

# Cletodes confusum sp. nov., C. pseudodissimilisoris sp. nov., and Stylicletodes longicaudatus (Copepoda: Harpacticoida: Cletodidae) from a coastal lagoon in south-eastern Gulf of California (Mexico)

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**Abstract:** The description of *Cletodes confusum* sp. nov. and *C. pseudodissimilisoris* sp. nov., and new records of *Stylicletodes longicaudatus* from a coastal lagoon in North-western Mexico are presented. *Cletodes confusum* sp. nov. proved closely related to *C. tenuipes* and *C. endopodita*. Autapomorphies for *C. confusum* sp. nov. are the shape of the female caudal rami, position of setae VII, I and II, female P5 morphology, and relative length of setae of female P5 exopod. *Cletodes pseudodissimilisoris* sp. nov. is closely related to *C. pseudodissimilis* Coull, 1971. These two species can be separated by subtle differences such as the dorsal ornamentation along the posterior edge of pro- and urosomites, ventral ornamentation of the fourth and fifth urosomites, ornamentation of caudal rami, position of the inner and subapical outer setae of the female P5 exopod, and relative size of the baseoendopodal setae of female P5. *Cletodes pseudodissimilisoris* is defined by the presence of two sets of spinule rows along the posterior edge of the female anal somite.

**Résumé:** Cletodes confusum *sp. nov.*, C. pseudodissimilisoris *sp. nov.*, *et* Stylicletodes longicaudatus, *d'une lagune côtière au sud-est du Golfe de Californie*. La description de *Cletodes confusum* sp. nov. *C. pseudodissimilisoris* sp. nov. et un nouveau signalement de *Stylicletodes longicaudatus*, provenant d'une lagune au nord-ouest du Mexique sont présentés. *C. confusum* est étroitement liée à *C. tenuipes* et *C. endopodita*, étant donné la forme générale similaire de la furca chez la femelle. Les autapomorphies observées pour *C. confusum* sp. nov. sont la forme de la furca et l'endroit d'insertion des soies VII, I et II, la morphologie de P5 chez la femelle, la longueur des soies de l'exopode des péréiopodes 5 de la femelle. *Cletodes pseudodissimilisoris* sp. nov. est étroitement liée à *C. pseudodissimilis*. Ces deux espèces peuvent être séparées par l'ornementation dorsale le long du bord postérieur des segments thoraciques et abdominaux, l'ornementation ventrale du quatrième et cinquième segment abdominal, l'ornementation de la furca, l'endroit d'insertion de la soie interne et subdistale de l'exopode des péréiopodes 5 de la femelle. *Cletodes pseudodissimilisoris* sp. nov est caractérisée par deux groupes d'epines au bord postérieur du segment anal de la femelle.

Keywords: Copepoda, Harpacticoida, Cletodidae, Systématique, Mexique

# Introduction

Reçu le 10 juin 1999; accepté après révision le 19 mai 2000. Received 10 June 1999; accepted in revised form 19 May 2000. In 1991, the Mazatlán Marine station of the Institute of Marine Sciences and Limnology (National Autonomous University of Mexico), began a short-term study on the impact of organic enrichment on the distribution and abundance of meiofauna in a coastal lagoon in the southeastern Gulf of California (Mexico) (Gómez-Noguera & Hendrickx, 1997), an area that had been neglected thus far. During this study 63 harpacticoid species were identified, most of which proved new to science. This contribution deals with the description of two new species of the genus *Cletodes*, and a new record of *Stylicletodes longicaudatus* (Brady & Robertson, in Brady (1880)).

## Material and methods

Quantitative triplicate sediment samples were taken in Ensenada del Pabellón lagoon (Sinaloa, North-western Mexico), using a 7 cm<sup>2</sup> plastic corer. Meiofauna was separated from macrofauna using 500 and 63 µm sieves. Harpacticoids were sorted under a dissecting microscope, counted and preserved in 70% ethanol. Dissected parts of the harpacticoids were mounted in glycerin and sealed with nail polish. Observations were made at 1000X, 1250X and 2500X, drawings were made at 1000X and 1250X, using a Leitz Periplan phase contrast light microscope equipped with a drawing tube. The type material was deposited in the collections of the Mazatlán Marine Station of the Institute of Marine Sciences and Limnology (National Autonomous University of Mexico). The terminology proposed by Huys & Boxshall (1991) was adopted. Abbreviations used in the text and tables: P1-P6, first to sixth leg; EXP, exopod; ENP, endopod.

# **Systematics**

Family Cletodidae T. Scott, 1905 Genus *Cletodes* Brady, 1872 *Cletodes confusum* sp. nov. (Figs 1-7)

Type locality: Ensenada del Pabellón lagoon, Sinaloa, Mexico (24°19'-24°35'N, 107°28'-107°45'W).

Type material: Female holotype (EMUCOP-030192-22), male allotype (EMUCOP-030192-23), three dissected male paratypes (EMUCOP-020591-10, EMUCOP-030192-27, EMUCOP-030192-28), three dissected female paratypes (EMUCOP-030192-25, EMUCOP-240691-11, EMUCOP-030192-26), and one female paratype preserved in alcohol (EMUCOP-030192-24); all collected from intertidal, mud to fine sand (June 1991, May 1991, January, 1992); coll. S. Gómez.

Etymology. The specific name is derived from the Latin *confusum* (confused) and alludes to the close relationship of the new species with *C. endopodita* (Schriever, 1984), and *C. tenuipes* T. Scott, 1896.

## Description Female

Habitus (Figs 1A-B) fusiform, tapering from the posterior margin of the cephalothorax to the anal somite. Length ranging from 409 to 422 µm, including rostrum and caudal rami. Body length/length of cephalothorax ratio 5.4; greatest width near posterior edge of cephalothorax and first pedigerous somite. Cephalothorax with folded lateral sides and dorsal pair of longitudinal ridges; posterior margin with sensilla. Rostrum fused to cephalothorax; with curved tip, set with fragile setules. Surface of free body somites (except anal somite) smooth except for a number of sensilla (6-8) around posterior margin; second to fourth urosomite with a lateral sensillum arising from a conical projection on each side; surface of fourth and fifth urosomites smooth, the former with only four dorsal sensilla around posterior margin, the latter having only two dorsal pores. Ventral



Figure 1. *Cletodes confusum* sp. nov., adult female. A habitus, dorsal; B habitus, lateral; C anal somite and caudal rami, dorsal.

