

THE GENERA *TRIATHRIX* GEE & BURGESS AND *SPHINGOTHRIX* GEN. NOV. (COPEPODA, CLETODIDAE *SENSU* POR) FROM THE BAY OF CAMPECHE, GULF OF MEXICO

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SARSIA



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Three closely related species of the recently defined cletodid genus *Triathrix* GEE & BURGESS, 1997 are reported from the southern bight of the Gulf of Mexico. *T. mayae* sp. nov. is assigned to the genus while, based on the setal morphology of the P1, the new genus *Sphingothrix* is defined to unify the species *S. goldi* sp. nov. and *S. kalki* (GEE & BURGESS) comb. nov. The descriptions of *S. kalki*, *S. goldi* and *T. montagni* GEE & BURGESS are complemented with observations on their copepodid stages. The particular characteristics of *T. nicobarica* are discussed in the light of these observations. The development of the rami and the successive addition of elements on the exopodites during copepodid development is found to agree with the scheme proposed by FIERS (1996) for the Cletodidae. Preliminary ecological data on two species from the Bay of Campeche are given.

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KEYWORDS: Harpacticoida; *Triathrix*; *Sphingothrix*; Bay of Campeche; copepodids.

INTRODUCTION

As part of an in-depth systematic study of the cletodid genus *Enhydrosoma* BOECK, 1872, GEE & BURGESS (1997) defined the genus *Triathrix* to encompass *T. montagni* from California, *T. kalki* from the Flower Gardens in the Gulf of Mexico, and *Enhydrosoma nicobaricum* SEWELL, 1940 known from the Nicobar Islands (Bay of Bengal) but described from a male fifth copepodid stage (GEE 1994; FIERS 1996).

During a monitoring study on sublittoral meiofaunal assemblages in the Bay of Campeche (southern bight of the Gulf of Mexico: GOLD-BOUCHOT & FIERS 1991), *Triathrix kalki* and two closely related new species were found. *T. mayae* sp. nov. is assigned to the genus *Triathrix*, and *S. goldi* sp. nov. is unified with *T. kalki* in the here defined genus *Sphingothrix* gen. nov. Besides the description of the adults, several copepodid stages of these species were studied and described. In addition, several copepodid stages of *T. montagni*, obtained during a similar program in the Santa Maria Basin, off California (MONTAGNA 1991), are described and compared with the juvenile stages of its congeners. The copepodid morphology is studied to complete the scheme of post-maxillipedal leg development presented in FIERS (1996). This study explicitly demonstrates that

copepodids of even closely related species are relatively easily distinguishable. This allows us to infer the annual population fluctuations of *S. goldi* and *S. kalki*.

The occurrence of three different species in such a limited area as the southern bight of the Mexican Gulf conclusively documents the statement of GEE & BURGESS (1997) that our knowledge of the sublittoral harpacticoids (and meiofauna in general) from this region is extremely poor. The present paper dealing with only a limited group of harpacticoids of the Cletodid family is just a further step in the study of the copepods from the western tropical Atlantic region and adjacent areas.

MATERIAL AND METHODS

Most of the specimens enlisted herein were collected during three oceanographic cruises in the Bay of Campeche (southwestern part of the Yucatan shelf) in 1993. Samples for meiofaunal analyses were taken with a 2 cm diameter plastic core from the sediments recovered with a 40 x 40 cm Hessler-Skandia MK III box-corer. Sediments were fixed in 4 % formaldehyde after being relaxed with MgCl₂. Animals were stored in 75 % ethanol after being sorted out from the sediments. Material from California (*T. montagni*) was obtained and treated in the same way (HYLAND & al. 1990). Additional material from the Bay of Campeche was

obtained from previous sampling campaigns during which the contents of a van Veen grab were subsampled.

Dissected specimens are mounted in glycerine with sealed coverglasses, but the majority of the specimens are stored in 75 % ethanol. Observations were made on a Leitz Diaplan light microscope equipped with a 100 X oil immersion lens and a drawing tube. Abbreviations used in text are P1-P6 (first to sixth leg) and exo/end (exopodite/endopodite). Setal arrangements of the legs given in the descriptions of the copepodids are according to HUMES & HO (1969).

The specimens are deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels. The catalogue numbers of the type series (COP) are given preceding the species descriptions. A detailed list of the catalogue numbers of the additional specimens reported herein is available by simple request to the author.

TAXONOMICAL ACCOUNT

Genus *Triathrix* GEE & BURGESS, 1997

Diagnosis (amended). As originally defined with following amendments: terminal elements of P1 rami setulose with a distal plume of setules; outer terminal seta of exopodite distinctly longer than outer subdistal spine; inner distal seta with normal position, in line with endopodal axis.

The genus assembles the following species: *T. montagni* (type-species, by original designation), *T. nicobarica* (SEWELL, 1940, see general discussion below), and *T. mayae* sp. nov., here described.

Discussion. The species studied herein match in almost every aspect the diagnosis of the genus *Triathrix* as defined by GEE & BURGESS. They display a remarkable homogeneity regarding the cephalic appendages and natatorial legs and discrimination between them is mainly a matter of proportion of the chitinous posterior cephalic extension and the number and shape of socles along the posterior and lateral margins of the body somites.

However, the setal morphology and their particular interrelation on the terminal P1 segments divide the genus in two species groups. The P1 rami of *T. montagni* (type species), and the here described *T. mayae*, are complemented distally with long setulose setae furnished with a plume of long setules close to their tip. The outer terminal seta of these species is distinctly longer than the outer subdistal spine on the third exopodal segment. In contrast, *T. kalki* and the here described new species *Sphingothrix goldi* display a completely different picture. In these species, the terminal bipinnate setae have a rigid appearance, apparently lacking the typical flexibility known for setae (i.e. a more spiniform appearance). Their tip lacks a plume of setules

and the outer terminal element is shorter than the outer subdistal spine in *T. kalki* or of equal length in *S. goldi*. Of particular interest is the outwardly inclined direction of the inner distal element, intersecting the outer distal one posteriorly, near its implantation. This remarkable position of the inner distal seta is already present from the first copepodid stage on, although the length of the outer seta is distinctly longer (equals the inner one) than the outer distal one at this stage. The typical setae with distal plume known in *T. montagni* are present from the first copepodid stage on (see Fig. 10G) and it is assumed that the first copepodid of *T. mayae* possesses a comparable setal morphology in the P1. GEE & BURGESS (1997) discussed at length the (auto)apomorphies of the genus and evidenced the separate position of *Triathrix* lineage within the Cletodidae *sensu* POR but placed little emphasis on the shape and ornamentation of the terminal elements on both rami of the first leg. With the discovery of two new species which undoubtedly belong to the cletodid lineage mainly characterized by the antennal exopodite with three appendages, the importance of the setal morphology and ornamentation on the P1 rami becomes explicitly significant in the diagnosis of genera.

Much attention was never paid to the exact nature of the P1 setae in the descriptions of cletodid species. So far, there seems to be at least three different setal types known: (1) flexible plumose setae without special arrangements near the distal end (e.g. *E. lacunae* JAKUBISIAK, 1933; pers. obs.), (2) flexible plumose setae having a plume of setules near the distal end (e.g. *E. curticauda* BOECK, 1872, see GEE 1994), and (3) one or two geniculated setae on the terminal exopodal segment (e.g. *Cletodes macrura* FIERs, 1991). Plumed terminal setae are almost certainly a diagnostic criterion for several cletodid genera (e.g. *Acrenhydrosoma* LANG, 1948; *Stylicletodes* LANG, 1936: pers. obs., *Enhydrosomella* MONARD, 1928: pers. obs.) and they have been demonstrated to be present in at least one *Enhydrosoma* species (*E. curticauda*). However, the homogeneity of the latter has been questioned previously (FIERs 1987; MIELKE 1990) and there are sufficient arguments advanced to suppose that the number of species in this genus should be drastically reduced (see GEE 1994 for review).

Normal, undifferentiated flexible setae on the P1 (type 1) seem to be displayed by many cletodid species. However, the plumed aspect of the distal part of the setae is easily overlooked and may occur more frequently than previously thought. The geniculated setae (type 3) probably occur only in those (all?) presently assembled in the genus *Cletodes* (pers. obs.) and seem not to occur within the lineage leading to *Enhydrosoma* and related genera.

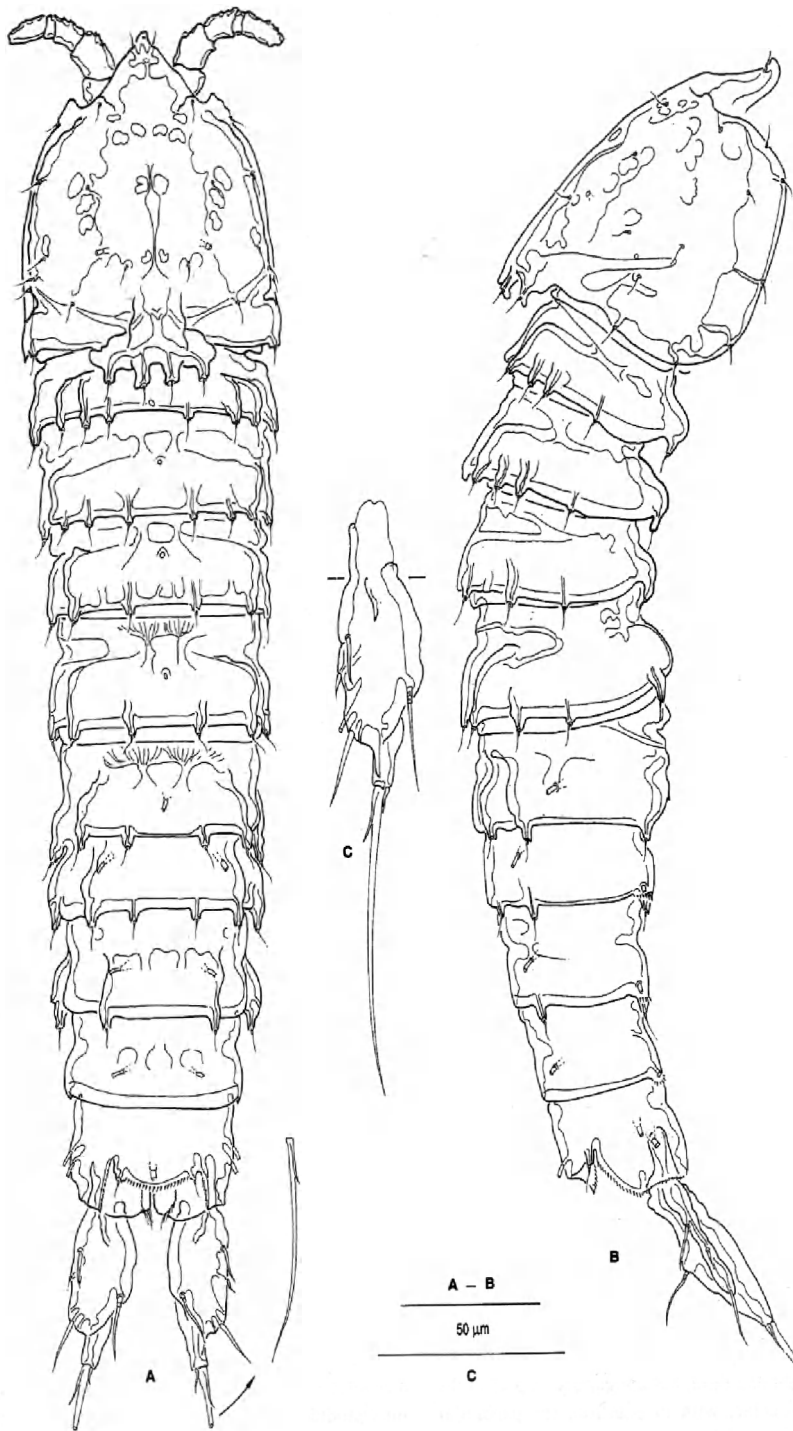


Fig. 1. *Triathrix mayae* sp. nov. A. Female habitus, dorsal. B. Female habitus, lateral. C. Caudal ramus, dorsal (horizontal bars indicate posterior margin of anal somite).

