



Taxonomic status of *Nimbecera* Reiss, 1972, a junior synonym of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)

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Abstract

In the past, the Nearctic *Tanytarsus limneticus* Sublette, 1964, as well as the Neotropical *T. rhabdomantis* (Trivinho-Strixino & Strixino, 1991) and *Caladomyia ortonii* Sæwedal, 1981 were erroneously placed in *Nimbecera* Reiss, 1972 due to the annulated Lauterborn organ pedicels of the larvae, a feature first thought to be unique to this genus. In the present paper, the systematic position of *T. limneticus*, *T. patagonicus* and *T. rhabdomantis* is discussed in detail. Complete morphological diagnoses of the adult males, pupae and larvae of *T. patagonicus* and *T. limneticus* are given, in addition to descriptions and drawings of the adult males and pupae of both species. As a result, *Nimbecera patagonica* Reiss, 1972, recorded from southern Chile and Argentina, is transferred to the genus *Tanytarsus* van der Wulp, 1874. The monotypic genus *Nimbecera* becomes a junior subjective synonym of *Tanytarsus*.

Key words: Diptera, Chironomidae, *Nimbecera*, *Tanytarsus*, new combination, synonymy, Neotropical Region

Introduction

Reiss (1972) described the genus *Nimbecera* based on larva, pupa and adult male of a single species, *Nimbecera patagonica*, from southern Chile and Argentina (Patagonia). The annulated Lauterborn organ pedicels were observed for the first time in the tribe Tanytarsini and was one of the characters used by Reiss to delimit *Nimbecera*.

This morphological character seemed to be so characteristic for the genus that further new *Nimbecera* species were described based on larval stage (Trivinho-Strixino & Sanseverino 2003). Steiner and Hulbert (1982) described the North American *Nimbecera pinderi*, but based on all life stages, the species was synonymised with *Tanytarsus limneticus* Sublette, 1964 (Epler 1992). In the same publication, Epler (1992) moved *T. limneticus* to *Nimbecera*, and thus *Nimbecera pinderi* became a junior synonym of *Nimbecera limnetica*. Later, Epler (1995) returned the species to the genus *Tanytarsus* (Caldwell *et al.* 1997). The Brazilian *Nimbecera rhabdomantis* and *N. paulensis* were described based on larvae by Trivinho-Strixino and Strixino (1991). After examination of reared pupae and adult males, *N. rhabdomantis* was transferred to the genus *Tanytarsus* (Trivinho-Strixino & Sanseverino 2003), while *N. paulensis* was synonymised with *Caladomyia ortonii* Sæwedal, 1981 (Trivinho-Strixino & Strixino 2003). *Nimbecera patagonica* is thus the only valid species in *Nimbecera*; all other species described later have been synonymised or placed in other genera (Trivinho-Strixino & Sanseverino 2003).

Epler (2001) pointed out that associations of life stages in several *Tanytarsus* species indicate that some of the characters used by Reiss (1972) to delimit *Nimbecera* may not hold as diagnostic characters for the genus. The features used to identify *Nimbecera* in the keys for Chironominae larvae and pupae (Pinder & Reiss 1983,

1986 respectively) are found also in *Tanytarsus* species. Cranston *et al.* (1989) pointed out that since only one species is known in the adult stage, the diagnosis of *Nimbecera* may require extension or revision. Some authors have questioned the validity of *Nimbecera* (Epler 1995) or the placement of at least certain species in *Tanytarsus* (Ekrem *et al.* 2003).

Tanytarsus is a species-rich genus, with more than 300 species world-wide (Ekrem 2003). The combination of several diagnostic characters of the adult males and pupae has been used to separate species groups (Reiss & Fittkau 1971; Cranston 2000; Ekrem 2001a, 2001b, 2002, 2003; Gifka & Paasivirta 2009).

In the present study, *Nimbecera patagonica* Reiss, 1972 is transferred to the genus *Tanytarsus* van der Wulp, 1874. The monotypic genus *Nimbecera* Reiss, 1972 becomes a junior subjective synonym of *Tanytarsus*. Complete morphological diagnoses, additional descriptions and drawings of the adult males and pupae of *T. patagonicus* and *T. limneticus* are given. The systematic placement of *N. patagonica* in *Tanytarsus* and the generic synonymy are discussed and argued. The systematic position of *Tanytarsus limneticus*, *T. patagonicus* and *T. rhabdomantis* is also discussed.

Material and methods

The male morphological terminology and abbreviations follow Sæther (1980) except for vannal fold (here called postcubitus), “lamellate setae” of median volsella (here called “lamellae”) and “sensilla basiconica” on anal point (here called “spines”). The antennal (AR), leg (LR, BV, SV), wing (L/WR) and hypopygium (Gc/Gs) ratios, as well as lengths and widths of all other characters were measured according to Sæther (1968), Schlee (1966) and Sponis (1977). The angle between the longitudinal axis of superior volsella and body was measured according to Fittkau and Reiss (1973). The terminology and abbreviations for the pupae follow Sæther (1980) with modifications suggested by Langton (1991) and Langton (1994). The terms “taenia” and “taeniae” are, respectively, singular and plural, while the term “exuviae” is used in both cases (Langton 1994). All species were mounted in Euparal on slides for light microscopy. The sampling methods and location of the material examined are given in the species descriptions. The types are housed in the following institutions: NHRS – Swedish Museum of Natural History, Stockholm, Sweden; ZSM - Zoologische Staatssammlung München (ZSM), Munich, Germany; ZMBN - Museum of Zoology, University of Bergen, Norway; Collection of J. E. Sublette - private collection of Prof. Dr. James E. Sublette, Scottsdale, Arizona, USA.

Results

Tanytarsus patagonicus (Reiss, 1972) comb. n.