**Figure 1**. *Cletodes confusum* sp. nov., femelle adulte. A habitus, vue dorsale ; B habitus, vue latérale ; C segment anal et furca, vue dorsale.

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Figure 2. *Cletodes confusum* sp. nov., adult female. A antennule; B antenna; C labrum; D mandible; E distal part of mandibular gnathobasis; F maxillule; G maxilla; H maxilliped.

**Figure 2**. *Cletodes confusum* sp. nov., femelle adulte. A antennule ; B antenne ; C labre ; D mandibule ; E partie distale de la mandibule ; F maxillule ; G maxille ; H maxillipède.

surface of genital double-somite (Fig. 3A) smooth except for fine setules along posterior margin, spinules on lateral conical projections and vestigial P6; fourth and fifth urosomites with similar ornamentation except for spinules around posterior margin being coarser. Dorsal surface of anal somite (Fig. 1C) smooth except for small spinules along posterior margin, with serrate operculum, flanked by a sensillum on either side; ventral surface (Fig. 3A) with few spinules along posterior margin. Caudal rami (Figs 1A-C, 3A), twice as long as anal segment, L/W ratio ranging from 3.7 to 5.6 measured at the maximum width; narrow at base and somewhat swollen in proximal half; with minute spinules near posterior edge; with seven elements, setae VII, I and II inserting at approximately the same level (seta VII slightly more distal than seta I and II), seta III located in distal third, setae V and IV fused, setae VI and IV about the same length (Fig. 1C).

Antennule (Fig. 2A) five-segmented; surface of segments smooth except for spinules on segment 1; segment 2 about 1.5 times as long as wide; segment 4 short and narrow; with aesthetasc on third and last segment. Armature formula: 1-[1], 2-[8], 3-[7+ae], 4-[1], 5-[10+ae]. Antenna (Fig. 2B): allobasis ornamented with spinules along inner edge, with abexopodal seta in distal half. Exopod one-segmented, elongate, with one distal plumose seta. Endopod with spinules along inner margin and subdistally; with two lateral spines, and six distal elements (two outermost setae fused, outermost very small).

Labrum as in Fig. 2C.

Mandible (Figs 2D-E): gnathobase with six distal teeth and two subdistal setae; palp short, ornamented with some spinules and with one lateral, one subdistal and three apical plumose setae.

Maxillule (Fig. 2F): arthrite ornamented with six terminal spines (two of them swollen medially), two lateral setae and two anterior surface elements; coxa with two slender setae; basis with four distal, and three subapical and two lateral setae representing incorporated endopod and exopod.

Maxilla (Fig. 2G): syncoxa ornamented with spinules along inner and outer edges, with two endites, proximal one with three, distal one with four setae; allobasis with bare claw and three setae. Endopod represented by two elements.

Maxilliped (Fig. 2H), subchelate; syncoxa ornamented with spinules, with one distal seta. Basis with spinules along inner margin;

endopodal claw barely armed, with one accompanying seta.

P1 (Fig. 3B): coxa ornamented with some median spinules and some spinules close to outer distal corner. Basis ornamented with some spinules at base of inner and outer seta, and between rami. Exopod three-segmented, reaching almost to tip of endopod, the latter two-segmented. The first endopodal segment small, slightly broader than long, second segment about five times longer than first one. Armature formula as follows:

EXP	0.0.022
ENP	0.011



Figure 3. *Cletodes confusum* sp. nov., adult female. A urosome, ventral; B P1; C, P2.

Figure 3. *Cletodes confusum* sp. nov., femelle adulte. A urosome, vue ventrale ; B P1 ; C P2.

P2-P4 (Figs 3C, 4A-B): coxa with row of spinules in the middle and close to outer distal corner; basis with (P2 and P3) or without (P4) spinules near base of endopod. Exopods three-, endopods two-segmented. Second endopodal segment with only one apical seta. Endopod of P2 slightly longer than second exopodal segment, of P3 hardly reaching tip of second exopodal segment, of P4 slightly beyond first exopodal segment. Armature formula as follows:

	P2	P3	P4
EXP	0.0.022	0.0.022	0.0.022
ENP	0.010	0.010	0.010

P5 (Fig. 4C): squarish baseoendopod with long cylindrical setophore bearing outer basal seta. Endopodal lobe represented by a single seta; with an inner hyaline tube-pore (arrowed in Fig. 4C). Exopod elongate, with one lateral and one subapical outer seta (the former shorter), one inner subdistal element and two apical setae; the inner subdistal

and the apical outermost setae of about the same length, and about 1/3 the length of the innermost apical seta; with a long distal tube-pore (arrowed in Fig. 4C).

P6 (Fig. 3A), represented by a plate in the middle of first genital somite; each vestigial leg represented by a single seta. Copulatory pore in posterior half of first genital somite, difficult to discern.

# Male

Habitus (Figs 5A-B, 6A-B) as in female, except for genital and first abdominal somites separate. Length ranging from 425 to 450 µm, including rostrum and caudal rami; slightly longer than in female. Ventral surface of third to fifth urosomites smooth except for spinules around posterior margin; anal somite as in female; caudal rami more cylindrical than in female, without swollen proximal part.

Antennule (Fig. 7A) six-segmented, sub-chirocer; fourth segment swollen, with longitudinal row of spinules; with aesthetasc on fourth segment. Armature formula: 1-[1], 2-[9], 3-[7], 4-[6+ae], 5-[2], 6-[9].

Mouthparts, P1 and P2 (not illustrated), as in female.

P3 (Fig. 7B): coxa, basis and first exopodal segment as in female. Second exopodal segment with strong outer spine; third segment narrower than in female. Endopod three-segmented, first segment as in female, second one with long inner hyaline distal apophysis, third segment small with one seta.

With regard to P4 (Fig. 7C), the second endopodal segment showed to be somewhat wider than in female.

P5 (Fig. 7D): baseoendopod as in female except for seta representing endopodal lobe. Exopod with four elements.