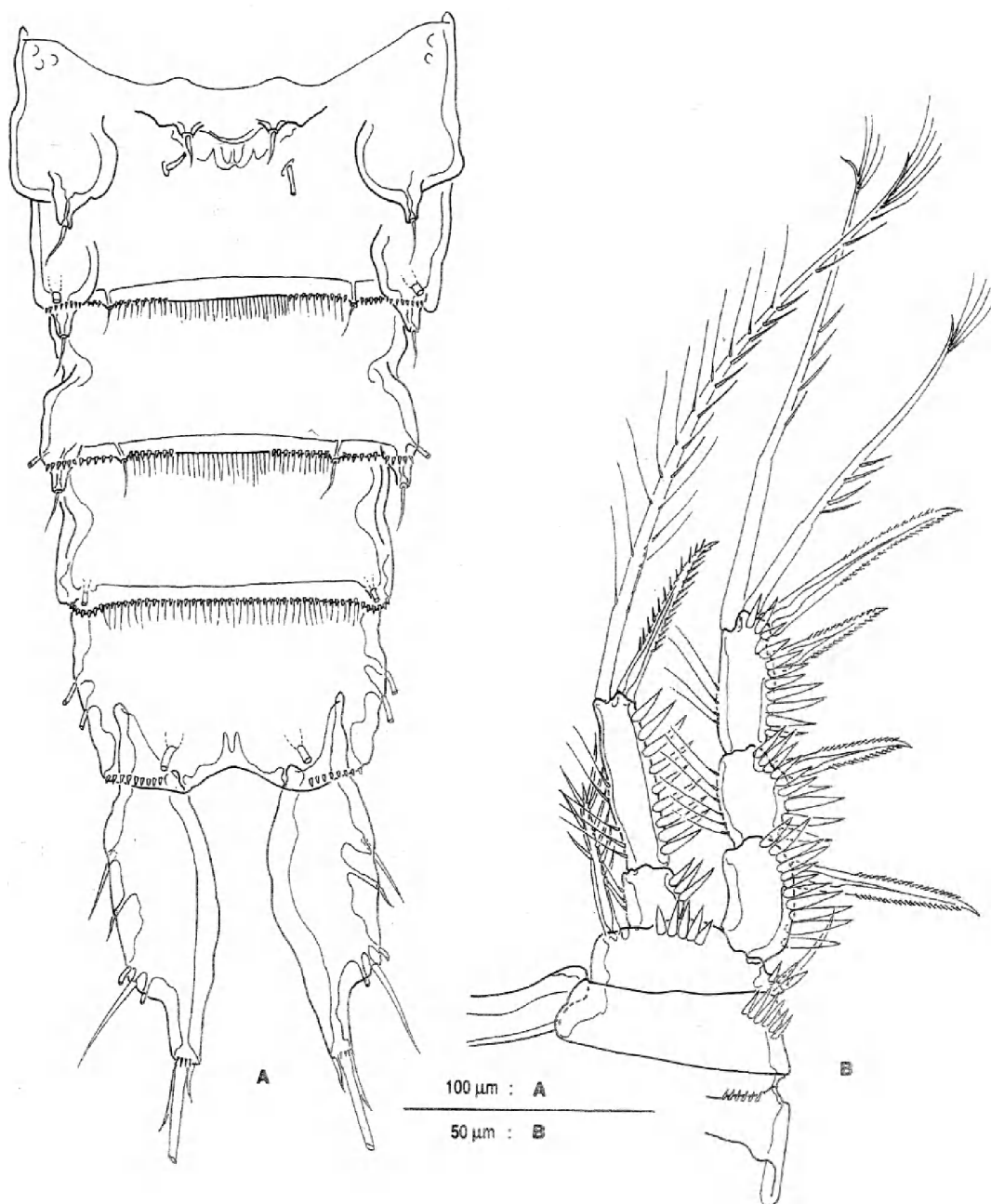


Fig. 2. *Triathrix mayae* sp. nov. A. Female urosome, ventral. B. P1, anterior.

The straight and rigid, but not plumed, aspect of the P1 terminal setae, with in addition, the particular inclined position of the inner one, as encountered in *T. kalki* and *S. goldi*, apparently is a novelty within the family. This advanced feature permits the definition of

a new taxon (the genus *Sphingothrix* gen. nov.) within the cletodid lineage which is basically characterized by its antennal exopodite bearing three setae and the allobasis with two setae on abexopodal margin.

Triathrix mayae sp. nov.
(Figs. 1-3)

Material. Holotype: dissected female, mounted on 5 slides, labeled COP 4165a-e.

Type locality. Yucatan Shelf, between Alacranes reef and Progreso Harbour (22°00'N 89°00'W), 38 m. Leg. CINVESTAV-IPN, Merida, May 1989.

Etymology. The specific name refers to the splendid Mayan culture for which this region is known.

Description

Female. Habitus (Fig. 1A). Length, from tip of rostrum to distal end of caudal rami, 430 µm; body typically curved in lateral view, cylindrical and slightly depressed in dorsal view; proportional length cephalothorax/body length about 1/4.

Cephalothorax with large chitinous posterodorsal extension having four broad and blunt socles; integument with pattern of rounded shallow depression arranged around a smooth median field; second and third pedigerous somites with 8 sensillum-bearing socles and two sensilla without socles, and a dorsomedian pore; fourth and fifth pedigerous somites with six sensillum-bearing socles and two sensilla without socles; genital somites with six sensillum-bearing socles, fourth urosomal somite with four socles; second genital somite and fourth urosomal somite with two additional sensilla without socles on posteroventral border; first genital somite with a single dorsomedian pore, second genital somite and third and fourth urosomal somites each with pair of pores on dorsal surface and one pore on posteroventral corner; pre-anal somite without sensilla; anal somite with two lateral pores and one ventral; anal operculum, finely dentate, flanked with two short sensillum-bearing socles, and having a median pore; dorsal and lateral surfaces of all somites finely striated.

Ventral surface of urosomal somites smooth (Fig. 2A); posteroventral borders of second genital somite and succeeding somites ornamented with minute spinules and fragile hairs; posteroventral margin of anal somites furnished with minute spinules.

Caudal rami (Fig. 1C; 2A) large, aspect foliaceous in dorsal view; anterior 2/3 broad with sinuate lateral margins and short anterior mediodorsal keel; posterior third slender, nearly cylindrical; biarticulate dorsal seta implanted in second half, close to inner margin; two lateral setae in anterior half and one in posterior half; outer and median distal setae fused at base, former short, latter one nearly 1.5 times as long as ramus, and smooth; inner distal seta half as long as outer one.

Antennule and mouthparts as in *T. montagni* GEE & BURGESS.

P1 (Fig. 2B) with sparsely ornamented protopodal components; medial spine on basis, bipinnate, reaching towards middle of second endopodal segment; outer exopodal spines armed with minute spinules; distal setae on third exopodal segment with few setules in middle of stem and short plume near distal tip; endopodite reaching not quite to middle of third exopodal segment, bearing two distal elements: outer spinulose spine and inner setulose seta with short plume near distal tip.

P2-P4 as in *T. montagni*; subdistal outer spine on second endopodal segments of P3 and P4, reaching just to distal edge of third exopodal segment. P5 (Fig. 3A) with strong appearance. Baseoendopodite with long cylindrical outer setiferous projection, bearing smooth seta; endopodal lobe slightly shorter than exopodite, with three attenuated spines: inner two with fine ornamentation, apical one set with rigid, widely spaced spinules; outer and inner margin of endopodal lobe with two and four rows of blunt spinules, apical margin ornamented with 5 rounded spinules (Fig. 3B); tubular pores in distal third of inner margin of endopodal lobe, and near articulation with outer setiferous extension; exopodite with sinuate lateral margins, bearing three bipinnate setae, and a wide tubular pore near outer proximal edge; inner margin ornamented with four rows of spinules, outer one with two rows.

P6 vestige (Fig. 3D) represented as small socle bearing a short smooth seta; copulatory pore leading to U-shaped slender duct; seminal receptacles (?) situated well posteriorly to gonopores, recurved posteriorly and slender.

Male. Unknown.

Comparison. *T. mayae* sp. nov. is at once recognizable from the two other species in the genus by its broad, foliaceous caudal rami, and the absence of lateral extensions of the anterior part of the cephalothorax. The species is easily distinguishable from *T. montagni* by its less pronounced dorsolateral extensions of the body somites and the reduced number of elements on the second endopodal segment of the P1.

Within the genus, only *T. nicobarica* is known to have only two terminal elements on the P1 endopodite. Although we are unaware of the exact adult morphology of this species, it seems apparent that *T. mayae* and *T. nicobarica* are not conspecific as the latter is characterized by the long inner distal seta on the caudal rami and the long outer subdistal spines reaching far beyond the distal margin of the exopodites in P3 and P4 (see also the general discussion, below).

