



Chalarosthrix gen. nov., a new taxon of the *Sphingothrix-Triathrix* clade (Harpacticoida: Cletodidae) from the Province of Cortez, Eastern Mexican Pacific

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Abstract

Seven species of four cletodid genera previously described or reported from Mexico (*Cletodes*, *Enhydrosoma*, *Geehydrosoma*, and *Stylicletodes*) and an undescribed genus presumably related to *Sphingothrix* and *Triathrix*, were found in sediment samples from a coastal system in north-western Mexico. The Bayesian analysis of 95 morphological characters of thirty-four cletodid genera revealed that the new genus, *Chalarosthrix* gen. nov., is closely related to *Sphingothrix*. The clade *Sphingothrix-Chalarosthrix* bears a sister group relationship with *Triathrix*. These three genera constitute a monophyletic group defined by the presence of a posterior chitinous extension of the cephalothorax with four sensillum-bearing socles, and the presence of a median tube-pore on the anal operculum. Other synapomorphies for *Sphingothrix* and *Triathrix* proposed by earlier researchers are re-evaluated upon the latest definition of the Cletodidae. Our analysis supports previous studies in that *Sphingothrix* can be objectively defined by i) the reduction of the distal outer seta of the last exopodal segment of the first swimming leg being at most as long as the subdistal outer spine, and ii) the distal inner seta of the same segment inclined outwards intersecting the distal outer element at its base. On the other hand, no (aut)apomorphies were detected for *Triathrix*. The new genus, *Chalarosthrix* gen. nov., is defined here by the apomorphic secondary loss of the inner element of the second endopodal segment of the first swimming leg. Some comments on the relationships of the new genus are given.

Keywords: Bayesian inference, maximum parsimony, new species, Mexico, phylogeny, taxonomy

Introduction

Gee & Burgess (1997) proposed the genus *Triathrix* Gee & Burgess 1997 to accommodate two species of the family Cletodidae *sensu* Por (1986), *T. montagni* Gee & Burgess 1997 found in sediment samples from the California continental shelf, and *T. kalki* Gee & Burgess 1997 from the Gulf of Mexico. They (Gee & Burgess 1997) noticed that their newly found species possess the most plesiomorphic antenna with two abexopodal setae on the allobasis and a one-segmented exopod with one lateral and two distal setae, which is similar to that of *Enhydrosoma nicobarica* Sewell 1940. Because of this resemblance, Gee & Burgess (1997) decided to remove *E. nicobarica* from that genus and reallocate it in *Triathrix*. Gee & Burgess (1997 pp. 223–224) defined *Triathrix* upon a series of characters (see below) that were thought to be autapomorphies within the family Cletodidae as defined by Por (1986 pp. 422–423). The same year of publication of Gee & Burgess' (1997) study, Fiers (1997) found some specimens of *T. kalki* and two closely related species in sediment samples from the Bay of Campeche (southern bight of the Gulf of Mexico). One of his newly found species, *T. mayae* Fiers 1997, was assigned to *Triathrix*, and the other species was attributed to a new genus, *Sphingothrix* Fiers 1997, as *S. goldi* Fiers 1997. Additionally, Fiers (1997) moved *T. kalki* from *Triathrix* to *Sphingothrix*, reassessed the position of *T. nicobarica*, and suggested that, pending the description of

the adults, *T. nicobarica* could be moved to a new genus, but concluded that, for taxonomic stability reasons, the species should be kept in *Triathrix*. Fiers (1997) discussed the relationships between *Triathrix* and *Sphingothrix* and defined the later upon the rigid apical elements of the P1 last exopodal and endopodal segments, the length of the distal outer seta relative to the length of the subdistal outer spine of the last exopodal segment of P1, and the position of the distal inner seta of the same segment (Fiers 1997 pp. 246). More recently, George (2020) proposed restructuring the family Cletodidae to incorporate some ancorabolids, and presented a new amended diagnosis of the Cletodidae (see George (2020 pp. 490–493)).

Cletodid species of some genera previously described or reported from Mexico were found in sediment samples from a polluted coastal system in north-western Mexico. Amongst the material collected, we found a specimen of an undescribed species closely related but not attributable to either *Triathrix* or *Sphingothrix*. The finding of this material prompted us to assess its position within the Cletodidae *sensu* George (2020) in the light of recent advances, as well as to reassess the (aut)apomorphies proposed by Gee & Burgess (1997) and Fiers (1997) for both *Triathrix* and *Sphingothrix*. As a result of this analysis, we propose a new genus, *Chalarosthrix* gen. nov., for *C. bisetosa* sp. nov., and give some comments on the (aut)apomorphies for the *Sphingothrix-Chalarosthrix-Triathrix* clade, and on the relationships of its constituent taxa.

Materials and methods

Field and laboratory work

Sediment samples were taken from ten sampling stations along Urias system, a polluted coastal system in north-western Mexico. The sediment samples were taken with an Eckman grab (sampling area 625 cm²) and triplicate cores were taken with acrylic tubes (sampling area 24.6 cm²). The upper 3 cm layer of each tube was retrieved. Sediment samples were fixed in pure ethanol and sieved through 500 and 38 µm sieves. Meiofauna (the material retained in the 38 µm sieve) was extracted through centrifugation with Ludox[®] HS-40 following Burgess (2001) and Rohal *et al.* (2016) and preserved in pure ethanol. Meiofauna was separated manually from the fine grains of sediment using an Olympus SZX12 stereomicroscope equipped with DF PLAPO 1X objective and WHS10X eyepieces, at a magnification of 40x. Harpacticoid copepods were stored separately in 1 ml vials with pure ethanol. Illustrations and figures of the material presented herein were made from the undissected individual and its dissected parts using a Leica DMLB microscope equipped with L PLAN 10X eyepieces, N PLAN 100X oil immersion objective, and drawing tube. The dissected parts were mounted on separate slides using lactophenol as mounting medium and sealed with Neo-Mount[®].

Huys & Boxshall (1991) was followed for general terminology. Abbreviations used in the text are : acro, acrothek; ae, aesthetasc; BENP, baseoendopod; ENP, endopod; EXP, exopod; EXP (ENP)1–3, first–third exopodal(endopodal) segments, P1–P6, first to sixth legs.

Phylogenetic analyses

We performed a Bayesian inference-based phylogenetic analysis of the cletodid genera with MrBayes (v. 3.2.5; Ronquist *et al.* 2012) to test the relationships between *Chalarosthrix* gen. nov., *Triathrix*, and *Sphingothrix*. Ninety-five morphological characters (Table 1) were extracted from the available literature on thirty-four genera of Cletodidae Scott T. 1904 *sensu* George (2020) (Table 2). However, not all the species of all genera were analyzed, and our results on the phylogeny of the entire Cletodidae are not conclusive. Instead, we chose only those species of each genus whose descriptions were informative and detailed enough to assess the position and relationships of *Sphingothrix*, *Triathrix*, and *Chalarosthrix* gen. nov. (see Table 3). The position of *Patagoniaella* Pallares 1968 is uncertain, and George (2020) relegated it to genus inquirendum within Harpacticoida, and was, therefore, excluded from our analyses. The monotypic *Monocletodes* Lang 1936 was also excluded. As outgroup taxa we included the Laophontidae Scott T. 1904, Normanellidae Lang 1944, Cletopsyllidae Huys & Willems 1989, and Adenopleuridae Huys 1990. All characters were unordered and with equal weights; unknown and missing data were coded as “?”; inapplicable data were coded as “–”. Following Huys & Boxshall (1991), oligomerization was considered the dominant trend in copepod evolution for character coding. Plesiomorphic character states inferred from out-group taxa were coded “0”; derived character states were coded “1” to “5”. Bayesian inference analysis was performed using the default options of the program except for rates which was set gamma (rates=gamma). Posterior probabilities were set 3500000 generations (ngen=3500000; with which an average standard deviation of split frequencies

<0.01 was reached) with four Markov Chain Monte Carlo (MCMC) chains (nchains=4) with every 100th tree saved (samplefreq=100), and “burn-in” was set 0.25% (burninfrac=0.25); default values were used for other parameters of the MCMC. The “sumt” command was used for the consensus tree using the “contype=allcompat” option with “burn-in” as for the MCMC. The output files were analysed using Tracer v. 1.7.1 (Rambaut et al. 2018) to assess convergence among different runs, and to confirm adequate effective sample size of the posterior distribution for all parameters (ESS>200), and appropriate burn-in. FIGTREE v.1.4.4 (Rambaut 2018; <http://tree.bio.ed.ac.uk/software/figtree/>) was used to visualize and edit the resulting tree, and Photoshop was used for final editing.