Variability. The only variability observed was in the L/W ratio of caudal rami, from 3.8 to 5.6 for females and from 6.7 to 7.7 for males.

#### **Comparison and discussion**

Seven species assigned to Cletodes (C. carthaginensis Monard, 1935, C. reductus Moore, 1977, C. smirnovi Bodin, 1970, C. setosus Marinov & Apostolov, 1985, C. tuberculatus Fiers, 1991, C. tenuipes T. Scott, 1896, and C. endopodita [Schriever, 1984]) share the reduced armature formula of the second endopodal segment of P1 (with two setae only). Cletodes carthaginensis, C. reductus and C. smirnovi have all been described as possessing two setae on the second endopodal segment of P2. Although Monard's collections are no longer available, there is no doubt about the presence of two well developed setae on the second endopodal segment of P2 in C. carthaginensis (see Monard, 1935, : 92, fig. 110). From the seven species mentioned above, C. carthaginensis is unique in the armature formula of P1-P4 and shares the same armature formula of P2 and P3 with C. millerorum Hamond, 1973, C. reyssi Soyer, 1964,



C P5.

Figure 4. Cletodes confusum sp. nov., femelle adulte. A P3; B P4; C P5.

C. dissimilis Willey, 1935, and C. pseudodissimilis Coull, 1971. The new species also shares the same armature formula of P2-P4 with C. limicola Brady, 1872. Cletodes carthaginensis seems to be unique in the armature of the female exopod of P5 (with four setae only) and its fusion to the baseoendopod. The antennule, antenna, mandible, maxillule, maxilla and maxilliped of C. carthaginensis have not been described and hence no comparisons can be made. Due to the deficiencies in Monard's original description and to the absence of any available material, Hamond (1973) suggested to exclude C. carthaginensis as a valid species until its rediscovery and redescription (a view not supported by Fiers, 1991).

Cletodes reductus was described by Moore (1977) with one well developed and one very small seta on the second endopodal segment of P2. Bodin (1970) also reported the presence of one well developed and one very small seta on the second endopodal segment of P2 in C. tenuipes and C. smirnovi from an intertidal mudflat at Châtelaillon (France), suggesting that this could be the right armature formula for C. tenuipes. As stated by Bodin (1970), the small inner seta could be mistaken for the surrounding spinules, a concept also supported by Hamond (1973 :478). Since the small inner seta is hard to discern should not be considered for phylogenetic analyses unless its presence or absence is definitely confirmed. Bodin (1970) also illustrated the female P5 of C. smirnovi with two setae on the baseoendopodal lobe. The innermost of these setae is in all probability a very long tube-pore which has

also been observed in C. confusum sp. nov., C. tuberculatus, and in Bodin's C. tenuipes. This could be the case for C. reductus and also C. endopodita, the latter also having been described with one well developed and one small inner seta on the second endopodal segment of P4. Schriever (1984: 65, 68, fig. 13) pointed out the presence of four setae on the lateral margin of the caudal rami of C. endopodita. This, however, must be a misinterpretation. The proximal set of setae on the lateral margin of the left caudal ramus most probably corresponds to setae VII, I and II.

Cletodes confusum sp. nov. appears most closely related to C. tenuipes and C. endopodita. These three species belong to Hamond's (1973, 480, table ·3A, B) type B (see also Fiers, 1996, :23), and Gee's (1994) type 3 according to the male P3 endopod being defined as the most advanced character state of the male P3 found within Cletodes (Fiers, 1996). These species have in common the armature formula of P1-P5, except for the small inner seta on the second Figure 4. Cletodes confusum sp. nov., adult female. A P3; B P4; endopodal segment of P2 observed by Bodin (1970) in C. tenuipes from Châtelaillon and the inner seta on the second endopodal segment of P4, observed by Schriever (1984) in C. endopodita, which may have been mistaken for spinules. The general morphology of the caudal ramus of C. confusum sp. nov, C. tenuipes and C. endopodita (about twice as long as the anal segment, rather conical with a clearly swollen proximal part; seta VII inserted slightly more distal than setae I and II [although the location of these setae in C. endopodita is not clear from the original description]), are synapomorphies for these three species. Some other Cletodes species (such as C. yotabis Por, 1967, C. smirnovi, C. tuberculatus, and C. longicaudatus [Boeck, 1872]), do exhibit similar caudal rami which are almost cylindrical without a clearly defined swollen part, and/or seta VII located far more distal to setae I and II. Autapomorphies for C. confusum sp. nov. are: female caudal ramus swollen at the level where setae VII, I and II are inserted (the caudal rami of C. endopodita and C. tenuipes are clearly swollen at the base of each ramus); overall shape of female P5, and relative length of the setae of female P5 exopod (see above description).

#### Cletodes pseudodissimilisoris sp. nov. (Figs 8-14)

Type locality: Ensenada del Pabellón lagoon, Sinaloa, Mexico (24°19'-24°35'N, 107°28'-107°45'W).

Type material: the following type material was deposited: dissected female holotype (EMUCOP-020591-11), dissected male allotype (EMUCOP-010591-23), one dissected female (EMUCOP-020591-12) and two dissected (EMUCOP-010591-24, EMUCOP-020591-14) male paratypes, and four male paratypes preserved in alcohol (EMUCOP-020591-13); all from intertidal, mud to fine sand (May 1991; coll. S. Gómez).



**Figure 5**. *Cletodes confusum* sp. nov., adult male. **A** habitus, dorsal; **B** urosome, dorsal (P5 and P6 bearing-somites omitted).

**Figure 5**. *Cletodes confusum* sp. nov., mâle adulte. **A** habitus, vue dorsale ; **B** urosome, vue dorsale (les segments qui portent les P5 et P6 ont été omis).

Etymology. The specific name (Latin *soris*, sister) alludes to the close relationship of the species with *Cletodes pseudodissimilis* Coull, 1971.