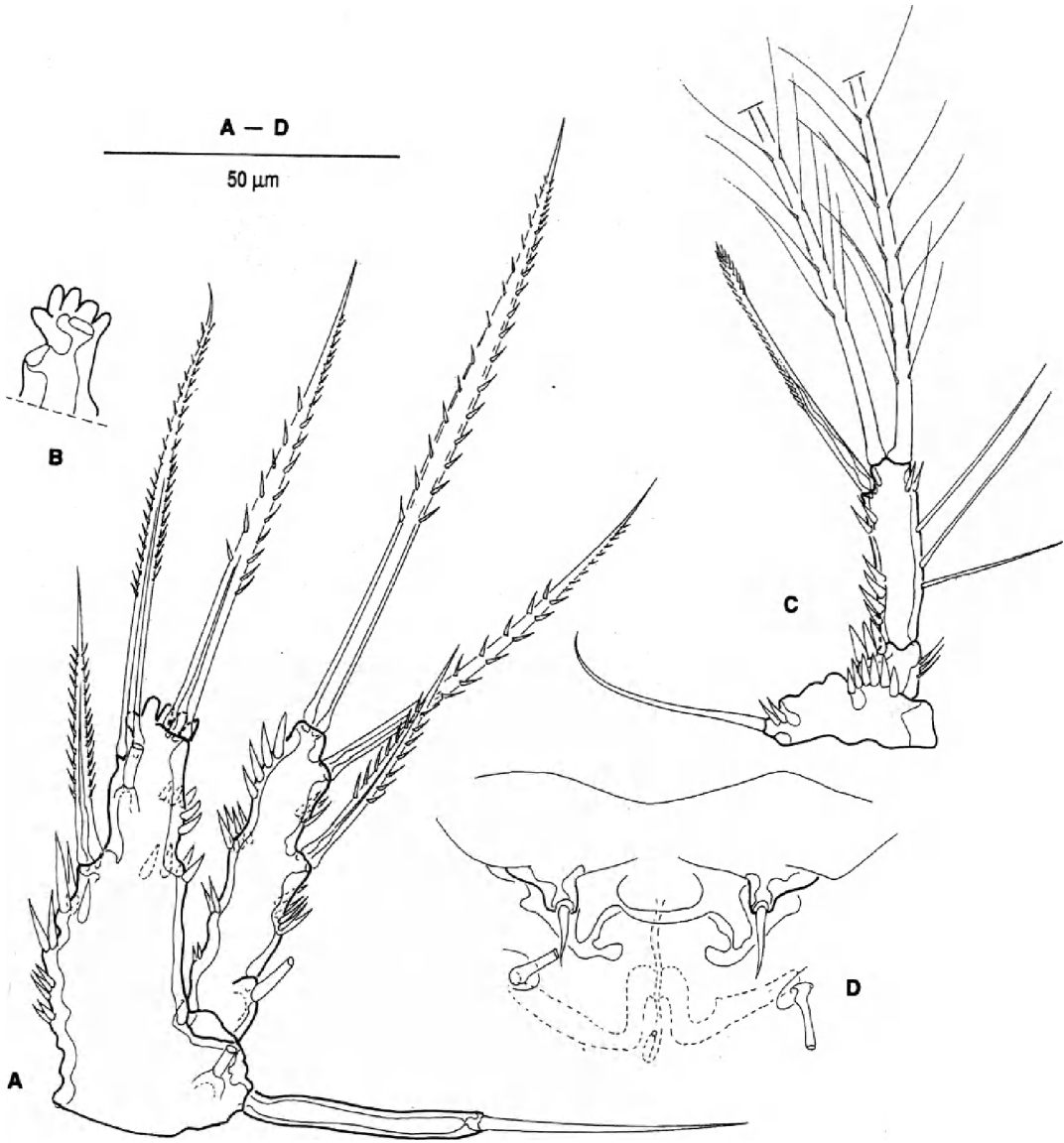


Fig. 3. *Triathrix mayae* sp. nov. A. Female P5, anterior. B. Distal margin of P5 endopodal lobe, setae omitted. C. Basis and endopodite P3, anterior. D. Female genital field.

Triathrix montagni GEE & BURGESS, 1997
(Figs. 4-5)

Material. Dissected: 1 ♀, 1 ♂, 1 CI (COP 4202, 4203, 4204, respectively) and ethanol preserved: 13 ♀♀ (3 ovigerous), 7 ♂♂ and 1 CIII and 1 C(♂)V, preserved in alcohol (COP 4183 - 4201).

Locality. Santa Maria Basin, off the Californian Pacific coast in the following stations R1 (35°05.83'N

120°49.16'W), 91 m; PJ1 (34°55.79'N 120°49.91'W), 145 m; PJ6 (34°54.71'N 120°49.91'W) 148 m; PJ7 (34°55.79'N 120°48.60'W), 123 m; PJ19 (34°55.03'N 120°49.91'W), 167 m; R4 (34°43.01'N 120°47.39'W, type-locality), 92 m; R5 (34°42.69'N 120°50.83'W), 154 m. For further information see HYLAND & al. (1990).

Description

This species was described in detail by GEE & BURGESS (1997). The description here only focuses on some ad-

ditional morphological details observed on adult specimens and on three copepodid stages.

Adults. Habitus. In addition to the sensillum-bearing socles and ventrolateral pores as originally described: each prosomal somite with a dorso-median pore in anterior half; second genital somite and following one with two dorsal pores situated on inner side of the ridge forming the sensillum-bearing socle; preanal somite with two dorsal pores, and anal somite with, on each side, two lateral pores and 1 ventral, and a single dorso-median one on anal operculum.

P3-P4 endopodites with outer subdistal spine on second segment reaching just to distal border of third exopodal segment.

Copepodid I. Habitus (Fig. 4A, B). Compact, and strongly recurved in lateral view; body with 5 tagmata with large head; length, measured laterally from tip of rostrum to distal end of caudal rami: 329 μ m. Rostrum fused with head with blunt and curved tip, bearing one pair of sensilla. Integument of all somites smooth; posterodorsal margin of head without socles, but posterodorsal margin of following somites each with two distinct socles: without sensilla on first and third free somite, with sensilla on second free somite; anal somite with rounded anal operculum flanked with two sensilla, and having median pore; ventral surface of anal somite with four short rows of spinules, arranged transversally (Fig. 4C).

Caudal rami (Fig. 4C-E) divergent, nearly three times as long as wide, tapering posteriorly; two lateral setae and biarticulate dorsal seta arising in anterior third; third lateral seta in middle of outer border; inner and median distal setae fused at base, the former nearly as long as ramus and feathered; future inner distal seta short, with dorsal position, and implanted on distal border; integument smooth, except for some spinules near implantation of median lateral seta, and along distal margin.

Antennule (Fig. 4I) three-segmented with following armature: I(3)-II(2+Aesth)-III(11+Aesth); integument smooth except for spinulose anterior lateral border of first segment.

Antenna as in adult but lacking a terminal spine on second endopodal segment; exopodite one-segmented with three elements and a row of distal spinules (Fig. 4F). Mouthparts as in adult.

P1 (Fig. 4G). Protopodal components differentiated, without medial spine on basis; rami one-segmented; exopodite with four outer spines and two apical pinnate setae having a plumed distal tip; endopodite with very slim inner distal seta, a pinnate median one with

plumed tip, and a spiniform outer element.

P2 (Fig. 4H). Protopodal components differentiated, rami one-segmented; exopodite with three outer spines and two distal pinnate setae; endopodite with two distal feathered setae.

P3 (Fig. 4J). Represented as a distinct lobe bearing three smooth setae.

Copepodid III. Habitus (Fig. 5A). Body with largest width along posterior margin of cephalothorax, strongly tapering post-cephalic region, and composed of 7 somites; length 527 μ m; length of cephalothorax about 1/3 of total body length.

Head with, on both sides, a small but distinct flattened extension of the anterolateral border, hardly visible in dorsal view (hidden behind anterodorsal edge); posterodorsal margin of head with six minute sensillum-bearing socles and two tubular pores; integument of head smooth. First to fourth free somites with 10, 10, 8 and 2 sensillum-bearing socles, respectively (ventralmost invisible in dorsal view); dorsolateral edges strongly produced posteriorly, bearing one of the sensilla; median part of posterior margin of each somite with two small triangular buds; preanal somite with produced lateral socles lacking sensilla, median region smooth; each body somite with a dorsal median pore and one pore on each side.

Anal somite rather large, having two dorsal depressions, and a transversal spinulose rows on ventral surface; anal operculum, crescentic, with median pore and flanked with two minute sensillum-bearing socles. Caudal rami divergent, tapering posteriorly, 2.5 times as long as wide, bearing lateral and dorsal setae in anterior half; inner and outer terminal setae short, equal in length.

Antennule four-segmented with following armament: I(1)-II(7+aesth)-III(1)-IV(11+aesth); segments smooth except for some spinules on first segment. Antenna and following buccal appendages as in adult.

P1 with two-segmented rami and setal complement as in adult; terminal setae on exopodite and endopodite setulose bearing a plume distally; medial spine on basis present.

P2 and P3 with two-segmented rami; setal complement as in adult in P2, with median outer exopodal spine wanting in P3; outer subdistal element on P3 endopodite reaching just to distal margin of exopodite; P4 with one-segmented rami, armament as follows: (exo) 0.2.III, (endo) 0.2.I; outer subdistal element on endopodal segment minute, with hyaline appearance.

P5 represented as a more or less globulous extension, bearing two smooth setae.