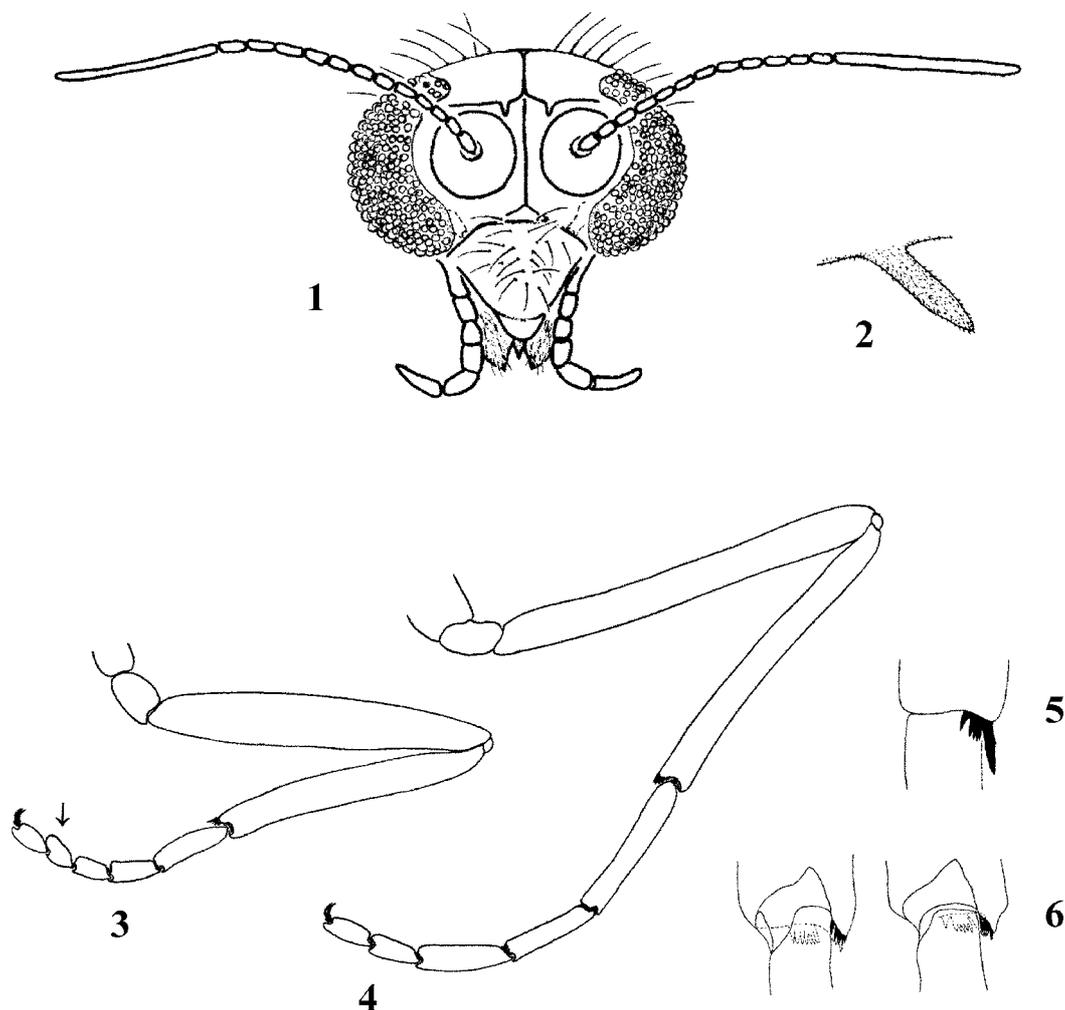
(Figs 1–15)

Type material. Holotype: 1 adult male, South Chile, Puerto Natales, Province of Magallanes, Laguna Diana, shore ponds, 2.I.1970, slide mounted in Euparal, leg. F. Reiss (NHRS). Paratypes: 4 adult males, same as holotype except deposited at ZSM; 4 pupal exuviae, same as holotype except deposited at ZSM; 2 pharate males as holotype except deposited at ZSM; 1 pharate male, South Chile, Lago Villarrica, 3.XI.1969, slide mounted in Euparal, leg. F. Reiss; 2 pupal exuviae, Lago Pellaifa, drift, 5.XII.1953, slides mounted in Euparal, leg. L. Brundin; 3 adult males, Argentina, Bariloche, Laguna Trebol (shallow littoral lake), 17.XI.1969, slides mounted in Euparal, leg. F. Reiss; 2 pupal exuviae as previous (all paratypes at ZSM).

Additional material examined: 1 adult male, Chile, 21.8.1970, slide mounted in Euparal; 1 pharate male, South Chile, Puerto Natales, Province of Magallanes, Laguna Diana, shore pond, 1. I.1970, slide mounted in Euparal, leg. F. Reiss; 1 adult male as previous (all material deposited at ZSM).

Diagnosis. Male Imago: Antenna short (brachycerous), plume reduced; low AR; palp reduced; wing somewhat reduced and cuneate, wing vein R_{2+3} distinct; wings with few setae, all wing setae shorter than those observed in Neotropical *Tanytarsus*; tarsomere 4 of mid leg cordiform; tergite IX without median setae; anal tergal bands separate, curved, ending “almost together” on the middle of tergite; anal point with pair of

weakly developed, low anal crests; with field of microtrichia on entire surface between the crests; spines absent, 5–7 short setae between anal crests; superior volsella circular, posteromedian margin well projecting and thumb-like, without microtrichia; digitus short and rounded; median volsella with ramose lamellae; gonostylus large, thick and curved inwards, distally rounded.



FIGURES 1–6. *Tanytarsus patagonicus* (Reiss), adult male. 1. Head. 2. Frontal tubercle. 3. Mid leg, cordiform tarsomere 4 marked by arrow. 4. Hind leg. 5. Comb of mid tibia. 6. Comb of hind tibia.

Pupa: Frontal setae thin and short, cephalic tubercles weakly developed; wing sheath without nose, prealar tubercle rectangular; thoracic horn thin, with small, weakly sclerotized spines; three precorneals not in triangular pattern, placed on a tubercle; tergite II with homogeneous shagreen, interrupted/ sparse medially; T III with pair of long bands of longer spines on posterior half of tergite, bands curving outward; T IV with bracket-shaped pair of long bands of longer spines directed to caudal, median and oral; T V and T VI with elongate spine patches; T VIII–IX with fine oral-lateral shagreen; posterolateral comb of segment VIII with 4–6 stronger marginal teeth and 12–17 smaller ones on pad; abdominal segment I without lateral seta; segments II–VII with 3 lateral setae; segment VIII with 4 lateral taeniae, 2 dorsal setae and 1 ventral seta and 1 ventral taenia.

Larva: Antennal pedestal with rounded, wrinkled spur, segment 2 of antenna with narrow, not sclerotized ring near base; AR 1.82; Lauterborn organs small, 3–4 μm long, situated on apex of very long and slim pedicels, pedicels annulated for more than 4/5 of their length; mentum with eleven brown to dark brown teeth, median tooth trifid; mandible with dorsal pale tooth, apical tooth and 4 inner teeth brown to dark brown;

clypeal seta S3 unequally bifid.

Emendations to previous diagnoses: The eyes of *Tanytarsus patagonicus* adult males have small dorsomedian extensions (Cranston *et al.* (1989) list this as absent), the thorax has 1 prealar (in Cranston *et al.* (1989) prealars are absent) and the wing vein R_{2+3} is "fused" with R_{4+5} along 2/3 of its length basally, ending midway between apices of R_1 and R_{4+5} .