TABLE 1. Characters and characters states used for the cladistic analyses. 1= apomorphic; 0= plesiomorphic.

1	Cephalothorax, frontal horns: (1) present; (0) absent.
2	P2–P4-bearing somites, paired dorsal process: (1) present; (0) absent.
3	Cephalothorax, sensillum-bearing socles on posterior border: (1) present; (0) absent.
4	Cephalothorax, chitinous extension bearing four socles: (1) present; (0) absent.
5	Prosomites and urosomites, sensillum-bearing socles on posterior border: (1) present; (0) absent.
6	Preanal somite, sensillum-bearing socles on posterior border: (1) present; (0) absent.
7	Anal operculum, median tube-pore: (1) present; (0) absent.
8	Rostrum: (1) not discernible, absorbed into anteroventral surface of cephalothorax; (0) discernible in dorsal aspect.
9	Rostrum: (1) fused with cephalothorax; (0) distinct.
10	Female antennule, number of segments: (0) 7; (1) 6; (2) 5; (3) 4; (4) 3.
11	Female antennule, first segment: (1) elongate; (0) not elongate.
12	Female antennule, protuberance on second segment: (1) absent; (0) present.
13	Antenna, exopod: (1) absent; (0) present.
14	Antenna, exopod when present, number of elements: (0) 4; (1) 3; (2) 2; (3) 1.
15	Antenna, allobasis, number of abexopodal elements: (0) 2; (1) 1; (2) 0.
16	Mandible, palp: (1) basis, endopod and exopod fused; (0) rami separated from basis.
17	Mandible, palp, number of elements: (1) at most 6 elements; (0) > 6 elements.
18	Maxillule, coxa, number of elements: (0) 2; (1) 1.
19	Maxillule, endopod and exopod: (1) fused to basis; (0) at least exopod distinct.
20	Maxillule, basal complex, number of setae: (0) >9; (1) 9; (2) <8
21	Maxilla, number of syncoxal endites: (0) 3; (1) 2.
22	Maxilla, endopod: (1) fused; (0) distinct.
23	Maxilla, endopod, number of elements: (0) 3; (1) 2; (2) 1.
24	Maxilliped, syncoxa, number of elements: (0) 3; (1) 2; (2) 1; (3) 0.
25	P1 basis: (1) elongated transversally; (0) not elongated.
26	P1 ENP, number of segments when present: (0) 2; (1) 1; (2) 0.
27	P1 ENP1, relative length and shape: (1) at most as long as endopod-1, endopod not prehensile; (0) endopod-1 elongate, endopod prehensile.
28	P1 ENP1, inner element: (1) absent; (0) present.
29	P1 ENP2, relative length: (1) elongate, at least as long as endopod-1; (0) shorter than endopod-1.
30	P1 ENP2 or only segment, number of elements: (0) 4; (1) 3; (2) 2; (3) 1.
31	P1 ENP2 or only segment, geniculate element: (1) absent; (0) present.
32	P1 ENP2 or only segment, claw: (1) absent; (0) present.
33	P1 EXP, number segments: (0) 3; (1) 2.
34	P1 EXP2 when EXP three-segmented, inner element: (1) absent; (0) present.
35	P1, last exopodal segment, number of elements: (0) 5; (1) 4.
36	P1, last exopodal segment, number of outer elements: (0) 3; (1) 2; (2) 0.
37	P1, last exopodal segment, geniculate element: (1) absent; (0) present.

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TABLE 1. (Continued)

38	P1, last exopodal segment, brush element: (1) present; (0) absent.
39	P1, last exopodal segment, relative length of the distal outer seta: (0) longer than subdistal outer spine; (1) as long as or shorter than subdistal outer spine.
40	P1 last exopodal segment, position of the distal inner seta: (0) not inclined outwards and not intersecting the distal outer element; (1) inclined outwards and intersecting the distal outer element.
41	P1, last exopodal and endopodal segment, shape of apical elements: (0) at least one seta whip-like; (1) both elements rigid, spiniform.
42	P2 ENP, number of segments: (0) 2; (1) 1; (2) 0.
43	P2 ENP1 when ENP present, inner element: (1) absent; (0) present.
44	P2 ENP, last segment when ENP present, number of inner elements: (0) 4; (1) 3; (2) 2; (3) 1; (4) 0.
45	P2 ENP, last segment when ENP present, number of apical elements: (0) 2; (1) 1; (2) 0.
46	P2 ENP, last segment when ENP present, number of outer elements: (0) 1; (1) 0.
47	P2 EXP, number of segments: (0) 3; (1) 2.
48	P2 EXP2 when EXP three-segmented, inner element: (1) absent; (0) present.
49	P2 EXP, last segment, number of inner elements: (0) 1; (1) 0.
50	P2 EXP, last segment, number of outer elements: (0) 3; (1) 2.
51	P2, sexual dimorphism: (1) present; (0) absent.
52	P3 ENP, number of segments: (0) 2; (1) 1; (2) 0.
53	P3 ENP1 when ENP present, inner element: (1) absent; (0) present.
54	P3 ENP last segment when ENP present, number of inner elements: (0) 3; (1) 2; (2) 1; (3) 0.
55	P3 ENP last segment when ENP present, number of apical elements: (0) 2; (1) 0.
56	P3 EXP, number of segments: (0) 3; (1) 2.
57	P3 EXP2 when EXP three-segmented, inner element: (1) absent; (0) present.
58	P3 EXP last segment, number of inner elements: (0) 2; (1) 1; (2) 0.
59	P3 EXP last segment, number of outer elements: (0) 3; (1) 2; (2) 1.
60	P3, sexual dimorphism: (1) present; (0) absent.
61	P4 ENP, number of segments: (0) 2; (1) 1; (2) 0.
62	P4 ENP1 when ENP present, inner element: (1) absent; (0) present.
63	P4 ENP last segment when ENP present, number of inner elements: (0) 3; (1) 2; (2) 1; (3) 0.
64	P4 ENP last segment when ENP present, number of apical elements: (0) 2; (1) 1.
65	P4 ENP last segment when ENP present, number of outer elements: (0) 1; (1) 0.
66	P4 EXP, number of segments: (0) 3; (1) 2.
67	P4 EXP2 when EXP three-segmented, inner element: (1) absent; (0) present.
68	P4 EXP last segment, number of inner elements: (0) 2; (1) 1; (2) 0.
69	P4 EXP last segment, number of outer elements: (0) 3; (1) 2; (2) 1.
70	P4 sexual dimorphism, outer spine absent in female: (1) present; (0) absent.
71	P2–P4 basis, shape: (1) transversally elongated; (0) not elongated.
72	Female P5 ENP and EXP: (1) fused; (0) distinct.
73	Female P5 EXP, tubular pore: (1) absent; (0) present.
74	Female P5 ENP lobe, tubular pore: (1) absent; (0) present.
75	Female P5 BENP: (1) reduced; (0) developed.
76	Female P5 BENP, mucroniform process: (1) present; (0) absent.
77	Female P5 EXP, number of elements: (0) 6; (1) 5; (2) 4; (3) 3; (4) 2; (5) 1.
78	Female P5 ENP lobe, number of elements: (0) 5; (1) 4; (2) 3; (3) 2; (4) 1.
79	Female P6, number of elements: (0) 3; (1) 2; (2) 1; (3) 0.