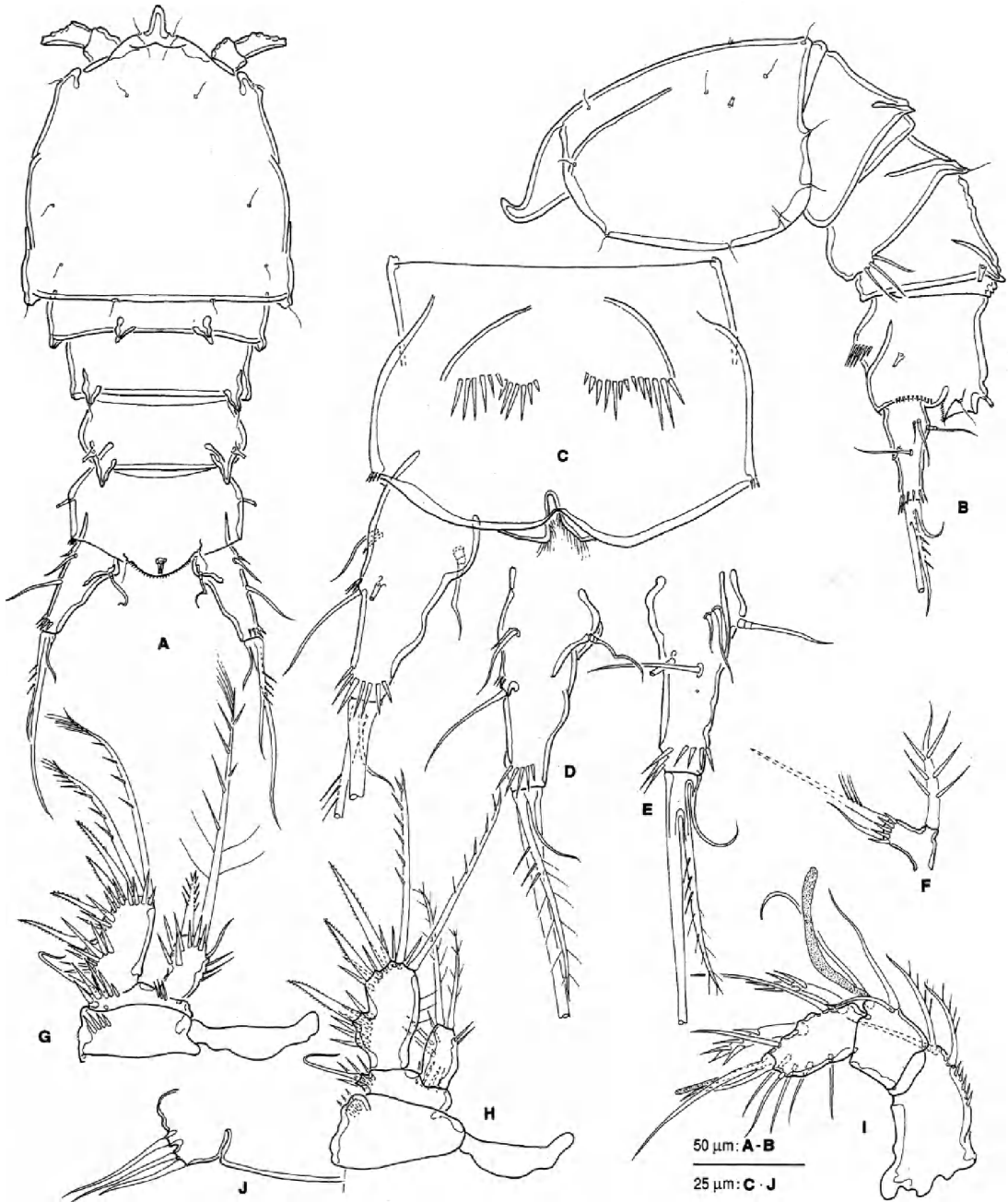


Fig. 4. *Triathrix montagni* GEE & BURGESS. Copepodid I. A. Habitus, dorsal. B. Habitus, lateral. C. Anal somite and right caudal ramus, ventral. D. Caudal ramus, dorsal. E. Caudal ramus, lateral. F. Exopodite of antenna. G. P1, frontal. H. P2, caudal. I. Antennule, ventral. J. P3.

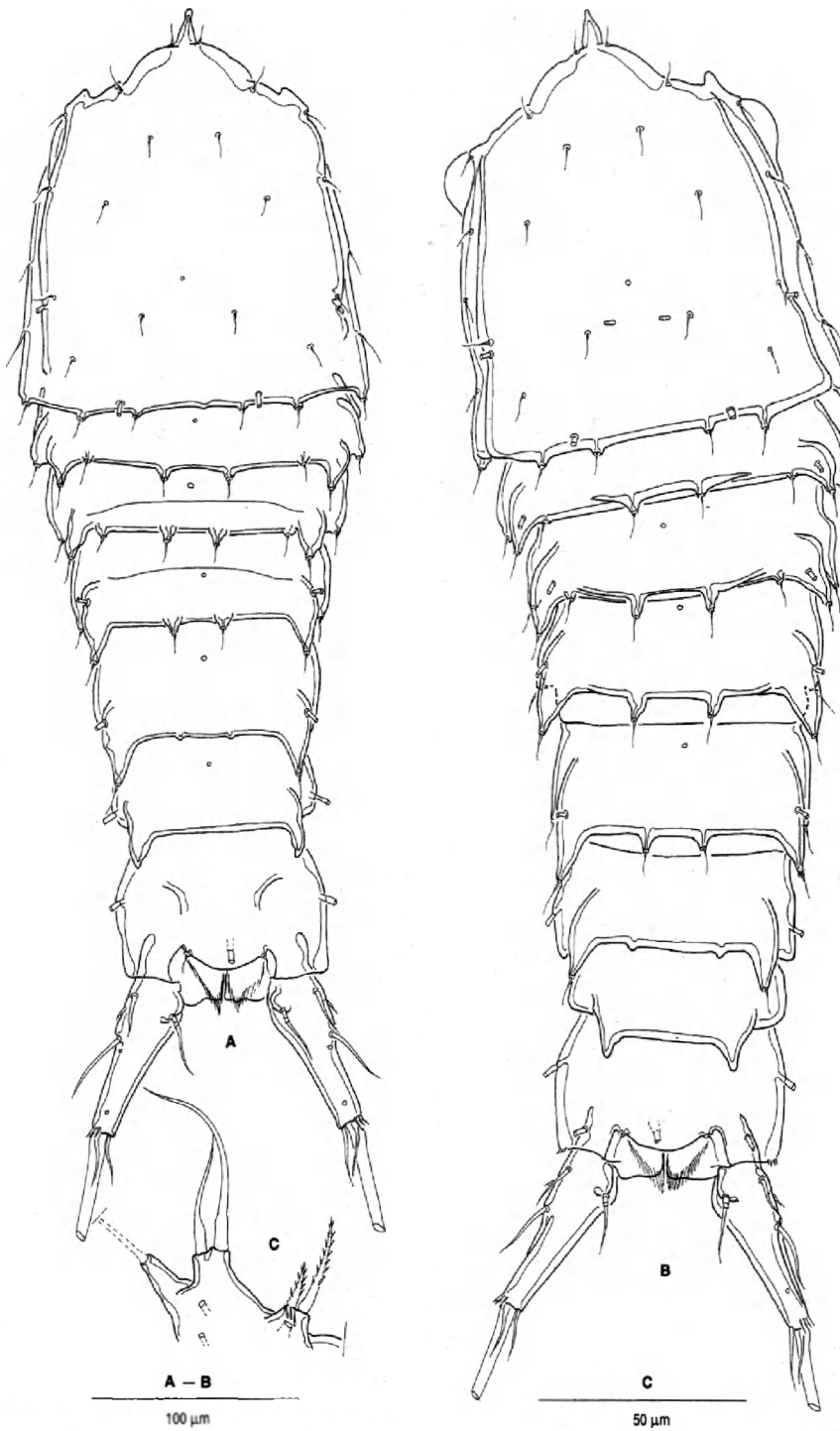


Fig. 5. *Triathrix montagni* GEF & BURGESS. A. Habitus of copepodid III, dorsal. B. Habitus of male copepodid IV, dorsal. C. P5 of male copepodid IV.

Copepodid IV (♂). Habitus (Fig. 5B). Body more cylindrical than in previous stage, 8 tagmata; length 614 µm; proportional length of head to whole body length about 1/3.5; anterolateral flaps of cephalothorax quite distinct, easily visible in dorsal view.

Posterior margin of cephalothorax and first three free somites with 10 sensillum-bearing socles: median ones distinctly more pronounced than in previous stage; fourth somite with 8, and fifth with four sensillum-bearing socles; the latter with two median rounded buds along posterior margin; preanal somite with two large dorsal conical buds, without sensilla.

Anal somite and caudal rami as in previous stage.

Antennule four-segmented, with armament as follows: I(1)-II(5)-III(7+aesth)-IV(11+aesth). Antenna and buccal appendages as in adult.

P1-P4 with two-segmented rami, showing adult setal complement; outer subdistal spine on second endopodal segments of P3 and P4 reaching just to distal margin of terminal exopodal segment.

P5 (Fig. 5C) not separated from supporting somite, having short, but distinct, endopodal and exopodal lobe; former with two smooth terminal setae, latter with two spinulose elements; outer seta of basis broken, arising from conical extension.

P6 not differentiated.

Remark. It is supposed here that this specimen is a juvenile male because of the presence of a four segmented antennule bearing 5 elements on segment II and 7 on segment III.

Sphingothrix gen. nov.

Diagnosis. As for *Triathrix* GEE & BURGESS, 1997 with in addition: P1 with terminal elements on exopodite and endopodite rigid and bipinnate; outer distal exopodal one at the most as long as outer subdistal spine, and inner terminal one inclined outwardly, intersecting outermost near base.

Etymology. The generic name *Sphingothrix* is derived from the Greek words *sphingein*, meaning to be drawn tight, and *thrix* meaning hair, and refers to the particularly tight position of the terminal elements on the P1 exopodite. Gender feminine.

Type species. *Sphingothrix goldi* sp. nov., here designated.

Other species. *Triathrix kalki* GEE & BURGESS, 1997

Sphingothrix goldi sp. nov. (Figs. 6-10)

Type material. Holotype: female, ethanol preserved, COP 4167; paratypes: 2 ♀♀, 2 ♂♂, 1 cop IV, 2 ♀♀ cop V, 1 ♂ cop V, ethanol preserved, COP 4166, 4162, 4163, and 1 ♀, 1 ♂, 1 ♂ cop V dissected, COP 4168a-b, COP 4169a-b, COP 4170a-b, respectively. All drawings from dissected specimens.

Type locality. Yucatan shelf, Campeche Bank: station 20°06.955'N 91°44.603'W, 41.5 m. (Leg. Xaman-Ek cruise II, 1 June 1993).

Additional material. 38 specimens: 7 ♀♀ (none ovigerous), 12 ♂♂, 7 cop I, 2 cop II, 3 cop III, 7 cop IV, 4 cop V (3 ♀♀, 1 ♂) from different samples in an area between 19°44.990' to 20°20.143'N and 91°31.417' to 92°00'W, ranging from depths between 35.0 m to 49.4 m. 1 ♀ specimen from the northern part of the shelf, 22°45'N 87°54.7'W, 57.5 m. All specimens ethanol preserved.

Etymology. The specific name honours Dr. Gerardo Gold Bouchot (Centro de Investigación y Estudios Avanzados, Mérida, Mexico).

Description

Female. Habitus (Fig. 6A, B). Body cylindrical, with slightly tapering urosome, and typically curved in lateral view; length, including rostrum and caudal rami, 730 µm; proportional length cephalothorax-body length: 1/5.

Integument of cephalothorax largely glabrous, showing some semi-circular shallow depressions beyond rostrum and along lateral margins and a ovate dorsomedian depression near posterior border; posterior border with four sensillum-bearing socles unified along a small but distinct chitinous extension, and two small sensillum-bearing socles forming dorsolateral edges.

