



## *Alotanypus vittigera* (Edwards) comb. nov.: adult redescription, immature description and a phylogenetic analysis of the genus (Diptera: Chironomidae: Tanypodinae)

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### Abstract

*Anatopynia vittigera* Edwards is transferred to *Alotanypus*. The male and female of *A. vittigera* comb. nov. are redescribed and immatures are described and illustrated. A cladistic analysis including one species of each Macropelopiini genus was conducted in order to assess the phylogenetic position of *Alotanypus* and to provide the first phylogenetic hypothesis for the genus. Adults and immatures were included in the analysis where discrete and continuous characters were considered. The cladistic analysis demonstrated that *Alotanypus* is a monophyletic genus, with *Guassutanypus oliveirai* as the sister group.

**Key words:** Diptera, Chironomidae, Macropelopiini, *Alotanypus*, phylogeny, Argentina, Neotropics

### Introduction

The genus *Alotanypus* is presently known by four species, *A. venustus* (Coquillett) and *A. aris* Roback from the Nearctic Region, *A. dalyupensis* (Freeman) from the Australian Region and *A. kuroberobustus* (Sasa *et* Okazawa) from the Palearctic Region (Niitsuma 2005). From the Neotropics, immatures of *Alotanypus* have been reported in various studies (i.e. Watson & Heyn 1992, Donato *et al.* 2008) however there are no species ascribed to this region. *Anatopynia vittigera* was described by Edwards (1931) from imagines collected in Southern Patagonia, citing the dark mark in the Cu vein as the most important character to differentiate this species from the other *Anatopynia*. Pupae of *Alotanypus* collected close to the localities described by Edwards have been recently reared, and the emerged adults show the obvious dark mark on Cu vein. The finding of these associations allowed us to conclude that *Anatopynia vittigera* belongs, in fact, to the genus *Alotanypus*.

In the present study, *Anatopynia vittigera* Edwards is formally transferred to *Alotanypus*, imagines are redescribed, immatures are described and a phylogenetic analysis of the genus is conducted in order to establish their possible relationships.

### Material and methods

Material collected by Edwards, including the pinned holotype and various paratypes housed in the Natural History Museum (London, England) (NHM), as well as the specimens recently collected, were mounted in Canada balsam. Female allotype was not studied. General terminology follows Roback (1976, 1977) and Sæther (1980). Larval cephalic setation follows Rieradevall and Brooks (2001). Measurements are in µm rounded to the nearest 5 unless

otherwise stated. The measurements are given as ranges followed by the measurements of the holotype in square brackets. The type material is deposited at the Natural History Museum (London, UK) (NHM) and the material recently collected is housed in the Museo de La Plata (La Plata, Buenos Aires, Argentina) (MLP).

**Phylogenetic analysis.** The characters and character states used for this analysis, are self-explanatory and are listed in Table 1. The characters consist in 56 continuous characters and 48 discrete ones (Table 2).

**TABLE 1.** List characters used in the phylogenetic analysis of *Alotanypus* Roback, 1971. M = male adult, F = female adult, P = pupa; L = larva.

N°	Character	Stage	Character state
0	AR	M	Range
1	Lateral anteprenotals	M	Range
2	Prealars	M	Range
3	Supralars	M	Range
4	Wing length	M	Range
5	LR I	M	Range
6	LR II	M	Range
7	LR III	M	Range
8	Spur ratio on Leg III	M	Range
9	HR	M	Range
10	AR	F	Range
11	Lateral anteprenotals	F	Range
12	Prealars	F	Range
13	Wing length	F	Range
14	LR I	F	Range
15	LR II	F	Range
16	LR III	F	Range
17	DC <sub>1</sub> length	P	Range
18	DC <sub>3</sub> length	P	Range
19	Sa length	P	Range
20	Thoracic horn length	P	Range
21	Thoracic horn width	P	Range
22	Thoracic horn L / W	P	Range
23	Plastron plate length	P	Range
24	Plastron plate L / W	P	Range
25	Anal lobe length	P	Range
26	Anal lobe width	P	Range
27	Anal lobe L / W	P	Range
28	Genital sac / anal lobe of the male pupa	P	Range
29	Relative position of LS I on anal lobe	P	Range
30	Relative position of LS II on anal lobe	P	Range
31	Relative position of LS I on segment VII	P	Range
32	Relative position of LS I on segment VIII	P	Range
33	Cephalic Index	L	Range
34	A <sub>1</sub> length	L	Range
35	A <sub>2</sub> length	L	Range

continued next page

TABLE 1. (continued)

N°	Character	Stage	Character state
36	A <sub>2</sub> L / W	L	Range
37	A <sub>3</sub> length	L	Range
38	BL <sub>1</sub>	L	Range
39	BL <sub>1</sub> / A <sub>2,4</sub>	L	Range
40	NB / BL <sub>1</sub>	L	Range
41	AR	L	Range
42	A <sub>1</sub> / position of RO	L	Range
43	Basal maxillary palp length	L	Range
44	Basal maxillary palp L / W	L	Range
45	CS on maxillary palp	L	Range
46	A <sub>1</sub> / basal maxillary palp	L	Range
47	Mandible length	L	Range
48	A <sub>1</sub> / mandible	L	Range
49	Ligula length	L	Range
50	Paraligula length	L	Range
51	Dorsomental teeth	L	Range
52	Pecten hypopharyngis	L	Range
53	Procercus length	L	Range
54	Procercus L / W	L	Range
55	Number of procercus setae	L	Range
56	Number of flagellomeres	M	0 = 14; 1 = <14
57	Postorbitals	M	0 = multiserial; 1 = uniserial; 2 = other
58	Scutal tubercle	M	0 = absent; 1 = present
59	Anepisternals	M	0 = absent; 1 = present; 2 = absent or present
60	Posnotals	M	0 = absent; 1 = present; 2 = absent or present
61	Preepisternals	M	0 = absent; 1 = present
62	Dark mark on FCu vein	M	0 = no; 1 = yes
63	Dark mark on RM vein	M	0 = no; 1 = yes
64	Dark mark on MCu vein	M	0 = no; 1 = yes
65	Dark mark on Cu vein	M	0 = no; 1 = yes
66	Wing spots	M	0 = absent; 1 = present
67	Tibial comb I	M	0 = absent; 1 = present
68	Tibial comb III	M	0 = reduced or absent; 1 = present
69	External spines of tibial comb III	M	0 = straight; 1 = "S" curved
70	Claws	M	0 = pointed; 1 = spatulate (at least on p II); 2 = pointed or spatulate
71	Spurs shape	M	0 = thorn like; 1 = other shape
72	Spurs teeth number	M	0 = <6; 1 = >15
73	Apex of spur Ti 1	M	0 = straight; 1 = curved
74	Setae on tergite IX	M	0 = absent; 1 = present
75	Ventral lobe of gonostylus	M	0 = absent; 1 = present
76	FCu position	M	0 = beyond MCu; 1 = before MCu

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TABLE 1. (continued)

N°	Character	Stage	Character state
77	Postorbitals	F	0 = multiserial; 1 = uniserial; 2 = other
78	Anepisternals	F	0 = absent; 1 = present
79	Preepisternals	F	0 = absent; 1 = present
80	Posnotals	F	0 = absent; 1 = present; 2 = absent or present
81	Dark mark on FCu vein	F	0 = no; 1 = yes
82	Dark mark on RM vein	F	0 = no; 1 = yes
83	Dark mark on MCu vein	F	0 = no; 1 = yes
84	Dark mark on Cu vein	F	0 = no; 1 = yes
85	Wing spots	F	0 = absent; 1 = present
86	Setae on tergite IX	F	0 = absent; 1 = present; 2 = absent or present
87	Setae on tergite X	F	0 = absent; 1 = present
88	Neck of seminal capsules	F	0 = symmetrical; 1 = asymmetrical
89	External membrane of thoracic horn	P	0 = smooth; 1 = reticulated
90	Tubercle on base of thoracic horn	P	0 = absent; 1 = present
91	Union between Plastron plate and horn sac	P	0 = connected directly ; 1 = connected by a neck
92	Thoracic horn: lumen and atrium	P	0 = atrium filling the lumen; 1 = atrium straight, do not filling the entire lumen; 2 = atrium sinuated, do not filling the entire lumen
93	Rods on atrium of thoracic horn	P	0 = absent; 1 = present
94	Thoracic comb	P	0 = absent; 1 = present
95	Outer fringed on anal lobe	P	0 = absent; 1 = present
96	Inner fringed on anal lobe	P	0 = absent; 1 = present
97	Scar	P	0 = absent; 1 = present
98	Shagreen	P	0 = single spines; 1 = serially arranged; 2 = single or serially arranged
99	Teniata setae on segment VII	P	0 = <5; 1 = 5; 2 = >5
100	Number of teeth on ligula	L	0 = 5; 1 = 4
101	Inner laterals teeth on ligula	L	0 = outcurved; 1 = straight; 2 = other
102	Coloration of ligula	L	0 = pale; 1 = dark
103	Teeth of paraligula	L	0 = bifid; 1 = <3 teeth

Problems related to quantitative characters are how to treat the measured data and the difficulty in assigning objectively character states (Pimentel & Riggins 1987; Cranston & Humphries 1988). Several authors such as Mickevich and Johnson 1976; Colless 1980, Almeida and Bisby 1984; Thorpe 1984; Archie 1985, Thiele 1993, Strait *et al.* 1996, and Wiens 2001, proposed different methods for converting the continuous variation into a series of discrete states. Several of them, have been criticized because taxa with significantly different values may be assigned to the same state, and/or taxa with non-significant differences may be assigned to different states (Farris 1990; Rae 1998). Goloboff *et al.* (2008a) implemented in the program TNT, the treatment of quantitative characters as additive characters and the use of Farris's (1970) algorithms for the down-pass optimization and Goloboff's (1993) algorithms for the up-pass. This method has the advantage to allow the analysis of ranges. Moreover, it is simple, faster, and more general than the other methods (Goloboff *et al.* 2006). Other problems related to continuous characters are character standardization and the use of the measurements as such or to compute some statistic descriptor. Donato (in prep.) explored these problems using different data sets expressing the measurements as ranges or means of a statistic descriptor (with or without standardization). The author finds that the standardized ranges are the more robust and informative between the competing data sets.