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TABLE 1. (Continued)

80	Male antennule, number of segments distal to geniculation: (0) 3; (1) 2; (2) 1.
81	Male P4 sexual dimorphism, inner element on ENP1: (1) present; (0) absent.
82	Male P3 ENP, number of segments: (0) 3; (1) 2.
83	Male P3 ENP2 when ENP three-segmented, inner element: (1) absent; (0) present.
84	Male P3 ENP, apophysis: (1) absent; (0) present.
85	P3 ENP last segment when ENP two-segmented, outer spine: (1) modified into a spinous process; (0) normal.
86	Male P4 ENP last segment, number of elements: (0) 6; (1) 5; (2) 4; (3) 3; (4) 2; (5) 1.
87	Male P5 BENP: (1) absorbed into somite; (0) distinct.
88	Male P5 ENP and EXP: (1) fused; (0) separate.
89	Male P5 ENP lobe, number of elements: (0) 3; (1) 2; (2) 1; (3) 0.
90	Male P5 EXP, number of elements: (0) 5; (1) 4; (2) 3; (3) 2.
91	Male P5 BENP, mucroniform process: (1) present; (0) absent.
92	Male P6, number of elements: (0) 3; (1) 2; (2) 1; (3) 0.
93	Furcal rami in both sexes, relative length: (1) slender, at least 3x as long as broad; (0) at most 2x as long as broad.
94	Caudal rami, position of seta I relative to seta II: (0) anterior or aligned to seta II; (1) posterior to seta II.
95	Character 91 preanal (fifth) urosomite, posterolateral non-sensillum bearing socles: (0) absent; (1) present.

Results

Systematics

Order Harpacticoida Sars 1903

Family Cletodidae Scott T. 1904

Genus Chalarosthrix gen. nov.

urn:lsid:zoobank.org:act:9142FF1A-0C5B-4828-86F5-52D3D0F7DA45

Type species. *Chalarosthrix bisetosa* sp. nov., by original designation.

Other species. *Enhydrosoma nicobarica* Sewell 1940 (= *Triathrix nicobarica* (Sewell 1940), *Chalarosthrix nicobarica* (Sewell 1940) comb. nov.), *Triathrix mayae* Fiers 1997 (= *Chalarosthrix mayae* (Fiers 1997) comb. nov.).

Diagnosis (based on female). Cletodidae. Cephalothorax with four sensillum-bearing socles along a small but distinct chitinous extension. Antennule five-segmented. Antennary allobasis with two abexopodal setae; exopod one-segmented, with three setae (one lateral and two distal). Mandibular palp with five setae. Maxillulary basis with two endites, distal endite with three, proximal endite with two setae; exopod and endopod fused to basis, the former represented by two, the latter by one seta; coxal endite with one seta. Maxillary syncoxa with two endites; allobasis with claw and two accompanying setae; endopod represented by two setae. Maxilliped subchelate; syncoxa and basis unarmed; endopodal claw slender, accompanied by long accessory seta. P1–P4 exopods three-segmented, endopods two-segmented. P1 EXP3 with four elements; distal outer seta whip-like, longer than subdistal outer spine; distal setae without setulose distal tuft, and distal inner seta not inclined outwardly and not intersecting base of distal outer seta; P1 ENP2 with two setae. Armature formula of P1–P4 EXP/ENP: (P1) 0,0,022/0,011; (P2) 0,0,022/0,020; (P3) 0,0,122/0,021; (P4) 0,0,122/0,021. P5 EXP and ENP elongate, with three setae each. Caudal rami elongate, with seven elements.

Etymology. The generic epithet comes from the Greek adjective χαλαρός, chalarós, loose, and from the Ancient Greek noun θρίξ, thrix, hair, and refers to the loose position of the apical elements on the P1 EXP3. Gender feminine.

TABLE 2. Data matrix of characters and character states used for the cladistic analyses (0 = plesiomorphic; 1 = apomorphic; 2–3 = further derived states; ? = unknown; – = not applicable).

	0	1	2	3	4	5	6	7	8	9
Adenopleurellidae	0000000013	0002111012	0012000102	0111110000	0012010000	0011000001	0120000000	0010002310	0010–20011	01000
Cleptosyllidae	0000000001	0002100002	0000000000	0000110000	0000000000	0000000000	0000000000	0000001001	01–1000001	02000
Laophontidae	0000000000	0000101002	0001000102	0001110000	0002010000	0000000001	0020000000	0011000001	0010–21010	01000
Normanellidae	0000000001	0100000000	0101000001	0000000000	0001000000	0000000001	0010000000	0010000001	01–1110001	00000
<i>Acrenhydryrosoma</i>	0010100012	0102111112	1112001112	1101111000	0014010111	0003001111	0130001110	0110013301	01–1130113	13100
<i>Australonannopus</i>	0010100001	0102111112	1122001111	1101111010	0014010011	0013001210	1–0–01111	01101033?0	11–10–0113	0110?
<i>Barbaracletodes</i>	00?0???010	0102011012	1002001110	1100111000	0012010001	0012000011	0120000011	01111020?1	0011–10102	0?0??
<i>Cletodes</i>	0010100012	0103111010	1012001111	1101111000	0014010011	0012000210	0120000210	0000101200	1010020011	02100
<i>Dyacrenhydryrosoma</i>	0010100012	0102211112	1112001112	1101111000	0014010111	0013001110	0130101110	0111014401	01–1040123	13000
<i>Echinocletodes</i>	0000000013	011–011012	112311–2	1101110000	0014010111	0012001211	0120001210	1000003110	0010–20012	02100
<i>Enhydryrosoma</i>	0010100012	0102111012	1112001112	1101111000	0014010111	0013001111	0130101110	0011002201	01–0140012	12001
<i>Enhydryrosomella</i>	00?????011	0102111012	1112001112	1101111000	0014011–11	001301–110	013011–110	00??0032?0	01–1040012	1?0??
<i>Geehydryrosoma</i>	0010110012	0102111112	1113001111	1101111000	0014010111	0013001111	0130001110	0111102211	01–1030013	0310?
<i>Interletodes</i>	0010110003	01??11???	??200111	1101110000	02–0–0111	02–0–01210	2–0–01210	00111012?0	02–0–0133	03100
<i>Kollerua</i>	??????012	0102111012	1122001112	1101111000	0014010111	0013001111	0130101110	00??0042?1	01–1140?13	0?00?
<i>Limnocletodes</i>	0010100012	0101111010	0111001012	1101111010	0014100011	0012100211	0121000211	0010014112	0010–31113	03000
<i>Mirostlavia</i>	?????????3	00021?????	???01–3	111–111000	0012010001	001200001?	012000001?	11100003???	???????????	??1??
<i>Nannopodella</i>	??????012	0100201???	??23001012	1101110000	0014010110	001300110?	013000110?	01??0010??	???????????	?????
<i>Neoacrenhydryrosoma</i>	0010100012	0102111012	1112001111	1101111010	0014011–11	001301–110	013011–110	0100104401	01–1041133	–?101
<i>Paracrenhydryrosoma</i>	0010100012	0102001012	1112001111	1101111000	0014010111	0013001111	0130001110	0000013301	01–1130012	13100
<i>Pyrocletodes</i>	0000000012	0102101012	1112001012	1100111000	01–0–0001	2–0–0011?	2–0–0011?	01??10????	???????????	??1??
<i>Schizacron</i>	0010100012	0103011010	1112001111	1101111000	0014000101	0013001111	0121001110	0100003211	0010–31112	03001
<i>Scintis</i>	00?0???013	0101110012	111302–	1100111000	0013010000	0013000000	0130100000	00??003011	01–1040112	0?0??
<i>Spinapetruris</i>	0010100012	0103011012	1112001111	1101111000	0014010101	0013001111	0130000110	0000101101	0010–30010	03000
<i>Strongylacron</i>	0010100012	0103011010	1112001111	1101111000	0014010111	0013001111	0121001110	0000003211	0010–31112	03001
<i>Stylocletodes</i>	0010100012	0102011112	111?001112	1101131100	0014010111	0013000111	0130000110	0011001102	0010–30010	0?1??
<i>Chalarosthrix</i> gen. nov.	0011101012	0101011111	1113001112	1101111000	0014010111	?01300111?	013000111?	000000321?	???????????	??110
<i>Sphingothrix</i>	0011101012	0101011111	1113001111	1101111011	1014010111	0013001110	0130001110	0000003211	01–1030013	0?110
<i>Triathrix</i>	0011101012	0101011111	1113001111	1101111000	0014010111	0013001110	0130001110	0000003211	01–1030013	03110

