ 1
	29	0.200	0 → 1
node 26 → *Leocrates chinensis*	13	0.250	2 ⇒ 1
	20	0.333	0 ⇒ 1
node 33 → node 32	25	1.000	0 ⇒ 1
	26	0.500	0 ⇒ 1
	28	0.500	0 → 1
	35	0.333	0 → 1
node 32 → node 28	4	0.500	1 ⇒ 0
node 28 → *Hesiospina aurantiaca*	34	0.500	0 ⇒ 1
node 28 → *Psamathe fusca*	5	0.500	0 ⇒ 1
node 32 → node 31	19	0.500	2 ⇒ 1
	22	0.500	2 ⇒ 1
	38	0.250	0 ⇒ 1
node 31 → *Micropodarke dubia*	37	0.500	0 ⇒ 1
node 31 → node 30	13	0.250	2 ⇒ 1
	14	1.000	0 ⇒ 1
	15	0.500	0 → 1
	28	0.500	1 → 0
	35	0.333	1 → 0
node 30 → node 29	12	0.500	0 ⇒ 1
	24	0.500	1 ⇒ 0
	26	0.500	1 ⇒ 0
	27	1.000	0 ⇒ 1
node 29 → *Nereimyra punctata*	11	0.333	0 ⇒ 1
	20	0.333	0 ⇒ 1
node 30 → *Sirsoe methanicola*	7	0.250	0 ⇒ 1
	10	0.333	1 ⇒ 0
	22	0.500	1 ⇒ 0
node 35 → *Parahesione* sp.	13	0.250	2 ⇒ 0
	21	0.429	2 ⇒ 0
node 38 → *Mahesia ammophila*	5	0.500	0 ⇒ 2
node 40 → node 39	30	0.333	0 ⇒ 1
node 39 → *Podarkeopsis arenicolus*	5	0.500	0 ⇒ 1
	6	0.250	1 ⇒ 0
	21	0.429	2 ⇒ 3
	31	0.333	0 ⇒ 1
node 39 → *Sinohesione genitaliphora*	29	0.200	1 ⇒ 0
	35	0.333	0 ⇒ 1
	37	0.500	0 ⇒ 1
	38	0.250	0 ⇒ 1
node 41 → *Ophiodromus flexuosus*	5	0.500	0 ⇒ 2
	13	0.250	1 ⇒ 0
	18	0.667	1 ⇒ 2
	31	0.333	0 ⇒ 1
node 42 → *Heteropodarke formalis*	29	0.200	1 ⇒ 0
node 43 → “*capricornia*”	32	0.250	0 ⇒ 1