Description. Male Imago (n = 6)

Head (Figs 1–2). AR 0.45–0.53. Antenna short (brachycerous) and more or less curved, plume reduced. Antennal flagellomeres one to twelve 400–428 μm long, thirteen 188–197 μm long, total length 588–625 μm . Eyes with dorsomedian extension; large frontal tubercles (length 18–22 μm), about 2.5 times as long as wide; 9–10 temporal setae; clypeus with 20–24 setae; lengths of palpomeres (in μm): 35–37, 38–40, 58–66, 60–61, 68–72, total length 259–276 μm .

Thorax. Length 892–1000 μm . Scutal tubercle absent; 7–8 dorsocentrals, 8–12 acrostichals, 1 prealar, 4–6 scutellars. Haltere with 4–5 setae.

Wing. Weak brachyptery, length 1500–1700 μm , width about 640 μm ; L/WR about 2.53. Brachiolum with 1 seta, Sc bare, R with 14 setae, R_1 with 9 setae, R_{2+3} distinct, bare, ending midway between apices of R_1 and R_{4+5} , R_{4+5} with 10 setae, M bare, M_{1+2} with 14 setae, M_{3+4} , Cu, Cu_1 and Postcubitus bare, An with 2 setae. Cell m and false vein bare, r_{4+5} with 42 setae, m_{1+2} with 32 setae (false vein bare), m_{3+4} with 5 setae, cu and an bare.

Legs (Figs 3–6). Fore tibia without spur (in the original description with small scales distal frayed), mid tibia with pair of small, separated combs (12 μm long), only 1 comb with spur, hind tibia with 2 separated combs (12 μm long) without spur, according to Cranston *et al.* (1989) occasionally 1 spur is present. Tarsomeres of mid (principally) and hind leg shorter, tarsomere 4 of mid leg cordiform. Lengths of leg segments and leg ratios as in table 1.

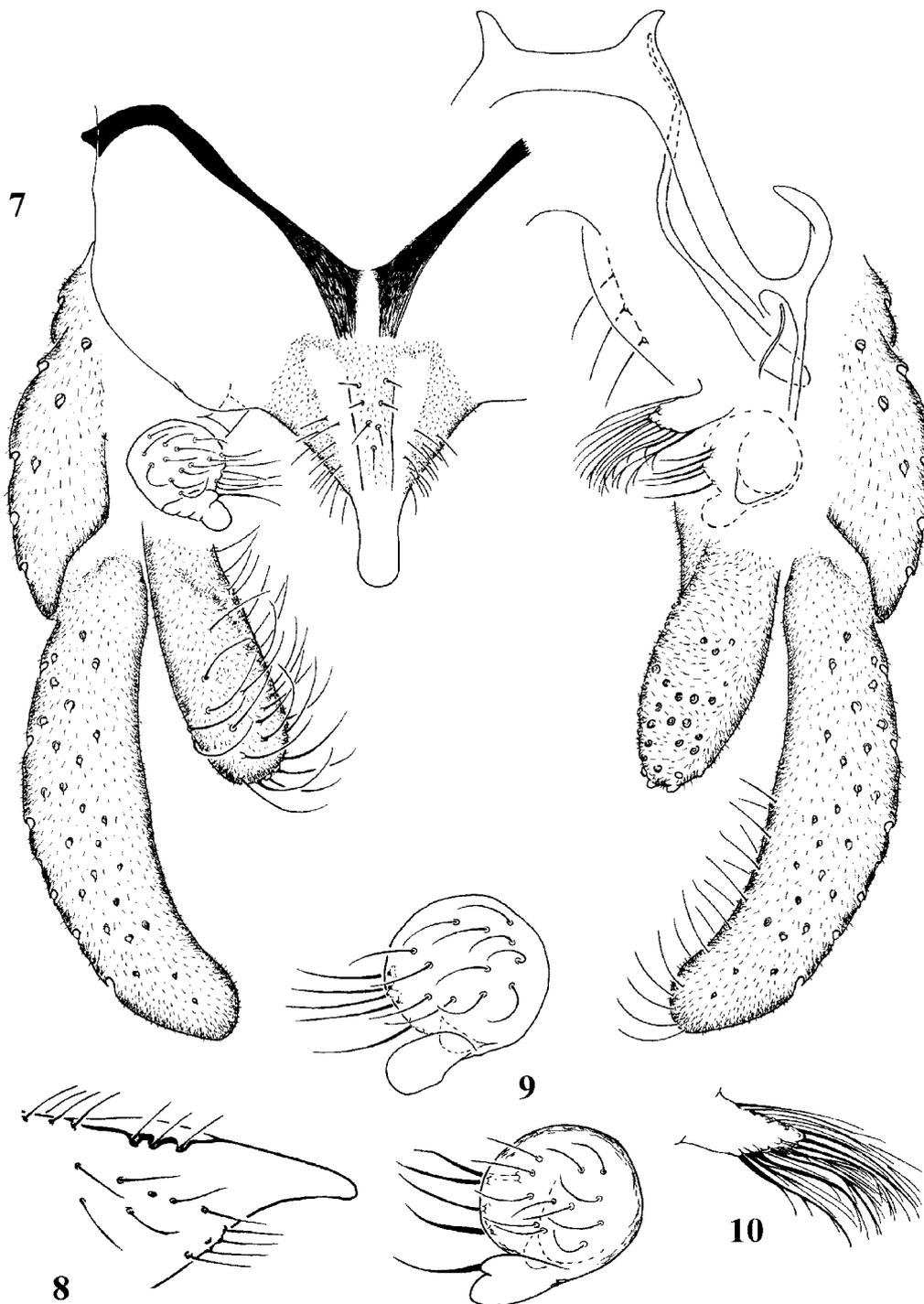
TABLE 1. Lengths (in μm) and proportions of leg segments of *Tanytarsus patagonicus* (Reiss) comb. n.

	fe	ti	ta ₁	ta ₂	ta ₃	ta ₄	ta ₅	LR	BV	SV
p ₁	800–815	518–580	*670–700	310–330	268–295	240–255	150–165	1.20–1.29	2.00–2.05	1.96–1.99
p ₂	667–700	510–560	150–165	90–100	70–90	51–60	68–75	0.29	4.38–4.75	7.63–7.84
p ₃	800–840	660–700	260–280	160–185	168–190	92–100	91–100	0.39–0.40	3.16–3.36	5.50–5.61

*In the original description the length of tarsomere 1 of fore leg is 435 μm .

Abdomen. Length 2340–3140 μm .