TABLE 2. (Continued)

	0	1	2	3	4	5	6	7	8	9
<i>Arthricornua</i>	110000013	111-011010	10121---	-1-020000	01---0001	0013000011	0130100110	1100101312	0010-41110	03100
<i>Ceratontus</i>	110000114	111-111010	1112101112	011-010000	0014010001	0013000111	0130100110	1000103311	0010-41022	03100
<i>Dendropsyllus</i>	110000114	111-111010	1012101113	011-020000	01---0001	0013000111	0131100210	1100103421	0010-51022	03100
<i>Dimorphipodia</i>	100000013	111-011010	10121---	-1-020000	01---0011	0013000211	0130100210	1100101312	0010-41010	03100
<i>Dorsiceratus</i>	010000013	111-011012	1112101112	0101020000	0014110001	0013000011	0130100111	1100101312	0010-31010	03100
<i>Echinopsyllus</i>	110000013	111-011112	11131---	-01110000	01---0011	11-3030211	1-30100211	1000102310	0010-31022	03100
<i>Polyasphortus</i>	110000013	111-011011	1012101113	011-020000	01---0001	0013000011	0131100111	1100101411	0010-31?1?	03000
<i>Pseudechinopsyllus</i>	110000013	111-011112	10131---	-1-020000	01---0001	11-310001?	1-3110011?	110010131?	??????????	??100
<i>Touphapleura</i>	010000013	111-011011	1112101112	011-020000	0014010001	0013000011	0130100110	1000101411	0010-41020	0?100

TABLE 3. List of cletodid species used for the Bayesian inference-based phylogenetic analysis to assess the position and relationships of *Sphingothrix*, *Triathrix*, and *Chalarosthrix* gen. nov.

Cletodidae Scott T. 1904 <i>sensu</i> George (2020)	<p> <i>Acrenhydrosoma perplexum</i> (Scott T.) <i>Arthuricornua anendopodia</i> Conroy-Dalton <i>Australonannopus aestuarinus</i> Hammond <i>Barbaracletodes carola</i> Becker <i>Ceratonotus elongatus</i> Gómez & Díaz <i>Ceratonotus thistlei</i> Conroy-Dalton <i>Cletodes confusum</i> Gómez <i>Cletodes meyerorum</i> Georg & Müller <i>Cletodes pseudodissimilisoris</i> Gómez <i>Dendropsyllus californiensis</i> Gómez & Díaz <i>Dendropsyllus thomasi</i> Conroy-Dalton <i>Dendropsyllus magellanicus</i> (George & Schminke) <i>Dendropsyllus kimi</i> Lee & Huys <i>Dimorphipodia changi</i> Lee & Huys <i>Dorsiceratus dinah</i> George & Plum <i>Dorsiceratus ursulae</i> George <i>Dorsiceratus wilhelminae</i> George & Plum <i>Dyacrenhydrosoma breviseta</i> Gee <i>Echinocletodes armatus</i> (Scott T.) <i>Echinocletodes voightae</i> Georg & Müller <i>Echinopsyllus brasiliensis</i> Wandeness, George & Santos <i>Echinopsyllus grohmannae</i> Wandeness, George & Santos <i>Echinopsyllus nogueirae</i> Wandeness, George & Santos <i>Enhydrosoma casoae</i> Gómez <i>Enhydrosoma curticauda</i> Boeck <i>Enhydrosoma parapropinquum</i> Gómez <i>Enhydrosoma serdarsaki</i> Sönmez, Yildiz & Karaytug <i>Enhydrosoma solitarium</i> Gómez <i>Enhydrosoma wellsii</i> Bodin <i>Enhydrosomella monardi</i> Por <i>Enhydrosomella setiensis</i> Raibaut <i>Geehydrosoma brevipodum</i> (Gómez) <i>Geehydrosoma intermedia</i> (Chislenko) <i>Intercletodes interita</i> Fiers <i>Kollerua longum</i> (Shen & Tai) <i>Kollerua radhakrishnai</i> (Ranga Reddy) <i>Limnocletodes angustodes</i> Shen & Tai <i>Limnocletodes behningi</i> Borutzky <i>Limnocletodes mucronatus</i> Gee <i>Miroslavia longicaudata</i> Apostolov <i>Nannopodella denisi</i> Monard <i>Neoacrenhydrosoma zhangii</i> Gee & Mu <i>Paracrenhydrosoma kiai</i> Sung, Dahms, Lee, Ryu & Khim <i>Paracrenhydrosoma normani</i> Gee <i>Polyascophorus martinezi</i> George <i>Pseudechinopsyllus sindemarkae</i> George <i>Pyrocletodes coulli</i> Dinert <i>Pyrocletodes desuramus</i> Coull <i>Schizacron barnishi</i> (Wells) <i>Schizacron intermedius</i> Gee & Huys <i>Scintis variifurca</i> Por <i>Spinapecuris curvirostre</i> (Scott T.) <i>Strongylacron buchholtzi</i> (Boeck) <i>Strongylacron glabrum</i> Kim, Jung & Yoon <i>Stylicletodes minutus</i> Bodin <i>Stylicletodes reductus</i> Wells <i>Stylicletodes oligochaeta</i> Bodin <i>Sphingothrix goldi</i> Fiers <i>Sphingothrix kalki</i> (Gee & Burgess) <i>Touphapleura schminkei</i> (George) <i>Triathrix mayae</i> Fiers <i>Triathrix montagni</i> Gee & Burgess <i>Triathrix nicobarica</i> (Sewell) </p>
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***Chalarosthrix bisetosa* sp. nov.**

(Figs. 1–6)

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Type locality. Urías estuary, Mazatlán, Sinaloa State, Mexico (stn. 10 (23.1815°N, 106.4214°W; depth 6.0 m, organic carbon content 1.2%, organic matter content 2.07%, sand 69.12%, clay 7.91%, silt 22.97%.)) (see also Gómez (2020 pp. 43, figure 1).

Material examined. Female holotype dissected and mounted onto nine slides (ICML-EMUCOP-180119-180); 18 Jan 2019. S. Gómez leg.

Description. Female. Total body length 625 µm measured from anterior tip of rostrum to posterior margin of caudal rami.

Habitus (Fig. 1A, C) semi-cylindrical, without clear demarcation between prosome and urosome. Rostrum (Fig. 1A, C) well-developed, fused to cephalothorax, with pointed tip recurved upwards, with two subdistal sensilla.

Prosome (Fig. 1A, C) consisting of cephalothorax with P1-bearing somite incorporated, and three free-pedigerous somites bearing P2–P4. Cephalothorax with dorsolateral surface sensilla as shown; postero-dorsal small chitinous extension with four sensillum-bearing socles; additionally, with one dorsolateral sensillum-bearing socle on each side. P2- and P3-bearing somites with four postero-dorsal sensilla, one dorsolateral and one lateral sensillum-bearing socle on each side, and with two lateral sensilla; with one dorsolateral tube pore on each side, but P3-bearing somite with additional medial tube pore dorsally; with lateral row of posterior slender spinules on each side. P4-bearing somite as previous somite but with two posterodorsal sensilla only.

Urosome (Figs. 1A, C, 2A) comprising fifth pedigerous somite, genital double-somite, two free abdominal somites, and anal somite. P5-bearing somite as in previous somite but with only one dorsolateral sensillum-bearing socle on each side. Second (genital somite) and third urosomites completely fused, original division indicated by lateroventral internal rib; both halves with two dorsal sensilla, and one dorsolateral and one lateral sensillum-bearing socle, of which each dorsolateral socle with one tube pore and lateral socle with row of spinules; posterior half with two dorsal pores and dorsolateral row of slender spinules along posterior margin; ventral surface of anterior half with P6, genital field and two tube pores as shown, posterior half with two tube pores, and two sensilla and row of slender spinules along posterior margin. Fourth urosomite as previous somite but dorsolateral socles less developed; ventrally with two sensilla and posterior spinules as shown. Fifth urosomite without socles or sensilla, with spinular ornamentation as in previous somite. Anal somite (Figs. 1A–D, 2A) with ventral cleft medially; with lateral, dorsal and ventral tube pores as shown; with posterior spinules close to caudal rami and on posterior margin of ventral cleft; anal operculum semicircular, posterior margin with row of minute spinules. Caudal rami slightly divergent, elongate, about 5x as long as wide (maximum width measured at proximal part); with seven setae as follows: lateral seta I in proximal third, very small; seta II 3x as long as seta I, issuing close to joint with anal somite, somewhat displaced dorsally; seta III lateral, posterior to seta I and as long as seta II; seta IV shorter than seta III, fused basally to seta V, the latter longest and sparsely pinnate; seta VI issuing at inner distal corner, as long as seta III; dorsal seta VII triarticulated, arising in the middle of ramus, somewhat displaced inwards.