**TABLE 2.** Data matrix for 18 taxa and 103 quantitative and discrete morphological characters used in the cladistic analysis. See Table I for explanation of coding. Value–value: range available; ?–?: no data is available; value–?: one data is available.

	0	1	2	3	4	5	6	7	8
<i>Pr. culiciformis</i>	1.80–2.80	?–?	20–30	2–4	2.40–3.50	0.67–0.74	0.52–0.60	0.60–0.68	?–?
<i>Dj. lacustris</i>	1.60–1.80	3–4	5–7	?–?	1.60–2.00	0.69–0.70	0.56–0.60	0.60–0.73	0.88–?
<i>N. baltimoreus</i>	1.70–2.00	7–15	20–58	3–8	2.70–3.40	0.70–0.76	0.53–0.60	0.66–0.74	0.45–0.52
<i>Al. dalyupensis</i>	1.80–?	?–?	?–?	?–?	3.00–?	0.60–?	?–?	?–?	?–?
<i>Al. aris</i>	1.60–1.80	15–22	102–108	1–?	2.70–3.00	0.69–0.71	0.55–0.59	0.85–0.90	?–?
<i>Al. kuroberobustus</i>	1.90–?	19–26	36–46	1–?	3.40–4.30	0.72–0.77	0.64–0.67	0.68–0.76	?–?
<i>Al. venustus</i>	1.50–1.80	11–12	31–?	1–2	3.60–4.20	0.59–0.66	0.52–0.55	0.70–0.73	0.29–?
<i>Al. vittigera</i>	1.90–2.10	14–19	23–38	1–?	3.10–3.80	0.68–0.76	0.60–0.66	0.68–0.76	0.63–0.76
<i>Ap. johnsonni</i>	2.00–2.10	14–?	22–?	3–?	3.60–?	0.68–0.74	0.57–0.69	0.67–?	0.33–?
<i>Be. floridensis</i>	2.90–?	9–?	20–22	1–2	3.00–?	0.75–0.76	0.48–0.55	0.66–?	?–?
<i>Bi. algens</i>	1.90–2.00	23–24	35–43	1–?	4.30–4.40	0.70–0.71	0.58–?	0.65–0.69	?–?
<i>Br. eumorpha</i>	1.70–?	16–?	29–38	2–3	3.00–3.70	0.72–?	0.60–0.61	0.75–?	0.28–?
<i>De. alaskensis</i>	2.50–3.50	22–35	44–70	5–10	4.80–5.10	0.56–0.61	0.46–0.52	0.58–0.62	0.21–0.33
<i>F. olivaceae</i>	2.00–2.10	2–3	9–12	1–?	2.70–3.20	1.03–1.08	1.06–1.07	0.86–0.96	?–?
<i>G. oliveirai</i>	1.94–2.16	10–13	9–12	?–?	2.90–3.30	0.67–0.71	0.55–0.60	0.64–0.71	?–?
<i>M. decedens</i>	2.00–?	17–?	46–?	4–6	4.20–4.80	0.74–0.75	0.60–?	?–?	0.28–?
<i>Ps. dyari</i>	1.90–2.10	13–?	41–57	7–12	2.70–4.20	0.60–0.64	0.49–0.57	0.62–0.68	0.29–0.35
<i>R. submarginella</i>	1.60–1.80	16–?	26–?	?–?	2.70–?	0.62–0.66	0.49–0.54	0.63–?	?–?

continued

	9	10	11	12	13	14	15	16	17
<i>Pr. culiciformis</i>	2.10–2.30	?–?	?–?	29–?	2.40–3.20	0.60–?	0.55–?	?–?	?–?
<i>Dj. lacustris</i>	1.50–2.00	0.27–0.33	3–4	7–8	2.70–2.80	0.65–0.66	0.48–0.52	0.64–?	?–?
<i>N. baltimoreus</i>	1.20–1.40	?–?	12–13	33–50	2.20–2.40	0.50–?	0.49–?	0.63–?	?–?
<i>Al. dalyupensis</i>	?–?	?–?	?–?	?–?	3.50–?	0.53–?	0.50–?	0.60–?	78–?
<i>Al. aris</i>	1.60–1.90	?–?	?–?	?–?	2.70–2.80	0.67–0.68	0.52–0.53	0.78–?	58–?
<i>Al. kuroberobustus</i>	1.92–?	0.18–0.21	20–33	42–65	3.30–3.80	0.66–0.71	0.56–0.61	0.67–0.71	?–?
<i>Al. venustus</i>	1.50–?	?–?	18–?	40–?	4.20–4.80	0.60–?	0.52–?	0.59–?	130–?
<i>Al. vittigera</i>	1.65–2.03	0.21–0.23	15–26	33–55	3.30–3.70	0.61–0.67	0.53–0.59	0.61–0.68	41–54
<i>Ap. johnsonni</i>	2.00–?	?–?	?–?	?–?	?–?	?–?	?–?	?–?	88–?
<i>Be. floridensis</i>	?–?	?–?	12–14	37–43	2.30–2.50	0.62–0.66	0.51–0.53	0.53–0.56	?–?
<i>Bi. algens</i>	1.60–1.70	0.25–?	10–?	57–?	4.40–?	0.69–?	0.58–?	0.70–?	55–88
<i>Br. eumorpha</i>	1.50–?	?–?	11–?	40–?	3.50–3.70	0.67–0.74	0.54–?	0.70–?	73–?
<i>De. alaskensis</i>	1.40–1.70	0.17–?	46–?	91–?	4.20–6.00	0.47–?	0.41–?	0.57–?	?–?
<i>F. olivaceae</i>	1.56–?	?–?	4–?	13–?	2.60–?	1.03–1.08	1.06–1.07	0.86–0.96	?–?
<i>G. oliveirai</i>	?–?	0.31–?	8–?	19–?	2.60–?	0.67–?	0.57–?	0.70–?	?–?
<i>M. decedens</i>	2.00–?	?–?	12–?	61–?	?–?	0.68–0.69	0.57–0.59	0.62–0.66	96–?
<i>Ps. dyari</i>	1.20–1.40	?–?	24–?	60–?	3.00–3.60	0.53–?	0.50–?	0.59–?	102–?
<i>R. submarginella</i>	1.52–?	?–?	?–?	?–?	3.20–?	0.59–?	0.49–?	0.58–?	?–?

continued.

	18	19	20	21	22	23	24	25	26	27
<i>Pr. culiciformis</i>	?–?	?–?	518–547	182–202	2.7–2.9	91–115	0.12–?	691–749	?–?	1.77–1.99
<i>Dj. lacustris</i>	?–?	?–?	487–?	185–?	2.6–?	?–?	0.09–?	385–?	247–?	1.56–?

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<i>N. baltimoreus</i>	?-?	?-?	285-?	337-?	2.3-3.5	74-115	0.26-0.34	336-384	150-155	2.20-2.50
<i>Al. dalyupensis</i>	?-?	?-?	662-?	221-?	3.0-?	67-?	0.10-?	797-?	509-?	1.57-?
<i>Al. aris</i>	110-?	219-?	518-576	?-?	3.6-3.8	?-?	0.30-0.33	806-845	?-?	2.05-2.10
<i>Al. kuroberobustus</i>	?-?	?-?	606-727	?-?	4.3-5.5	80-110	0.15-?	909-1111	?-?	1.80-2.00
<i>Al. venustus</i>	73-?	220-?	691-?	192-?	3.6-?	201-?	0.29-?	1104-?	566-?	1.95-?
<i>Al. vittigera</i>	95-140	203-?	524-596	106-135	4.4-5.0	58-85	0.11-0.15	803-996	400-450	1.93-2.05
<i>Ap. johnsonni</i>	?-?	?-?	442-509	154-192	2.5-?	?-?	0.27-?	691-864	336-394	2.15-2.17
<i>Be. floridensis</i>	?-?	?-?	?-?	?-?	4.0-?	?-?	0.27-?	?-?	?-?	2.62-?
<i>Bi. algens</i>	3-8	?-?	495-636	?-?	1.6-2.1	202-343	0.41-0.54	1167-1624	?-?	2.70-2.90
<i>Br. eumorpha</i>	20-?	75-?	?-?	?-?	1.8-?	?-?	0.15-0.30	778-826	172-221	2.27-2.58
<i>De. alaskensis</i>	?-?	?-?	834-?	365-?	2.3-?	?-?	0.28-?	1430-?	922-?	1.55-?
<i>F. olivaceae</i>	?-?	?-?	440-556	?-?	2.3-2.6	?-?	0.10-0.14	727-859	?-?	1.70-1.90
<i>G. oliveirai</i>	?-?	?-?	480-680	200-240	2.0-3.4	75-?	0.23-?	470-?	?-?	2.50-?
<i>M. decedens</i>	?-?	140-?	672-768	278-301	2.2-2.8	211-?	0.30-?	1046-1073	461-463	2.27-2.32
<i>Ps. dyari</i>	55-?	?-?	557-768	125-230	3.3-4.5	106-163	0.19-?	816-1104	394-576	2.02-2.03
<i>R. submarginella</i>	?-?	?-?	?-?	?-?	1.5-?	?-?	0.06-?	?-?	?-?	2.60-2.90

continued.