Hypopygium (Figs 7–10). Tergite IX 172–200 μm long, without median setae and with 28–32 apical setae, lateral tooth absent. T IX with microtrichia-free areas on each side of anal point. Orolateral spine of laterosternite IX present, 4–5 μm long. Anal tergal bands separate, curved, running parallel and ending "somewhat together" on the middle of tergite, more or less close to anal point. Anal point 57–70 μm long, elongate with rounded tip, with pair of weakly developed, low anal crests (29–37 μm long) not extending posterior to tergite IX; with field of microtrichia on entire surface between the crests; spines absent, 5–7 shorter setae between anal crests. Superior volsella oval, posteromedian margin well projecting and thumb-like, without microtrichia; anterior, median, lateral and posterior margins curved; 13–14 setae on dorsal surface, 1–2 setae proximal on projection of posteromedian margin, 4 setae on median margin (1–2 dorsal, 2–3 ventral) and 1 seta ventral, close to anterior margin. Longitudinal axes of superior volsella and body at angle of 36–40°. Digitus short and blunt, not reaching median margin of superior volsella. Median volsella 22–27 μm long with 18–25 μm long simple lamellae and 32–40 μm long ramose lamellae, not reaching apex of inferior volsella. Inferior volsella 150–153 μm long elongate and thick, expanded in distal half, area carrying setae with moderately large dorsoapical swelling. Gonocoxite length 148–155 μm ; gonostylus 185–198 μm , large, thick and curved inwards, distally rounded; hypopygium ratio (HR) 0.77–0.82.



FIGURES 7–10. *Tanytarsus patagonicus* (Reiss), adult male. 7. Hypopygium, dorsal view. 8. Anal point, lateral view. 9. Superior volsella and digitus, variation. 10. Median volsella.

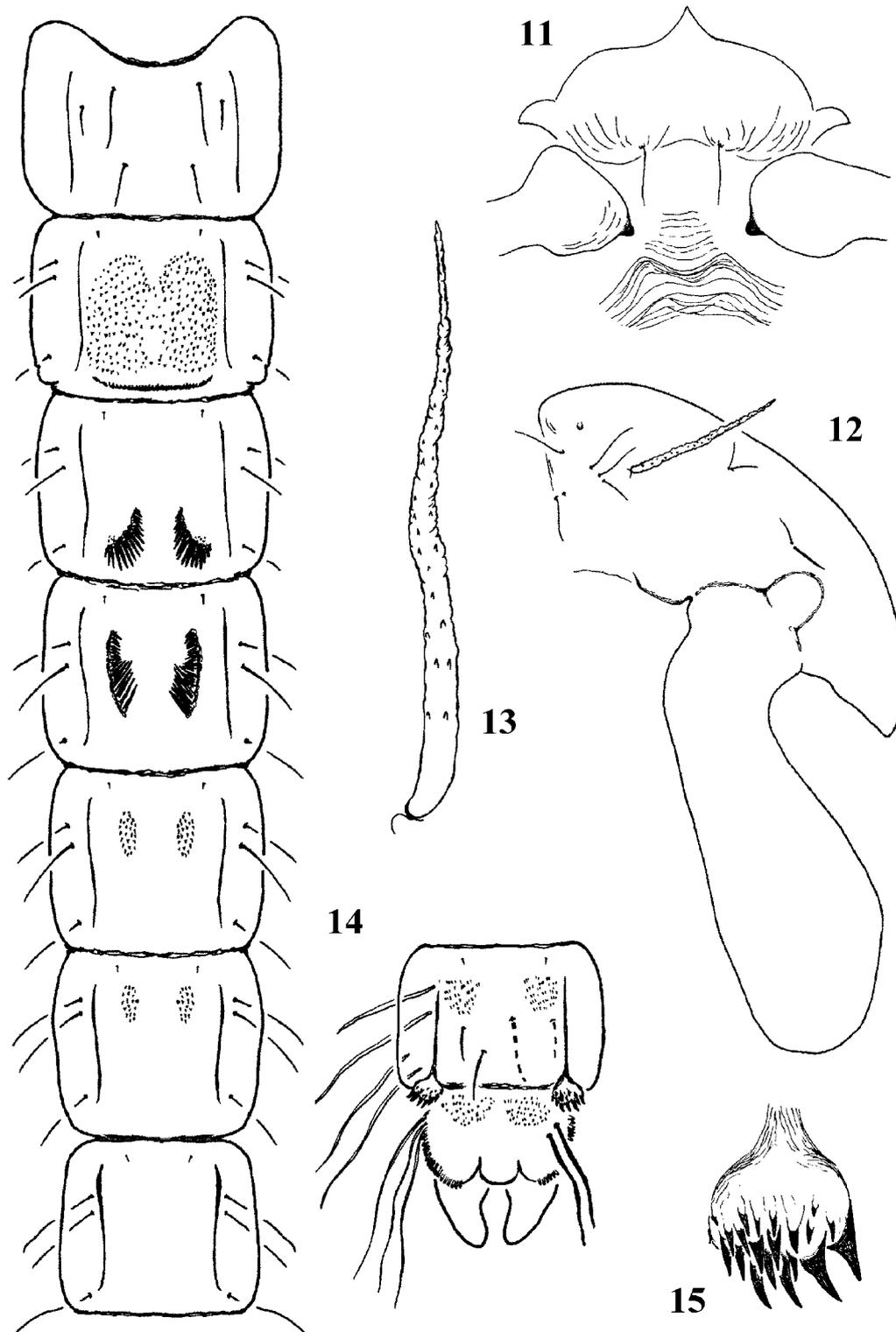
Pupa (n=5)

Total length 3840–4510 μm long.

Pupal exuviae pale brown, thorax and lateral muscle marks somewhat brownish.

Cephalothorax (Figs 11–13). Frontal apotome smooth, with wrinkles on area of cephalic tubercles. Frontal setae thin and short, 50–62 μm long, mounted apical on weakly developed cephalic tubercles; frontal warts absent. Pedicel sheath tubercle well developed. Thorax smooth, 1040–1100 μm long, with points along median suture; a small, rounded tubercle is present anteriorly near median anteprenotal. Thoracic horn thin, 292–373 μm long, with small, weakly sclerotized spines. Wing sheath without nose, prealar tubercle well

developed, rectangular. Three precorneals in row, apparently placed on a tubercle, another small tubercle is present close to Pc_3 . Anterior precorneal stronger ($100\text{--}125\ \mu\text{m}$), Pc_2 ($85\text{--}102\ \mu\text{m}$) and Pc_3 ($92\text{--}110\ \mu\text{m}$) closer to each other; 1 median ($100\text{--}115\ \mu\text{m}$) and 2 lateral antepronotals ($4\text{--}5\ \mu\text{m}$ and $62\text{--}79\ \mu\text{m}$, the latter one difficult to measure, appearing to be broken in most of the specimens); 2 pairs of dorsocentrals, anterior pair $73\text{--}100\ \mu\text{m}$ (thin) and $42\text{--}53\ \mu\text{m}$ (thick), posterior pair $68\text{--}76\ \mu\text{m}$ (thin) and $110\text{--}120$ (thick), the latter one stronger than other three.