Posterodorsal region of other somites densely furnished with minute spinules; ventral surface of urosomal somites smooth, their posteroventral border ornamented as in *T. kalki*; first and second free pedigerous somites with 8 sensillum-bearing socles, and four sensilla without socle; third and fourth free pedigerous somites with six sensillum-bearing socles, and two sensilla without socle; first genital somite with four dorsal sensillum-bearing socles, interconnected with a transverse ridge, and two ventrolateral ones; second genital somite with 3 sensillum-bearing socles (dorsal and lateral) and two sensilla without socles (ventrally); fourth urosomal somite with two sensillum-bearing socles (dorsal and lateral) and two sensilla without socles (ventral); prea-

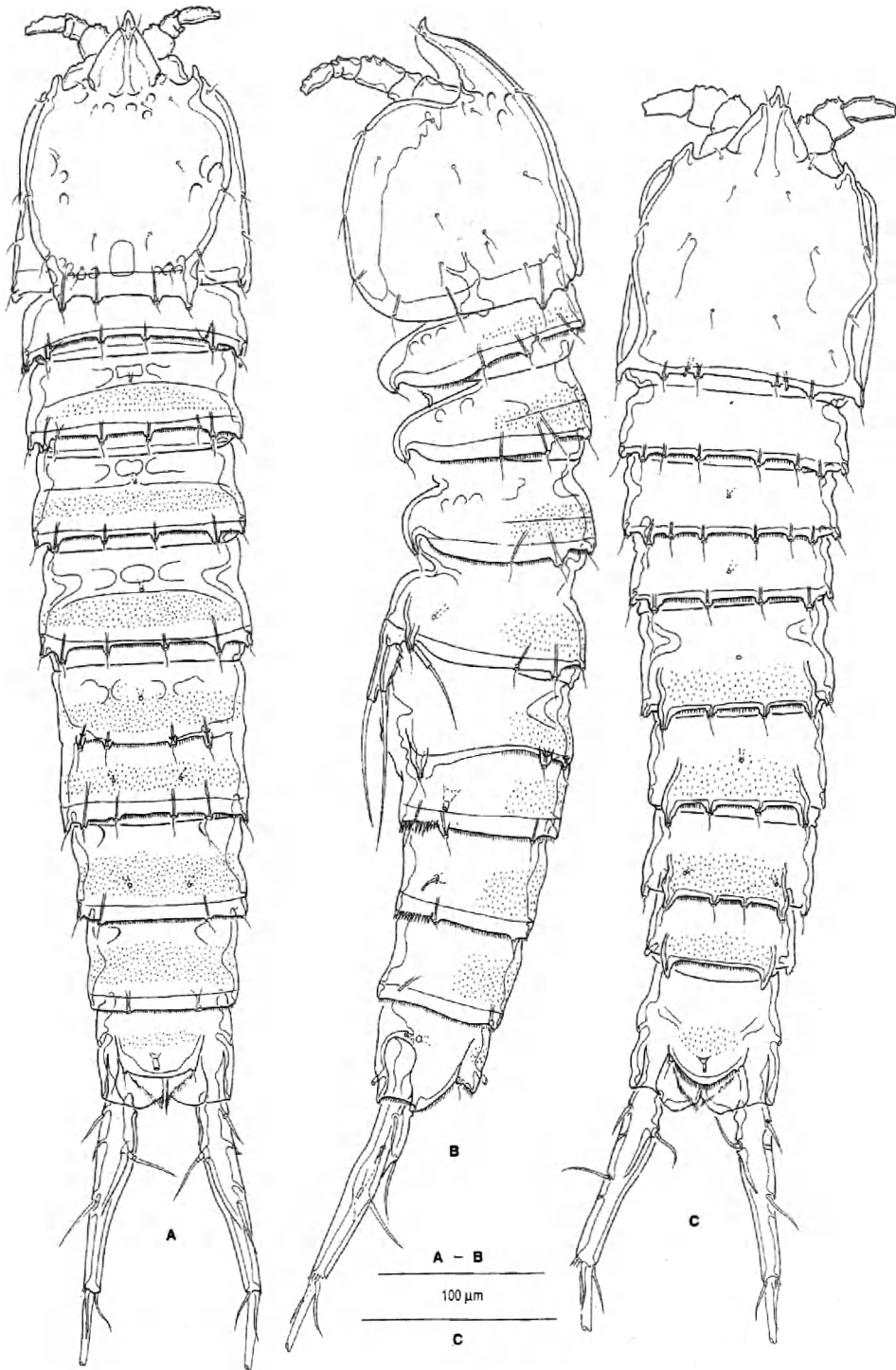


Fig. 6. *Sphingothrix goldi* sp. nov. A. Female habitus, dorsal. B. Female habitus, lateral. C. Habitus of male copepodid V, dorsal.

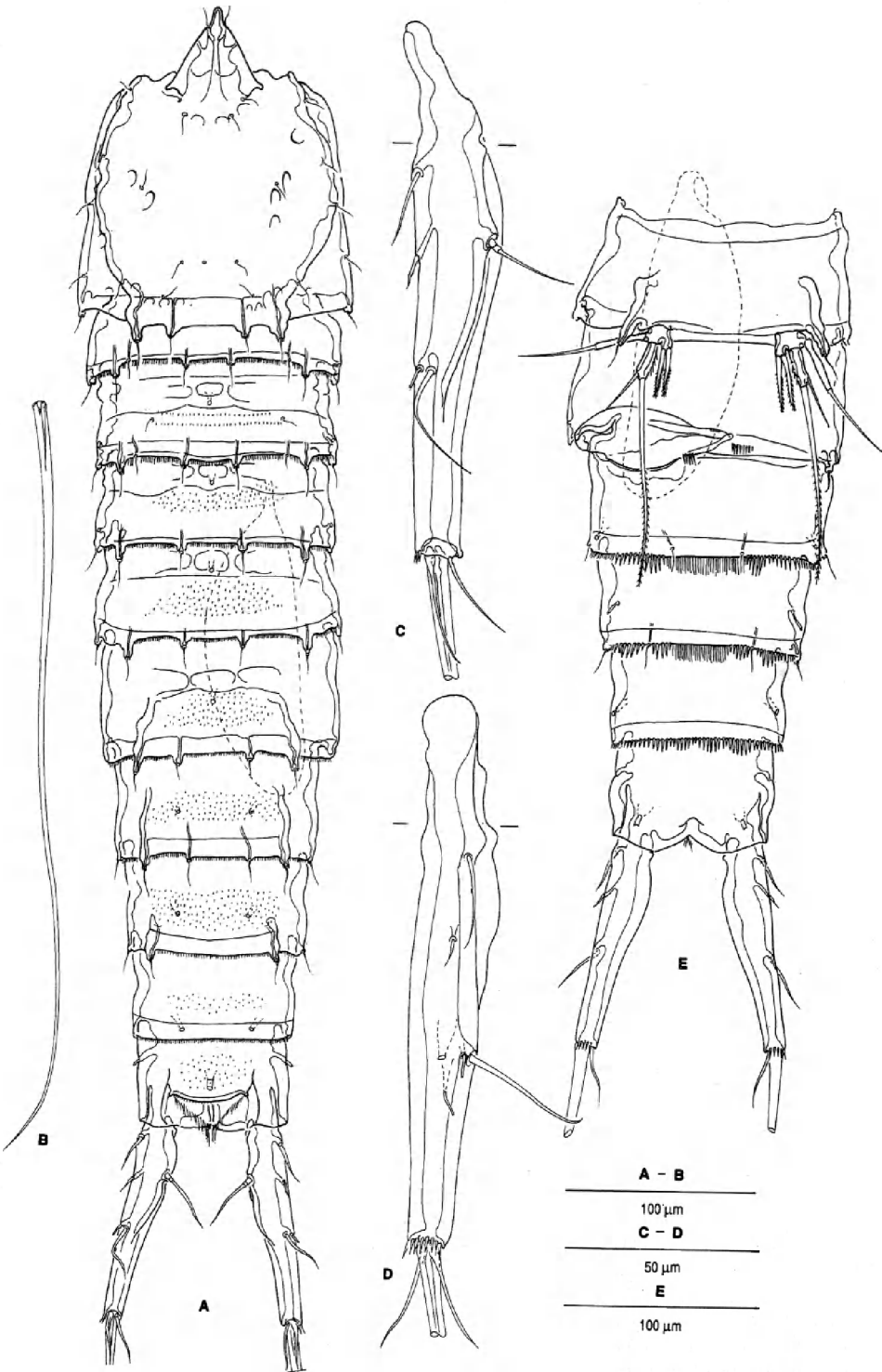


Fig. 7. *Spingothrix goldi* sp. nov. A. Male habitus, dorsal. B. Principal distal caudal setae. C. Male caudal ramus, dorsal. D. Male caudal ramus, lateral. E. Male urosome, ventral (horizontal bars in D and E indicate posterior margin of anal somite).



Fig. 8. *Sphingothrix goldi* sp. nov. A. P5 of male (?) copepodid IV. B. P5 of male copepodid V. C. P5 of copepodid III. D. P5 of female copepodid V (aberrant). E. P5 of female copepodid V (normal). F. P1 of male copepodid V, posterior. G. P5 of adult female, anterior. H. P5 of adult male, anterior. *T. kalki* GEE & BURGESS. I. P5 of female copepodid V. J. Baseoendopodite P5 of adult female, anterior.

nal somite without sensilla. Each pedigerous somite with a dorsomedian pore and one on each side; second genital to preanal somites with two dorsal and one lateral pore on each side.

Border of anal operculum almost straight, ornamented along border with minute spinules; operculum with a

dorsal median pore, and flanked by a sensillum-bearing socle on each side. Anal somite with two pairs of lateral and 1 pair of ventral pores.