# Description

#### Female

Habitus (Figs 8A-B) fusiform, tapering from posterior margin of cephalothorax; length ranging from 590 to 607 µm including tip of rostrum and caudal rami. Cephalothorax about 1/5 of total body length. Greatest width in the middle and posterior edge of cephalothorax, and in first prosomite, the former with folded lateral sides and posterior margin with eight sensilla arising from distinct cones. Rostrum fused to cephalothorax; pitted; with slightly bilobed tip set with fragile setules and two lateral sensilla. Surface of prosomites pitted, with 8, 10 and 10 sensilla arising from distinct conical projections on posterior margin. Urosomites Figure 6. *Cletodes confusum* sp. nov., adult male. A urosome, ventral; B urosome, lateral (P5 and P6 bearing-somites omitted).

**Figure 6.** *Cletodes confusum* sp. nov., mâle adulte. **A** urosome, vue ventrale; **B** urosome, vue latérale (les segments qui portent les P5 et P6 ont été omis).

pitted; first to third urosomite with six, fourth with four conical projections each bearing one sensillum. Fifth urosomite with four conical projections with one pore each. Genital double-somite and fourth and fifth urosomites (Fig. 9B) plain ventrally, except for tiny spinules close to posterior edge of genital double-somite, and long spinules close to posterior margin of fourth and fifth urosomite. Dorsal surface of anal somite pitted (Figs 8A-B, 9A), with two sets of strong spinules close to joint with caudal rami; rounded denticulate anal operculum with a sensillumbearing conical projection on each side; ventral surface of anal somite plain except for short row of minute spinules close to outer distal corner and row of long spinules along posterior edge (Fig. 9B). Caudal rami pear-shaped, nearly as long as wide at the widest part, and as long as anal somite; outer proximal edge convex, rather straight distally; with dorsal ridge at about 1/2 the length; with seven setae; seta II



Figure 7. *Cletodes confusum* sp. nov., adult male. A antennule; B P3; C P4; D P5.

Figure 7. *Cletodes confusum* sp. nov., mâle adulte. A antennule ; B P3 ; C P4 ; D P5.

longer than seta I, both arising from distinct lateral projection; seta IV very small and fused to seta V; seta VII arising from distinct dorsal projection (Fig. 9A); with a conspicuous hyaline pear-shaped tube between seta III and V-IV (indicated in Fig. 9A).

Antennule (Fig. 10A) four-segmented; surface of segments smooth except for spinules on first segment; segment 3 longest, about 1.5 times as long as wide; with aesthetasc on third and last segment. Armature formula: 1-[1], 2-[5], 3-[6+ae], 4-[11].

Antenna (Fig. 10B): allobasis ornamented with spinules along inner edge; with abexopodal seta in distal half. Exopod represented by one plumose seta. Endopod with spinules along inner margin and subdistally along outer edge; with two strong lateral spines and six apical elements (two outermost fused).

Mandible (Fig. 10C): gnathobase with four teeth, one strong spine and one seta; palp with six setae.

Maxillule (Fig. 10D): arthrite ornamented with one subdistal strong spine and four terminal elements (one tridentate, one serrate and two dentate spines, and two



Figure 8. *Cletodes pseudodissimilisoris* sp. nov., adult female. A habitus, dorsal; B habitus, lateral.

Figure 8. *Cletodes pseudodissimilisoris* sp. nov., femelle adulte. A habitus, vue dorsale; B habitus, vue latérale.

slender setae), and two anterior surface setae; coxa with two slender setae; basis with two proximal and three median lateral setae representing incorporated exopod and endopod, respectively, two pairs of fused apical setae and one single subapical element.

Maxilla (Fig. 10E): syncoxa ornamented with spinules along outer edge; with two endites, proximal endite bifurcate, with three slender setae, distal endite with two smooth and one spinulose element; allobasis with claw, with two slender setae and one pinnate spine. Endopod represented by two naked setae.

Maxilliped (Fig. 10F) subchelate; syncoxa ornamented with spinules, without armature. Basis with spinules along inner margin; endopodal claw with minute spinules, without accompanying seta.

P1 (Fig. 11A): basis smooth. Exopod three-, endopod two-segmented. First endopodal segment smaller than

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Figure 9. *Cletodes pseudodissimilisoris* sp. nov., adult female. A anal somite and caudal rami; B urosome, ventral; C, P5.

Figure 9. *Cletodes pseudodissimilisoris* sp. nov., femelle adulte. A segment anal et rame caudale ; B urosome, vue ventrale ; C, P5.

second one, the latter as long as entire exopod and armed with minute inner seta and two apical elements. Armature formula as follows:

EXP	0.0.022
ENP	0.111

P2-P4 (Figs 11B, 12A-B): praecoxa with spinules close to joint with coxa, the latter ornamented with spinules close to inner proximal and outer distal corner; basis with spinules between rami and at base of outer seta. Exopod threesegmented; first and third segment without, second with inner seta. Endopod two-segmented, of P2 reaching just past second exopodal segment, of P3-P4 hardly reaching to insertion level of inner seta of second exopodal segment; first segment smaller than second one, as long as wide; second endopodal segment of P2 and P3 without, of P4 with inner seta. Armature formula as follows:

	P2	P3	P4
EXP	0.1.022	0.1.022	0.1.022
ENP	0.020	0.021	0.121



Figure 10. *Cletodes pseudodissimilisoris* sp. nov., adult female. A antennule; B antenna; C mandible; D maxillule; E maxilla; F maxilliped.

Figure 10. *Cletodes pseudodissimilisoris* sp. nov., femelle adulte. A antennule ; B antenne ; C mandibule ; D maxillule ; E maxille ; F maxillipède.

P5 (Fig. 9C): baseoendopodal lobe almost triangular, with one inner short and strong spine, one apical and one outer seta, ornamented with spinules at base of apical and outer seta with cylindrical outer extension furnished with fragile setules and bearing outer seta. Exopod long, about 6.4 times longer than wide, ornamented with spinules close to inner seta and with long setules along inner and outer margin; with one median lateral outer seta, one subdistal outer seta, two apical setae, and one inner plumose seta.

P6 (Fig. 9B): represented by a median pitted plate in proximal half of genital double-somite. Each vestigial leg represented by a single seta.



Figure 11. *Cletodes pseudodissimilisoris* sp. nov., adult female. A P1; B P2.

Figure 11. *Cletodes pseudodissimilisoris* sp. nov., femelle adulte. A P1 ; B P2.