	28	29	30	31	32	33	34	35	36
<i>Pr. culiciformis</i>	?-?	?-?	?-?	0.49-?	0.30-?	?-?	185-?	32-?	4.00-?
<i>Dj. lacustris</i>	0.82-?	0.31-?	0.50-?	?-?	0.76-?	0.71-?	130-?	18-?	4.10-?
<i>N. baltimoreus</i>	0.69-0.75	0.27-?	0.44-?	?-?	?-?	?-?	139-152	?-?	?-?
<i>Al. dalyupensis</i>	?-?	0.17-?	0.28-?	0.51-?	0.27-?	?-?	237-?	25-?	4.50-?
<i>Al. aris</i>	0.43-0.48	0.21-0.23	0.30-0.35	0.52-?	0.21-?	?-?	252-270	28-31	4.67-5.00
<i>Al. kuroberobustus</i>	0.40-0.45	0.15-?	0.22-0.27	0.46-0.52	0.23-0.31	0.78-0.83	290-335	30-40	6.00-7.00
<i>Al. venustus</i>	?-?	0.13-?	0.23-?	0.57-?	0.20-?	0.84-?	225-?	28-?	4.20-?
<i>Al. vittigera</i>	0.42-0.44	0.16-0.17	0.28-?	0.45-0.51	0.22-0.27	0.76-0.85	233-266	28-35	4.30-6.60
<i>Ap. johnsonni</i>	0.31-0.33	0.12-0.16	0.19-0.23	0.58-?	0.29-?	?-?	159-182	13-?	2.25-?
<i>Be. floridensis</i>	0.36-?	0.18-?	0.26-?	0.55-?	0.76-?	?-?	?-?	?-?	3.50-?
<i>Bi. algens</i>	0.32-0.35	?-?	?-?	0.47-0-60	0.60-0.67	0.69-0.78	238-275	18-23	2.70-4.00
<i>Br. eumorpha</i>	0.31-?	0.09-?	0.15-?	0.08-?	0.20-?	1.03-?	185-199	18-?	2.20-?
<i>De. alaskensis</i>	0.48-?	0.27-?	0.32-?	0.48-?	0.45-?	1.06-?	374-380	35-?	2.20-?
<i>F. olivaceae</i>	0.42-0.48	?-?	0.18-0.24	?-?	?-?	0.72-?	270-?	29-?	5.80-?
<i>G. oliveirai</i>	0.29-?	0.33-?	0.43-?	0.50-?	0.33-?	1.17-?	324-356	32-36	?-?
<i>M. decedens</i>	0.36-0.40	0.08-0.10	0.14-0.17	0.25-?	0.28-?	1.25-?	215-248	23-?	3.90-?
<i>Ps. dyari</i>	0.38-0.40	0.13-?	0.22-?	?-?	?-?	1.03-1.08	185-241	22-25	4.40-?
<i>R. submarginella</i>	0.25-?	0.06-?	0.11-?	0.10-?	0.29-?	1.00-?	116-173	15-16	2.30-?

continued.

	37	38	39	40	41	42	43	44	45
<i>Pr. culiciformis</i>	?-?	35-?	1.05-?	?-?	4.77-?	0.72-?	?-?	?-?	?-?
<i>Dj. lacustris</i>	6-?	55-?	1.89-?	0.16-?	4.48-?	0.83-?	40-?	2.7-?	0.33-?
<i>N. baltimoreus</i>	?-?	73-?	1.00-?	0.79-?	1.93-2.08	0.66-?	31-34	2.5-?	0.65-?
<i>Al. dalyupensis</i>	13-?	38-?	0.93-?	0.61-?	5.78-?	0.75-?	67-?	2.7-?	0.50-?
<i>Al. aris</i>	7-8	47-51	0.50-?	0.61-0.72	5.31-5.74	0.71-0.76	55-64	3.0-?	0.45-0.51
<i>Al. kuroberobustus</i>	8-10	43-53	0.86-?	0.77-?	5.80-6.40	0.71-0.76	65-75	3.4-?	0.50-0.54
<i>Al. venustus</i>	4-?	?-?	?-?	?-?	?-?	0.72-?	73-?	2.5-?	0.46-?
<i>Al. vittigera</i>	7-11	35-42	0.80-0.88	0.83-0.90	4.90-5.60	0.70-0.76	60-73	2.4-3.0	0.59-0.67

<i>Ap. johnsonni</i>	3-?	24-30	0.93-1.13	0.73-0.88	6.19-6.90	0.72-0.82	44-54	2.8-3.1	0.40-0.50
<i>Be. floridensis</i>	?-?	?-?	0.92-?	0.89-?	6.05-?	0.69-?	?-?	2.9-?	0.24-?
<i>Bi. algens</i>	5-?	30-?	0.89-?	0.78-?	6.80-8.30	0.77-0.80	60-75	2.5-3.1	0.21-0.27
<i>Br. eumorpha</i>	3-?	31-32	1.10-1.17	0.68-0.76	7.10-7.30	0.76-0.81	37-44	2.7-3.1	0.31-0.45
<i>De. alaskensis</i>	6-?	58-?	0.92-?	0.71-?	7.31-7.48	0.81-?	100-?	3.8-?	0.69-?
<i>F. olivaceae</i>	?-?	?-?	?-?	?-?	?-?	0.63-?	65-?	3.3-?	0.80-?
<i>G. oliveirai</i>	8-12	48-56	1.08-?	?-?	6.70-8.10	0.75-?	76-80	?-?	0.38-?
<i>M. decedens</i>	6-?	40-?	1.00-1.04	0.69-0.77	6.10-6.70	0.69-0.77	73-88	4.0-4.5	0.24-0.29
<i>Ps. dyari</i>	3-4	32-35	0.95-0.97	0.59-0.65	5.60-6.80	0.79-0.82	44-67	2.3-2.8	0.53-0.57
<i>R. submarginella</i>	2-?	21-22	1.00-?	0.91-?	7.60-8.00	0.90-?	42-46	2.3-2.4	0.54-?

continued.

	46	47	48	49	50	51	52	53	54	55
<i>Pr. culiciformis</i>	?-?	192-?	0.96-?	111-?	48-?	?-?	?-?	?-?	?-?	14-?
<i>Dj. lacustris</i>	3.25-?	151-?	0.86-?	75-?	30-?	9-?	11-12	151-?	3.15-?	9-10
<i>N. baltimoreus</i>	3.52-?	102-124	1.19-1.38	69-73	?-?	?-?	?-?	160-?	4.32-?	7-?
<i>Al. dalyupensis</i>	3.54-?	192-?	1.23-?	122-?	96-?	6-?	?-?	296-?	3.79-?	16-17
<i>Al. aris</i>	4.05-4.58	196-215	1.22-1.32	104-111	61-70	6-?	14-16	278-322	3.80-4.70	12-13
<i>Al. kuroberobustus</i>	?-?	225-255	?-?	125-150	70-80	5-7	15-22	?-?	4.00-4.60	13-?
<i>Al. venustus</i>	3.49-?	241-?	1.06-?	126-?	58-?	7-?	18-?	352-?	3.96-?	13-?
<i>Al. vittigera</i>	3.64-4.08	191-213	1.17-1.26	108-145	60-95	5-7	14-18	250-350	3.00-3.50	13-?
<i>Ap. johnsonni</i>	3.34-3.93	167-203	0.91-0.95	105-131	54-66	4-5	16-20	192-222	4.50-?	10-?
<i>Be. floridensis</i>	2.90-?	?-?	?-?	?-?	?-?	5-6	14-?	?-?	?-?	?-?
<i>Bi. algens</i>	3.67-?	212-245	1.20-?	115-143	58-65	6-7	?-?	?-?	3.80-4.10	8-?
<i>Br. eumorpha</i>	4.50-5.00	148-155	1.20-1.30	81-?	41-44	5-?	11-13	163-?	3.40-?	?-?
<i>De. alaskensis</i>	3.80-?	384-407	0.93-0.97	192-?	64-?	6-7	27-29	480-?	3.43-?	18-?
<i>F. olivaceae</i>	4.15-?	193-?	1.40-?	128-?	55-?	?-?	20-?	?-?	?-?	?-?
<i>G. oliveirai</i>	4.40-?	240-252	1.40-?	120-144	64-72	14-?	21-?	360-400	?-?	13-?
<i>M. decedens</i>	3.00-?	204-237	1.06-?	133-148	67-74	6-7	15-18	?-?	3.00-?	12-13
<i>Ps. dyari</i>	3.59-4.40	178-229	1.05-1.14	93-118	63-80	6-?	14-20	370-432	4.02-4.16	18-20
<i>R. submarginella</i>	?-?	148-153	?-?	98-102	53-58	5-?	16-20	95-98	4.00-?	10-12

continued.

	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
<i>Pr. culiciformis</i>	0	?	0	0	0	0	?	?	?	?	?	0	1	?	0	1	0
<i>Dj. lacustris</i>	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>N. baltimoreus</i>	1	1	0	1	1	1	0	1	0	0	0	1	1	0	1	1	0
<i>Al. dalyupensis</i>	1	?	0	?	0	?	?	?	?	?	?	1	1	?	?	0	1
<i>Al. aris</i>	1	0	0	1	0	1	1	1	1	0	0	1	1	1	[01]	0	1
<i>Al. kuroberobustus</i>	1	0	0	0	0	0	1	1	1	0	1	1	1	?	1	0	1
<i>Al. venustus</i>	1	0	0	1	0	0	1	1	1	0	1	1	1	0	1	0	1
<i>Al. vittigera</i>	1	0	0	[01]	[01]	0	1	1	1	1	1	1	1	1	1	0	1
<i>Ap. johnsonni</i>	1	0	0	1	1	1	0	0	0	0	1	0	1	?	0	0	1
<i>Be. floridensis</i>	1	2	1	1	1	1	0	0	0	0	0	0	0	?	0	0	1
<i>Bi. algens</i>	1	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1
<i>Br. eumorpha</i>	1	0	0	1	1	0	0	0	0	0	1	0	1	?	0	0	1
<i>De. alaskensis</i>	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1
<i>F. olivaceae</i>	1	?	1	1	1	0	0	0	0	0	0	0	1	0	?	0	1

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<i>G. oliveirai</i>	1	2	0	1	1	0	1	1	1	0	0	0	1	0	0	0	1
<i>M. decedens</i>	1	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	1
<i>Ps. dyari</i>	1	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	1
<i>R. submarginella</i>	?	2	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1

continued.