Caudal rami (Fig. 7C, D) divergent, tapering posteriorly, up to 5 times as long as maximum width. Anterior lateral setae and biarticulate dorsal seta positioned in

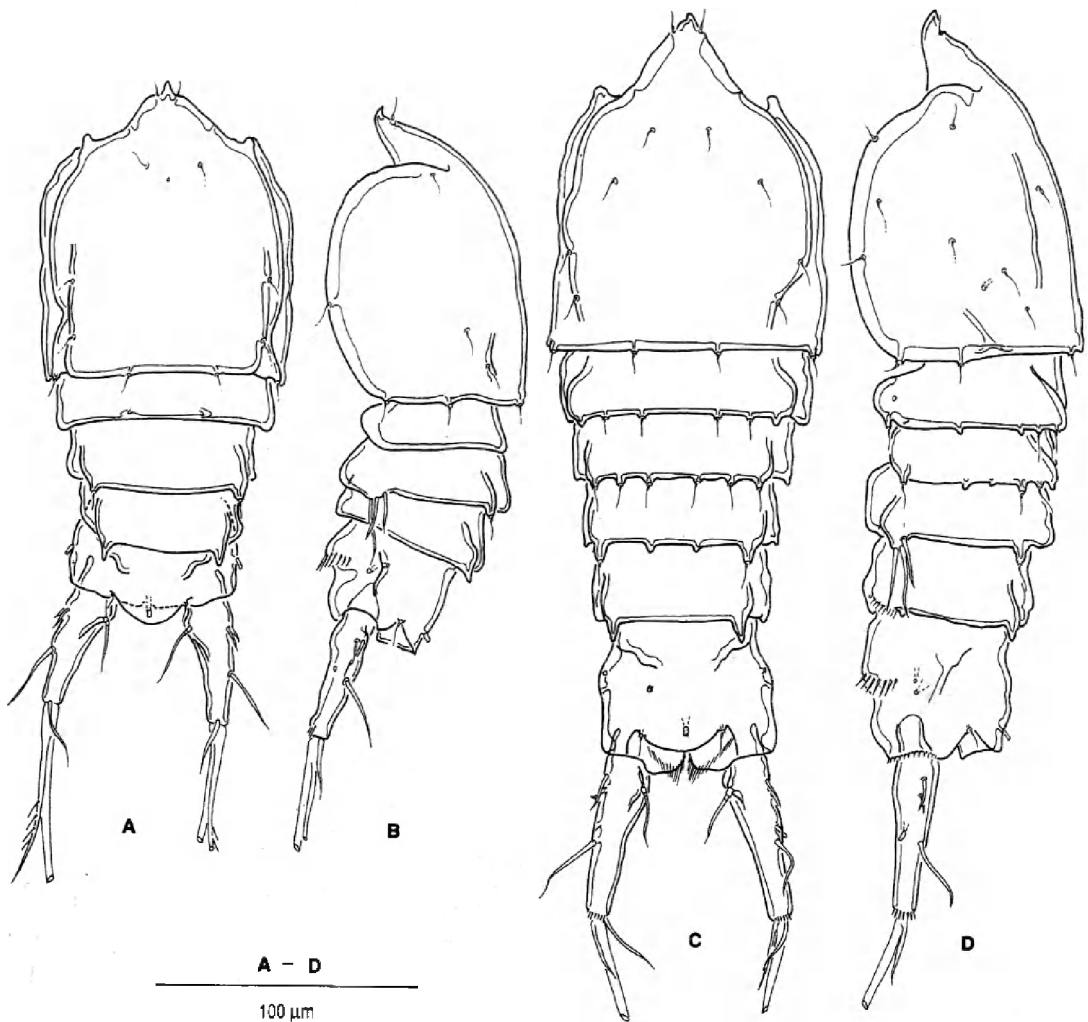


Fig. 9. *Sphingothrix goldi* sp. nov. Copepodid I. A. Habitus, dorsal. B. Habitus, lateral. Copepodid II. C. Habitus, dorsal. D. Habitus, lateral.

anterior half; the latter arising from a rigid transversal ridge parallel with inner margin; distal lateral seta implanted in distal half of outer margin; outer distal one fused with median one at base, and as long as inner distal seta. Integument of rami smooth, except for row of spinules along ventrodistal and outer lateral margin.

Cephalic appendages, rostrum, and setal shape and ornamentation of P1 and P2 as in *S. kalki*. P3-P4 as in the latter, except for outer subdistal spines on second endopodal segments being distinctly shorter, just reaching distal edge of third exopodal segments.

P5 (Fig. 8G) distinctly more compact than in *S. kalki*: endopodal lobe of baseoendopodite three times as long as wide, and exopodite two times as long as wide. Outer

setae on exopodite smooth, terminal one spinulose. Endopodal elements spinulose, inner ones shorter than length of lobe. Ornamentation and position of pores as in *S. kalki*.

Male. Habitus (Fig. 7A) as in female, except for separated genital somites; length: 693 μm (allotype, 675-700 μm paratypes). Antennule as in *T. montagni*; mouthparts and natatorial legs as in female.

P5 (Fig. 7E, 8H). Exopodite three times as long as wide, bearing a short (as long as segment) smooth outer seta and a spinulose distal element. Endopodal lobe minute, with two equally sized distal spines, reaching beyond exopodite.

P6 (Fig. 7E) roughly ovate, situated on right side, without setae. Spermatophore large, about 150 μm long, 50 μm wide.

Variability. The rigidity of the transversal ridge, marking the posterior border of the first genital somite, is less pronounced in some females than in the type-specimens. The four associated sensillum-bearing socles remain present in those specimens but are not explicitly connected. The female copepodid V (COP 4107) bears an additional inner subdistal seta on the exopodal lobe of the left P5 (arrowed in Fig. 8D).

Copepodid I. Habitus (Fig. 9A, B). Body composed of 5 tagmata, length: 240 μm , slightly curved in lateral view; proportional lengths head/body length: 1/2.5; posterodorsal margin of cephalothorax and first free somite without socles, former with two sensilla, latter without; second and third free somite with two posterodorsal socles, former sensillum-bearing, latter non-sensillum-bearing; anal somite with convex smooth operculum flanked by two sensilla, and having a median pore; ventral surface with a transverse row of spinules.

Caudal rami slightly divergent, conical, tapering posteriorly; 2.7 times as long as largest width. Both anterior lateral setae and bi-articulate dorsal seta implanted in anterior half; third lateral seta arising in posterior half of outer margin; outer terminal seta 1.5 times as long as ramus, fused with median one, and spinulose in distal half; future inner terminal seta short, smooth, and arising from dorsal distal margin.

Antennula three-segmented with following armament: I(1)-II(3+aesth)-III(1+aesth); first segment furnished with some minute spinules along anterior border, other segments smooth.

Antenna with one-segmented exopodite, bearing three elements as in adult; abexopodal setae present on allobasis; second endopodal segment bearing 1 spine less than in adult.

P1 without medial spine on basis; protopodal components defined in P1 and P2; rami of P1 and P2 one-segmented with following complement on exo/end: (P1) 0.2.IV/1.II; (P2) 0.2.III/0.2.0; position and shape of terminal elements on P1 exopodite as in adult, but outer element twice as long as outer subdistal spine.

P3 represented as a small lobe, bearing 3 smooth setae.

Copepodid II. Habitus (Fig. 9C, D). Body composed by six tagmata, length: 350 μm ; proportional lengths cephalothorax/body length: 1/3; cephalothorax with two minute posteromedian sensillum-bearing socles; first free somite with 10 socles along posterior margin: ventral one and four dorsomedian ones sensil-

lum-bearing, two lateral (on both sides) without sensilla; second free somite with 10 socles: 8 sensillum-bearing, two (one on both sides) without; third free somite having pair of strong dorsolateral sensillum-bearing socles and pair of dorsomedian non sensillum-bearing bumps; preanal somite with pair of non sensillum-bearing socles.

Anal somite and caudal rami as in previous stage, the latter slightly longer (L/W: 1/3) and with short outer terminal seta.

Antennule four-segmented with following armament: I(1)-II(5+aesth)-III(1)-IV(11+aesth); ornamentation as in Cop I. Antennule with full complement on second endopodal segment, aspect as in adult; mouth parts as in adult.

P1 and P2 with two-segmented rami; P1 having medial spine on basis; outer distal element shorter than outer subdistal one; P1 chaetotaxy as in adult, of P2 (exo/end): 0.I-0.2.II/0.0-0.2.0. P3 with one-segmented rami, complemented as follows (exo/end): 0.2.III/0.2.0; P4 as P3 in previous stage.

Copepodid III. Habitus (Fig. 10A) as in previous stage, except for additional somite; length, 385 μm ; cephalothorax showing more evolved longitudinal dorsal and lateral ridges; posterior margin of head and first two free somites each with 10 sensillum-bearing socles, with in addition two pores on head and central dorsal pore on somites; third free-somite having six (two lateral, four dorsal) sensillum-bearing socles, and following somite with four sensillum-bearing socles and two dorsomedian bumps; preanal somite showing two large and two smaller dorsal socles.

Anal somite and caudal rami as in previous stage, except for the L/W ratio of the latter, being 1/4.

Antennule four-segmented, with following armament: I(1)-II(10+aesth)-III(1)-IV(11+aesth), segmental integument as in previous stage.

P1 unchanged; chaetotaxy of P2 (exo/end): 0.I-0.2.III/0.0-0.2.0 (as in adult), and P3: 0.I-1.2.II/0.0-0.2.I with inner subdistal element on exopodite and outer subdistal element on endopodite minute, having a hyaline appearance; P4 with one-segmented rami, complemented as (exo/end): 0.2.III/0.2.0.

P5 (Figs 8C; 10B) represented as a small rounded socle, bearing two smooth setae.

Copepodid IV (σ). Habitus (Fig. 10D) resembling previous stage closely, differs in following aspects: (1) length: 460 μm ; (2) fourth free somite with six sensillum-bearing socles (two lateral, four dorsomedian); (3) fifth free somite having two sensillum-bearing and two non sensillum-bearing socles; (4) preanal somite with two distinct dorsal socles

