



Clarification of the taxonomic status of *Notodiaptomus anisitsi* (Daday, 1905) and related species, with description of a new species from Argentina (Crustacea: Copepoda: Diaptomidae)

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Abstract

The diaptomids discussed represent a group of incompletely known and, at first glance, closely related species. The most conspicuous feature shared among them is the general aspect of the exopodite segment 2 of the male leg 5. Through a study of literature and comparison of descriptions with material from several localities, some of them type localities, of northern Argentina, Uruguay and Paraguay, *N. anisitsi* Daday, 1905 and *N. spinuliferus* Dussart, 1985 are redescribed and one new species is described. The validity or possible conspecificity of *N. inflexus* (Brian, 1925), *N. bidigitatus* Brehm 1958, and *N. perelegans* (Wright, 1927) is discussed. Additionally, the variability and the value as diagnostic character of several morphological features, mainly, ornamentation of distal segment of prosome, setation of antennules, basipodite and exopodite of right leg 5 of male, and shape of outer caudal seta are analysed.

Introduction

The taxonomy of the South American diaptomids is still incomplete, and many problems about the validity of several species remain unsolved (Brehm, 1958; Brandorff, 1976; Dussart, 1985; Reid, 1985, 1987). Part of this situation arises because a significant number of the available descriptions are fragmentary and incomplete, and also because current knowledge about the intra- and interpopulation variability of the diagnostic characters is rather poor. In some cases, variability has been overestimated, with different populational variations being described as distinct species. On the other hand, the variability of some features has been underestimated, and some populations, which could be correctly interpreted as different species, have been assigned to a single species. In *Notodiaptomus anisitsi* Daday (1905), it is feasible that both situations have occurred.

The intricate taxonomical history of this species involves three nominal species (*D. anisitsi* Daday, *D. inflexus* Brian, *D. bidigitatus* Brehm) and one form, assigned to *N. anisitsi* but close to *N. spinuliferus* Dus-

sart, which is described here as a new species. The present study is an attempt to clarify the taxonomic status of *N. anisitsi* and the diagnostic value of some morphological features, taking into account the intra- and inter population variability.

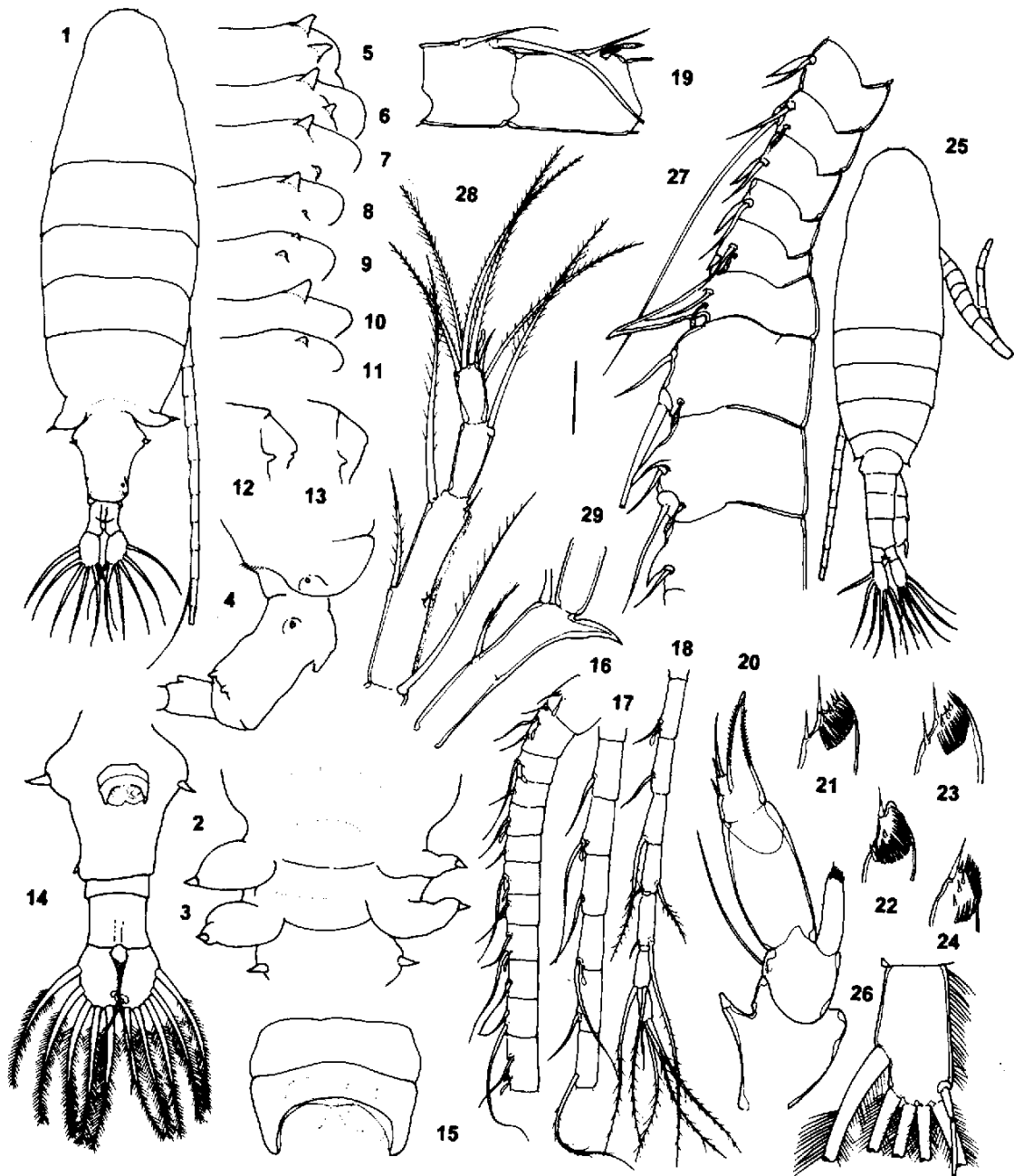
In order to present the material in an intelligible way, initially *N. anisitsi* and *N. spinuliferus* are redescribed and the new species is described, and finally, the variability of the main diagnostic characters is discussed.

Taxonomy

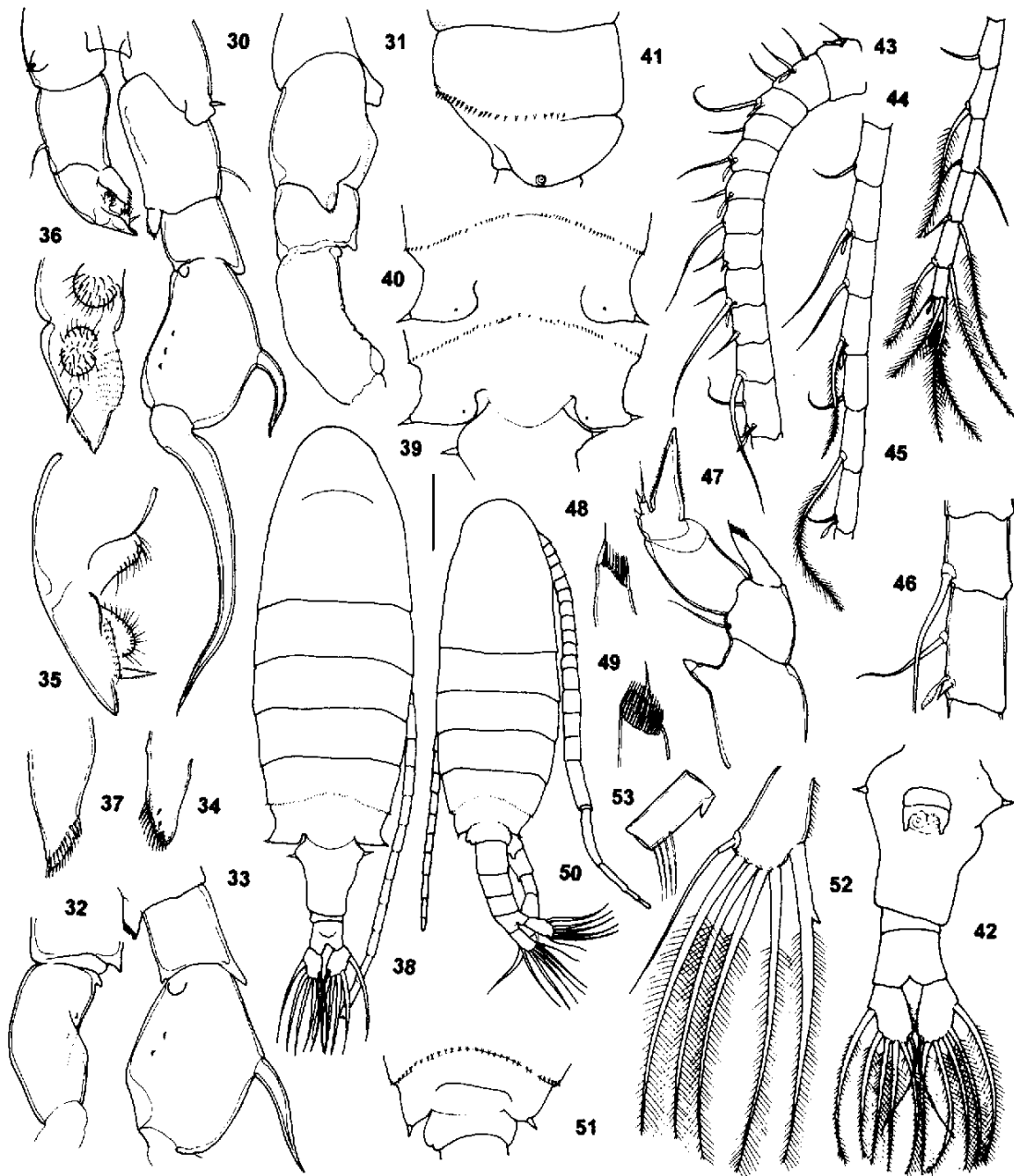
Notodiaptomus anisitsi Daday (1905) (Figs 1–37 and 92).