Male

Habitus (Figs 13A-C) as in female, except for caudal rami and separation of genital and first abdominal somites; length ranging from 496 to 533 µm including rostrum and caudal rami, the latter cylindrical and from 3.1 to 3.3 times longer than wide, and 1.5 times longer than anal somite.

Antennule (Fig. 14A), six-segmented, sub-chirocer; fourth segment swollen, pitted, with longitudinal row of spinules; with aesthetasc on fourth and ultimate segment. Armature formula as follows: 1-[1], 2-[8], 3-[7], 4-[5+ae], 5-[2], 6-[11+ae].

Mouthparts, P1, P2 and P4 (not illustrated) as in female. P3 (Fig. 14B) as in female.

P5 (Fig. 14C): baseoendopod without seta; outer seta of basis as in female, except for lack of ornamentation. Exopod with one small outer lateral seta and two apical setae (outermost smaller).

### **Comparison and discussion**

Coull (1971) described *Cletodes pseudodissimilis* from North Carolina, and observed that his species, *C. dissimilis* and *C. spinulipes* Por, 1967, share the armature Figure 12. *Cletodes pseudodissimilisoris* sp. nov., adult female. A P3; B P4.

Figure 12. Cletodes pseudodissimilisoris sp. nov., femelle adulte. A P3 ; B P4.

formula of the second endopodal segment of P2-P4 (with two, three and four setae, respectively). Since Coull's (1971) description of C. pseudodissimilis, one more species, C. millerorum, associated with a hermit crab at Green Island (North Queensland), was described with the same armature formula. Cletodes pseudodissimilisoris sp. nov. is the fourth species described possessing two, three and four setae on the second endopodal segment of P2-P4. However, the armature formula of the second endopodal segment of P2-P4 of these species is a symplesiomorphy and does not indicate common ancestry. It is probable that the setation of the mouthparts, especially of the maxillule, would provide elements of phylogenetic significance among Cletodes species but this is still unclear (Hamond, 1973). The shape of the female and male caudal rami are regarded here as synapomorphies for C. limicola, C. pseudodissimilis, C. hartmannae Lang, 1965, and C. pseudodissimilisoris sp. nov. The female caudal rami of all these species are convex along the outer proximal edge and rather straight distally; with a dorsal ridge at about 1/2 the length of the ramus. The male caudal rami of these species show similar sexual dimorphism, being more cylindrical and straight than in female, and from 1 to 1.5 times longer than the anal somite.



Figure 13. *Cletodes pseudodissimilisoris* sp. nov., adult male. A habitus, dorsal; B habitus, lateral; C anal segment and caudal ramus, dorsal.

Figure 13. *Cletodes pseudodissimilisoris* sp. nov., mâle adulte. A habitus, vue dorsale ; B habitus, vue latérale ; C segment anal et rame caudale.

Por (1964) observed great variablity in the female caudal rami in material identified as C. limicola, and Bodin (1970) suggested that this could be due to confusion with C. spinulipes and/or C. longicaudatus. Hamond (1973) described Cletodes millerorum from a single female, and showed some variability with regard to the armature formula of the P5 exopod: the left P5 was shown to possess six setae on the exopod, while the right P5 possesses only five. All Cletodes species exhibit five setae only on the female P5 exopod, and this must be the normal condition in C. millerorum also. The female P5 exopod of C. millerorum with 6 setae is in all probability an aberration. The female P5 of C. pseudodissimilis, C. hartmannae and C. pseudodissimilisoris sp. nov. are similar to the female P5 of C. limicola, C. spinulipes, C. macrura, C. longicaudatus, C. latirostris Drzycimski, 1967, and C. yotabis in that they possess three elements on the baseoendopodal lobe



Figure 14. *Cletodes pseudodissimilisoris* sp. nov., adult male. A antennule; B P3; C P5.

Figure 14. *Cletodes pseudodissimilisoris* sp. nov., mâle adulte. A antennule ; B P3 ; C P5.

(C. tuberculatus, C. setosus, C. smirnovi, C. tenuipes, C. endopodita, C. confusum sp. nov. possess only one seta; C. reductus, C. carthaginensis, C. pussilus Sars, 1920, C. longifurca and C. reyssi possess two setae), but differ in the innermost element which is transformed into a spine in C. hartmannae, C. pseudodissimilis and C. pseudodissimilisoris sp. nov., and is considered a synapomorphy for these three species. The innermost element of the female P5 baseoendopod is a single seta in C. limicola, C. spinulipes, C, macrura, C. longicaudatus, C. latirostris and C. yotabis. An autopomorphy for C. hartmannae is the long baseoendopodal lobe reaching beyond the middle of the exopod.





**Figure 15**. *Cletodes pseudodissimilis* Coull, 1971, adult female paratype (USNM-128180). A habitus, dorsal; **B** anal segment and caudal rami, dorsal; **C** urosome (P5 bearing-somite and first genital somite omitted); **D** P5 (ornamentation of setae omitted).

**Figure 15**. *Cletodes pseudodissimilis* Coull, 1971, femelle adulte, paratype (USNM-128180). A habitus, vue dorsale ; B segment anal et rame caudale, vue dorsale ; C urosome, vue ventrale (le segment qui porte P5 et le premier segment génital ont été omis) ; D P5 (l'ornementation des soies a été omise).

Cletodes pseudodissimilis and C. pseudodissimilisoris sp. nov. are very closely related, and can easily be mistaken for each other. After careful examination of the paratypes of C. pseudodissimilis deposited in the United States National Museum (USNM-128180), only subtle differences were found between these two species. The armature of the antennule, antenna, mandible, maxillule, maxilla and maxilliped proved to be identical. Also the general body morphology and armature formula of P1-P5 is the same. The two species can be separated by: the dorsal ornamentation along posterior margin of the body somites (without ornamentation in C. pseudodissimilisoris sp. nov., with setules in C. pseudodissimilis (Fig. 15A)); ventral ornamentation of the fourth and fifth urosomites (with spinules along posterior edge in C. pseudodissimilisoris sp. nov., with spinules and delicate setules (spinules?) along posterior edge in C. pseudodissimilis (Fig. 15C, 16B)); caudal rami (without spinules close to seta I and II in C. pseudodissimilisoris sp. nov., with spinules close to setae I and II in C. pseudodissimilis (Fig. 15A-C, 16A)); inner and subapical outer seta of female P5 exopod (insertion of these

**Figure 16**. *Cletodes pseudodissimilis* Coull, 1971, adult male paratype (USNM-128180). **A** anal segment and caudal ramus, dorsal; **B** urosome, ventral.