	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
<i>Pr. culiciformis</i>	0	?	1	1	?	1	0	0	?	?	?	?	?	0	0	0	?	1	0	
<i>Dj. lacustris</i>	0	1	1	1	1	1	0	0	0	1	0	0	0	0	?	0	1	1	1	0
<i>N. baltimoreus</i>	0	0	0	0	1	1	1	?	0	1	0	0	0	0	1	0	0	1	0	1
<i>Al. dalyupensis</i>	0	1	0	0	0	?	?	1	1	1	1	0	?	?	?	?	0	1	0	2
<i>Al. aris</i>	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	2
<i>Al. kuroberobustus</i>	1	1	0	0	?	2	0	0	1	1	1	0	1	0	1	1	0	?	0	2
<i>Al. venustus</i>	0	1	0	0	?	1	0	0	1	1	1	0	1	1	?	1	0	1	0	1
<i>Al. vittigera</i>	1	1	0	0	0	1	0	0	1	1	1	1	1	[01]	1	1	0	1	0	1
<i>Ap. johnsonni</i>	0	1	0	0	?	?	?	?	?	?	?	?	?	0	1	1	0	1	0	0
<i>Be. floridensis</i>	0	1	0	0	2	1	1	1	0	0	?	?	0	1	1	0	0	?	1	1
<i>Bi. algens</i>	0	1	0	0	?	1	1	1	0	0	0	0	1	?	0	0	0	?	0	0
<i>Br. eumorpha</i>	0	0	0	0	?	1	0	0	0	0	0	0	1	0	?	?	0	1	0	0
<i>De. alaskensis</i>	0	0	0	0	?	1	1	0	1	1	0	0	0	?	?	0	0	0	0	0
<i>F. olivaceae</i>	0	0	0	0	?	1	0	1	0	0	0	0	0	0	0	0	0	?	1	0
<i>G. oliveirai</i>	0	1	0	0	1	1	0	1	1	1	1	0	0	?	?	1	0	1	0	2
<i>M. decedens</i>	0	1	0	0	?	1	1	0	0	1	0	0	0	0	2	0	0	1	0	0
<i>Ps. dyari</i>	0	0	0	0	?	1	1	?	1	1	0	0	1	0	1	0	0	1	0	0
<i>R. submarginella</i>	0	1	0	0	?	?	?	?	?	?	1	?	0	?	?	?	1	?	0	0

continued.

	93	94	95	96	97	98	99	84	85	86	87	88	89	90	91	92	93	94	95
<i>Pr. culiciformis</i>	0	0	0	0	?	0	0	?	?	0	0	0	0	?	1	0	0	0	0
<i>Dj. lacustris</i>	0	1	0	0	0	0	0	0	0	0	?	0	1	1	1	0	0	1	0
<i>N. baltimoreus</i>	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0
<i>Al. dalyupensis</i>	0	0	1	1	1	0	1	0	?	?	?	?	0	1	0	2	0	0	1
<i>Al. aris</i>	0	0	1	1	1	0	1	0	0	0	1	1	0	1	0	2	0	0	1
<i>Al. kuroberobustus</i>	0	0	1	1	1	0	1	0	1	0	1	1	0	?	0	2	0	0	1
<i>Al. venustus</i>	0	0	1	1	1	0	1	0	1	1	?	1	0	1	0	1	0	0	1
<i>Al. vittigera</i>	0	0	1	1	1	0	1	1	1	[01]	1	1	0	1	0	1	0	0	1
<i>Ap. johnsonni</i>	1	0	1	1	1	0	1	?	?	0	1	1	0	1	0	0	1	0	1
<i>Be. floridensis</i>	0	0	1	0	1	1	2	?	0	1	1	0	0	?	1	1	0	0	1
<i>Bi. algens</i>	0	0	1	0	1	1	1	0	1	?	0	0	0	?	0	0	0	0	1
<i>Br. eumorpha</i>	0	0	1	1	1	0	2	0	1	0	?	?	0	1	0	0	0	0	1
<i>De. alaskensis</i>	1	0	1	1	1	0	2	0	0	?	?	0	0	0	0	0	1	0	1
<i>F. olivaceae</i>	?	0	1	1	0	[01]	0	0	0	0	0	0	0	?	1	0	?	0	1
<i>G. oliveirai</i>	0	0	1	1	1	0	1	0	0	?	?	1	0	1	0	2	0	0	1
<i>M. decedens</i>	1	0	1	0	0	1	2	0	0	0	2	0	0	1	0	0	1	0	1
<i>Ps. dyari</i>	0	0	1	1	1	0	2	0	1	0	1	0	0	1	0	0	0	0	1
<i>R. submarginella</i>	0	0	1	1	1	0	2	?	0	?	?	?	1	?	0	0	0	0	1



continued.

	96	97	98	99	100	101	102	103	96	97	98	99	100	101	102	103
<i>Pr. culiciformis</i>	0	?	0	0	0	?	1	1	0	?	0	0	0	?	1	1
<i>Dj. lacustris</i>	0	0	0	0	0	?	0	1	0	0	0	0	0	?	0	1
<i>N. baltimoreus</i>	0	1	0	0	0	?	0	0	0	1	0	0	0	?	0	0
<i>Al. dalyupensis</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Al. aris</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Al. kuroberobustus</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Al. venustus</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Al. vittigera</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>Ap. johnsonni</i>	1	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1
<i>Be. floridensis</i>	0	1	1	2	0	1	0	0	0	1	1	2	0	1	0	0
<i>Bi. algens</i>	0	1	1	1	0	1	0	0	0	1	1	1	0	1	0	0
<i>Br. eumorpha</i>	1	1	0	2	0	1	0	0	1	1	0	2	0	1	0	0
<i>De. alaskensis</i>	1	1	0	2	1	1	0	1	1	1	0	2	1	1	0	1
<i>F. olivaceae</i>	1	0	[01]	0	0	2	0	1	1	0	[01]	0	0	2	0	1
<i>G. oliveirai</i>	1	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0
<i>M. decedens</i>	0	0	1	2	0	1	0	0	0	0	1	2	0	1	0	0
<i>Ps. dyari</i>	1	1	0	2	1	1	0	1	1	1	0	2	1	1	0	1
<i>R. submarginella</i>	1	1	0	2	0	1	0	0	1	1	0	2	0	1	0	0

Based on the above-mentioned, a data set with all standardized quantitative characters expressed as ranges together with discrete characters coded as non-additive, were analyzed with the program TNT version 1.1 (Goloboff *et al.* 2008a) under implied weights as optimality criteria (Goloboff 1993). Analyses with implied weighting were conducted by means of values for the concavity constant  $k=5-16$  as suggested by Goloboff *et al.* (2008b). All tree searches were performed using a Wagner tree as starting tree and 1000 random addition sequences plus TBR with 10 trees to save per replication, followed by TBR branch swapping. Four character support measures were calculated. Absolute and relative Bremer supports were calculated saving up to 6 steps longer suboptimal trees obtained with branch-swapping. The presence of characters with weights or costs can lead to wrong conclusions with regard to support using Bootstrap and Jackknife (Goloboff *et al.* 2003). The results obtained in this analysis were estimated as absolute and GC (Group present/Contradicted) frequencies with 1000 replicates of jackknife symmetrical resampling plus TBR (jackknife symmetric resampling is not affected by weighted characters), 10 random addition sequences, and saving 100 trees per replicate.

## Results

### *Alotanypus vittigera* (Edwards, 1931), comb. nov.

*Anatopynia vittigera* Edwards 1931: 242–243, fig. 36b; Spies & Reiss 1996: 82 (listed as unplaced valid species).

**Type material (all in NHM).** **HOLOTYPE male** (NHM) L. Nahuel Huapi, Eastern end, Río Negro province, Argentina, 28–31.x.1926, F.W. Edwards. **Paratypes.** 3 males and 2 females same date as holotype; 1 male and 2 females, L. Correntoso, Río Negro province, Argentina, 18–25.xi.1926, F.W. Edwards; 1 male, Bariloche, Río Negro province, Argentina, 25–28.xi.1926, F.W. Edwards; 1 male, Puerto Montt, Llanquihue province, S. Chile, 24.xii.1926, F.W. Edwards.

**Recently collected material.** 1 male and 2 females from 41°00'56''S, 71°49'54''W, 856 m, Mallín La Heladera, Puerto Blest, PNNH, Río Negro province, Argentina, 07.i–04.ii.2007, Garré & Montes de Oca, Malaise trap, and 3 fourth instar larvae from same site, 04.ii.2007, Garré & Montes de Oca, Kick sample; 4 males with their pupal exuviae and 2 females with their pupal exuviae (all adults emerged same day of collection) from

41°36'06''S, 71°36'25''W, temporary pool beside Vertiente stream, Manso Inferior, PNNH, Río Negro province, Argentina, 10.i.2008, G. Orpella; 1 male with its pupal exuviae (adult emerged on 12.ii.2009), 2 females with their pupal exuviae (both adults emerged on 11.ii.2009), 1 prepupa and 2 fourth instar larvae, 41°00'05''S, 71°50'53''W, 855 m, Mallín La Heladera, Puerto Blest, PNNH, Río Negro province, Argentina, 11.ii.2009, A. Siri, kick sample.