FIGURES 11–15. *Tanytarsus patagonicus* (Reiss), pupa. 11. Frontal apotome. 12. Thorax. 13. Thoracic horn. 14. Abdomen, dorsal view; dorsal setae of segments II–VII not drawn. 15. Posterolateral comb of abdominal segment VIII.

Abdomen (Figs 14–15). Total length 2800–3420 μm . Tergites I and VII without armament. T II with homogeneous shagreen, interrupted/ sparse medially. T III with pair of long bands of longer spines placed on posterior half of tergite, bands curved outward. T IV with bracket-shaped pair of long bands of longer spines directed to caudal, median and oral. T V and T VI with elongate spine patches. T VIII–IX with fine oral-lateral shagreen. Sternites I, IV–VII without armament. S II–III with very fine oral-lateral shagreen. S VIII with fine oral-lateral shagreen. Conjunctives and pleura unarmed. Hook row 204–260 μm , about 1/2 width of tergite II. Pedes spurii A absent; pedes spurii B present on segment II. Posterolateral comb of segment VIII 60–76 μm wide, with 4–6 strong marginal teeth and 12–17 smaller ones on pad. Abdominal setation: segment I with 3 D, the most anterior longer, 0 L and 0 V; segment II with 4 D, 3 L and 4 V; segments III–VII with 5 D, 3 L and 5 V; segment VIII with 2 D, 4 lateral taeniae and 1 V and 1 ventral taenia. Anal lobe well developed, with fringe of 17–20 taeniae in single row and with two pairs of dorsal taeniae. Tergites II–VIII with O-setae.

Distribution and ecological notes. *Tanytarsus patagonicus* is recorded from southern Chile and Argentina (Patagonia). Larvae and pupae inhabit ponds, lakes and coastal lagoons. According to Reiss (1972), the larvae probably prefer to inhabit nutrient-rich sediments of standing waters, where mass-developments can occur. Since adults were never trapped at the surrounding vegetation of the corresponding water-body, Reiss (1972) presumed that the brachypterous males do not form swarms and the mating probably takes place on water surface.

***Tanytarsus limneticus* Sublette, 1964** (Figs 16–25)

Nimboecera pinderi (Steiner & Hulbert, 1982); 4th instar larvae. Synonymised by Epler (1992).

Type material (USA). Paratypes: 1 adult male, Louisiana, Natchitoches, U.S. Fish Hatchery, 20.IX.1958, leg. R. F. Tyler (Collection of J. E. Sublette); 1 adult male as previous except 12.IX.1958, specimen remounted in Euparal, leg. J. E. Sublette (Collection of J. E. Sublette).

Additional material examined: *Nimboecera pinderi* (Steiner & Hulbert, 1982): 1 adult male, USA, Florida, Boca Grande, a lab pond, 27.XII.1982, R. Rutter (ZMBN); 1 adult male plus 1 pupal exuviae as previous, 2 pharate males as previous.

Diagnosis. Male Imago: AR about 1.37; large frontal tubercles; dorsocentrals in one row, close to scutellum in a group of 2–4 setae; high number of acrostichals and scutellars; 2–3 prealars; M and Sc veins with setae; tergite IX without microtrichia-free areas; anal tergal bands separate, curved; anal point with pair of well developed anal crests; spines placed irregularly between anal crests, 2 shorter setae are present anteriorly between crests; superior volsella with field of microtrichia on anterolateral margin, posteromedian corner projecting; digitus pointed, triangular to somewhat cone-like, not extending or extending a little beyond margin of superior volsella; median volsella with foliate lamellae.

Pupa: Frontal setae short, cephalic tubercles weakly developed; prealar somewhat rounded to quadrate and inwardly folded; thoracic horn thin and with spinules; three precorneals not in triangular pattern, placed on an tubercle; tergite II with median homogeneous shagreen; T III with pair of long bands of longer spines placed on posterior half of tergite and lateral fields of fine shagreen, bands anteriorly straight, posteriorly curved outward; T IV with bracket-shaped pair of long bands of spines, anterior part with thin short spines directed to caudal and median, posterior part with longer spines directed to oral; T V–VI with anterior pair of rounded spine patches; T VIII with fine anterolateral shagreen; T IX with anterior shagreen; posterolateral comb of segment VIII quite broad; abdominal segment I with 2 dorsal long taeniae and without lateral seta, segment II–VII with 3 lateral setae, segment VIII with 3 lateral taeniae, 1 dorsal seta and 1 ventral taenia.

Larva: Antennal pedestal without spur, segment 2 of antenna with narrow, not sclerotized ring near base; AR 1.66; Lauterborn organs small, situated on apex of long and slim pedicels, pedicels annulated for about 4/5 of their length; mentum with pale, pentamerous median tooth and 5 pairs of brown lateral teeth; mandible with dorsal pale tooth, apical tooth and 3 inner teeth brown to dark brown.



FIGURES 16–19. *Tanytarsus limneticus* Sublette, adult male. 16. Hypopygium, dorsal view. 17. Anal point, dorsal view. 18. Superior volsella and digitus variation. 19. Median volsella.

Description. Male Imago (n = 4)

Head. AR 1.33–1.44. Antennal flagellomeres one to twelve 442–470 μm long, thirteen 590–680 μm long, total length 1032–1150 μm . Eyes with dorsomedian extension; large frontal tubercles (length 16–18 μm), about 2.5 times as long as wide; 12–13 temporal setae; clypeus with 19–23 setae; lengths of palpomeres (in μm): 32–40, 38–44, 80–90, 98–118, 168–192, total length 416–484 μm .

Thorax. Length 1140–1230 μm . Scutal tubercle absent; 12–15 dorsocentrals in one row + group of 2–4 dorsocentrals posteriorly, 23–30 acrostichals, 2–3 prealars, 13 scutellars. Haltere with 6–8 setae.

Wing. Wing length 1780–1882 μm , width 548–575 μm ; L/WR 3.21–3.24. Brachiolum with 1 seta, Sc with 1–5 setae, R with 46–56 setae, R_1 with 50–67 setae, R_{4+5} with 80–105 setae, M with 16–28 setae, M_{1+2} with 74–92 setae, M_{3+4} with 47–63 setae, Cu with 18–39 setae, Cu_1 with 24–34 setae, Postcubitus with 42–63 setae and An with 44–70 setae. Cell m with 35–44 setae (+20–26 setae on false vein), r_{4+5} with more than 200 setae, m_{1+2} with more than 200 setae (+43–55 setae on false vein), m_{3+4} with about 182 setae, cu with about 134 setae and an with about 142 setae.