Diaptomus anisitsi Daday 1905, p. 149, pl. 9, Figs 16–22; Wright 1927, p. 77, pl. 1, Figs 4–6; 1937, p. 76; 1938, p. 562; 1939, p. 647; Kiefer, 1928, p. 172, Figs 4–6.

Notodiaptomus anisitsi, Kiefer 1936, p. 197; Ringuelet 1958, p. 45, 50; Brehm 1958, p. 575; Brehm, 1965, p. 11; Brandorff, 1976, p. 625; Dussart & Defaye 1983; p. 135; Matsumura Tundisi, 1986, p. 551; Reid, 1991, p. 738.



Figures 1-29. *Notodiptomus anisitsi* (Daday). 1: mature female, dorsal; 2-3: pedigers 4 and 5, dorsal; 4: distal pedigers and urosome, lateral; 5-11: right distal angle of genital segment (drawn reversed); 12-13: distal left corner; 14: urosome; 15: genital operculum; 16-18: antennula; 19: segments 11-12; 20: leg 5; 21-24: tip of endopodite; 25: male, dorsal; 26: caudal ramus; 27: right antennula, segments 8-12; 28: segments 23-25; 29: segment 23 with 'spur'. Scale bars: 0.2 mm (Figs 1 and 15), 0.1 mm (Figs 2-4, 14 and 16-18), 0.05 mm (Figs 5-13, 19, 20, 26-29), 0.04 (Fig. 15), 0.025 (Figs 21-24).



Figures 30–53. *Notodiptomus anisitsi* (Daday) male. 30: legs 5, caudal; 31: lateral; 32: exopodites 1 and 2, lateral; 33: caudal; 34: endopodite of right leg; 35: left leg, lateral; 36: caudal; 37: left endopodite; Figures 38–40. *Notodiptomus dentatus* sp. n. 38: female, dorsal; 39–40: pedigera 4 and 5, dorsal; 41: lateral; 42: urosome; 43–45: antennula; 46: segments 11–12; 47: leg 5; 48–49: tip of endopodite; 50: male, dorsal; 51: pedigera 4 and 5, dorsal; 52–53: detail of outer caudal seta. Scale bars: 0.17 mm (Figs 38 and 50), 0.09 mm (Figs 39–45 and 51), 0.05 mm (Figs 30–33), 0.04 mm (Figs 46, 47 and 52), 0.025 mm (Figs 34–37), 0.02 mm (Figs 48, 49 and 53).

Diaptomus inflexus Brian 1925, p. 180, Figs 4–6; Brehm, 1965, p. 3, 7.

Notodiaptomus inflexus; Brehm, 1938, p. 29.

Notodiaptomus bidigitatus; Brehm, 1958; Dussart & Defaye, 1983, p. 135.

Diaptomus bidigitatus Brehm, 1965, p. 3; Brandorff, 1976, p. 625; José de Paggi, 1978, p. 150–151; 1984, p. 141; 1985, p. 17; Dussart, 1985, p. 214.

Material examined

Argentina:

1 – Roadside pond near Resistencia, Chaco Province, Sept. 1968. 2 – Shallow lake No 3, on island near Formosa, floodplain of Paraguay River, Formosa Province, Sept. 1971. 3 – Shallow lake No 17, on island near Formosa, floodplain of Paraguay River, Formosa Province, June 1972. 4 – Laguna Yema, Formosa Province, Nov. 1974. 5 – Los Matadores Lake, Los Mellados Island, Paraná River, near Santa Fe, Prov. Santa Fe, Nov. 1975. 6 – Ponds connected to Ayuí Grande Creek, Concordia, Entre Ríos Province, Sept. 1968; Dec. 1971. 7 – Temporary roadside pond near San José de Feliciano, Entre Ríos, Sept. 1969. 8 – Roadside pond between San José de Feliciano and Sauce, Entre Ríos Province, Sept. 1969. 9 – Uruguay River, at Federación, Entre Ríos Province, Sept. 1968. 10 – Uruguay River at Colón, Entre Ríos Province, Aug. 1971. 11 – Pool near Margarita, Santa Fe Province, Nov. 1984. 12 – Roadside pond near San Justo, Santa Fe Province, Sept. 1996. 13 – Laguna La Cuarentena, Carabajal Island (shallow lake on Paraná River floodplain), Santa Fe Province, March 1981; May 1981; Dec. 1982. 14 – Main channel of Paraná River, at Paraná, March 1981; Oct. 1981. 15 – Laguna Los Espejos, Sirgadero Island (shallow lake on Paraná River floodplain), Santa Fe Province, Dec. 1969. 16 – Pool on Sirgadero Island, (shallow lake of Paraná River floodplain), Santa Fe Province, Nov. 1971. 17 – Madrejón Don Felipe, ox-bow lake near Santa Fe, Santa Fe Province, May 1986; Feb. 1969; Apr. 1969; Aug. 1969. 18 – Laguna Los Matadores, Los Mellados Island (shallow lake of Paraná River floodplain), Santa Fe Province, Jan. 1975; Nov. 1975. 19 – Lower Paraná River, Isla Las Palmas, Buenos Aires Province, Sept. 1995. 20 – Middle Paraná River, Diamante, Entre Ríos Province, Sept. 1995. 21 – Main channel of Paraná River, Paso Muelles, Santa Fe Province, Sept. 1995. 22 – Main channel of Paraná River, Paso Alvear, Santa Fe Province, Sept. 1995. 23 – Lower Paraná River, Florida, Santa Fe Province, Sept. 1990. 24 – Paraná Las Palmas River, Ñacurutú, Buenos Aires Province,

Sept. 1990.

Paraguay:

25 – Ipacaráí Lake, La Capital District, Feb. 1981.

Uruguay:

26 – Small pool connected to Vïboras Stream near Carmelo, Colonia Department, Dec. 1982.

Description

Female: Body widest at junction of pedigers 1 and 2, dorsal view (Fig. 1). Suture between pedigers 4 and 5 indistinct dorsally, sometimes with 1–3 rows of spinules of variable extension near posterior part of pediger 4 (Figs 2 and 3) and with 1 row of tiny spinules at distal border of pedigers 2 and 3 (specimens from localities 6 and 10). Convexity of pediger 4, in lateral view, more pronounced in some specimens because of presence of short dorsal hump, sometimes with group of tiny spinules. Pediger 5 expanded posterolaterally into moderately developed asymmetrical wings; left wing oblong, somewhat inflated, directed latero-obliquely, larger than right wing, ending in stout sensillum; right wing smaller, produced into narrow and irregular lobe directed laterally, ending in stout sensillum (Figs 2 and 3). Distal part of pediger 5, between wings, with 1 row of stiff hair-like setulae, perpendicular to body axis (Figs 2–4).

Urosome with 3 segments, about 1/4 of body length. Genital segment slightly longer than broad, well expanded anterolaterally and slightly asymmetrical, right expansion larger than left; each expansion with 1 stout sensillum, sensillum on right side lateral at tip of expansion and anteriorly curved, sensillum on left side straight, dorsal and posterior to the tip of expansion (Fig. 14). Right postero-dorsal corner of genital segment with 2 finger-like protuberances, rarely one of them very reduced or absent (Figs 4–11). Left corner with 1 small protuberance, normally smaller than and not so conspicuous as protuberances of right side; sometimes with no protuberances (Figs 12 and 13). Genital operculum (terminology after Cicchino, 1994) with proximal plate sub-trapezoidal, little broader than distal plate. Junction between distal and proximal plate gently curved. Distal plate narrow and gently curved, with lateral arms somewhat convergent and as long as transverse bar. Inner side of lateral arms and distal border of transverse bar concave (Fig. 15). Urosomite 2 without notable structure. Inner margins of caudal rami haired, outer margins smooth. Caudal

setae with normal armature. Rostral points acute and well developed, with no process at base.