**Figure 16**. *Cletodes pseudodissimilis* Coull, 1971, mâle adulte, paratype (USNM-128180). A segment anal et rame caudale, vue dorsale; **B** urosome, vue ventrale.

two seta at the same level in *C. pseudodissimilisoris* sp. nov., at different levels in *C. pseudodissimilis* (Fig. 15D)); and outermost seta of baseoendopod (somewhat shorter than apical seta in *C. pseudodissimilis* (Fig. 15D), apical seta about 2 times as long as outermost seta in *C. pseudodissimilisoris* sp. nov.). The presence of two dorsal sets of long spinules on the posterior edge of anal somite in the female is an autapomorphy for *C. pseudodissimilisoris* sp. nov.

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**Figure 17.** *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), adult female. A habitus, dorsal; **B** urosome, lateral (P5 bearing-somite omitted).

**Figure 17**. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), femelle adulte. **A** habitus, vue dorsale ; **B** urosome, vue latérale (le segment qui porte P5 a été omis).

# Genus Stylicletodes Lang, 1936 Stylicletodes longicaudatus (Brady & Robertson in Brady (1880)) (Figs 17-22)

Original description. *Cletodes longicaudata* Brady & Robertson in Brady (1880): 92, figs 13-19

Cletodes leptostylis Sars, 1920, Cletodes numidicus Monard, 1935, Stylicletodes leptostylis (Sars, 1920) Lang, 1936, Stylicletodes numidicus (Monard, 1935) Petkovski, 1955

Material examined. Two dissected adult females (EMUCOP-010591-25, EMUCOP-030192-29), and one dissected male (EMUCOP-030192-30), were deposited in the collection of the Mazatlán Marine Station of the Institute



Figure 18. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), adult female. A urosome, ventral; B anal segment and caudal rami, dorsal.

**Figure 18**. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), femelle adulte. **A** urosome, vue ventrale; **B** segment anal et rame caudale, vue dorsale.

of Marine Sciences and Limnology; intertidal, mud to fine sand (May 1991, January 1992); coll. S. Gómez.

Distribution. Argentina: Ria Deseado (Santa Cruz) (Pallares, 1975); Black Sea (Por, 1959); Bulgaria (Marinov, 1971); Crimean coast of Ukraine (Griga, 1963); England: Northumberland (Moore, 1973); Mexico: South-eastern Gulf of California (present study); Scotland: Loch Nevis and Fladen (Wells, 1965); Spanish Sahara coast (Marinov, 1977); U. S. A.: Santa Maria Basin (Fiers in litt.); Yugoslavia: Budva (Montenegro) (Petkovski, 1955); see also Lang (1948, 1965).

Redescription

Female

Habitus (Figs 17A-B, 18A-B) fusiform, tapering from



Figure 19. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), adult female. A antennule; B antenna; C mandible; D mandible, another view; E maxillule; F maxilla; G rostrum.

Figure 19. Stylicletodes longicaudatus (Brady & Robertson in Brady (1880)), femelle adulte. A antennule ; B antenne; C mandibule ; D mandibule, un autre angle ; E maxillule ; F maxille ; G rostre.

posterior margin of cephalothorax; length ranging from 569 to 571 µm including tip of rostrum and caudal rami. Cephalothorax/body length ratio, 4.4. Greatest width in the posterior edge of cephalothorax, and in first prosomite, the former with folded lateral sides and posterior margin with two sensilla. Rostrum (Fig. 19G), fused to cephalothorax; with bilobed tip set with fragile setules and two lateral sensilla. Surface of pro- and urosomites smooth, with sensilla in posterior margins, except for fifth urosomite. Genital double-somite with vestigial P6 represented by two setae (outermost more than two times longer than innermost seta) in proximal half of first genital somite. Genital pore (Fig. 18A) in anterior half of genital double-somite. Fourth and fifth urosomites with setules on posterior edge ventrally. Dorsal surface of anal somite smooth; with lateral spinules close to posterior margin; anal operculum flanked with two sensilla and ornamented with fine spinules; with two porebearing projections close to caudal edge ventrally. Length of urosome/length of caudal ramus ratio, 2.2; caudal rami

about 2.4 times longer than anal somite, and about 10 times longer than broad, ornamented with setules along proximal half of inner margin, with small dorsal spinules on posterior edge, with seven setae. Following Huys & Boxshall (1991) nomenclature, setae I and II located rather proximally (the latter about twice as long as seta I); seta VII in proximal third, setae III, IV, V and VI in posterior margin, setae IV and V fused at base, the former smooth and slender, and longer than setae III and VI (Fig. 18B).

Antennule (Fig. 19A) five-segmented; surface of segments smooth except for three rows of fine spinules on first segment; segment 3 about two times as long as wide; with aesthetasc on third and last segment. Armature formula: 1-[1], 2-[5], 3-[6+ae], 4-[1], 5-[11+ae].

Antenna (Fig. 19B): surface of allobasis smooth; with one proximal and one subdistal abexopodal seta. Exopod one-segmented, with two setae. Endopodal segment with spinules along inner margin and subdistally on outer edge; with two strong lateral spines; with five apical elements.

Mandible (Fig. 19C-D): coxa slender; with one long serrate spine and three smooth subapical setae and one spine; gnathobase with bidentate teeth; palp represented by two slender setae fused at base.

Maxillule (Fig. 19E): arthrite ornamented with four terminal elements, two lateral setae, and one (or two?) anterior surface elements; coxa with one seta; basis with two lateral and two apical setae.

Maxilla (Fig. 19F): syncoxa ornamented with distal spinules on outer edge; with two endites, proximal endite with one, distal endite with two setae; allobasis with claw, with one accompanying seta; endopod represented by two slender setae.

Maxilliped lost during dissection.