Legs. Foreleg bearing single tibial spur (22–28 μm). Lengths of combs of mid tibia 20–23 μm (with 32–35 μm long spur) and 21–23 μm (with 40–42 μm long spur); lengths of combs of hind tibia 23–28 μm (with 42–46 μm spur) and 22–26 μm (with 44–48 μm long spur). Lengths of leg segments and leg ratios as in table 2.

TABLE 2. Lengths (in μm) and proportions of leg segments of *Tanytarsus limneticus* Sublette.

	fe	ti	ta ₁	ta ₂	ta ₃	ta ₄	ta ₅	LR	BV	SV
p ₁	910–990	508–560	1074–1190	610–638	550–562	478–495	180–190	2.11–2.15	1.36–1.46	1.23–1.39
p ₂	920–952	760–794	498–530	298–310	235–252	148–170	100–107	0.65–0.66	2.74–2.78	3.28–3.37
p ₃	953–1000	949–964	670–695	400–420	330–342	210–213	127–130	0.70–0.72	2.40–2.43	2.82–2.83

Abdomen. Length 2950–3060 μm .

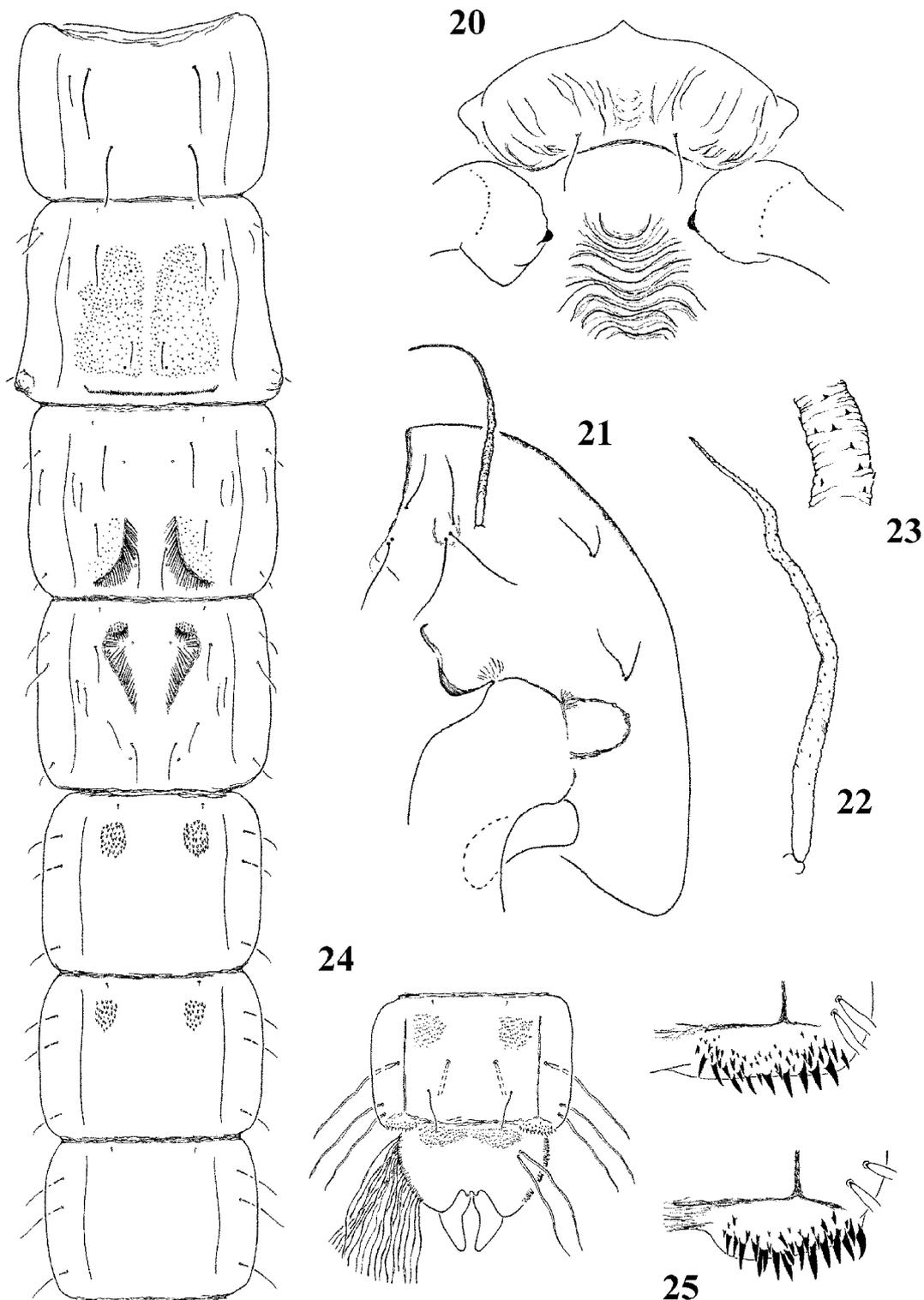
Hypopygium (Figs 16–19). Tergite IX 186–200 μm long with 9–10 median setae (not placed between anal tergal bands, not separated into groups, placed from well anterior to anal point base to close to anal point base), 18–20 apical setae, apparently without lateral teeth. T IX without microtrichia-free areas. Orolateral spine of T IX present, 2–3 μm long. Anal tergal bands separate, curved, short, not running parallel and ending well anterior to anal point base. Anal point 80–84 μm long, elongate with rounded to slightly pointed tip, with pair of well developed anal crests (34–50 μm long); field of microtrichia on entire surface between the crests; spines placed irregularly between anal crests; 2 shorter setae are present anteriorly between crests. Superior volsella with small to large field of microtrichia on anterolateral margin, anterior margin slightly curved, lateral and posterior margins curved, median margin concave, posteromedian corner projecting; 6–14 setae on dorsal surface, 2–3 setae on median margin and 1 seta on a ventral tubercle, close to anterior margin. Longitudinal axes of superior volsella and body at angle of 28–34°. Digitus pointed, triangular to somewhat cone-like, not extending or extending a little beyond margin of superior volsella. Median volsella 24–30 μm long, surpassing superior volsella but not reaching apex of inferior volsella, with 26–33 μm long simple lamellae and 30–40 μm long foliate lamellae. Inferior volsella 130–135 μm long, somewhat thick and slightly straight, distal part oval, only slightly swelled. Gonocoxite length 138–150 μm ; gonostylus 150–156 μm , somewhat elongate, straight and thin; hypopygium ratio (HR) 0.92–0.98.

Pupa (n = 4)

Total length 5135–5800 μm .

Pupal exuviae pale brown, thorax and lateral muscle marks somewhat brownish.