Antennula reaching end or beyond of caudal rami (% of body length: mean=113, range=100–124), setation (s=setae, cs=conical setae, ae=aesthetascs; terminology after Santos Silva et al., 1999) of each segment as follows: 1(1s, 1ae), 2(3s, 1ae), 3(1s, 1ae), 4(1s), 5(1s, 1ae), 6(1s), 7(1s, 1ae), 8(1s, 1cs), 9(2s, 1ae), 10(1s), 11(2s), 12(1s, 1ae, 1cs), 13(1s), 14(1s, 1ae), 15(1s), 16(1s, 1ae), 17(1s), 18(1s), 19(1s, 1ae), 20(1s), 21(1s), 22(2s), 23(2s), 24(2s), 25(4s, 1ae) (Figs 16–19). Length of seta of segment 7 and longest seta of segment 9, 7.5–8.5% length of antenna. Of the terminal setae, 3 are several times longer than segment 25, 1 slightly longer than segment, and remaining setae shorter than segment.

Remaining cephalic appendages and swimming legs with normal setation. Swimming legs with segmentation and armature normal for the genus. Segment 1 of exopodite of leg 1 with 1 spine at outer distal corner. Endopodite segment 2 of leg 2 with Schmeil's organ.

Leg 5 (Fig. 20) coxopodite with prominent posteroventrally directed process tipped with stout, blunt spine. Basipodite with inner proximal angle smooth, and long lateral seta reaching end of exopodite segment 1. Exopodite segment 1 about twice as long as broad, lateral margin slightly convex, medial margin even, exopodite segment 2 2.5 times longer than broad and shorter than segment 1, with shorter spine as long as segment 3, claw coarsely serrated along middle half of both margins. Exopodite segment 3 not clearly distinct from segment 2, with 2 spines, shortest spine as long as segment and longest spine 4–6 times longer than it. Endopodite slender, as long as 3/5 of exopodite segment 1, bearing at tip a row of hair-like setulae, 2 setae, and 1–4 short denticles (Figs 21–24). Endopodite unsegmented, but in some specimens there is a constriction near proximal third, suggesting incomplete segmentation.

Length (caudal setae excluded): mean=1.48 mm, range=1.31–1.64 mm, $n=79$.

Male: Body widest at junction of pedigers 1 and 2 in dorsal view. Suture between pedigers 4 and 5 complete dorsally, usually without spinules or convexity on pediger 4. Distal border of pedigers 2–4, sometimes with 1 row of tiny spinules (specimens from localities 6 and 10). Pediger 5 expanded posterolaterally into 2 small, nearly symmetrical wings, each with minute hair and short spine at tip. There is no other orna-

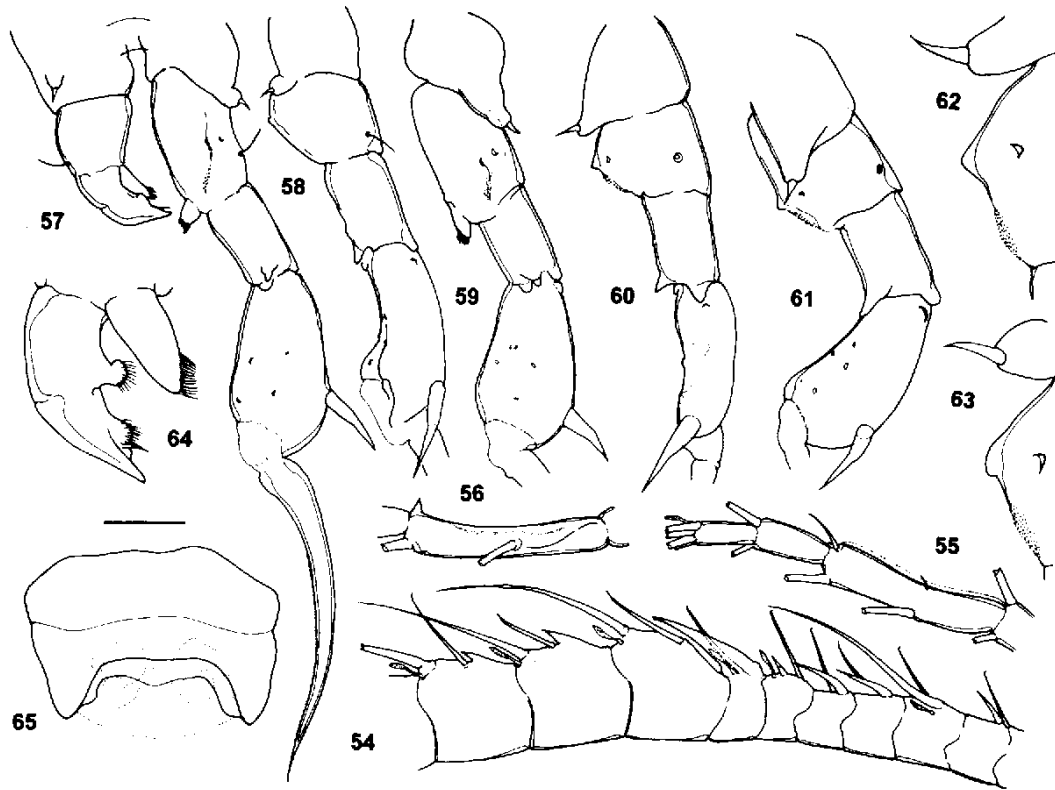
mentation on this pediger except for few pores (Fig. 25).

Urosome about 1/3 of body length, of 5 segments, first segment slightly asymmetrical, with short spine at left distolateral corner. Inner margins of caudal rami haired, outer margins smooth. Caudal setae with normal armature (Fig. 26). Rostral points acute and well developed, with 1 rounded process on right side of base.

Right antennula with small conical seta on segment 12 and well developed modified setae on segments 8, 10 and 11, and spine-like process on segments 13, 15 and 16; modified seta of segment 11 longer than modified seta of segment 10 and shorter than that of segment 8; process on segment 13 bifid at tip, large, extending to midlength of segment 14, 2.5–4 times longer than process on segments 15 and 16; process of segment 15 longer than that of segment 16 (Fig. 27). Antepenultimate segment with longitudinal, narrow lamella (Fig. 28) and, sometimes, with stout curved process longer than diameter of segment (Fig. 29). Left antennula with armature identical to that of females except for setae of segments 7 and 9, which are two times longer than corresponding setae of females, about 17% length of antenna.

Mouthparts and swimming legs identical to those of female. Right leg 5, coxopodite distocaudally expanded into well-developed mammiform process with 1 short spine at tip (Figs 30 and 31). Basipodite longer than broad, with surface smooth or with a short ridge on caudal surface. Lateral seta short, extending only slightly past distal end of segment (Fig. 30). Exopodite segment 1 longer than broad (Figs 30, 33 and 91), distal width larger than proximal width, with small blunt process at distal inner corner and larger and more pointed process at distal outer corner. Exopodite segment 2 oblong, with outer margin more convex than inner margin. Caudal surface with a row, parallel to inner margin, of 1–3 chitinous knobs (Figs 30 and 33), sometimes barely visible. Lateral spine as long as width of segment (Figs 30 and 33), sharply bent downward and slightly recurved at tip, with a row of minute hairs on distal half of posterior side, inserted at widest part of segment near middle of outer margin (Fig. 90). Terminal claw nearly twice longer than segment. Right endopodite unsegmented, moderately developed with oblong ring of hairs, which are stronger on one side of ring (Fig. 34).

Left leg 5, coxopodite longer than wide, expanded into short rounded protuberance near distal outer angle, with one short spine. Basipodite longer than



Figures 54–65. *Notodiptomus dentatus* sp. n., male. 54: right antennula, segments 8–16; 55: segments 23–25; 56: segment 23 with 'spur'; 57: legs 5; 58: right leg, lateral; 59: caudal; 60: lateral; 61: oblique; 62–63: basipodite, lateral; 64: left leg, exopodite and endopodite; 65: female, operculum. Scale bars: 0.04 mm (Figs 54–61), 0.02 mm (Figs 62–65).

wide, without noticeable structure, and lateral seta inserted at distal third. Exopodite segment 1 with proximal haired pad well developed. Exopodite segment 2 with proximal haired pad and flat middle pad covered with tiny spinules. Distal and proximal processes approximately equal in length and lined bilaterally with fine denticles (Figs 35 and 36). Endopodite similar to that of right leg (Fig. 37).

Length (caudal setae excluded): mean=1.29 mm, range=1.13–1.48 mm, $n=83$.

Notodiptomus dentatus n. sp. (Figs 38–64)

Notodiptomus anisitsi; Ringuelet & Martínez de Ferrato 1967, p.417, Figs 7–10, José de Paggi 1978, p. 150–151; 1980, p. 72; 1981, p. 199; 1983, p. 168; 1984, p. 141.

Material examined

Argentina:

1 – Madrejón Don Felipe, ox-bow lake near Santa Fe, Santa Fe Province, April 1969, May 1969; Aug. 1969; Oct. 1969; Dec. 1969 (type locality). 2 – Santa Fe River (secondary channel of Paraná River), Santa Fe Province, March 1975. 3 – Laguna La Cuarentena, Carabajal Island (shallow lake on Paraná River floodplain), Santa Fe Province, June 1980; Dec. 1980. 4 – Laguna No. 12, Sirgadero Island (shallow lake on Paraná River floodplain), Santa Fe Province, March 1972. 5 – Laguna Los Matadores, Los Mellados Island (shallow lake on Paraná River floodplain), Santa Fe Province, Jan. 1975; March 1975; Nov. 1975. 6 – Lower Paraná River, Florida, Santa Fe Province, Sept. 1990. 7 – Paraná Las Palmas River, Ñacurutú, Buenos Aires Province, Sept. 1990.