Antennule (Fig. 3A) five-segmented; all segments smooth except for two spinular rows on first one; all setae smooth except for one and three setulose setae on first and second segments, respectively, and for two strong thick spinulose elements on last segment. Armature formula as follows: 1[1], 2[7], 3[6+(1+ae)], 4[1], 5[9+acrothek]; acrothek of last segment consisting of two slender setae fused basally to aesthetasc.

Antenna (Fig. 3B) with allobasis armed with two abexopodal setae (one proximal, one medial), with outer remainder of original division between basis and first endopodal segment. Free endopodal segment as long as allobasis, with proximal and subdistal strong outer spinules and two subdistal inner frills; with two inner lateral spines, distally with three spines one of which bipinnate, one single geniculate seta, and one geniculate element fused basally to small slender seta. Exopod one-segmented, ornamented with few subdistal spinules, armed with one lateral and two distal setae as shown.

Mandible (Fig. 4A) with well-developed coxa ornamented with short spinular row; gnathobase well-developed; distally with seven spines as depicted, and one long ventral element. Palp one-segmented, with two lateral and three apical setae.

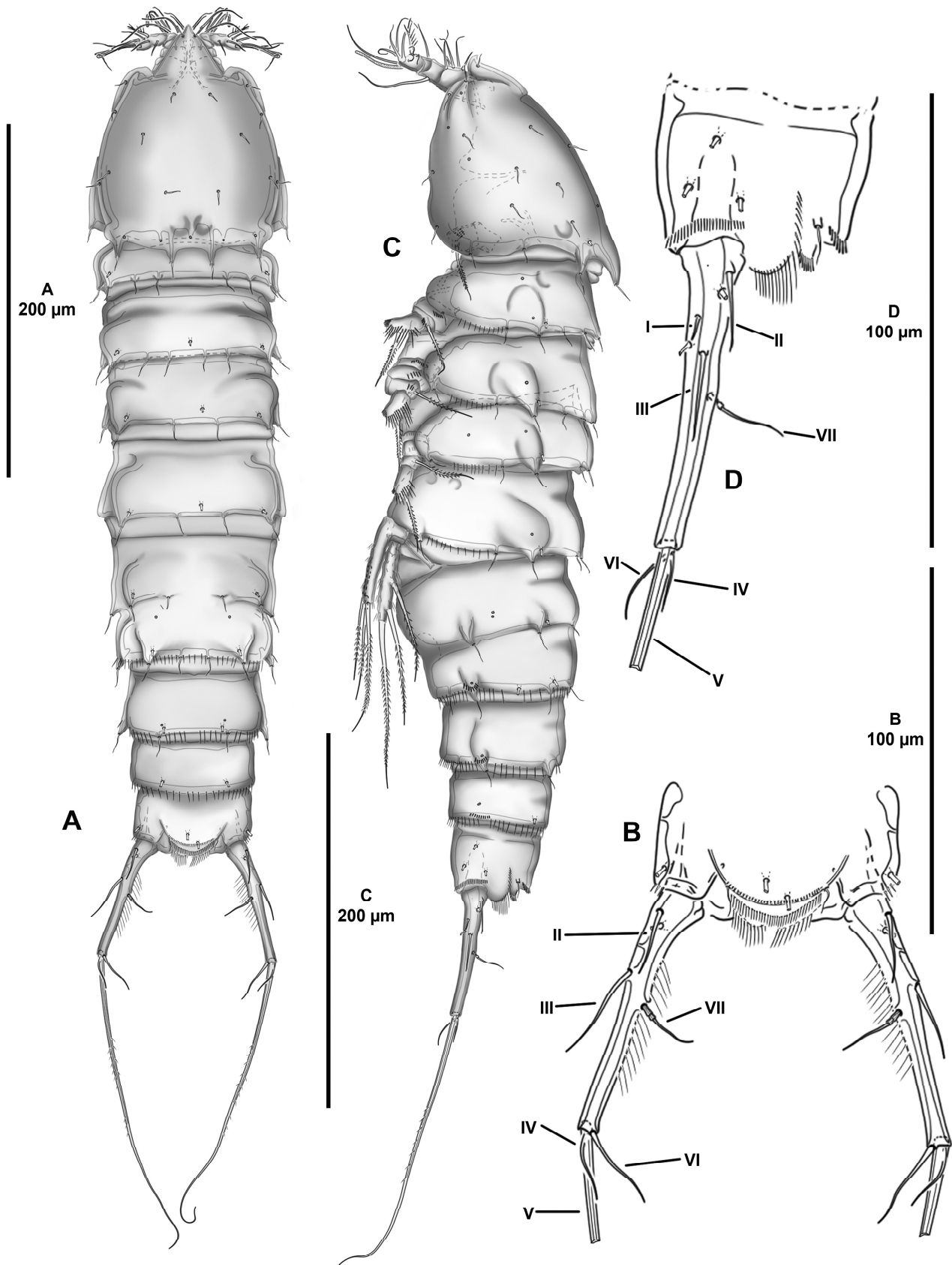


FIG. 1. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, habitus, dorsal; B, anal somite and caudal rami, dorsal (Roman numerals indicate each caudal seta); C, habitus, lateral; D, anal somite and left caudal ramus (Roman numerals indicate each caudal seta).