Cephalothorax (Figs 20–23). Frontal apotome smooth, with some wrinkles. Frontal setae short, 49–52 μm long, mounted apically on weakly developed cephalic tubercles; frontal warts absent. Pedicel sheath tubercle well developed. Thorax smooth, 1290–1320 μm long, with small teeth along median suture and granulation close to the basis of thoracic horn. Wing sheath with weakly developed nose, prealar tubercle well developed, somewhat rounded to quadrate and inwardly folded. Thoracic horn thin, 680–720 μm long, with spinules. Three precorneals not in triangular pattern, placed on a tubercle. Anterior precorneal 170–238 μm , Pc_2 (196–204 μm) and Pc_3 (212–248 μm) closer to each other, Pc_3 thicker and longer; 1 median (136–154 μm) and 2 lateral antepnotals (100–110 μm , 1 seta base); 2 pairs of dorsocentrals, anterior pair 102–140 μm (thin) and 69–82 μm long (thick), posterior pair 100–104 μm (thin) and 94–96 μm (thick).



FIGURES 20–25. *Tanytarsus limneticus* Sublette, pupa. 20. Frontal apotome. 21. Thorax. 22. Thoracic horn. 23. Detail of thoracic horn armament. 24. Abdomen, dorsal view; dorsal setae of segments V–VII not drawn. 25. Posterolateral comb of abdominal segment VIII.

Abdomen (Figs 24–25). Total length 3845–4480 μm . Tergites I and VII without armament. T II with median homogeneous shagreen, sparse/interrupted medially. T III with pair of long bands of long spines on posterior half of tergite, fields of fine shagreen lateral to spine bands, bands anteriorly straight, posteriorly

curved outward. T IV with bracket-shaped pair of long bands of spines, anterior part with thin short spines directed to caudal and median, occasionally sparse or absent, posterior part with longer spines directed to oral. T V–VI with anterior pair of rounded spine patches. T VIII with fine anterolateral shagreen. T IX with anterior shagreen, sparse or interrupted on median part. Sternites I–VII apparently without armament. S VIII with fine oral-lateral shagreen. Conjunctives and pleura unarmed. Hook row 280–372 µm, about 1/2 width of tergite II. Pedes spurii A absent; pedes spurii B present on segment II, weakly developed. Posterolateral comb of segment VIII broad, 112–120 µm wide, consisting of 9–14 strong marginal teeth and 28–42 smaller ones. Abdominal setation: segment I with 2 dorsal taeniae and 1 dorsal seta, 0 L and 1 pair of ventral seta bases; segment II with 3 D, the most anterior and posterior setae somewhat taeniate, and two pairs of dorsal seta bases, 3 L and 4 V; segment III with 5 D, the most anterior and posterior setae somewhat taeniate, and two pairs of dorsal seta bases, 3 L and 5 V; segments IV–VII with 3 L, dorsal and ventral setae difficult to see; segment VIII with 1 D, 3 lateral taeniae and 1 ventral taenia. Anal lobe well developed, with complete fringe of 18–20 taeniae in single row and two pairs of dorsal taeniae. Tergites II–VIII with O-setae.

Distribution and ecological notes. *Tanytarsus limneticus* is a Nearctic species recorded from the USA. Caldwell *et al.* (1997) pointed out that "although originally listed by Hudson *et al.* (1990) as occurring in lakes, rivers, and streams, *T. limneticus* appears to occur only in lentic habitats. Larvae of similar, typically stream dwelling species (possibly *Tanytarsus guerlus* Roback or similar species), have probably been confused with *T. limneticus*". Epler (2001) mentioned that most *T. limneticus* larvae collected by him are from bottom sediments of eutrophic ponds or slowly flowing rivers.

Discussion

Taxonomy of *Tanytarsus patagonicus* and *Tanytarsus limneticus*

The pupa and imago of *Tanytarsus patagonicus* are associated through a pharate male, while the larva should be considered "tentatively associated" since no rearing was made. Reiss (1972) found many larvae occurring in sediments at the same place where imagines and pupae of *T. patagonicus* were encountered, and he believed these larvae belonged to *T. patagonicus*.

The principal characters used by Reiss (1972) to delimit *Nimbocera* larvae and pupae from other genera were the spines pattern on pupal tergites, especially the bracket-shape pair of bands of spines directed to caudal and oral on tergite IV, and the annulated Lauterborn organ pedicels of the larva. The keys and diagnoses of pupa and larva of *Nimbocera* also take these characters into account (Pinder & Reiss 1986; Pinder & Reiss 1983). *Tanytarsus limneticus* and *T. rhabdomantis* also present bands of spines on tergite IV directed to oral and caudal, as do pupae of *Tanytarsus cuieirensis* (Sanseverino & Wiedenbrug 2000). In *T. cuieirensis*, however, the spines of the mid and posterior band sections are cone-shaped. Ekrem (2003) and Ekrem *et al.* (2003) argued that such pupal spine pattern is typical for a group of North American *Tanytarsus* species placed in the *Tanytarsus confusus* aggregate. The larvae of the *confusus* aggregate have non-annulated Lauterborn organ pedicels (Ekrem *et al.* 2003).

Thus, the annulations of Lauterborn organ pedicels and the bands of spines caudally and orally directed on pupal tergite IV are not exclusive for *Nimbocera*, as also pointed out by Epler (2001) and Trivinho-Strixino and Sanseverino (2003).

The Lauterborn organ pedicels of *Caladomyia ortonii* larvae are partially annulated, i.e. the annulations occur in about half of the pedicel length (Trivinho-Strixino & Strixino 1991, 2003).

Larvae of *Tanytarsus patagonicus*, *T. limneticus* and *T. rhabdomantis* are similar in having small Lauterborn organs on apex of completely annulated pedicels, the 2nd antenna segment with narrow, unsclerotized ring near base, mandible with 3 inner teeth and mentum with 11 teeth. The species can be separated by the antennal length (*T. patagonicus* 290 µm, *T. limneticus* 323 µm and *T. rhabdomantis* 601 µm), antennal ratio (*T. patagonicus* 1.82 µm, *T. limneticus* 1.66 µm and *T. rhabdomantis* 1.38 µm), length of antennal blade (in *T. patagonicus* and *T. limneticus* blade about as long as segment 2, while in *T. rhabdomantis* blade about 1/4 length of segment 2), spur of antennal base (present in *T. patagonicus*, absent in *T. limneticus*

and *T. rhabdomantis*) and indentation and colour of median tooth of mentum (trifid in *T. patagonicus* and *T. rhabdomantis*, pentamerous in *T. limneticus*, dark in *T. patagonicus* and pale in *T. limneticus* and *T. rhabdomantis*).