Holotype: Male preserved in a mixture of formaldehyde and glycerol (1/10), deposited in Museo Ar-

gentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires (No. 34203).

Allotype: Female preserved in a mixture of formaldehyde and glycerol (1/10), deposited in Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires (No. 34204).

Paratypes: One female and one male, preserved in a mixture of formaldehyde and glycerol (1/10), deposited in Museo Provincial de Ciencias Naturales 'Dr Florentino Ameghino'.

Description

Female: Body widest at junction of pedigers 1 and 2, dorsal view (Fig. 38). Suture between pedigers 4 and 5 distinct at middle and lateral part, with single row of irregularly spaced spinules near distal part of pediger 4 (Figs 39–41). Distal border of pedigers 1–3, sometimes with 1 short row of tiny spinules (Fig. 40). Convexity of pedigers 4 and 5, in lateral view, even, without dorsal hump (Fig. 41). Pediger 5 expanded posterolaterally into moderately developed symmetrical wings; ending in stout sensillum, with 1 short hair on dorsal surface. Distal part of pediger 5, between wings, smooth.

Urosome (Fig. 42) with 3 segments, about 1/4 of body length. Genital segment slightly longer than broad, well expanded anterolaterally and slightly asymmetrical, right expansion tapered and larger than left; each expansion with 1 stout sensillum, sensillum on right side lateral to the tip of expansion, and sensillum on left side dorsal and posterior to tip of expansion. Right side with rounded protuberance near proximal expansion. Postero-dorsal corners of genital segment smooth.

Genital operculum with proximal plate subtrapezoidal, somewhat longer than transverse bar of distal plate. Junction between distal and proximal plates concave at middle and slightly convex on sides. Distal plate narrow, with distal border slightly curved or irregularly straight. Lateral arms clearly convergent, little more than twice longer than transverse bar, with a rounded protuberance on inner side (Fig. 65). Urosomite 2 without noticeable structure.

Inner margins of caudal rami setose, outer margins smooth. Caudal setae with normal armature. Rostral points acute and well developed, with no process at base.

First antenna reaching end of caudal rami (% of body length: mean=105, range=95–113), setation (s=setae, cs=conical setae, ae=aesthetascs) of each segment as follows: 1(1s, 1ae), 2(3s, 1ae), 3(1s, 1ae),

4(1s), 5(1s, 1ae), 6(1s), 7(1s, 1ae), 8(1s, 1cs), 9(2s, 1ae), 10(1s), 11(1s), 12(1s, 1ae, 1cs), 13(1s), 14(1s, 1ae), 15(1s), 16(1s, 1ae), 17(1s), 18(1s), 19(1s, 1ae), 20(1s), 21(1s), 22(2s), 23(2s), 24(2s), 25(4s, 1ae). (Figs 43–46). Length of seta of segment 7 and longest seta of segment 9, 10–15% length of antennula. Of terminal setae, 3 setae several times longer than segment 25, 1 seta slightly longer than segment 25, and remaining setae shorter than segment 25.

Remaining cephalic appendages and swimming legs with normal setation. Swimming legs with segmentation and armature normal for genus. Segment 1 of exopodite of leg 1 with one spine at outer distal corner. Endopodite segment 2 of leg 2 with Schmeil's organ.

Leg 5 (Fig. 47) coxopodite with prominent posteroventally directed process tipped with stout blunt spine. Basipodite with inner proximal angle smooth, lateral seta as long as width of segment. Exopodite 1 about 1.5 times longer than broad, outer and inner margins convex. Segment 2 of exopodite more than twice longer than broad and nearly as long as segment 1, with lateral spine as long as segment 3; claw coarsely serrated along middle 3/5 of both margins. Exopodite segment 3 not clearly distinct from segment 2, with 2 spines, shorter spine as long as segment, and longest spine about 3 times longer than segment. Endopodite unsegmented, slender, as long as 2/3 length of exopodite segment 1, bearing at tip a row of hair-like setulae and 1 apical seta (Figs 48 and 49).

Length (caudal setae excluded): mean=1.28 mm, range=1.15–1.40 mm, $n=53$.

Male: Body widest at junction of pedigers 1 and 2 in dorsal view (Fig. 50). Suture between pedigers 4 and 5 complete, with single row of irregularly spaced spinules, like female, along distal border of pediger 4. Pediger 5 expanded posterolaterally into 2 small, nearly symmetrical wings, each with 1 minute hair and 1 short spine at tip (Fig. 51).

Urosome length shorter than 1/3 of body length, of 5 segments, segment 1 slightly asymmetrical with short spine at left distolateral corner. Inner margins of caudal rami haired, outer margins smooth. Outer caudal seta frequently with a lateral spiniform process of variable development, at proximal end of normal row of setulae (Figs 52 and 53). Rostral points acute and well developed, with 1 rounded process on right side of base.

Right antennula with small conical seta on segment 12 and well-developed modified setae on segments 8,

10 and 11, and spine-like process on segments 13, 15 and 16; modified seta of segment 11 longer than modified seta of segment 10 and shorter than that of segment 8 (Fig. 89); process on segment 13 bifid at tip, large, extending to midlength of segment 14, 2.5–4 times longer than process on segments 15 and 16; process of segment 15 longer than that of segment 16 (Fig. 54). Antepenultimate segment with narrow longitudinal lamella (Fig. 55) and, sometimes, with stout curved process longer than diameter of segment (Fig. 56). Left antennula: armature identical to that of females except for setae of segments 7 and 9, which are 16–17% length of antenna, longer than those of females.

Mouthparts and swimming legs identical to those of female.

Right fifth leg coxopodite distocaudally expanded into conspicuous mammiform process with one short spine at tip (Figs 62 and 63). Basipodite longer than broad, caudal surface expanded into longitudinal, somewhat oblique ridge with 1 blunt thickening at tip of elevation and 1 field of fine granulation along distal part of ridge. Near blunt thickening is 1 rounded chitinous knob (Figs 62 and 63). Lateral seta short, extending only slightly past distal end of segment. Exopodite segment 1 elongate, about twice longer than broad (Figs 57–61 and 91), distal width equal to proximal width, distal inner corner with 1 blunt process, outer corner with 1 larger pointed process, this process oblique or almost perpendicular to axis of segment.

Exopodite segment 2 broad and pear-shaped, widest part at distal 1/4, with 2 proximal thickenings coincident with distal protuberances of first exopodite. Distal half of caudal surface with 3–6 chitinous knobs located at vertices of imaginary triangle, rhombus, or pentagon (Figs 57, 59 and 61). Proximalmost knob often longitudinally divided (Fig. 59). Lateral spine stout, shorter than width of segment, smooth, gently curved and inserted at widest part of segment (Fig. 90). Diameter of distal half of spine sharply and asymmetrically reduced. Terminal claw gently curved, nearly twice longer than segment, with single row of fine spinules along inner margin. Right endopodite unsegmented, moderately developed, with curved row of hair-like setulae at tip.

Left fifth leg coxopodite longer than wide, expanded into a short rounded protuberance near distal outer angle, with one short spine. Basipodite as long as wide, proximal width larger than distal width, lateral seta similar to that of right leg, located at distal third. Exopodite segment 1 with prominent, well-developed

haired pad. Exopodite segment 2 with proximal haired pad and 1 small pad covered with barely visible tiny spinules. Distal process longer than proximal one, both processes smooth. Endopodite unsegmented, similar to but longer than endopodite of right leg (Fig. 64).

Length (caudal setae excluded): mean=1.14 mm, range=1.09–1.24 mm, $n=50$.