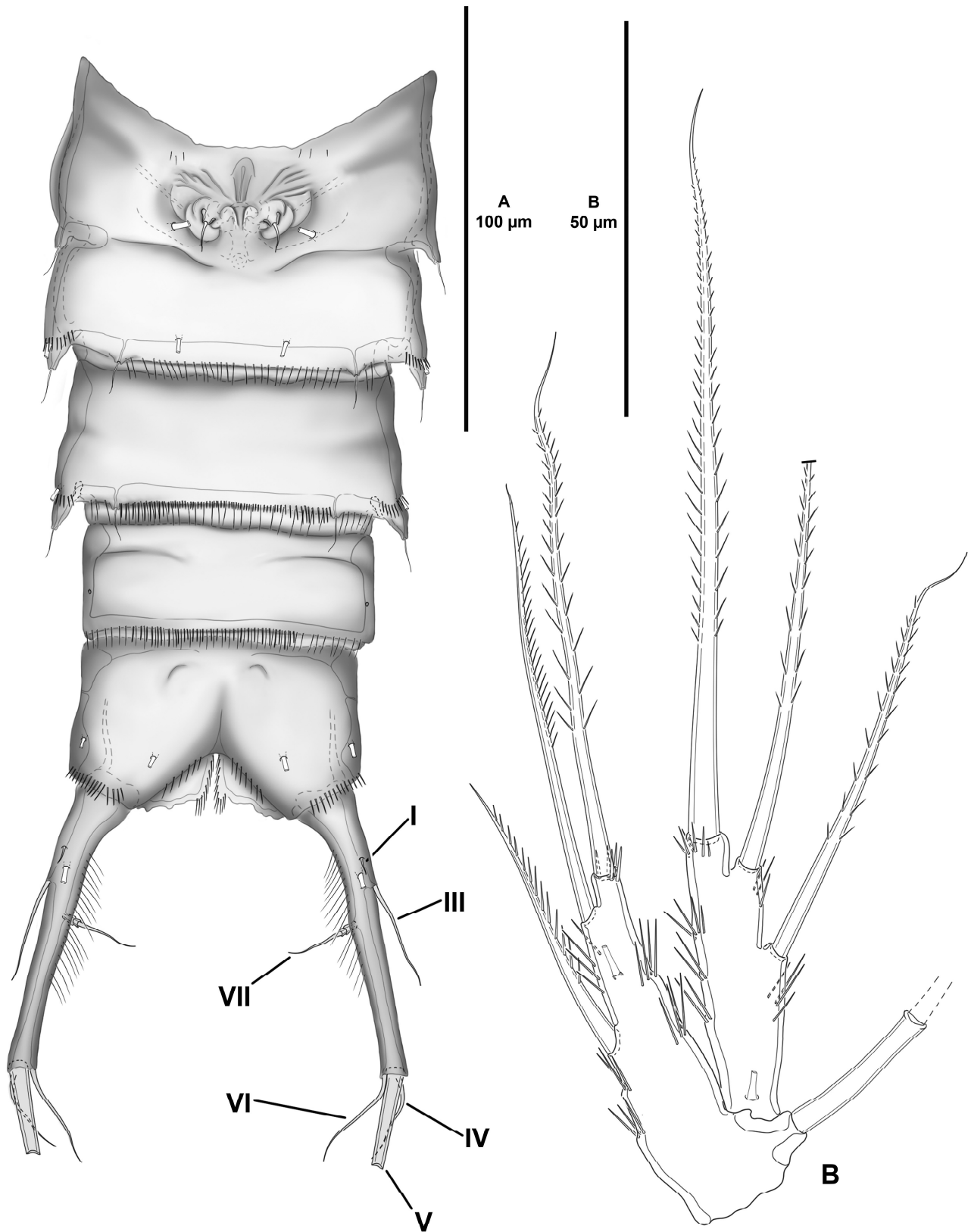


FIG. 2. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, urosome, ventral (P5-bearing somite omitted); B, P5, anterior.

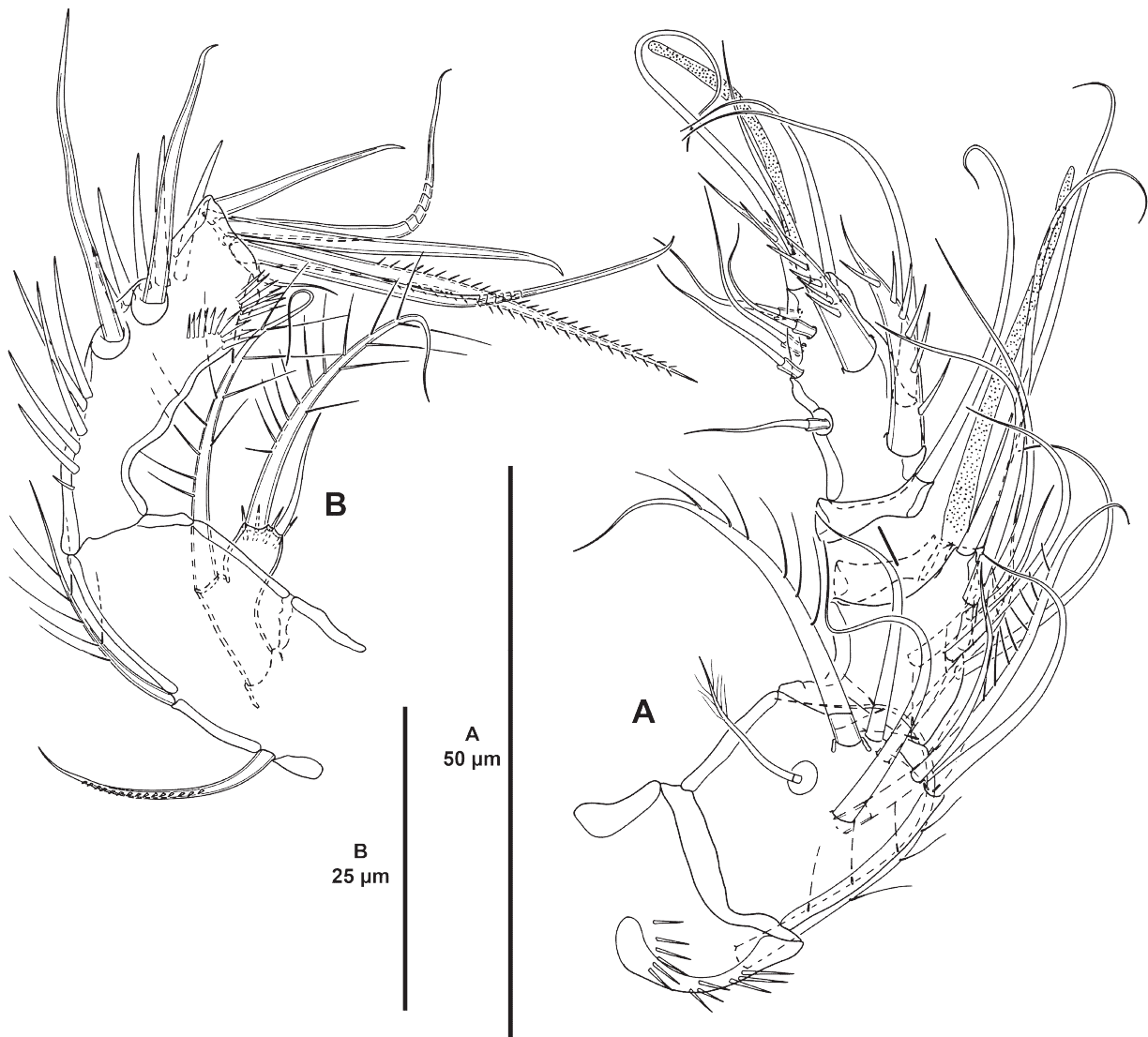


FIG. 3. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, antennule; B, antenna.

Maxillule (Fig. 4B) with praecoxal arthrite armed with two surface setae one of which displaced subdistally, and five distal spines. Coxal endite with one seta. Basis with two endites, distal endite with three, proximal endite with two setae. Exopod and endopod fused to basis, the former represented by two, the latter by one seta.

Maxilla (Fig. 4C) with syncoxa ornamented with small proximal inner and outer subdistal spinules; with two endites, each with one spinulose and one slender seta. Allobasis drawn out into claw, the latter with one posterior and one anterior accompanying seta. Endopod completely incorporated to basis, represented by two setae.

Maxilliped (4D) subchelate. Syncoxa ornamented with few subdistal outer spinules, unarmed. Endopod one segmented, with long claw accompanied by long slender seta.

P1 (Fig. 5A) with elongate bare intercoxal sclerite. Praecoxa triangular, unornamented. Coxa rectangular, with few subdistal outer spinules. Basis with spinules at base of outer and inner setae and at base of endopod; outer seta setulose, inner spine strongly spinulose. Exopod three-segmented; segments subequal in length and ornamented with long outer spinules as shown; first and second segments without inner armature, outer spines very long; third segment without inner armature, with two outer spines (proximal visibly shorter than subdistal), and two distal setae without setulose distal tufts (distal inner shorter than distal outer, longer than subdistal outer spine, not inclined outwardly, and not intersecting base of distal outer element). Endopod two-segmented, reaching proximal third of EXP3; first segment about one third the length of second segment, with inner and outer spinules as shown, unarmed; second segment elongate, about 4x as long as wide, with inner and outer spinules as depicted, with two distal elements (one inner distal seta and one outer distal spine).