P1 (Fig. 20A): coxa with row of spinules close to outer distal corner; basis with spinules at base of outer and inner spine. Exopod three-, endopod two-segmented. Exopod barely reaching to distal third of second endopodal segment; third exopodal segment as long as first and second segments combined. Second endopodal segment about five times longer than first one. Armature formula as follows:

EXP	0.0.121
ENP	0.110

P2-P4 (Figs 20B-C, 21A): coxa with spinules close to inner proximal and outer distal corner; basis somewhat prolonged transversally, with spinules at base of outer spine. Exopod three-segmented; third segment as long as the first and second segments combined. Endopod two-segmented, of P2 as long as entire exopod, of P3 reaching the middle of third exopodal segment, of P4 barely beyond second exopodal segment; first segment small, of P2 1/9, of P3 1/8, of P4 1/6 the length of the second segment. Armature formula as follows:

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Figure 20. Stylicletodes longicaudatus (Brady & Robertson in Brady (1880)), adult female. A P1; B P2; C P3.
Figure 20. Stylicletodes longicaudatus (Brady & Robertson in

Brady (1880)), femelle adulte. A P1 ; B P2 ; C P3.





Figure 21. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), adult female. A P4; B P5.

**Figure 21**. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), femelle adulte. A P4 ; **B** P5.

	P2	P3	P4
EXP	0.0.022	0.1.231	0.1.231
ENP	0.020	0.021	0.021

P5 (Fig. 21B): basis with a pore-bearing conical projection ornamented with some spinules; with elongate baseoendopodal lobe reaching distal fourth of exopod, ornamented with spinules along inner margin and with setules along outer edge, with two inner strong setae and two apical elements (outermost spine-like). Exopod long, ornamented with setules along inner margin and at base of apical setae, with three strong outer setae, one apical and one subapical inner element.

P6 (Fig. 18A): represented by a plate in proximal half of genital double-somite. Each vestigial leg represented by two setae.

**\_\_\_\_ Figure 22.** *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), adult male. **A** antennule, exploded; **B** P3; **C** P5.

Figure 22. *Stylicletodes longicaudatus* (Brady & Robertson in Brady (1880)), mâle adulte. A antennule; B P3 ; C P5.

Male

Habitus (not shown) as in female, except for separation of genital and first abdominal somites.

Antennule (Fig. 22A) five-segmented, chirocer; fourth segment swollen, with longitudinal row of spinules; with aesthetasc on fourth and ultimate segment. Armature formula as follows: 1-[1], 2-[7], 3-[7], 4-[9+ae], 5-[11+ae].

Mouthparts, P1, P2 and P4 (not illustrated) as in female. P3 (Fig. 22B): exopod as in female; endopod threesegmented; first segment as in female, second segment slightly shorter than third one, with outer apophysis reaching far beyond the tip of third exopodal segment and ornamented with setules along inner edge; third segment reaching about the middle of third exopodal segment, ornamented with sets of spinules along inner margin, with two apical setae.

P5 (Fig. 22C): as in female, except for baseoendopodal lobe with two elements (outermost spine-like and shorter than innermost one).

## **Comparison and discussion**

So far, six species of the genus *Stylicletodes* have been described: *S. longicaudatus* (Brady & Roberston in Brady (1880)); *S. stylicaudatus* (Willey, 1935); *S. reductus* Wells, 1965; *S. verisimilis* Lang, 1965; *S. oligochaeta* Bodin, 1968; and *S. minutus* Bodin, 1968. *Stylicletodes reductus* and *S. minutus* are unique within the genus as they exhibit a very elongated anal operculum.

Stylicletodes oligochaeta and S. stylicaudatus share the same chaetotaxy at least of P1, P2, and endopod of P4 (the male of S. oligochaeta and the female of S. stylicaudatus remain unknown), and only some differences can be found when comparing the armature of the caudal rami (seta VII is situated in the proximal third of the ramus in S. stylicaudatus [(Willey, 1935): 69, fig. 68], and in the middle of the ramus in S. oligochaeta [Bodin, 1968: 92, fig. 55]).

As suggested by Bodin (1968) in his key to the species of *Stylicletodes*, *S. longicaudatus* and *S. verisimilis* could be closely related. These species share the same chaetotaxy of P1-P5, but differ in the general shape of the caudal rami (lack of setules along inner margin, shape of proximal half of the ramus, and length of seta II), and location of the antennal exopod (Lang, 1965).

Although amphiamerican distribution patterns do not seem to be uncommon within harpacticoids (pers. obs.), the occurrence of the same species on both sides of the Atlantic seems to be the result of "lack of attention to morphological details" that "caused people to lose sight of relationships and generic boundaries in interstitial families" (Huys, 1992). This was nicely shown by Huys (1992) in his analysis of the amphiatlantic distribution of *Leptastacus macronyx* (T. Scott, 1892) and seems not to be an isolated case.

Stylicletodes longicaudatus has been reported repeatedly from distant localities, particularly from both sides of the Atlantic. However, the supposed amphiatlantic distribution of this species seems to be supported by poor descriptions in which only some morphological details are shown and many others have been overlooked, namely the relative size of the exo- and endopod of P1-P4, relative size of the antennal allobasis and endopodal segment, location of the antennal exopod, antennular armature, and structure of female P6 and genital field. On the other hand, Lang (1965) found a number of specimens (three females, the abdomen of one female and two males) in a sample taken in the Gullmar Fjord, which were identified as S. longicaudatus, and implicitly suggested that the differences observed could be best explained by intraspecific variability. Unfortunately, Lang (1965) did not give any comment on the two males, and he only presented the P5 and the endopod of P3 of male I, and P5 of male II, probably because he considered them conspecific. In my opinion the females found by Lang (1965) could belong to different species, and the males found in the same sample could belong to at least two different species. Such assumption is based on the shape of the insertion lobe of the apical seta of the P5 exopod of male I and male II. The insertion lobe of the apical seta of P5 exopod of male II seems to be larger than in male I, and is similar to that of female 3. Unfortunately Lang (1965) did not present any comment on other sexually dimorphic characters.