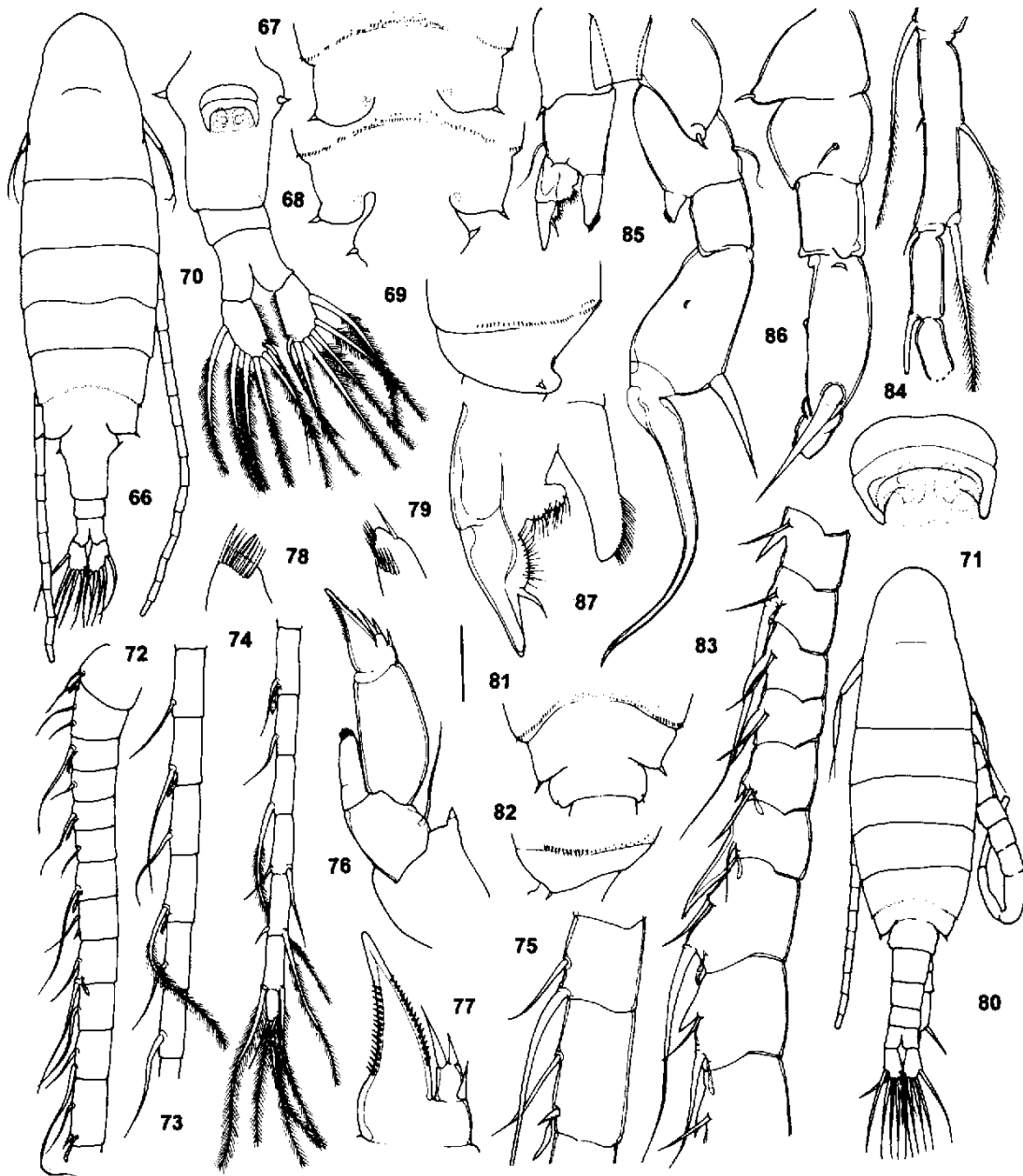
Differential diagnosis

This species is easily distinguished from the other species of *Notodiptomus* by at least two typical features of males: the arrangement of the chitinous outgrowths on the exopodite segment 2 of right leg 5, and the presence of one conspicuous spine on the outer caudal seta. *Notodiptomus dentatus* n. sp. is quite similar to *N. spinuliferus* Dussart 1985 in several aspects. Both males and females, in fact, have a row of spines along the distal border of pediger 5, and they share the general aspect of the leg 5 of male, particularly the shape of the right exopodite segment 2. On the other hand, they can be distinguished by a number of features, apart from those previously mentioned which are exclusive to *N. dentatus*. In both females and males of *N. dentatus*, there is a continuous row of spinules on the fourth prosomal somite. This spinule row is discontinuous in *N. spinuliferus*, sometimes with a gap in the middle part. The male of *N. dentatus* has a ridge and a patch of fine granules on the basipodite of right leg 5, that is absent in *N. spinuliferus*. Females differ in a number of aspects of the fifth legs, segmentation of the endopodite and relative length of the endopodite and the exopodite segments.

A detailed comparison with the most closely related species is given in Table 1. The presence of fine granules on the basipodite of the right leg 5 in males is an uncommon feature in *Notodiptomus* Kiefer, but it is shared with *Argyrodiaptomus* Brehm and *Austrinodiptomus* Reid. However, *N. dentatus* differs from the species of these genera in a number of features, mainly the shape of pediger 5 of the female and several details of the leg 5 of the male. Also, *N. dentatus* differs from *Austrinodiptomus* because it has one instead of two setae on segment 11 of antennula.

Notodiptomus spinuliferus Dussart, 1985.

Notodiptomus spinuliferus Dussart, 1985, p. 208–210, Fig. 6; Dussart & Frutos, 1985, p. 307, 308; Dussart & Matsumura-Tundisi, 1986; Matsumura-Tundisi, 1986, p. 537, Figs 34–37; Reid, 1987, p. 377.



Figures 66–87. *Notodiaptomus spinuliferus* Dussart. 66: female, dorsal; 67–68: pedigers 4–5, dorsal; 69: lateral; 70: urosome; 71: operculum; 72–74: antennula; 75: segments 11–12; 76: leg 5; 77: exopodite, segments 2–3; 78–79: tip of endopodite; 80: male, dorsal; 81: pedigers 4–5, dorsal; 82: lateral; 83: right antennula, segments 8–12; 84: segments 23–25; 85: fifth legs; 86: right leg, lateral; 87: left leg, endopodite and exopodite. Scale bars: 0.15 mm (Figs 66 and 80), 0.08 mm (Figs 67–70, 72–74, 81 and 82), 0.04 mm (Figs 75–76, 83–86), 0.03 mm (Fig. 71), 0.02 mm (Figs 77–79 and 87).

Table 1. Morphological differences among *Norodiptomus amsitsi* (Daday), *N. dentatus* n. sp. and *N. spinuliferus* Dussart. Symbols: * = no constant presence; ⁽¹⁾ = with a simple row according to Dussart (1985); ⁽²⁾ = also valid for males

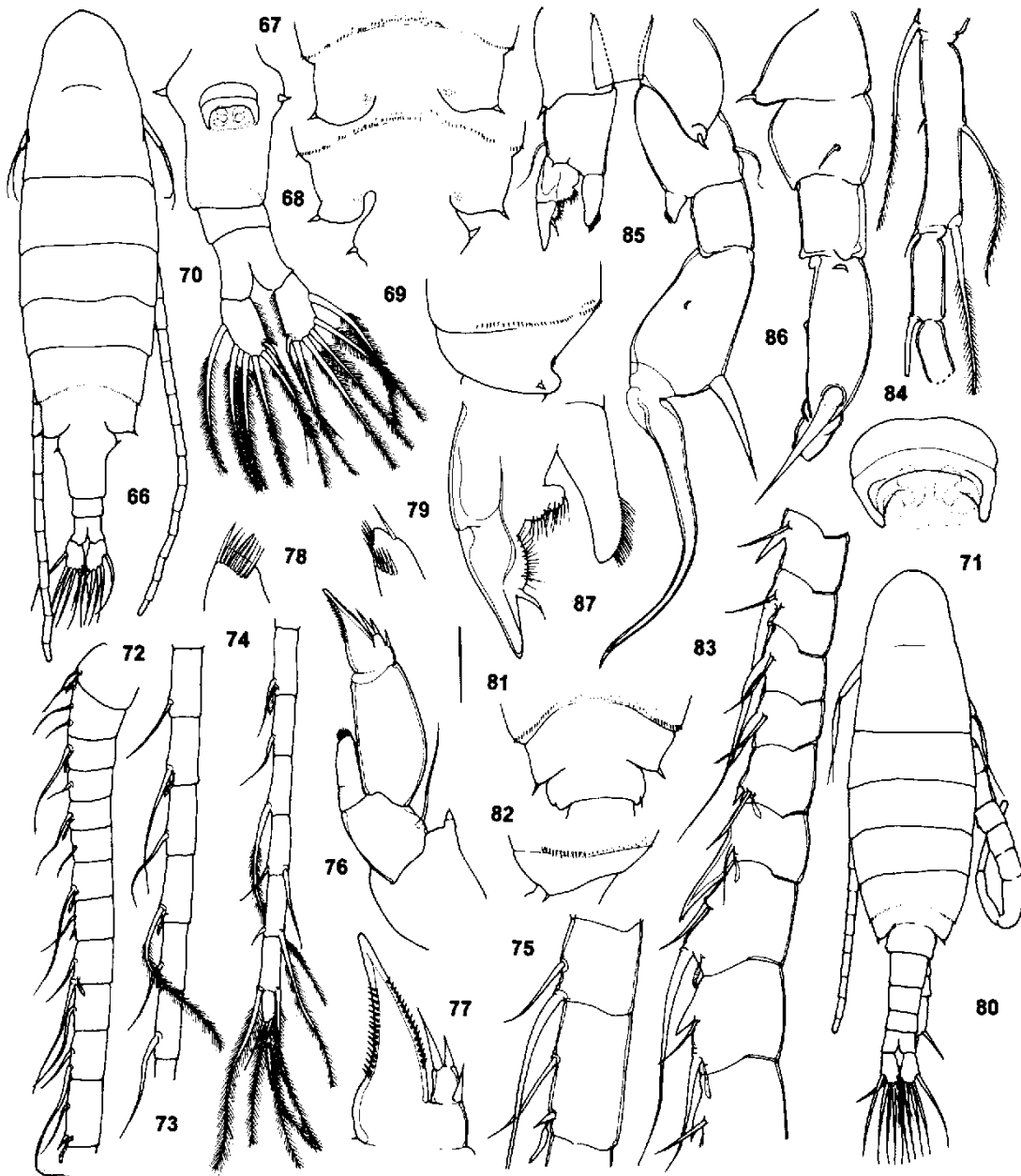
Character	<i>amsitsi</i>	<i>dentatus</i>	<i>spinuliferus</i>
Females			
(1) Dorsal suture between pediger 4 and 5	indistinct	distinct	distinct
(2) Distal border of pediger 5 with hairs	yes	no	no
(3) Distal border of pediger 4 with spinules	yes*	yes	yes
(4) Distal border of pediger 4, row of spinules: multiple=M, simple=S	M	S	M/S ⁽¹⁾
(5) Patch of spinules on middle of pediger 5	yes	no	no
(6) Wings of pediger 5 asymmetrical	yes	no	no
(7) Genital segment with finger-like protuberances	yes	no	no
(8) Genital segment; W=width, L=length	W=L	W<L	W<L
(9) Antennula, number of setae on segment 11 ⁽²⁾	2	1	2
(10) Basipodite 2 of leg 5: W=width of segment, L=length of lateral seta	W<<L	W>L	W>L
(11) Leg 5, ratio: length of exopodite 2/length of longest seta of exopodite 3 (approximate)	2	3	3
Males			
(1) Distal border of pediger 4 with spinules	no	yes	yes
(2) Outer caudal seta with lateral spine	no	yes*	no
(3) Right antennula, relative size of modified setae of segments 8 and 10	8>10	8<10	8<10
(4) Antepenultimate segment of right antennula; width of segment (W), length of 'spur' (S)	W<S	W>S	W>S
(5) Basipodite 2 of right leg 5 with a patch of fine granules	no	yes	no
(6) Exopodite 2, length:width ratio	1-1.2	1.7	1.3
(7) Exopodite 2 with maximum width at:	middle	distal third	distal third
(8) Number of chitinous knobs on caudal surface	2-3	3-4	1
(8) Arrangement of chitinous knobs: S=straight row, TR=triangular or rhomboidal	S	TR	-
(10) Location of lateral spine on exopodite 2	middle	distal third	distal third
(9) Shape of lateral spine: S=sigmoid; C=straight or gently curved	S	C	C
(10) Lateral spine, L=length, W=maximum width of segment.	L=W	L<<W	L>>W