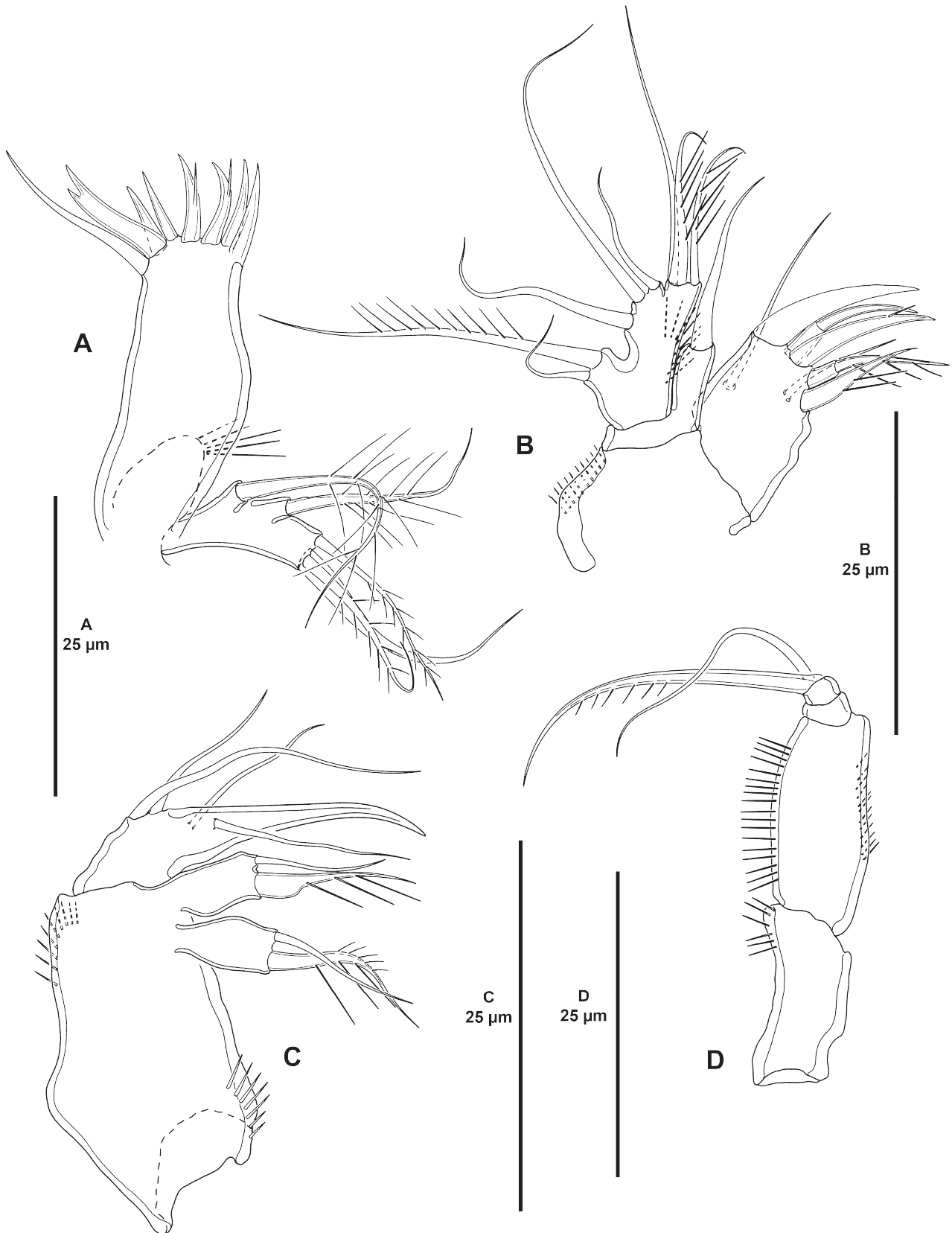


FIG. 4. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, mandible; B, maxillule; C, maxilla; D, maxilliped.

P2–P4 (Figs. 5B, 6A, B) with elongate bare intercoxal sclerites. Praecoxa triangular; with transverse row of small spinules. Coxa with inner and outer short spinular rows, of P2 with two, of P3 with one, of P4 without medial minute spinules. Basis with outer long plumose seta, with spinules at base of outer seta and at base of endopod. Exo-

pod three-segmented; segments with outer spinules as shown, EXP1 and EXP2 with inner distal frill, without inner armature, outer spines elongate; P2 EXP3 with four (two apical setae, and two outer spines), P3–P4 EXP3 with five elements (one inner and two apical setae, and two outer spines). Endopod two-segmented; segments ornamented with spinules as shown; first segment small, unarmed; second segment elongate, of P2 with two apical setae, of P3 and P4 with two apical setae and one outer spine.



FIG. 5. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, P1, anterior; B, P2, anterior.



FIG. 6. *Chalarosthrix bisetosa* gen. et sp. nov., female holotype. A, P3, anterior; B, P4, anterior.

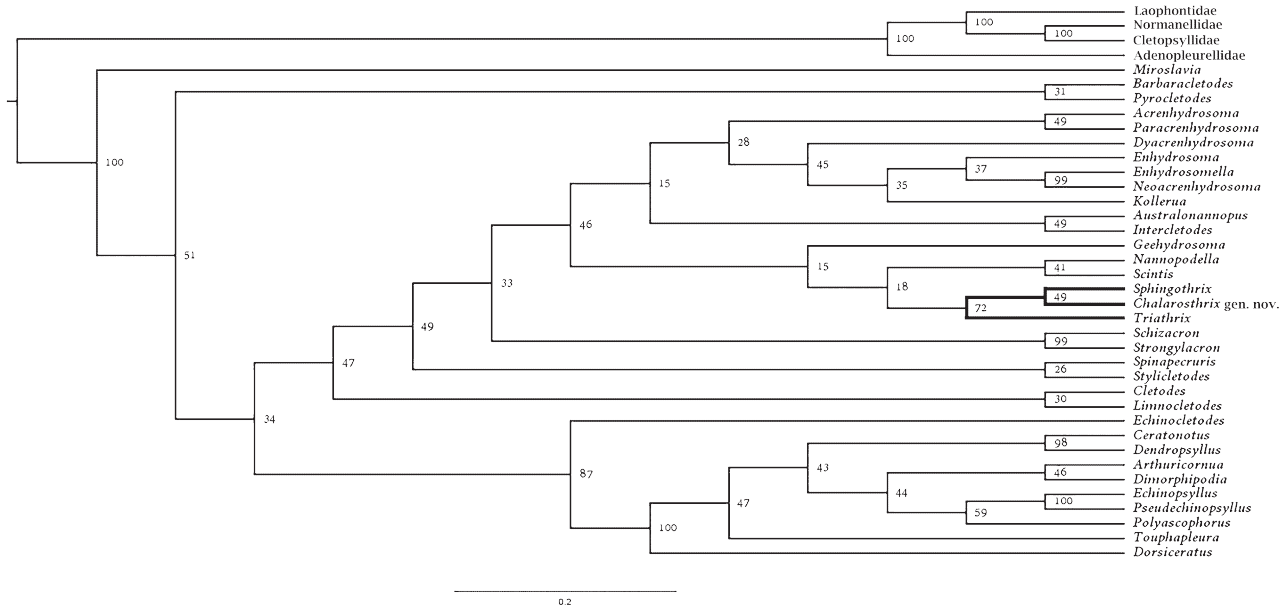


FIG. 7. “Allcompat” consensus tree of the Bayesian analysis (equivalent to the majority-rule consensus tree) using MrBayes showing the most probable relationships amongst *Sphingothrix*, *Triathrix*, and *Chalarosthrix*. Numbers indicate the Bayesian Posterior Probability values (BPP %).

P1–P4 armature formulae as follows:

	P1	P2	P3	P4
Exopod	0,0,022	0,0,022	0,0,122	0,0,122
Endopod	0,020	0,020	0,021	0,021

P5 (Fig. 2B) with baseoendopod and exopod distinct, elongate and narrow, ornamented with spinules as depicted. Baseoendopod with outer seta arising from long setophore; endopodal lobe with two inner (one medial, one subdistal) and one distal seta, and with one medial tube pore subdistally. Exopod with two outer (one medial, one subdistal) and one distal seta, and one proximal tube pore.

Genital field (Fig. 2B) with median copulatory pore; each P6 represented by one small seta.

Male. Unknown.

Variability. No variability was observed in the only female inspected.

Etymology. The specific epithet comes from the Latin suffix *bi*, two, and from the Latin adjective *sētōsa*, setaceous, and refers to the presence of two setae only on the P1 ENP2. It is in the nominative singular, gender feminine.

Phylogenetics

The “allcompat” consensus tree (see Materials and Methods) of the Bayesian analysis (equivalent to the majority-rule consensus tree) with ninety-five characters and thirty-four ingroup taxa is shown in Fig. 7. The output files of MCMC ran in MrBayes were analysed using Tracer v. 1.7.1. The sampling of the posterior probability for all parameters reached a sufficiently effective sampling size (ESS= 3383.8 > 200) for meaningful parameter estimation. Also, the convergency of two independent runs and appropriate burn-in were confirmed.