**Emended diagnosis.** The diagnosis of *Alotanypus vittigera* (Edwards) comb. nov. should be emended as follows:

Male: vittae strongly or not indicated; AR lesser or slightly higher than 2.0; anepisternals, preepisternals and postnotals present or absent; LR I = 0.60–0.75.

Pupa: Thoracic seta DC<sub>1</sub> shorter or longer than DC<sub>3</sub>.

**Descriptions. Male** (n = 5–12, except when otherwise stated) (Figs. 1–8)

Total length 5.15–6.23 mm. Total length / wing length 1.61–1.89.

Coloration: Thorax yellowish brown to dark brown, with or without evident vittae. Anepisternum, preepisternum and postnotum dark brown; abdomen as Fig. 1.

Wing with several dark spots on membrane; macrotrichia above dark spots thick and densely grouped; central section of Cu, cross-veins RM and MCu, FCu and basal section of M<sub>3+4</sub> darkened (Fig. 2).

Head: Antenna; AR 1.9–2.1 [1.95]. Temporals multiserial 42–76 [71]; postorbitals bi to multiserial, 21–26 [21]. Clypeus with 7–20 [11] setae. Tentorium 257–274 [270] long (4). Palpomere lengths (1–5) 59–84 [70]; 101–148 [145]; 153–195 [150]; 227–282 [250]; 315–415.

Thorax. Anteprepronotum with 12–19 [17] lateral setae; humerals 14 (1); acrostichals biserials between vittae, diverging as uni to multiserial, merging with the dorsocentrals in the prescutelar area; dorsocentrals 44 (1); prealars 26–38 [35]; supraalar 1; anepisternals 0–3 [3]; scutellars 35–86 [76]; postnotum with 0–10 [0]; preepisternals absent.

Wing with macrotrichia in all cells except to r<sub>1</sub> and r<sub>2+3</sub>; length 3.10–3.80 [3.30] mm; width 0.90–1.06 [0.93] mm. L / W = 3.26–4.12 [3.55]. VR 0.88–0.97 [0.94]. C extended beyond R<sub>4+5</sub>. Brachiolum with 4–8 distal setae, plus 4–5 proximal setae. Squama fringed with up to 65 setae.

Legs. Tibial spur on p<sub>1</sub> with slightly curved apex, 102–116 [113] long; comb on p<sub>1</sub> with 9–13 [10] short spines (Fig. 3). Tibial spurs on p<sub>2</sub> 95–120 [115] and 63–83 [75] long (Fig. 4). Tibial spurs on p<sub>3</sub> 91–120 [113] and 69–81 [75] long (Fig. 5); spur ratio 0.65–0.74 [0.66]; comb on p<sub>3</sub> with 10–12 [12] spines, the outer slightly "S" curved (Fig. 6). Two pseudospurs on ta<sub>1-2</sub> of p<sub>2</sub> and ta<sub>1</sub> of p<sub>3</sub>. Lengths and proportions of legs in Table 3.

**TABLE 3.** Lengths (µm) and proportions of legs of *Alotanypus vittigera* comb. nov., male (n = 5–10); value for the holotype in brackets.

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>
p <sub>1</sub>	1307–1563 [1540]	1652–1880 [1750]	1224–1351 [1200]	625–717 [625]	415–497 [463]
p <sub>2</sub>	1452–1629 [1588]	1593–1805 [1750]	1017–1152 [1063]	525–612 [525]	350–418 [350]
p <sub>3</sub>	1245–1468 [1325]	1780–2095 [2000]	1328–1544 [1413]	665–795 [725]	428–530 [475]

continued.

	ta <sub>4</sub>	ta <sub>5</sub>	LR	BV	SV
p <sub>1</sub>	259–327 [275]	172–226 [200]	0.68–0.76 [0.69]	2.65–2.93 [2.87]	2.38–2.74 [2.74]
p <sub>2</sub>	208–249 [225]	165–200 [200]	0.60–0.66 [0.61]	3.13–3.39 [3.39]	2.91–3.17 [3.14]
p <sub>3</sub>	268–324 [288]	180–207 [200]	0.68–0.76 [0.71]	2.59–2.96 [2.81]	2.27–2.52 [2.35]

Hypopygium (Fig. 7). Setae on tergite IX, 17–24. Gonocoxite 249–291 [280] long. Gonostylus 135–161 [145] long. Aberrant specimens (3) with a very thick megaseta-like lateral to the megaseta; 1 aberrant specimen with the very thick megaseta-like, plus 1 additional strong spine (Fig. 8). HR 1.65–2.04 [1.93]; HV 1.97–2.41.

**Female** (n = 5–7, except when otherwise stated) (Figs. 9–11)

Total length 4.50–5.15 (4). Total length / wing length 1.27–1.44 (4).

Coloration: Thorax and wing spots as in male; cercus yellowish.



**FIGURE 1.** *Alotanypus vittigera* (Edwards) **comb. nov.** Male: abdomen in dorsal view. Scale bar = 500  $\mu$ m.

Head. Antenna with 14 flagellomeres, AR 0.21–0.23 (4). Temporal setae multiserial, 74 (1), postorbitals bi to multiserial, 45 (1). Clypeus with 16–21 setae. Palpomere lengths (I–V) 70–90; 102–150; 150–200; 220–303; 210 (1) long.

Thorax. Anteprepronotum with 15–26 lateral setae and 0–4 dorsal setae. Acrostichals as in male; prealars 33–55; supraalar 1; anepisternals 1–6 (4), scutelars 86–118. Preepisternals and postnotals absent.

Wing with macrotrichia in all cells except to  $r_1$  and  $r_{2+3}$ ; length 3.40–3.70 mm; width 1.16–1.50 mm; L / W = 2.39–2.90. VR 0.92–0.97. C extended beyond  $R_{4+5}$ . Squama fringed with 60–87 setae. Macrotrichia above dark spots thick and densely grouped

Legs. Tibial spur on  $p_1$  95–120 long; on  $p_2$  93–128 and 66–88 long; on  $p_3$  93–120 and 73–83 long. Spur ratio on  $p_3$  0.65–0.78. Comb on  $p_3$  with 9–12 spines; no tibial comb on  $p_1$ . Two pseudospurs on  $ta_{1-3}$  of  $p_2$  and  $ta_1$  of  $p_3$ . Lengths and proportions of legs in Table 4.

**TABLE 4.** Lengths ( $\mu$ m) and proportions of legs of *Alotanypus vittigera* comb. nov., female (n = 5–7).

	fe	ti	$ta_1$	$ta_2$	$ta_3$
$p_1$	1370–1700	1680–2100	1121–1325	564–700	405–488
$p_2$	1525–1900	1660–2025	934–1100	477–600	332–425
$p_3$	1287–1625	1836–2375	1183–1500	633–800	436–550

continued.

	$ta_4$	$ta_5$	LR	BV	SV
$p_1$	250–325	200–250	0.61–0.67	2.74–2.98	2.64–2.96
$p_2$	208–250	166–208	0.53–0.59	3.23–3.48	3.15–3.65
$p_3$	270–325	200–228	0.61–0.68	2.65–2.89	2.43–2.73

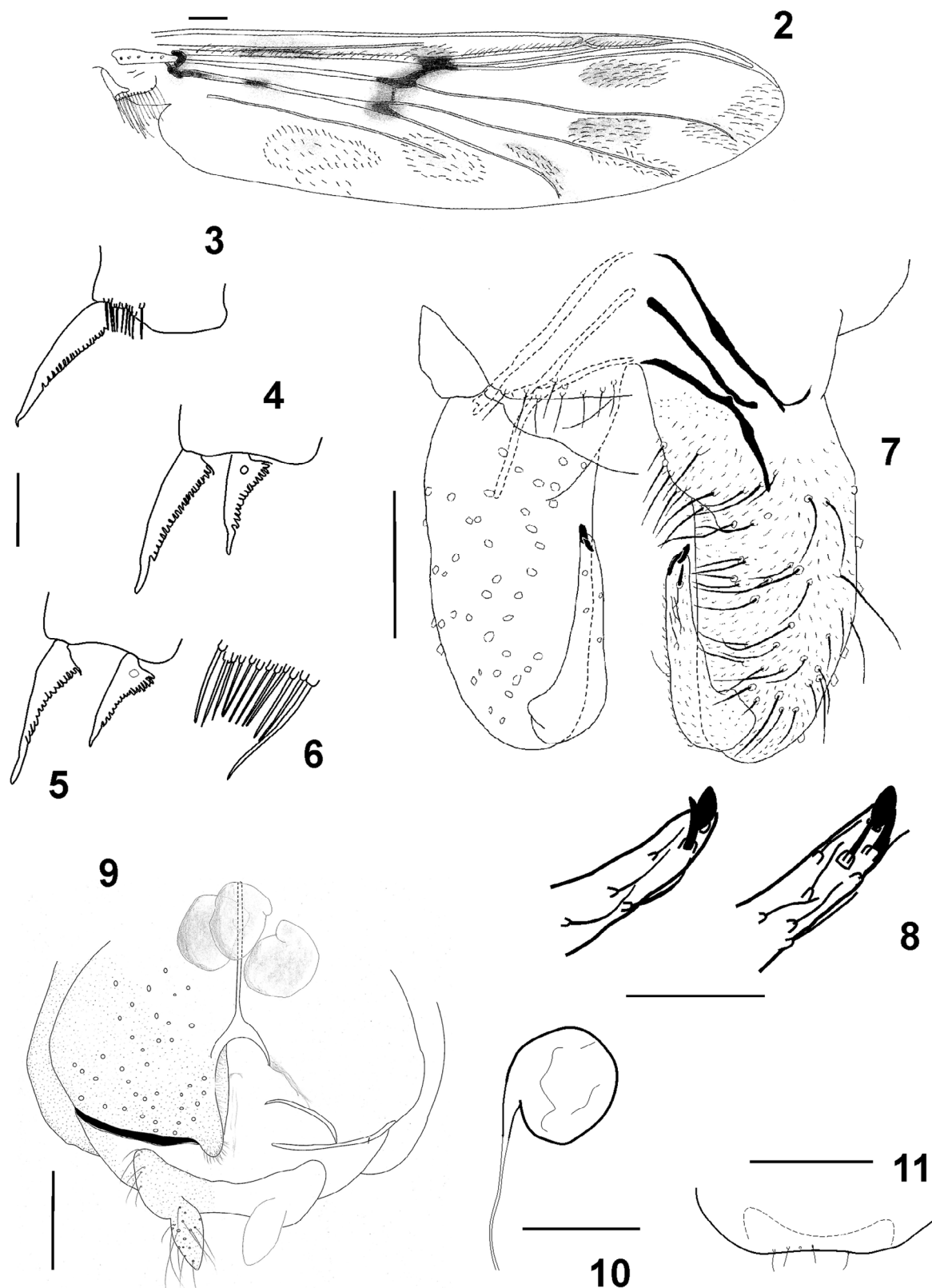
Genitalia (Fig. 9). Cercus 81–125 long. Seminal capsule 91–125 long (Fig. 10); notum 216–300 long (2); tergite IX with 0–5 setae (3) (Fig. 11); segment X with 6–13 setae (4).