Material examined

Argentina:

1-Pool near Formosa, Formosa Province, Sept. 1971. 2-Madrejón Don Felipe, oxbow lake near Santa Fe, Santa Fe Province, Apr. 1969. 3-Middle Paraná River, Diamante, Entre Rios Province, Sept. 1995. 4-Lower Paraná River, Paso Borghi, Sept. 1995. 5-Lower Paraná River, Km 412, Sept. 1995. 6-Lower Paraná River, Km 405, Sept. 1995. 7-Middle Paraná River,

Paraná, Entre Rios Province, Nov. 1990. 8-Lower Paraná River, San Nicolas, Buenos Aires Province, Nov. 1990. 9-Lower Paraná River, Florida, Santa Fe Province, Nov. 1990. 10-Lower Paraná River, Isla Las Palmas, Buenos Aires Province, Nov. 1990. 11-Paraná, Las Palmas River, Ñacurutú, Buenos Aires Province, Nov. 1990. 12-Paraná, Las Palmas River, Canal 6, Buenos Aires Province, Nov. 1990. 13-Confluence of Uruguay River and La Plata River, Entre Rios Province, Nov. 1990.



Figures 66–87. *Notodiptomus spinuliferus* Dussart. 66: female, dorsal; 67–68: pedigers 4–5, dorsal; 69: lateral; 70: urosome; 71: operculum; 72–74: antennula; 75: segments 11–12; 76: leg 5; 77: exopodite, segments 2–3; 78–79: tip of endopodite; 80: male, dorsal; 81: pedigers 4–5, dorsal; 82: lateral; 83: right antennula, segments 8–12; 84: segments 23–25; 85: fifth legs; 86: right leg, lateral; 87: left leg, endopodite and exopodite. Scale bars: 0.15 mm (Figs 66 and 80), 0.08 mm (Figs 67–70, 72–74, 81 and 82), 0.04 mm (Figs 75–76, 83–86), 0.03 mm (Fig. 71), 0.02 mm (Figs 77–79 and 87).

Description

Female: Body widest at junction of pedigers 1 and 2, dorsal view (Fig. 66). Suture between pedigers 4 and 5 distinct at middle and lateral part, with a row of spinules parallel to this junction. This row multiple on dorsal part and single on both sides, and sometimes with one short row of spinules on lateral part of pediger 4 (Figs 67–69). Pedigers 4 and 5 evenly curved, in lateral view, without dorsal hump (Fig. 69). Pediger 5 expanded posterolaterally into moderately developed symmetrical wings; ending in stout sensilla, with one group of fine spines on inner proximal surface of each wing. Distal part of pediger 5, between wings, smooth.

Urosome with three segments, about 1/4 of body length. Genital segment 1.5 times longer than broad, well expanded anterolaterally and slightly asymmetrical, right expansion larger than left; each expansion with 1 stout sensillum, sensillum on right side lateral to tip of expansion and that on left side dorsal and posterior to top of expansion. Postero-dorsal corners of genital segment smooth (Fig. 70).

Genital operculum (Fig. 71) with proximal plate, slightly longer than transverse bar of distal plate, with proximal border irregularly undulate. Junction between distal and proximal plate evenly curved. Distal plate narrow, with distal border somewhat curved or irregularly straight. Lateral arms clearly convergent, about three times longer than transverse bar, with evenly curved inner side. Urosomite 2 without noticeable structure. Inner margin of caudal rami haired, outer margin smooth. Caudal setae with normal armature. Rostral points acute and well developed, with no process at base.

Antennula reaching end of caudal rami (% of body length: mean=112, range=101–121), setation (s=setae, cs=conical setae, ae=aesthetascs) of each segment as follows: 1(1s, 1ae), 2(3s, 1ae), 3(1s, 1ae), 4(1s), 5(1s, 1ae), 6(1s), 7(1s, 1ae), 8(1s, 1cs), 9(2s, 1ae), 10(1s), 11(1s), 12(1s, 1ae, 1cs), 13(1s), 14(1s, 1ae), 15(1s), 16(1s, 1ae), 17(1s), 18(1s), 19(1s, 1ae), 20(1s), 21(1s), 22(2s), 23(2s), 24(2s), 25(4s, 1ae) (Figs 72–75). Length of seta of segment 7 and longest seta of segment 9, 8.5–9.5% length of antennula. Of terminal setae, 3 setae several times longer than segment 25, one seta slightly longer than segment 25, and remaining seta shorter than segment 25.

Remaining cephalic appendages and swimming legs with normal setation. Swimming legs with segmentation and armature normal for genus. Segment 1 of exopodite of leg 1 with one spine at outer distal

outer corner. Endopodite segment 2 of leg 2 with Schmeil's organ.

Leg 5 (Fig. 76) coxopodite with prominent, posteroventrally directed process tipped with short, blunt spine. Basipodite with inner proximal angle smooth, lateral seta longer than width of segment. Exopodite segment 1 slightly less than twice as long as broad, outer margin convex, inner margin straight or somewhat convex. Segment 2 of exopodite about twice longer than broad and shorter than segment 1, with lateral spine as long as segment 3; claw with one proximal row of long spines on each side. Exopodite segment 3 not clearly distinct from segment 2, with two spines, shortest spine as long as segment, and longest spine about two times longer than it (Fig. 77). Endopodite partially segmented, half length of exopodite segment 1 bearing at tip one curved row of hair-like setulae and one apical seta (Fig. 79).

Length (caudal setae excluded): mean=1.13 mm, range=1.05–1.23 mm, $n=25$.

Male: Body widest at junction of pedigers 1 and 2 in dorsal view (Fig. 8). Suture between pedigers 4 and 5 complete, with one row of spinules parallel to this junction, this row multiple on dorsal part and single on both sides, as in female (Figs 81 and 82). Pediger 5 expanded posterolaterally into two small, nearly symmetrical wings, each with one short spine at tip.

Urosome little shorter than one third of body length, of 5 segments, segment 1 slightly asymmetrical, with short spine at left distolateral corner. Inner margins of caudal rami haired, outer margins smooth. Caudal setae with normal armature. Rostral points acute and well developed, with 1 rounded process on right side of base.

Right antennula with small conical seta on segment 12 and well developed modified setae on segments 8, 10 and 11, and spine-like process on segments 13, 15 and 16; modified seta of segment 11 longer than modified seta of segments 10 and 8 (Fig. 89); process on segment 13 bifid at tip, extending to distal 2/3 of segment 14, 3.5–4 times longer than process on segments 15 and 16; process of segment 15 longer than that of segment 16 (Fig. 83). Antepenultimate segment sometimes with stout process shorter than diameter of segment, similar to that of *N. dentatus*.