Pupae of *T. limneticus*, *T. rhabdomantis* and *T. patagonicus* share some similarities such as the armament of abdominal tergites, especially the bracket-shaped spine bands on tergite IV, but they can be separated by the form of the posterolateral comb on segment VIII (broad in *T. limneticus* and *T. rhabdomantis*, narrower in *T. patagonicus*), setation of segment VIII (3 lateral taeniae, 1 dorsal seta and 1 ventral taenia/taeniate seta in *T. limneticus* and *T. rhabdomantis*, 4 lateral taeniae, 2 dorsal and 1 ventral setae plus 1 ventral taenia in *T. patagonicus*) and presence of wing sheath nose in *T. limneticus* and *T. rhabdomantis* (absent in *T. patagonicus*). A broad anal comb is also found in *T. cuieirensis* (Sanseverino & Wiedenbrug 2000) as well as in the genus *Virgatanytarsus* (Cranston 2000).

Characters of the adult males of *T. limneticus* and *T. rhabdomantis* show that both species seem to be closely related. The species have many features in common: high antennal ratio, large frontal tubercles, wing vein M with setae, anal tergal bands of similar form, well developed anal crests, foliate lamellae on median volsella, and anal point tip, superior volsella, inferior volsella and gonostylus of similar design. The digitus of *T. limneticus* and *T. rhabdomantis* do not extend or extend a little beyond margin of the superior volsella, but in *T. limneticus* the digitus is somewhat shorter and triangular to cone-shaped (in *T. rhabdomantis* it is finger-like). *Tanytarsus limneticus* can be separated from *T. rhabdomantis* by the armament of anal point (*T. limneticus* has spines and two shorter setae between anal crests, while *T. rhabdomantis* does not have spines but short, thick setae between crests), by the presence of microtrichia on the superior volsella (absent in *T. rhabdomantis*) and wing setosity (wing of *T. limneticus* with much more setae). The males of both species do not have much in common with those of *T. patagonicus*. Trivinho-Strixino and Sanseverino (2003) pointed out that *T. rhabdomantis* shares only one character with *T. patagonicus*, i.e. the presence of short setae between the crests on the anal point, and can be separated by having a higher antennal ratio, setose wing veins and cells, normally developed antennae, wings, palps, tarsomeres of mid and hind legs, tibial combs and spurs (all reduced or shorter in *T. patagonicus*), and by having a differently shaped superior volsella, digitus, and median volsella. Regarding *T. limneticus*, not even the character "short setae on the anal point" is shared, since the species has spines and only two short setae between the anal crests.

Nimbecera as a junior synonym of *Tanytarsus*

The adult male of *Tanytarsus patagonicus* is characterized by the low antennal ratio, short antenna (brachycery), a somewhat reduced antennal plume, reduced palps and wings (brachyptery), low ratio of wing length to width (more than 3.1 in most Neotropical *Tanytarsus* species, about 2.5 in *T. patagonicus*), few and short wing setae (shorter than those observed in other Neotropical *Tanytarsus* species), shortened tarsomeres of mid and hind legs, low leg ratio (LR), high "Beinverhältnis" (BV) and "Schenkel-Schienerverhältnis" (SV), by the cordiform 4th tarsomere of mid leg, absence of median setae on tergite IX, presence of short setae on the anal point (spines absent) and a peculiar superior volsella, robust inferior volsella and gonostylus.

Morphological reductions should be treated carefully before the characters are used as arguments in creation of new taxa. With regard to *Nimbecera*, it is difficult to decide if such peculiar features and reduced characters of the adult male are sufficient to diagnose the genus, because of its already mentioned monotypy and its habitat. The species is recorded from the southern part of South America, occurring in coastal lagoons and ponds. If this habitat is interpreted as a restricted or an extreme environment, the reductions and modifications could be associated with limitations or adaptations for such an environment.

Oliver and Dillon (1997) studied chironomids from the Arctic region and reported some groups with structural reductions and modifications such as shortened or modified antennae, enlarged hypopygia, brachyptery, strengthened legs, flattened scutum and shortened palps. Such structural modifications are usually associated with loss of aerial mating habit and with mating on the ground or other substrate (Butler *et al.* 1980). As an example, Oliver and Dillon (1997) reported a *Tanytarsus* species with such modifications. This species first recorded by Butler *et al.* (1980) and later described by as *Tanytarsus aquavolans* Butler, 2000, shows a peculiar hypopygium and several morphological reductions (Butler 2000).

Tanytarsus aquavolans has shortened antenna and reduced antennal plume, short palps, legs and wings, low LR, few setae on wings, the hypopygium is robust in form and does not have median setae on the anal tergite, microtrichia or spine groups between anal point crests are absent and the digitus is also absent. Butler (2000) pointed out that such developments generally are considered adaptations to pelagic swarming or surface mating, but that they also could be beneficial under strong selection pressure against flight in habitats subjected to persistent high winds. Some sensillar structures of the antenna interpret wind speed in normally plumed males; non-plumed males are poor fliers or brachypterous, and normally mate on the ground of water surface (Sublette 1979). Reiss (1972) presumed that other features of *Tanytarsus patagonicus*, besides its slight brachyptery and brachycery, would be an indicative that the copula occurs on water surface and the males apparently do not form swarms. Similar to *T. aquavolans*, the structures most involved in flight, swarm behaviour and aerial location of a mate are also reduced in *T. patagonicus* while the genitalia is relatively robust. Furthermore, comparing *T. patagonicus* with all described Neotropical *Tanytarsus*, the species shows the lowest LR and the highest BV and SV; these ratio values of the legs could be more an indicative that the mating occurs on the ground or on water surface.

The Afrotropical *Tanytarsus minutipalpus* Ekrem & Harrison, 1999 inhabits extremely salty lakes in the Rift Valley. The adult males have reduced palpomeres and the anal tergite median setae are also absent (Ekrem & Harrison 1999; Ekrem 2001b).

According to Ashe and Cranston (1990), where male swarming is limited, particularly in extreme environments, there is associated variable feminization of the male antennae, and there may be brachyptery or aptery in both sexes. Lloyd (1999) pointed out that the strand habitat (shores of lakes, rivers and oceans, and around islands) has often been associated with wing reduction and loss; since flyers can be blown away over open water, wings may often be "fatal" in such situations. Geographical isolation, high energetic cost of flight and habitat stability are probably the major factors thought to be responsible for the loss of flight in insects (Roff 1990).

Conclusions

The modifications and reductions of the *Nimbecera* adult male apparently are related to its habitat preference and geographical distribution. The characters in the immature stages previously used as diagnostic for *Nimbecera* are shared by members of *Caladomyia* and *Tanytarsus*. Due to the absence of good diagnostic characters to delimit the genus, its similarity with the genus *Tanytarsus* and its monotypy, we propose to transfer *Nimbecera patagonica* to the genus *Tanytarsus*. The genus *Nimbecera* is to be regarded as a junior subjective synonym of *Tanytarsus*.

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