**Pupa** (n = 4–9, except when otherwise stated) (Figs. 12–17)

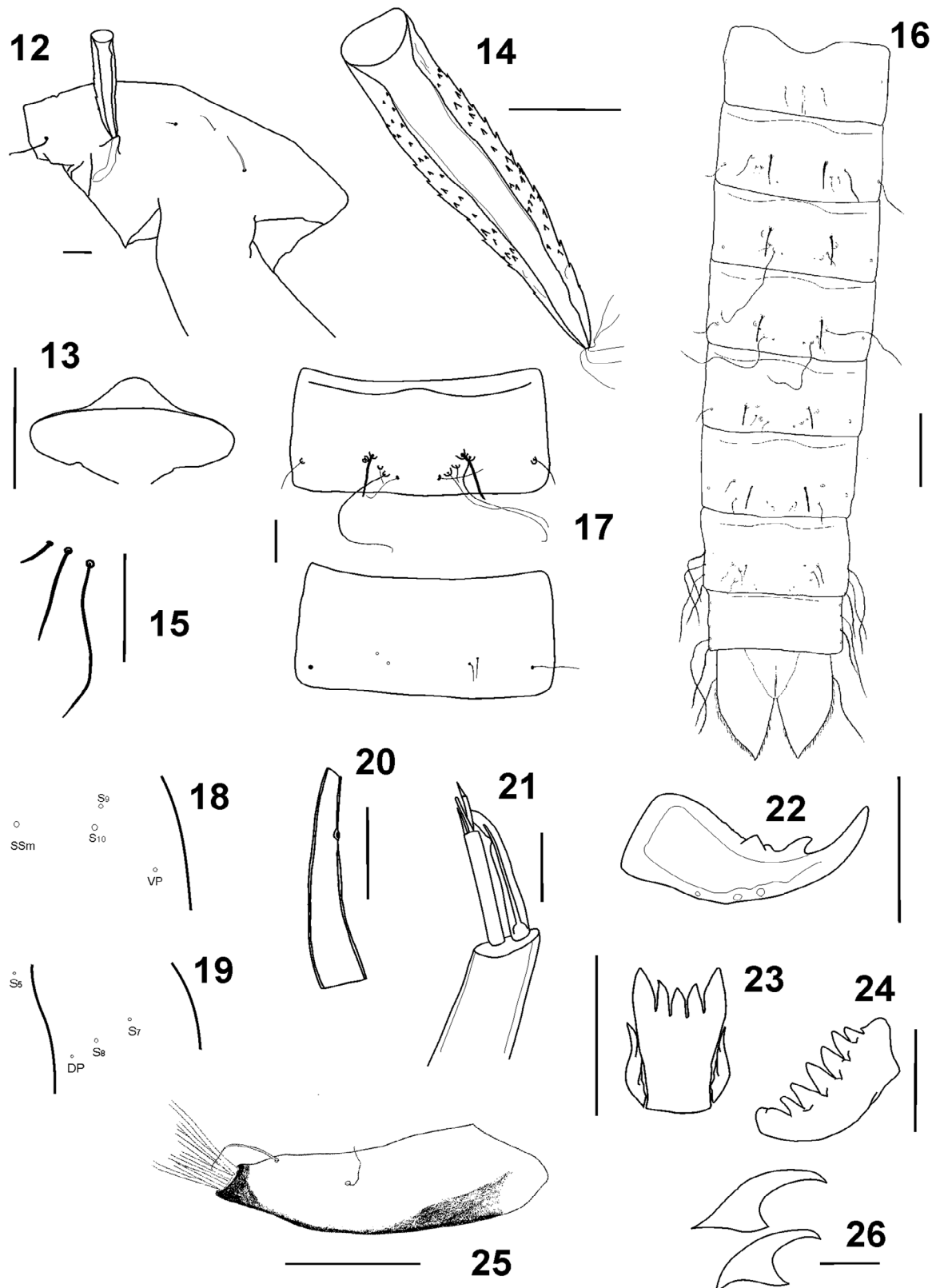
Total length 6.25–8.30 mm.

Cephalothorax (Fig. 12). Frontal apotome as in Fig. 13. Thoracic horn (Fig. 14) arising from a distinct tubercle; external membrane with spines; respiratory atrium almost straight. Length 524–596; width 106–135; L / W 4.41–4.95; plastron plate 58–85 long; 97–132 wide; plastron plate length / thoracic horn length 0.11–0.15. Thoracic setation (Fig. 15):  $DC_1$  41–54;  $DC_3$  95–140; Sa 203 long (1); MAs 175–188 long (2).

Abdomen. Scar on segment I, 216–249 long. Shagreen with single spines. Chaetotaxy (Figs. 16, 17):  $D_1$  more or less straight, arising from a distinct tubercle on segments I–VII.  $D_1$  is situated in the same line or slightly posteriorly to  $D_2$  in segments VI and VII.  $D_2$  and  $D_4$  longer than  $D_1$ , arising from a distinct tubercle in segments II–VII.  $D_3$  and  $D_5$  short and thin, arising from a very short tubercle or tubercle absent. Segments I–VI with two pairs of



**FIGURES 2–11.** *Alotanypus vittigera* (Edwards) **comb. nov.** adults. Male: 2, wing; 3, tibial spur and comb on fore leg; 4, tibial spurs on mid leg; 5, tibial spurs on hind leg; 6, tibial comb on hind leg; 7, Hypopygium, dorsal view to the left and ventral view to the right; 8, apex of gonostylus of two aberrant form. Female: 9, genitalia; 10, detail of seminal capsule and the first portion of the duct; 11, abdominal setation of tergite IX. Scale bars = 50  $\mu$ m for Figs. 3–6, 8; 100  $\mu$ m for Figs. 7, 9–11; 200  $\mu$ m for Fig. 2.



**FIGURES 12–26.** *Alotanypus vittigera* (Edwards) **comb. nov.** immatures. Pupa: 12, cephalothorax; 13, frontal apotome; 14, thoracic horn; 15, thoracic setae:  $Dc_1$ ,  $Dc_2$  and  $Sa$  from left to right; 16, complete abdominal setation; 17, tergite and sternite of abdominal IV segment. Fourth-instar larva: 18, ventral cephalic setation; 19, dorsal cephalic setation; 20, antennite I; 21, apex of antenna; 22, mandible; 23, ligula; 24, dorsomental teeth; 25, procercus; 26, simple claws of posterior parapod. Scale bars = 20  $\mu$ m for Fig. 21; 50  $\mu$ m for Figs. 13, 24, 26; 100  $\mu$ m for Figs. 12, 15, 20, 22, 23, 25; 200  $\mu$ m for Figs. 14, 17; 500  $\mu$ m for Fig. 16.

short lateral setae. Segments VII and VIII with 5; anal lobe with 2 pairs of long and teniated lateral setae. Position of  $LS_1$  / segment length = 0.45–0.51 on segment VII; 0.22–0.27 on segment VIII. Anal lobe 803–996 long; 400–450 wide; L / W 1.93–2.05. Position of LS / anal lobe length 0.16–0.18 for  $LS_1$  and 0.27–0.28 for  $LS_2$ .

Male genital sac 355–387 long; length of male genital sac / length of anal lobe 0.42–0.44.

**Fourth-instar larva** (n = 5–6, except when otherwise stated) (Figs. 18–26)

Total length 0.77–0.91 mm (2). Head: capsule 620–800; 820–1000 wide. CI 0.76–0.85.