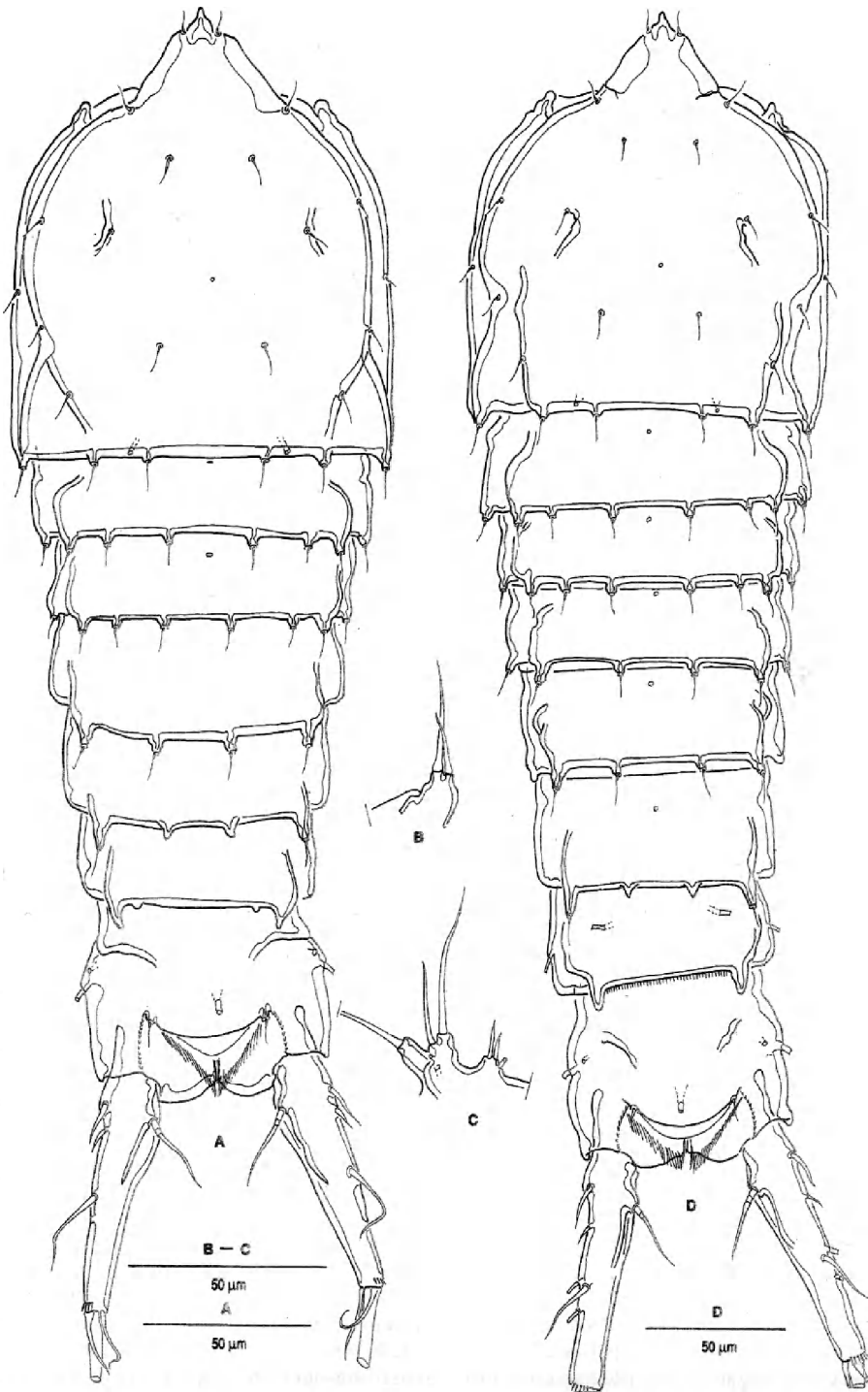


Fig. 10. *Sphingothrix goldi* sp. nov. Copepodid III. A. Habitus, dorsal. B. P5. Male copepodid IV. C. P5. D. Habitus, dorsal.

and being furnished with fragile hairs along dorsomedian border.

Antennule four-segmented with following armament: I(1)-II(6)-III(8+aesth)-IV(11+aesth). P1 and P2 as in previous stage.

P3 and P4 with two-segmented rami, having following chaetotaxy (exo/end): 0.I-1.2.III/0.0-0.2.1; inner sub-distal element on second exopodal segment, smooth, reaching just to distal end of exopodite; outer subdistal element on second endopodal segment minute, and hyaline.

P5 (Figs 8A; 10C) not separated from supporting somite, having distinct outer setiferous process, endopodal and exopodal lobe; latter two each with two short and smooth setae.

P6 not differentiated.

Copepodid V (♀ & ♂). Habitus (Fig. 6C) as in previous stage, except for additional somite; length: 600 µm; all somites with sensillum-bearing socles except preanal one; posterodorsal process of cephalothorax not differentiated.

Antennule as in adult for female, still four-segmented in male (several setae and spines broken off in observed specimen). P1-P4 with adult chaetotaxy and resembling adult appearance closely (see as example P1 Fig. 8F); outer sub-distal spine on second endopodal segment in P3 and P4 not reaching distal end of exopodite ultimate segment.

P5 not separated from supporting somite and non-articulating exopodal lobe; female P5 (Fig. 8E) with three elements on both rami, male P5 (Fig. 8B) with two elements on both rami.

P6 not differentiated

Comparison. *S. goldi* differs from its closest relative, *S. kalki*, in the following aspects: (1) the dorsomedian sensillum-bearing socles on pedigerous somites are separate, (2) the chitinous extension of cephalothorax is distinctly smaller, (3) the posterior lateral seta on caudal rami arises in second half of margin, (4) the compact aspect of the P5 in both sexes, and (5) the distinctly shorter elements on exopodite and baseoendopodite of the P5 in male and female.

The first copepodid stage of *S. goldi* is immediately distinguishable from that of *S. kalki* by the absence of socles along the posterior border of the head (sensillum-bearing) and the first free somite (non sensillum-bearing). Other differences are the more posterior position of the distalmost lateral seta on the caudal rami in *S. goldi* (positioned in anterior half in *S. kalki*), and the long outer terminal seta of the caudal rami (longer than ramus in *S. goldi*, half as long as ramus in *S. kalki*).

Copepodid stages II to IV of *S. kalki* were not avail-

able, but it is assumed that these stages are separable from those of *S. goldi* by their distinctly shorter socles on each somite, and by the proximal position of the lateral seta on the caudal rami.

Fifth copepodid stages were present for both species, and they are easily separable by the dimensions of the sensillum-bearing socles (small in *S. goldi*, distinctly larger in *S. kalki*), the length/width ratio of the caudal rami (4.85/1 in *S. goldi*; 3.75/1 in *S. kalki*), and the number of sensillum-bearing socles along the posterior border of the sixth free (future second genital) somite (6 in *S. goldi*; four in *S. kalki*).

Sphingothrix kalki (GEE & BURGESS, 1997) comb. nov. (Figs. 11; 8I-J)

Material. 4 ♀♀ (3 ovigerous), 2 ♂♂, 1 Cop I, 1 Cop II, 1 ♀ Cop V, all ethanol preserved (COP 4111-4113, 4116, 4119).

Locality. Yucatan shelf, Campeche Bank: station 19°25.231'N 91°50.355'W, 39.5 m, (3 March 1993); station 19°24.792'N 91°50.791'W, 40.2 m, (1 July 1993).

Description

The species was described in detail by GEE & BURGESS (1997). The description is amended here with some additional morphological details observed on adult specimens and on two of its copepodid stages.

Adult. Habitus. In addition to the sensillum-bearing socles and ventrolateral pores as originally described: each prosomal somite with a dorso-median pore in anterior half; second genital somite and following one with two dorsal pores situated on inner side of the ridge forming the sensillum-bearing socle; preanal somite with two dorsal pores, and anal somite with, on each side, two lateral pores and 1 ventral, and a single dorso-median one on anal operculum.

Integument glabrous, except for some ovate shallow depressions on cephalothorax near the fusion line with rostrum; posterodorsal and lateral borders of all free somites ornamented with slender setules.

P3-P4 endopodites with outer subdistal spine on second segment reaching far beyond distal margin of third exopodal segment.

P5 (Fig. 8J) with general appearance and ornamentation as originally described, except for the following: distinctly larger spinules along inner margin and on posterior face of baseoendopodite, and more rigid and curved appearance of the subdistal spine of baseoendopodite.

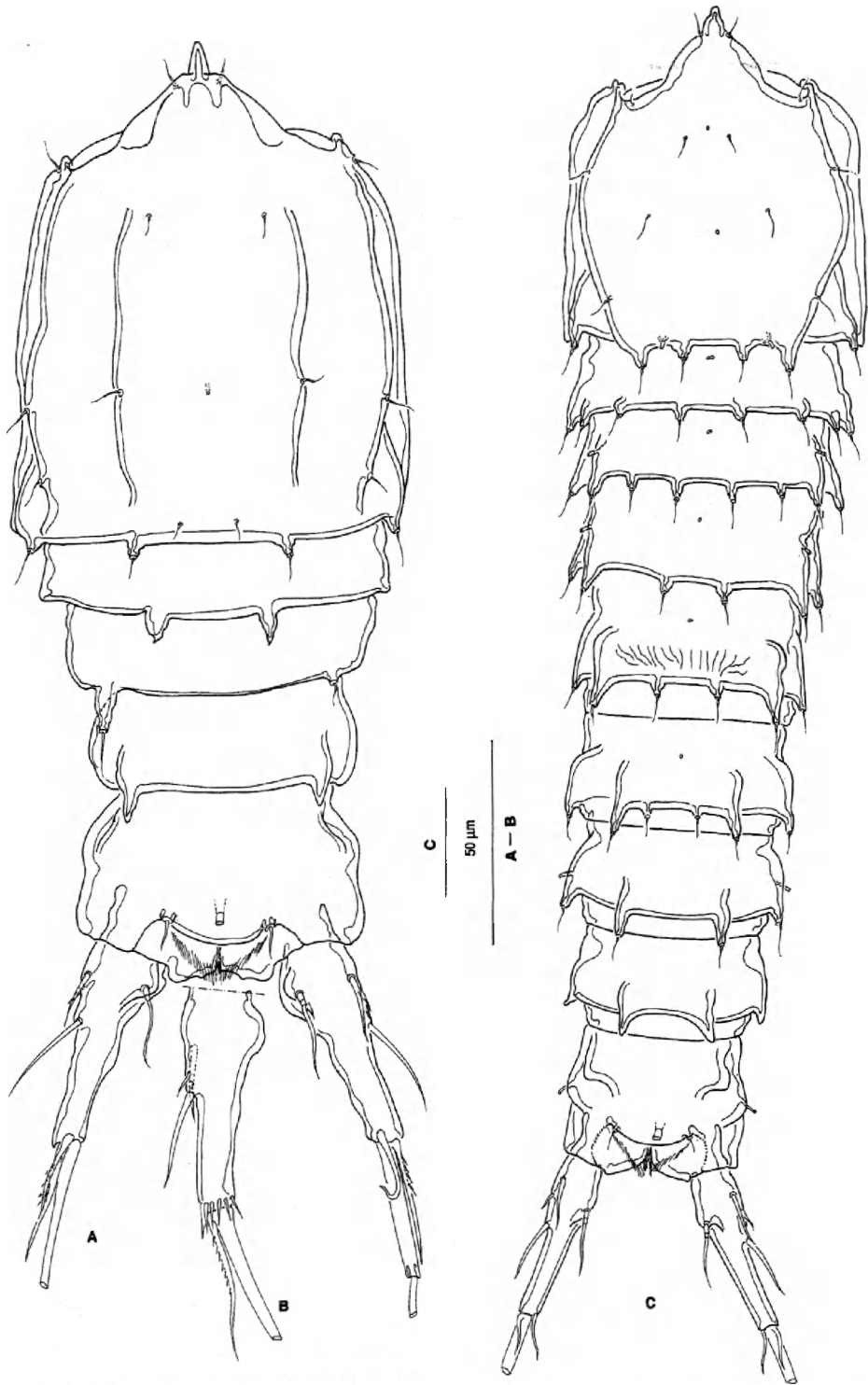


Fig. 11. *Sphingothrix kalki* (GEE & BURGESS, 1997) comb. nov. A. Habitus, copepodid I, dorsal. B. Caudal ramus copepodid I, ventral. C. Habitus female copepodid V, dorsal.

Copepodid I. Habitus (Fig. 11A). Compact body, distinctly curved in lateral view, with divergent caudal rami; body with 5 tagmata; length, including rostrum and caudal rami, 267 μ m. Cephalothorax with folded lateral margins and two longitudinal sclerotized dorsal lines; posterior border with four sensillum-bearing socles; first and third pedigerous somites without sensilla but with two conical socles along posterior border; second pedigerous somite with two sensillum-bearing socles (left one small, right one large, the latter probably the normal appearance).