Left antennula armature identical to that of females except for setae of segments 7 and 9, which are about twice longer than those of females, about 16–17% length of antenna.

Mouthparts and swimming legs identical to female.

Right leg 5 (Figs 85 and 86) coxopodite distocaudally expanded into moderately developed mammiform process with one short spine at tip. Basipodite longer than broad, with caudal surface smooth. Lateral seta short, extending only slightly past distal end of segment. Exopodite segment 1 somewhat longer than broad (Fig. 91), distal width equal to proximal width, distal inner corners with blunt process, outer process larger than inner one. Exopodite segment 2 broad and pear-shaped, widest part at distal quarter, with two proximal thickenings coincident with distal protuberances of first exopodite, and with one conspicuous chitinous knob on caudal surface. Lateral spine large, longer than width of segment, smooth, gently curved, and inserted at widest part of the segment (Fig. 90). Terminal claw gently curved, nearly twice longer than segment, with single row of fine spinules along inner margin. Right endopodite unsegmented, short, with curved row of hair-like setulae at tip.

Left leg 5 coxopodite longer than wide, expanded into short rounded protuberance near distal outer angle, with one small spine. Basipodite as long as wide, proximal width larger than distal width, lateral seta similar to that of right leg, located at distal third. Exopodite segment 1 with bilobed haired pad well developed. Exopodite segment 2 with rounded, short and haired proximal process. Distal process longer than proximal one, both processes smooth. Endopodite unsegmented, longer than that of right leg (Fig. 87).

Length (caudal setae excluded): mean=1.03 mm, range=0.99–1.07 mm, $n=18$.

Remarks

There are three available descriptions of this species: Dussart (1985), Dussart & Matsumura-Tundisi (1986), and Matsumura-Tundisi (1986). However, they are relatively brief and some details were not considered. Therefore, for a close comparison with *N. dentatus*, additional observations on Argentine material were necessary and consequently new data were obtained.

One of the hitherto undescribed features is the presence of a group of spines on each wing of the pediger 5. This feature is shared, in the Neotropical region, with *N. brandorffi* Reid 1987, *N. leonicollinus* (Marsh) 1913, *N. maracaibensis* Kiefer 1954, and *N. gatunensis* (Marsh) 1913.

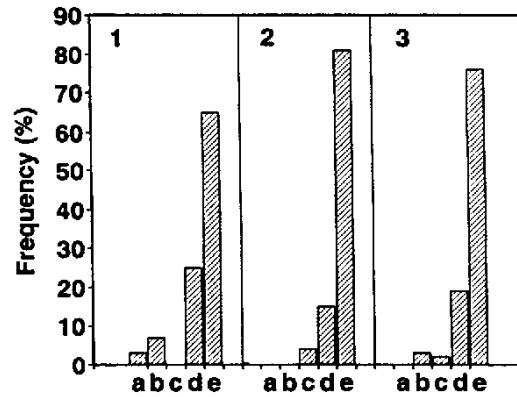


Figure 88. *Notodiptomus anisitsi* (Daday). Frequency of the variations of theinger-like process at right distal angle of genital segment of female (a=absent, b=one small, c=one large, d=one small+1 large, e=two large) in the following localities: (1) Laguna Yema, (2) Margarita, (3) Concordia.

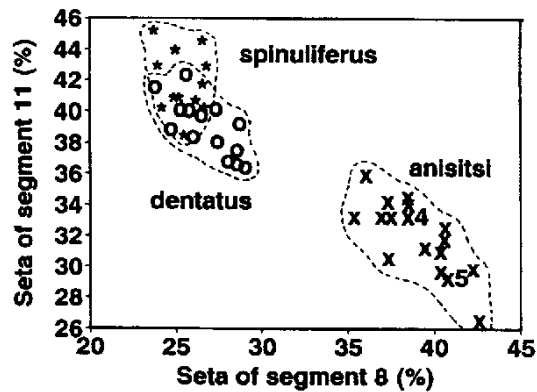


Figure 89. Length of modified setae on segments 8 and 11 of the right antennula of the male (calculated as percentages of the sum of the modified setae of the segments 8, 10 and 11). Symbols 4 and 5 correspond to *N. 'bidigitatus'* Brehm (1958) from Calchaquí and Laguna Yema, respectively.

This feature was not mentioned in the text or drawn in the figures by Dussart & Matsumura Tundisi (1986). Although it could be considered a variable feature, this spine group was present in all females from all localities studied.

Discussion

Notodiptomus anisitsi was originally described from several localities in Paraguay (Daday, 1905). Some years later, Brian (1925) described *D. inflexus* from

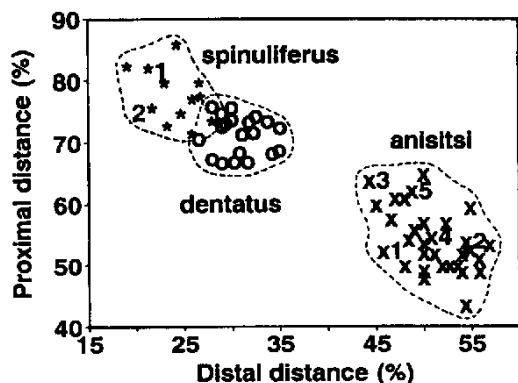


Figure 90. Location of the lateral spine of right leg 5 of male (calculated as the percentage of the length of exopodite 2). Proximal distance (proximal right angle of the segment lateral spine). Distal distance (lateral spine—base of terminal claw). Measurements from literature, according to symbols: 1=Dussart (1985), 2=Daday (1905), 3=Brian (1925), 4 and 5=Brehm (1958).

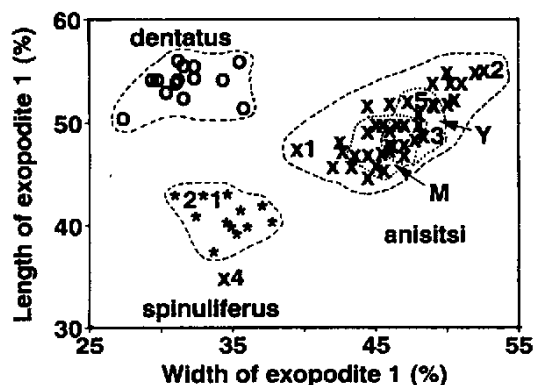


Figure 91. Length:width ratio of exopodite 1 (calculated as percentage of the length of exopodite 2). Measurements from literature, according to the same symbols of Fig. 90. Other symbols: M=specimens from Margarita, Y=specimens from Laguna Yema.

Argentina and Uruguay; which is undoubtedly related to Daday's species. The presence of a row of three chitinous knobs on the second exopodite of the male right leg 5 is the most conspicuous difference between these species.

A few years later, Kiefer (1928) stated that *D. inflexus* should be considered conspecific with *D. anisitsi*, and he emphasised the poor diagnostic value of the supposed differences and the schematic nature of Daday's illustrations. The interpretation offered by Kiefer (1928) was not accepted by Brehm (1938), who believed that they are two different species. The same author (Brehm, 1939) described material from Ur-

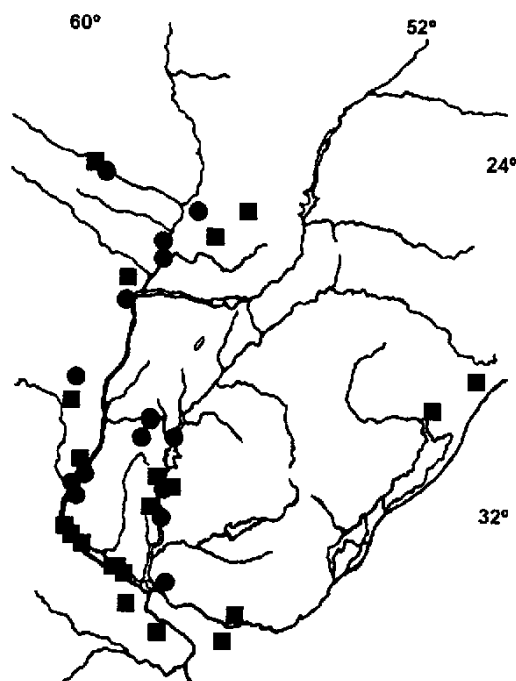


Figure 92. Distribution of *Notodiptomus anisitsi* (Daday, 1905). Squares=records from literature; circles=original records.

uguay related to *D. anisitsi*, but he was not convinced whether to assign them to the mentioned species or to two different species, because of the presence of two finger-like protuberances on the genital segment of females and one process on the antepenultimate segment of the right antennula of some males. About the presence of the chitinous knobs on the exopodite of the male leg 5, I suppose that Brehm (1939) did not observe them in his material, since they were not mentioned in the description.

Brehm (1958), along with a comparison between *Notodiptomus perelegans* (Wright, 1927), and *N. anisitsi*, dealt again with *D. anisitsi*-like populations from northern Argentina in which females had two finger-like protuberances on the distal right angle of genital segment. Because of this feature and the shape of the exopodite segment 1 of the male right leg 5, he described the specimens from Calchaquí and Laguna Yema as an intermediate form between *N. anisitsi* and *N. perelegans*, under the name *N. 'bidigitatus'*.