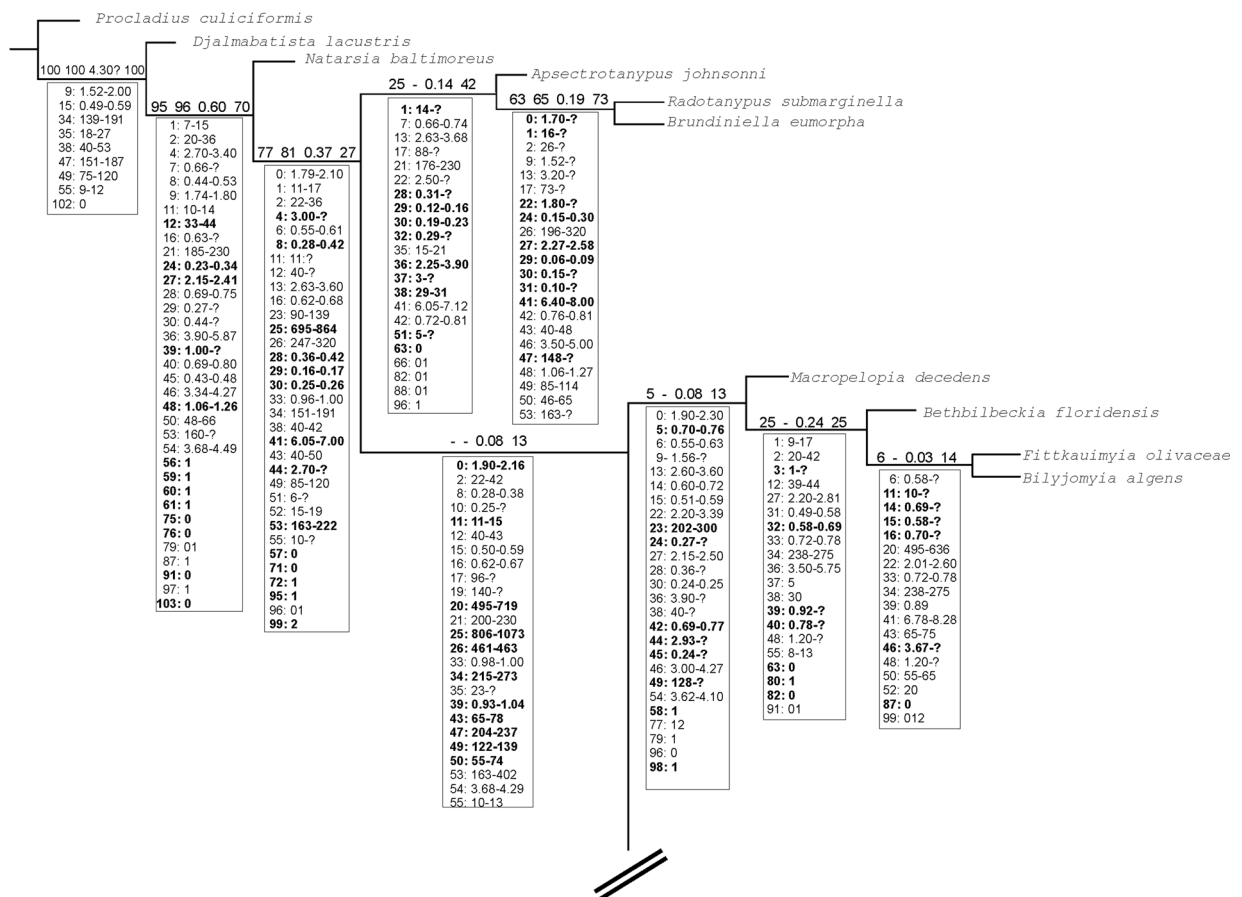
Cephalic setation: Ventral (Fig. 18):  $SS_m$  between  $S_9$  and  $S_{10}$ ;  $SS_m$  close to  $S_{10}$  and VP posterior to  $S_{10}$ . Dorsal (Fig. 19):  $S_7$ ,  $S_8$  and DP arranged in a line;  $S_6$  anterolaterally to  $S_{7-}$ .

Antenna (Figs. 20, 21). AR 4.9–5.6;  $A_1$  233–266 long, ring organ situated at 0.70–0.76 from base;  $BL_1$  35–42 long; NB 33–37 long; NB /  $BL_1$  0.83–0.90;  $BL_1$  /  $A_{2-4}$  0.80–0.88;  $A_2$  28–35 long, length  $A_2$  / width  $A_2$  4.3–6.6 (3);  $BL_2$  10–11;  $A_3$  7–11 long; length  $A_3$  / width  $A_3$  3.6–4.4;  $A_4$  5 long.

Maxillary palp: basal segment 60–73 long, length / basal width 0.59–0.67; relative distance of CS 0.59–0.67.  $A_1$  / PMx 3.64–4.08. Mandible (Fig. 22) 191–213 long.  $A_1$  / Mn 1.17–1.26. Hypopharyngeal complex: Ligula 108–145 long (Fig. 23), the outermost inner teeth slightly outcurved; paraligula bifid, 60–95 long; pecten hypopharyngis with 14–18 teeth; dorsomental teeth 5–7 (Fig. 24).

Abdomen. Procercus 250–350 long (Fig. 25); L / W 3.00–3.50; with 13 setae 855–1050 long. Preanal seta 780–830 long. Posterior parapods: smallest claws simple curved (Fig. 26).

Figure 27 (Part I)



**FIGURE 27 (part I).** Cladogram obtained under K 5. Synapomorphies are in bold. Numbers below nodes represent, from left to right, the support as Frequency Differences, as Absolute Differences, the Bremer support and the Relative Bremer Support respectively (unavailable data scored as "-").

Figure 27 (Part II)

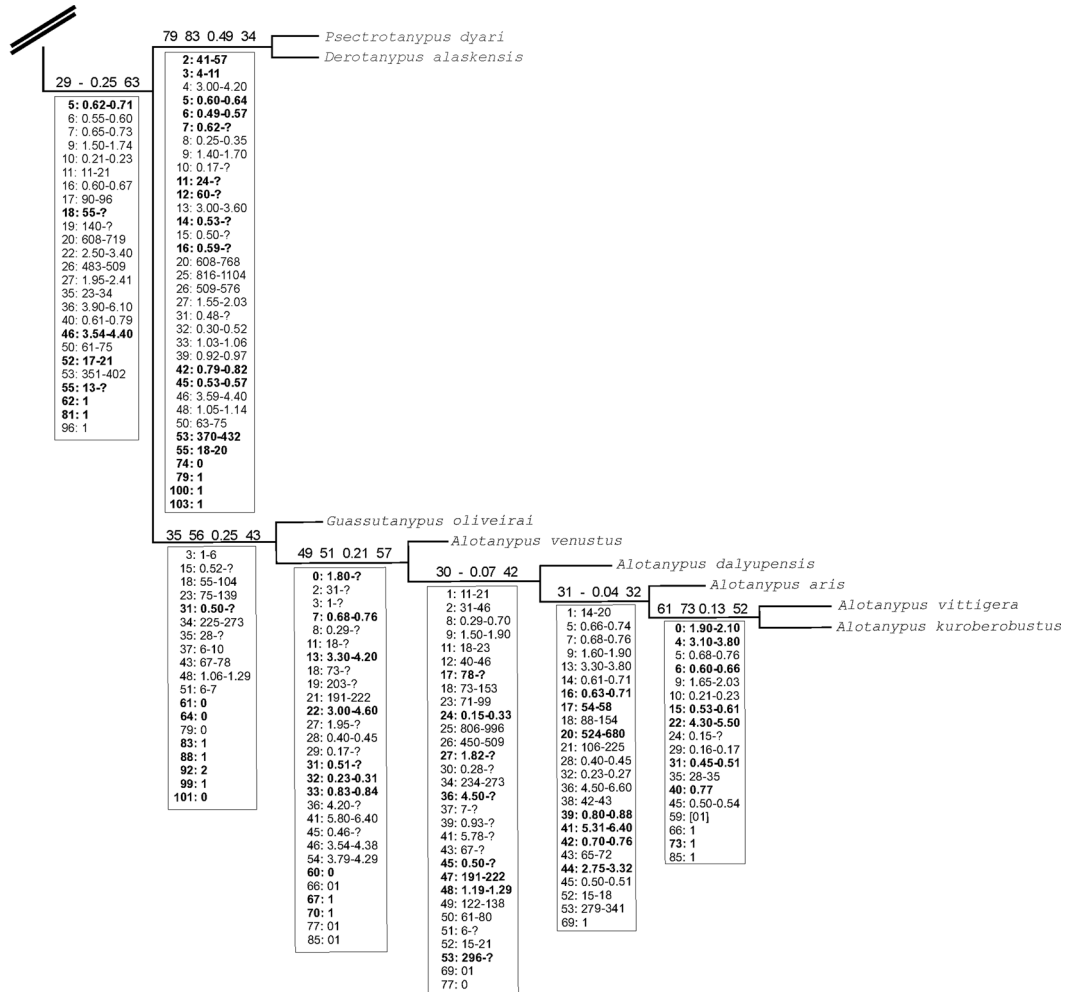


FIGURE 27 (part II). Cladogram obtained under K 5. Synapomorphies are in bold. Numbers below nodes represent, from left to right, the support as Frequency Differences, as Absolute Differences, the Bremer support and the Relative Bremer Support respectively (unavailable data scored as "-").

**Biology.** The species *A. vittigera* was found in a wide range of standing water environments such as lakes, temporary pools and “mallines” (singular “mallín”). A “mallín” can be characterized as a humid meadow with a dense cover mainly dominated by Juncaceae, Cyperaceae and Gramineae. The mallín soil contains a high percentage of organic matter and always associated with either surface water or ground water discharge. This kind of wetland in the Andes mountains is characterized by harsh environmental conditions, as the plant growth season is relatively short (about 4 months) and snow cover remains for about 6 months during the year (Raffaele 1996).

**Cladistic analysis.** The data set analyzed under  $K = 5$  to 16 yielded the same tree topology (Fig. 27) in each of the concavities (CI = 0.47, RI = 0.42). The tree derived from  $K = 5$  (score = 30.37) showed the best character measure support calculated as absolute frequencies, frequency differences and absolute Bremer support. The best relative Bremer support measures were those of  $K = 7$  (score = 29.7).

The genus *Alotanypus* is a monophyletic group supported by the synapomorphies male AR of 1.8, male LR III of 0.68–0.76, female wing length of 3.30–4.20 mm, L / W of thoracic horn 3.00–4.60, relative position of  $LS_1$  on segment VII of 0.51, relative position of  $LS_1$  on segment VIII of 0.23–0.31, CI of 0.83–0.84, postnotal setae absent, tibial comb I present, claws spatulate (at least on pII). *Alotanypus venustus* is the basal species of the genus followed by *A. dalyupensis* and *A. aris*. The species *A. vittigera* is closely related with *A. kuroberobustus* and shares the characters male AR of 1.90–2.10, male wing length of 3.10–3.80, male LR II of 0.60–0.66, female LR II of 0.53–0.61, L / W of thoracic horn of 4.30–5.50, relative position of  $LS_1$  on segment VII of 0.45–0.51, NB /  $BL_1$  of 0.77 and curved apex of spur I on male.