Anal somite with convex and smooth anal operculum, flanked by two small sensillum-bearing socles; median pore on anal operculum present; two short median rows of slender spinules on ventral surface.

Caudal rami conical, slightly longer than 2.5 times the width, bearing 7 elements; both anterior lateral setae implanted closely together at same height of biarticulate dorsal setae; outer distal seta long and ornamented with spinules along outer margin of stem; median distal seta smooth (not fully expanded in specimen at hand); future inner distal seta with dorsal position, half as long as outer one; posteroventral margin of rami with six slender spinules (Fig. 11B).

Rostrum broadly triangular with distinctly upward curved blunt tip and two sensilla. Antennule three-segmented with following armature: I(1)-II(4+aesth)-III(11+aesth); third segment with trithek formed by two setae and aesthetasc. Antenna with allobasis, bearing two pinnate setae on the abexopodal margin; exopodite as in adult, except for proportional larger distal smooth seta; endopodite with three lateral elements; distal margin with five elements: two geniculate setae, two spines and a minute smooth seta fused to basis of outer spine. Mouthparts as in the adult.

P1 and P2 with distinct protopodal segments, and one-segmented rami. Chaetotaxy of P1 as in adult, except for absence of medial spine on basis; exopodite with outer distal seta pinnate, straight, about 1.5 times longer than outer subdistal spine, and inclined in front of inner distal seta. P2 exopodite with three outer spines and two distal setae; endopodite P2 with one apical seta. P3 represented as a small but distinct lobe on third pedigerous somite, bearing three smooth setae.

Copepodid V (♀). Habitus (Fig. 11C) resembling adult habitus closely, but less recurved in lateral view; body with 9 tagmata, 600 μ m long including rostrum and caudal rami.

Chitinous postorodorsal extension of head differentiated, but less pronounced than in adult, having four sensillum-bearing socles and one pair of pores; posterolateral margin with an additional sensillum-bearing socle; first and second free pedigerous somites with 8,

third to fifth with six sensillum-bearing socles, all with a dorsomedian pore orifice; sixth free somite with four sensillum-bearing socles and two lateral pore orifices; seventh with free somite having four socles without sensillum. Integument of all tagmata finely striated dorsally and laterally.

Anal somite large, with strongly folded lateral margins, and a smooth convex anal operculum; two pairs of lateral pores, 1 pair ventrally, and 1 dorsomedian on operculum; ventral surface with a transversal row of long spinules.

Caudal rami resembling those of adult, but only four times as long as wide; lateral setae and dorsal setae implanted in anterior half; inner and outer distal setae short, about 20 % of ramus length.

Antennule five-segmented with aesthetascs on segment III and V, and chaetotaxy as in adult; antennule of specimen with several setae and spines detached. Antenna and mouthparts as in adult.

P1-P4 with three-segmented exopodites and two-segmented endopodites; chaetotaxy as in adult; appearance of rami more compact than in adult (see for example Fig. 8F).

P5 (Fig. 8I) not articulating with supporting somite, having equally long endopodal and exopodal (not articulating) lobe, each bearing three elements; one pore orifice on endopodite, two on exopodite; outer seta of basis arising from cylindrical extension; P6 vestiges not differentiated.

GENERAL DISCUSSION

Including the here described species, four out of the five known species attributed to the genera *Triathrix* and *Sphingothrix* are fully described and can be compared in detail. Only the adult morphology of *T. nicobarica* is unknown and the copepodid morphology of the appendages is far less precisely known than for its congeners. Unfortunately, this specimen seems to be lost for good, and we will have to wait until new material is collected to fill out the gaps in our knowledge. However, from SEWELL's illustration (1940: fig. 85) we obtain the following 6 features: (1) the distal exopodal segment of P1 has two seemingly rigid long elements, (2) the P1 endopodite has only two terminal elements on its distal segment, (3) the outer subdistal spines on the second endopodal segments of P3 and P4 are very long reaching beyond the distal margin of the third exopodal segment, (4) the inner (?) distal seta on the caudal rami equals approximately 75 % of the supporting ramus, (5) the dorsal seta on the caudal rami has a nearly median position close to the inner margin, and (6) the preanal somite of the fifth copepodid stage shows no modification into socles.

Based upon the observations on copepodid morphology of *S. kalki*, *S. goldi* and *T. montagni*, it is assumed that from the six juvenile features mentioned above, 5 (numbers 1 to 5) will be present in the adult stage of *T. nicobarica*. These key characteristics displayed by the juvenile allow us to discriminate *T. nicobarica* definitely from all other species of this lineage and assigned to the genera *Triathrix* and *Sphingothrix*.

Two of the juvenile features exhibited in *T. nicobarica* deserve closer attention in order to illustrate its particular place within the herein discussed lineage.

The illustration of the P1 of this species (SEWELL 1940: fig. 85) shows that there are two long rigid spinulose terminal elements (longer than the subdistal outer spine) on the third exopodal segment. Except for the length of the outermost terminal element, only the species in *Sphingothrix* show a comparable rigid morphology of both terminal elements in this leg. In addition, the outwardly tilted position of one of these elements in *T. nicobarica* resembles strongly the setal direction of the terminal appendages in two known species of the genus *Sphingothrix*. Although the illustrations in SEWELL (1940) may appear rudimentary at first sight, it is believed here that this author explicitly drew attention upon the shape and morphology of setae and spines. This can easily be conceived from his illustrations made from the appendages of the other harpacticoids collected during the John Murray 1933-34 expedition.

When in *Sphingothrix* the inner element is outwardly directed and the outer one is produced vertically, it seems that we have a reversed situation in *T. nicobaricum* with the outer one inclined and the inner element in a vertical position. But it should be noted that only close examination of the implantation of both terminal elements reveals the exact implantation. As a matter of fact the distal border of the distal exopodal segment is quite narrow, and the implantation of the inner seta is rather hidden behind that of the outer appendage (see GEE & BURGESS 1997: fig. 8D). Thus it seems reasonable to suggest that SEWELL overlooked the exact implantation of both elements on the P1.

In addition, it is quite interesting to note that the length of the outer terminal exopodal segment of the P1 in the first copepodid of *S. goldi* and *S. kalki* is much longer than the outer subdistal one. During the moult to stage II, the outer terminal element receives its typical length, being at the most equal in length with the outer distal one. Thus it appears that this copepod constraint is not present in *T. nicobarica*, which will result in an adult P1 with two (nearly equally sized) terminal elements on the exopodite.

Secondly, the absence of socles (non sensillum-bearing) on the preanal somite in the fifth copepodid stage

of *T. nicobarica* contrasts fundamentally with the substantial modifications along the posterior border of this somite observed in the juveniles of *T. montagni*, *S. goldi* and *S. kalki* (see Figs. 5B; 6C; 11C, respectively). In fact, the dorsal aspect of the fifth copepodid stage *T. nicobarica* resembles more the adult body of the other species (except for the absence of a cephalic process and the preanal somite) than their preadult stage. As such it is speculated that the dorsum of the last urosomal somites in the adults of *T. nicobarica* may be quite differently ornamented (without socles ?) than in its congeners.

Taking these two points in consideration, it is reasonable to think that when adults of *T. nicobarica* or related species will be discovered, it will be necessary to remove this species from its present genus and to define a separate taxon within the *Triathrix-Sphingothrix* lineage of the Cletodidae. For the moment, and for the sake of taxonomic stability, the species is kept in the genus *Triathrix* in accordance with GEE & BURGESS (1997), solely on the fact that the terminal elements on the P1 exopodite are longer than the outer spines.

FIERS (1996) speculated on the ramal development constraints in the family Cletodidae, and considered the copepodid leg morphology of *T. nicobarica* (named *Enhydrosoma nicobaricum*) as intermediate between the classical development displayed in *Cletodes* and the advanced developmental constraint in *Enhydrosoma*. The observations on the copepodids of the herein described species confirm the intermediate position of the genera *Triathrix* and *Sphingothrix* between the two other developmental suites. In addition, it was shown that the setal complement evolves in the same way during development of *Cletodes* and *Enhydrosoma*. The serial addition of setal armament in the genera *Triathrix* and *Sphingothrix* follows the same succession as in the two other genera with a full complement for P1 from copepodid I on, and an adult number of setae and spines is present on the other legs in the third (for P2) and fourth (for P3 and P4) copepodid stage.

PRELIMINARY ECOLOGICAL DATA

The genera *Triathrix* and *Sphingothrix* form part of the deeper sublittoral meiofaunal associations. *T. montagni* was found at depths ranging from 91 m to 167 m in the Santa Maria Basin off California (GEE & BURGESS 1997; Fiers pers. obs.) while *S. kalki* was recovered from Flower Garden Banks, off Louisiana, at depths ranging from 110 to 160 m (GEE & BURGESS 1997). In the southern bight of the Gulf of Mexico, *S. kalki* was collected in a single station at 40 m depth, and the sole specimen of *T. mayae* was found at 38 m depth. The third species

occurring in the Campeche Bay, *S. goldi*, has a depth distribution ranging from 29 m to 144 m deep. Only *T. nicobarica* seems to have been collected at more shallow depths in Nankauri Harbour (Nicobar Islands, SEWELL, 1940).

Densities of *S. goldi* are low. The maximum density for the species was estimated at 10.01 ind/10 cm², representing 6 % of the total harpacticoid community in this station. The maximum density found for *S. kalki* was 12.40 ind/10 cm² in March. In this sample *S. kalki* constituted 21.21 % of the total harpacticoid community. However this station is situated close to the oil drilling sites (19°25.231'N 91°50.355'W) and shows an aberrantly low meiofaunal density (maximum of only 219 ind/10 cm² of total meiofauna).

Specimens are rarely found in sediments below the 2 cm top interval. Only two copepodids of *S. goldi* (CI and CIII), and 1 adult male of *S. kalki* were sorted out from the sediment fraction between 2 and 4 cm deep but were probably displayed towards this level during the extrusion of the sediments from the cores.

S. goldi was found in the samples obtained during the three cruises (March, July and October 1993) with most (70 %) of its copepodids present in the March samples. Throughout the year adult male specimens were present but female adults were most abundant in July. The younger copepodid stages (CI-CIV) were found in the March and October samples. The July samples, characterized by their low densities of this species, contained only older copepodids (CIV and CV) among adult males and females.

S. kalki was present in the March samples of one station (see above) with 8 adults (3 ovigerous ♀♀ out of 4 and 4 ♂♂) and a single copepodid I. The July samples of the same station contained only copepodids (1 CII and 1 ♀CV) whereas this species was not detected anymore in the samples obtained in October.

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