Brandorff (1976), Dussart & Defaye (1983) and Dussart (1985) dealt with *N. bidigitatus* as a species different from *N. anisitsi*, though they did not agree about the generic status and its validity as a new

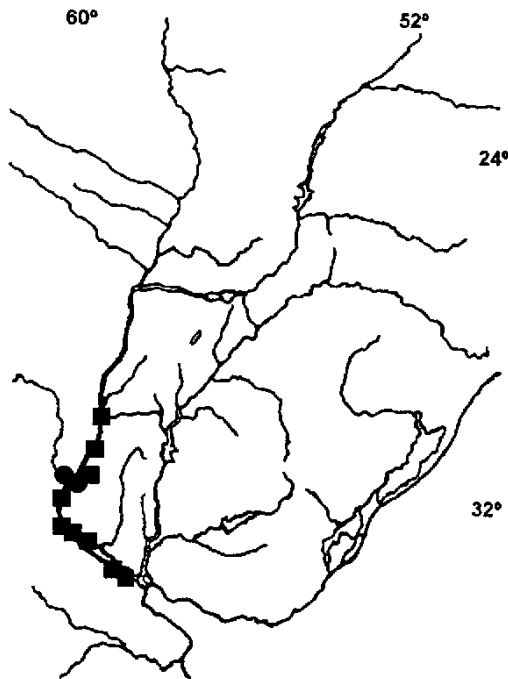


Figure 93. Distribution of *Notodiaptomus dentatus* n. sp. Squares=records from literature; circles=original records.

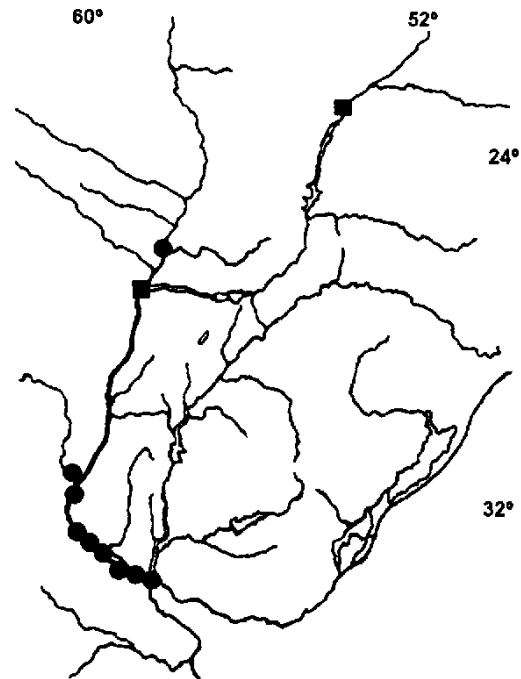


Figure 94. Distribution of *Notodiaptomus spinuliferus* Dussart, 1985. Squares=records from literature; circles=original records.

species. Brandorff (1976) considered that the location of '*bidigitatus*' as a member of *Notodiaptomus* is not clear and should be revised, suggesting to assign it provisionally to '*Diaptomus*'. On the other hand, Dussart & Defaye (1983), in agreement with Brehm (1958), considered '*bidigitatus*' as a member of *Notodiaptomus*, but pointed out that it is a doubtful species, close to *N. perelegans* and *N. anisitsi*.

Ringuet & Martinez de Ferrato (1967) offered a description of a diaptomid copepod from Santa Fe, Argentina, and assigned it to *D. anisitsi*. The identification was based mainly on the presence of chitinous knobs on the exopodite segment 2 of the right leg 5, though the arrangement of these knobs was not the same as that described by Brian (1925) and Kiefer (1928). In their brief description, they did not mention the ornamentation of the female genital segment.

Hence, at least three diagnostic features were involved in the intricate history of this complex of species: the chitinous knobs on the exopodite segment 2 of the right leg 5 of males; the finger-like protuberances on the distal right angle of genital segment; and presence or absence of one 'spur' on the antepenultimate segment of the right antennula.

Although the number and shape of the finger-like process on the right angle of genital segment are variable (Figs 5–11), all or most of the females studied had two processes (Fig. 88). The material studied was obtained from type localities, or nearby, of *N. anisitsi* (Ipacará Lake, Paraguay River), *N. inflexus* (Uruguay River at Concordia and Colón) and *N. bidigitatus* (Laguna Yema and Margarita).

The protuberance on the left angle, distinctly drawn by Daday (1905) and not so clear in Brian's (1925) figures, was a quite frequent feature in the specimens studied, though the shape and size were variable, and sometimes the protuberance was barely visible.

In none of the populations studied did any female have one process on the right distal angle of urosomite 2, like that present in *N. perelegans* (Wright, 1927).

Therefore, there are no valid arguments to sustain, based on these characters, the separation of *N. anisitsi*, *N. inflexus* and *N. bidigitatus* as three different species. On the contrary, the location of these protuberances was constant, and no intermediate form between them and *N. perelegans* was observed.

The chitinous knobs on the caudal surface of exopodite 2 of the male right leg 5 were always present, but they were not always easily visible in caudal view. In general, these protuberances are observed better in lateral view. The specimens of *N. 'bidigitatus'* described by Brehm (1958) seemingly lacked these protuberances. However, all the specimens that I studied from Laguna Yema ('type locality') and Margarita (near to Calchaquí, the other 'type locality') of *N. 'bidigitatus'*, had the chitinous knobs.

Though the size of these knobs seems to be somewhat exaggerated in Brian's (1925) figures, I often found specimens in which they were almost as conspicuous. The relative location of these knobs was always along an imaginary straight line parallel to the inner border of the segment.

Ringuelet & Martínez de Ferrato (1967), who agreed with Kiefer's (1928) opinion about the synonymy of *N. anisitsi* and *N. inflexus* on the basis of the chitinous knobs, supposed that the specimens from the Paraná River studied by them should be assigned to *N. anisitsi*, because of the presence of this feature alone. However, not only the arrangement and the number of these knobs are different, but there are a number of other differences regarding *N. anisitsi* (see Table 1).

Brehm (1939), dealing with a *N. anisitsi*-like population from the La Plata River, suggested that it could be composed of more than one species because of the existence of two kinds of males, one of them with a 'spur' on the antepenultimate segment of the right antennula.

The presence of a curved distal process, or 'spur', on some of the males in the populations studied was a constant feature. However, not all males exhibited this feature; in general only a low percentage of the population had the 'spur'. The highest percentage (29%) was observed in one population from the Paraguay River, near Formosa. In all the populations studied, this character was present in the larger specimens, but not in all them.

It is also possible to add another feature to the discussion about the validity of *N. 'bidigitatus'* and its supposed intermediate location between *N. anisitsi* and *N. perelegans*: the length/width relationship of the exopodite 1 of the male's fifth right leg. In *N. anisitsi*, the exopodite 1 is longer than wide, in *N. perelegans* it is wider than long, and in *N. 'bidigitatus'* this relationship is intermediate, especially in the population from Calchaquí (Brehm, 1958).

From the two populations of *N. 'bidigitatus'* described by Brehm (1958), the specimen from Laguna

Yema (Fig. 91, 5; measurements taken from the original figures), falls within the limits of those studied by me (Fig. 91, Y), but that from Calchaquí (Fig. 91, 4) is far from this group. Although I was not able to study specimens from Calchaquí, I observed one population from Margarita near that locality. The specimens from Margarita (Fig. 91, M) also fall among the group corresponding to *N. anisitsi*. Moreover, the remaining features of the male specimen from Calchaquí described by Brehm (1958) are consistent with those of *N. anisitsi*, even the distinctive size relationship of the modified setae of the right antennula (Fig. 89, 4). Therefore, I believe that Brehm's (1958) figures of the exopodite 1 may have been based on an atypical specimen or an artifact.

The patterns of geographical distribution of *N. anisitsi*, *N. dentatus* and *N. spinuliferus*, as far as we know, are quite similar (Figs 92–94), and we often find two of them co-existing in the same habitat. These species inhabit lentic and lotic environments of the Paraná River basin, and *N. anisitsi* has also been recorded in the Uruguay River, and in Rio Grande do Sul, Brazil.

Conclusions

The validity of *N. inflexus* (Brian) and *N. 'bidigitatus'* Brehm as species different from *N. anisitsi* (Daday) cannot be sustained. Analysis of the morphological variability of the populations of *N. anisitsi* demonstrated that inclusion of *N. perelegans* within the range of variations of *N. anisitsi* cannot be sustained. Some populations of *Notodiptomus* from Paraná River assigned to *N. anisitsi* are representative of a new species, *N. dentatus*. It is apparent that *N. spinuliferus* and *N. dentatus* are very much alike, which suggests a close phylogenetic relationship. Although the presence or absence of one 'spur' on the male's right antennula cannot be used to differentiate a species, the shape and relative size of this process can be used as a diagnostic character to separate *N. anisitsi* from *N. spinuliferus* and *N. dentatus*. Several of the diagnostic characters analysed here were constant, but most of them exhibited some variability and therefore can be used only in populational analysis.

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