The analysis of the phylogeny of the Cletodidae and George's (2020) concept of the family are beyond the scopes of this study and will not be discussed here. The characters used for the analysis are self-explanatory and will not be explained here. The “allcompat” consensus tree (Fig. 7) supports the monophyly of the *Sphingothrix-Chalarosthrix-Triathrix* clade (SCT clade) with a Bayesian posterior probability of 72%, being *Triathrix* the sister taxon of *Sphingothrix-Chalarosthrix* gen. nov., the latter clade supported by a BPP of 49%. The SCT clade appears as the

sister taxon of the clade *Nannopodella-Scintis* being this relationship supported by a relatively low BPP of 18%. In our analysis, the SCT clade is defined by the synapomorphic characters 4, 7, and 94 (presence of chitinous extension with four socles, median tube pore on anal operculum, and seta I of caudal rami posterior to seta II; see tables 1 and 2). No autapomorphies were detected for *Triathrix*, but this is the only genus within the STC clade with apical brush setae on P1 EXP3 (character 38; see tables 1 and 2). *Sphingothrix* is defined by the autapomorphic characters 40 (distal inner seta of P1 EXP3 inclined outwards and intersecting the distal outer element at its base; see table 1) and 41 (both apical elements of P1 EXP and ENP rigid and spiniform; see table 1). *Sphingothrix* is unique within the SCT clade also in the distal outer exopodal seta of P1 EXP at most as long as the subdistal outer spine (character 39; see tables 1 and 2) which is also present in some other cletodid genera (see table 2). No autapomorphies were detected for *Chalarothrix* gen. nov., but this genus is unique within the SCT clade in the reduction of the distal armature complement of P1 ENP2 from three (as in *Sphingothrix* and *Triathrix*) to two elements.

Discussion

The genus *Triathrix* was created for *T. montagni* Gee & Burgess 1997 and *T. kalki* Gee & Burgess 1997 collected by Dr. Paul Montagna 15 km off the central Californian coast, and SE of Galveston Texas, in the Gulf of Mexico, respectively. Gee & Burgess (1997) detected and discussed several—potential—autapomorphies of their newly created genus. These are i) the presence of a chitinous plate with four socles on the posterior margin of the cephalothorax, ii) absence of socles on the preanal somite, iii) presence of a medial tube pore on the anal operculum, iv) caudal seta I situated posterior to seta II, v) maxillary coxa with one seta only, and vi) maxillary basal complex with eight setae. Additionally, they (Gee & Burgess 1997) characterized *Triathrix* by i) a sharply pointed triangular rostrum, ii) mandibular palp with five setae, iii) proximal endite of the maxillary syncoxa with two elements, iv) maxillary allobasis with a claw and two setae, v) maxillary endopodal setae not fused basally, vi) syncoxa of maxilliped unarmed, vii) shape of the female P5 with elongate rectangular rami subequal in length and with only three setae each, and viii) lack of sexual dimorphism in swimming legs. Gee & Burgess (1997) noticed the resemblance of their new genus and *E. nicobarica* from Nicobar Island in the presence of three setae on the antennary exopod and two abexopodal setae on the antennary allobasis and removed that species from *Enhydrosoma* Boeck 1872 and reallocated it into *Triathrix*. That same year, Fiers (1997) amended the diagnosis of the genus *Triathrix* by adding the presence of a distal setulose tuft on the distal setae of the P1 EXP and ENP, length of the distal outer seta relative to the length of the subdistal outer spines, and position of the distal inner seta, added *T. mayae* to the genus *Triathrix*, and erected the genus *Sphingothrix* for *T. kalki* Gee & Burgess 1997 and for *S. goldi*, the latter from the Yucatan shelf. Fiers (1997) defined *Sphingothrix* by i) the rigid and bipinnate distal elements of the P1 EXP and ENP, ii) reduction in length of the distal outer exopodal seta—at most as long as the subdistal outer spine—, and position of the distal inner seta—inclined outwards and intersecting the distal outer element at its base. By the time of publication of Fiers' (1997) paper, *Triathrix* was composed of *T. montagni* from the central California continental slope, *T. nicobarica* from Nicobar Island, and *T. mayae* from the Yucatan shelf, and *Sphingothrix* included two species only, *S. kalki* from the US Gulf of Mexico, and *S. goldi* from the Yucatan shelf.

In a recent study on the systematics and phylogeny of the Ancorabolidae Sars 1909 and the Cletodidae, George (2020) confirmed the polyphyletic status of the Ancorabolidae and the Ancorabolinae Sars 1909, and the paraphyletic status of the Laophontodinae Lang 1944. As a result of his analyses, he (George 2020) redefined the Ancorabolidae, restructured and redefined the Ancorabolinae by disposing off the previous concept of the subfamily and giving subfamily rank to the *Ancorabolus*-lineage *sensu* Conroy-Dalton & Huys (2000) as the new restructured Ancorabolinae. He also restructured the Laophontodinae, and removed the *Ceratonotus*-group *sensu* Conroy-Dalton (2001) from the Ancorabolinae to the Cletodidae, and proposed the Cletodinae Scott T. 1904 for the *Ceratonotus*-group and its sister taxon *Cletodes* Brady 1872. A list of the taxa included in the restructured Cletodidae and Cletodinae can be found in George (2020 pp. 467–468). George's (2020) concept of the Cletodidae was followed here. Also, following George (2020 pp. 493–494) we excluded *Patagoniaella* from our analyses, as well as the monotypic genus *Monocletodes*. The detailed phylogenetic analysis of the Cletodidae is beyond the scope of the present study and will not be discussed here, as well as neither George's (2020) concept of the Cletodidae.

The genera *Triathrix* and *Sphingothrix* were diagnosed upon several autapomorphies (see Gee & Burgess (1997 pp. 223, 224) for *Triathrix*, and Fiers (1997 pp. 246) for *Sphingothrix*) following Por's (1986) concept of the Cle-

todidae. These autapomorphies have been listed above. However, recent advances and restructuring of the Cletodidae by George (2020) makes necessary the re-evaluation of the putative autapomorphies for these two genera. Our results indicate that the SCT clade is defined objectively by the following synapomorphies: i) presence of chitinous extension with four sensillum-bearing socles, ii) presence of a median tube pore on anal operculum, and iii) seta I of caudal rami situated posterior to seta II. In the light of recent evidence and as a result of restructuring of the Cletodidae by George (2020), no autapomorphies are left for *Triathrix*, being those proposed by Gee & Burgess (1997) present in other taxa. However, *Triathrix* is the only genus within the SCT clade with apical brush setae on P1 EXP3. On the other hand, in agreement with Fiers (1997) the distal inner seta of P1 EXP3 inclined outwards and intersecting the distal outer element at its base, and the rigid spiniform apical elements of P1 EXP and ENP are the only autapomorphies for *Sphingothrix*. This genus is also unique within the SCT clade in the distal outer exopodal seta of P1 EXP being at most as long as the subdistal outer spine. However, this character state is present also in some other cletodid genera (see table 2). We could not detect any autapomorphies for *Chalarosthrix* gen. nov., but this genus is unique within the SCT clade in the reduction of the distal armature complement of P1 ENP2 from three (as in *Sphingothrix* and *Triathrix*) to two elements. This reduction is regarded here as the sole apomorphy for the genus, being a secondary loss within the clade.

Triathrix nicobarica and *T. mayae* stand out within *Triathrix* by the reduction in armature complement of the P1 ENP2 from three to two elements—one distal outer spine and one distal inner seta—which is also displayed in *C. bisetosa* sp. nov. Pending the discovery of the males of *T. mayae*, *T. nicobarica*, and of the new Mexican material, and of the adult female of *T. nicobarica* (the latter is known from a stage V female copepodid), we formally remove *T. nicobarica* and *T. mayae* from *Triathrix* to *Chalarosthrix* gen. nov., the latter characterized by the apomorphic secondary loss of the inner element of the P1 ENP2.

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