Lang (1965) found a single female of a new species, S. verisimilis, in Monterey Bay. He suggested that the location of the antennal exopod and the presence/absence of setules along the inner margin of the caudal rami could be used as a taxonomic character to separate the American and the European Stylicletodes species. The distinction of the antennal exopod seems to be valid when comparing the illustrations of the European specimens of S. longicaudatus of Lang (1965), Petkovski (1955), and Marinov (1971), with the Northamerican specimens of S. verisimilis of Lang (1965) and the Mexican specimens of S. longicaudatus herein described. Unfortunately, this character state is not clear for the European S. longicaudatus of Por (1959), Griga (1963), and Marinov (1977), and for the Southamerican S. longicaudatus of Pallares (1975). On the other hand, the character state of the caudal rami regarding the setules along the inner margin has been overlooked in Petkovski (1955), Por (1959), Griga (1963), and Marinov (1971, 1977). Pallares (1975) gave no comments on the absence/presence of such setules in the Southamerican representatives.

The alleged amphiatlantic distribution of *S. longicaudatus* could be the result of lack of detail when describing new records of specimens identified with this species. Although some differences were found, the Mexican specimens proved closely related to

*S. longicaudatus.* I suggest to tentatively allocate the Mexican specimens to *S. longicaudatus* pending a thorough revision of the genus, and particularly of *S. longicaudatus.* 

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# References

- Bodin P. 1968. Copépodes harpacticoïdes des stages bathyal et abyssal du Golfe de Gascogne. *Mémoires du Muséum National d'Histoire Naturelle*, **55A**: 1-107.
- Bodin P. 1970. Copépodes harpacticoïdes marins des environs de La Rochelle. 1- Espèces de la vase intertidale de Châtelaillon. *Téthys*, 2: 385-436.
- Brady G. S. 1880. A monograph of the free and semi-parasitic Copepoda of the British Islands, 2. Ray Society: London. 182 pp.
- Coull B. C. 1971. Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf. *Cahiers de Biologie marine*, **12**: 195-237.
- Fiers F. 1991. Three new harpacticoid copepods from the Santa Maria basin off the Californian Pacific coast (Copepoda, Harpacticoida). *Beaufortia*, 42: 13-47.
- Fiers F. 1996. Redescription of *Enhydrosoma lacunae* Jakubisiak, 1933 (Copepoda, Harpacticoida); with comments on the *Enhydrosoma* species reported from West Atlantic localities, and a discussion of cletodid development. *Sarsia*, 81: 1-27.
- Gee J. M. 1994. Towards a revision of *Enhydrosoma* Boeck, 1872 (Harpacticoida: Cletodidae *sensu* Por); a re-examination of the type species, *E. curticauda* Boeck, 1872, and the establishment of *Kollerua* gen. nov. *Sarsia*, **79**: 83-107.
- Gómez-Noguera S. E. & Hendrickx M. 1997. Distribution and abundance of meiofauna in a subtropical coastal lagoon in the South-eastern Gulf of California, Mexico. *Marine Pollution Bulletin*, 34: 582-587.
- Griga R. E. 1963. Harpacticoids of the benthonic biocenoses in the southern coast of the Crimea and Caucasus. *Trudy Sevastopolskoj Biologicesky Stancii*, 16: 159-172.

- Hamond R. 1973. A review of *Cletodes* (Crustacea: Harpacticoida), with the description of a new species from Queensland. *Memoirs of the Queensland Museum*, 16: 471-483.
- Huys R. 1992. The amphiatalntic distribution of *Leptastacus* macronyx (T. Scott, 1892) (Copepoda: Harpacticoida): a paradigm of taxonomic confusion; and a cladistic approach to the classification of the Leptastacidae Lang, 1948. Academiae Analecta 54: 1-194.
- Huys R. & Boxshall G. A. 1991. Copepod evolution. The Ray Society. 468 pp.
- Lang K. 1948. *Monographie der Harpacticiden, I, II.* A-B. Nordiska Bokhandeln: Stockholm. 1682 pp.
- Lang K. 1965. Copepoda Harpacticoidea from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar*, 10: 1-566.
- Marinov T. 1971. Harpacticoids of the Bulgarian Black Sea coast. Proceedings of the Institute of Oceanography and Fisheries, Varna, 11: 43-87.
- Marinov T. 1977. Harpacticoida from the Eastern Central Atlantic coast. *Proceedings of the Institute of Oceanography and Fisheries, Varna*, 15: 83-98.
- Monard A. 1935. Les harpacticoïdes marins de la région de Salammbô. *Bulletin de la Station Océanographique de Salammbô*, 34: 1-94.
- Moore P. G. 1973. The kelp fauna of northeast Britain II. Multivariate classification: turbidity as an ecological factor. *Journal of Experimental Marine Biology and Ecology*, 13: 127-164.
- Moore P. G. 1977. Une forme nouvelle de *Cletodes* Brady (Copepoda, Harpacticoida) de la Côte Catalane française. *Vie et Milieu*, 27: 255-262.
- Pallares R. E. 1975. Copépodos marinos de la Ría Deseado (Santa Cruz, Argentina). Contribución sistemático-ecológica IV. *Physis*, 34A: 213-227.
- Petkovski T. K. 1955. Weitere Beiträge zur Kenntnis der Grundwasser-Copepoden der Adriatischen Küste. Acta Musei Macedonici Scientiarum Naturalium, 3: 209-225.
- Por F. D. 1959. Harpacticoide noi (Copepoda, Crustacea) din mîlurile Marii Negre. *Studii si Cercetari di Biologie, Seria Biologie Animala*, 11: 347-368.
- Por F. D. 1964. A study of Levantine and Pontic Harpacticoida (Crustacea: Copepoda). Zoologische Verhandelingen, 64: 1-227.
- Schriever G. 1984. New Harpacticoida (Copepoda) from the North Atlantic Ocean. IV. Four new species of the families Diosaccidae, Ameiridae, and Ancorabolidae. *Crustaceana*, 47: 52-71.
- Wells J. B. J. 1965. Copepoda (Crustacea) from the meiobenthos of some Scottish marine sub-littoral muds. *Proceedings of the Royal Society of Edinburg*, 69B: 1-33.
- Willey A. 1935. Harpacticoid Copepoda from Bermuda. Part II. Annals and Magazine of Natural History, 15: 50-100.