The clade [*A. aris*-*A. vittigera*-*A. kuroberobustus*] shares the characters female LR III of 0.63–0.71, DC<sub>1</sub> of 54–58 um long, thoracic horn of 524–680 um long, larval AR of 5.30–6.40, BL<sub>1</sub> / A<sub>2-4</sub> of 0.80–0.88, A<sub>1</sub> / Ring 0 of 0.70–0.76 and L / W PMx of 2.75–3.30.

The clade [*A. dalyupensis*-*A. aris*-*A. vittigera*-*A. kuroberobustus*] shares the characters DC<sub>1</sub> of 78 um long, plastron plate / thoracic horn of 0.15–0.33, L / W of anal lobe of 1.82, L / W of A<sub>2</sub> of 4.50, relative position of CS on PMx of 0.50, mandible of 191–220 um long, A<sub>1</sub> / mandible of 1.19–1.29 and procercus of 296 um long.

*Guassutanypus oliveirai* is the sister group of *Alotanypus*. This clade shares the presence of preepisternals, RM, FCu and MCu darkened veins on male and female, assymetrical neck position on seminal capsules, relative position of LS<sub>1</sub> on abdominal segment VII, horn sac of the thoracic horn not filling the entire horn lumen, number of teniated setae on segment VIII on pupa. This last clade is the sister group of the clade [*P. dyari*-*D. alaskensis*] by sharing characters: LR I on male; FCu vein darkened in male and female; length of DC<sub>3</sub> on pupa, A<sub>1</sub> / PMx, pecten hypopharnix and number of setae on procercus.

The tribe Macropelopiini is monophyletic and it is supported by the synapomorphies male wing length of 3.00, male spur ratio of 0.28–0.42, female anal lobe length of 695–864, genital sac / anal lobe of 0.36–0.42, relative position of 0.16–0.17 for LS<sub>1</sub> and 0.25–0.26 for LS<sub>2</sub> on anal lobe, larval AR of 6.05–7.00, L / W PMx of 2.70, procercus length of 163–222, postorbitals multiserials, male spur thorn like. Spur teeth bigger than 15, outer fringed on anal lobe present and teniata setae on abdominal segment VII bigger than 5.

## Discussion

The genus *Alotanypus* was erected by Roback (1971) for *A. aris* and *Anatopynia venusta*. Roback notes the similarity between the male of *Alotanypus* and *Macropelopia*, distinguishing them by the absence of both the scutal tubercle and postnotals in *Alotanypus*. This author differentiates the male of *Alotanypus* from *Apsectrotanypus* by the presence of the tibial comb on the fore leg, spatulated claws, spurs on some tarsal segments and absence of postnotals. In the diagnosis of *Alotanypus* male adult, he also notes the presence of anepisternals, and the presence or absence of preepisternals. At the same time, he differentiates the pupa of *Alotanypus* from the related *Psectrotanypus* by the shagreen. Later, based on a numerical taxonomic studies, the full genus *Alotanypus* was established as a subgenus of *Macropelopia* (Roback & Moss 1978). However, posterior papers (i.e. Fittkau & Roback 1983, Fittkau & Murray 1986, Murray & Fittkau 1989, Epler 2001) re-consider *Alotanypus* as a full genus.

Murray and Fittkau (1989) also consider the presence of the tibial comb on the fore leg in *Alotanypus* and *Macropelopia* male as a distinct character missing in the other Macropelopiini genera. According to Roback (1971), these authors note the absence of scutal tubercle and the absence of postnotals in *Alotanypus* male as the further differences that separate this genus from *Macropelopia*. In the diagnosis of male adults of *Alotanypus* Murray and Fittkau (1989) describe the presence of both anepisternals and preepisternals.

As it was mentioned above, the monophyletic genus *Alotanypus* is distinguished from the other Macropelopiini by a combination of characters. However, we found some difficulties to differentiate male adults of *A. vittigera* from the genus *Macropelopia*, because some specimens of *A. vittigera* comb. nov. have postnotals. Therefore, the absence of the scutal tubercle represents the most important character to separate male of both genera. In addition, the marks present in the wing vein FCu and MCu together with the spatulated claws also differentiated male of *Alotanypus* from *Macropelopia*. Contrarily, both genera are easily distinguished at pupal and larval stages. In contrast of previous *Alotanypus* male adult diagnosis (Roback 1971, Murray & Fittkau 1989), the preepisternals are absent in *A. vittigera*, but anepisternals are present in some specimens. Summarizing, the presence-absence of preepisternals, anepisternals and postnotals are not enough characters to separate this genus from other Macropelopiini

On the basis of adult and pupal characters, the genus *Alotanypus* was considered as an early derivative of the line leading to *Psectrotanypus*-*Apsectrotanypus* (Roback 1971). In our cladistic analysis, *Psectrotanypus* and *Apsectrotanypus* are not closely related, being *Alotanypus* more related with the former genus.

*Alotanypus vittigera* is closely related to the Japanese *A. kuroberobustus* by the foretibial male spur recurved sharply at the apex, which does not occur commonly in Tanypodinae (Niitsuma 2005). The LR II of these species is the highest within *Alotanypus*. Pupae of both species are distinguishable by the extremely sinuated respiratory atrium existing in *A. kuroberobustus*. Differences in the measures and ratios of the larval antenna clearly distin-



guish both larvae, with differences in AR,  $A_1$  length, L / W of  $A_2$  and NB /  $BL_1$  ratio. The relative distance of CS in the maxillary palp, and the length / width of procercus also differs in the larvae.

Male adult of *A. vittigera* shares with *A. aris* the apices in concave arc in the spines of the comb III. Male adult of *A. aris* has a very high number of prealars than other species of *Alotanypus* and is the only *Alotanypus* with preepisternals. The AR of the male of *A. aris* is lower than *A. vittigera*. The male and female adults of *A. aris* have a lower LR II and a higher LR III than *A. vittigera*, as well as shorter and unmarked wings. Compared to *A. vittigera*, pupa of *A. aris* differs by the lower L / W ratio of the thoracic horn, by the strongly sinuated respiratory atrium, by the shorter thoracic horn and by the length of plastron plate length / thoracic horn length ratio. Larvae of both species differ by the NB /  $BL_1$  ratio; by the position of the CS in the basal segments of the maxillary palp, by the  $A_1$  / PMx ratio and by the L / W ratio of the procercus.

*Alotanypus dalyupensis* is poorly described and a redescription of all its stages is needed. The major difference with *A. vittigera* seems to be the very low L / W ratio of the thoracic horn, with strongly sinuated respiratory atrium, and the strongly outcurved inner teeth of ligula in the larva. The male adult LR I of *A. dalyupensis* is the smallest within the genus. Postnotals were described for the female of this species.

*Alotanypus venustus* is the basal species of the genus. The adult male of this species resembles *A. vittigera*, but differs in the LR I and II (Roback 1978). The LR II of *A. venustus* is the smallest within the *Alotanypus*. The pupa of *A. vittigera* shares the almost tubular respiratory atrium with *A. venustus*, but the L / W ratio of the thoracic horn differs. The thoracic seta  $Dc_1$  of *A. venustus* is almost twice longer than  $Dc_3$ , while in *A. vittigera* the  $Dc_1$  is at least 2X shorter than  $Dc_3$  (named as  $Dc_2$  in Fittkau & Murray 1986), as well as, the Sa is only 2X longer than  $Dc_3$ . Larva might be differentiated by the relative position of CS on the PMx, with centro-basal position in *A. venustus* and centro-apical in *A. vittigera*.

Character values or states of the species used in the phylogenetic analysis were obtained from the published bibliographic data. Description of *A. kuroberobustus* is the most detailed of all *Alotanypus* species description, and includes some characters which have not been previously studied. Therefore, there is more available data of *A. kuroberobustus* than other *Alotanypus* species. Therefore, this might be the result of the close relationship of *A. vittigera* and *A. kuroberobustus*.

The genus *Natarsia* shares characters with Macropelopiini and Pentaneurini. Thus, its taxonomical placement consisted a problem for chironomid taxonomists (Roback & Moss 1978). This genus was originally included in Pentaneurini (Fittkau 1962) and transferred later to Macropelopiini (Roback 1971). According to the analysis of the female genitalia (Sæther, 1977), *Natarsia* fits within Macropelopiini. Lately, Roback and Moss (1978) transferred the genus *Natarsia* from Macropelopiini to a new tribe named Natarsiini. As in Roback (1971) and Sæther (1977) in our cladistic analysis *N. baltimoreus* is closely related to Macropelopiini. Further studies including more species of Macropelopiini and all described species of *Natarsia* will be necessary in order to corroborate the position of this genus in Natarsiini, or consider *Natarsia* as the basal genus of Macropelopiini.

## Remarks on larval cephalic setation

The larval cephalic setation is a widely used tool to distinguish Tanypodinae genera in subfossil studies because most of the taxonomical characters are not present in larval subfossil head capsules (Rieradevall & Brooks 2001). The setation in *Alotanypus* was firstly described for *A. kuroberobustus* (Niitsuma 2005). The genus is included in the "Group A5" of Rieradevall and Brooks (2001), where  $SS_m$  is located between  $S_9$  and  $S_{10}$ , and VP is below  $S_{10}$ , with the difference that in *Alotanypus* the  $S_9$  is external to  $S_{10}$ . In addition, the intersection of a line connecting  $S_9$ - $S_{10}$  and another line connecting  $SS_m$  and VP shows an angle of 90 degrees.

*Macropelopia*, *Apsectrotanypus* and *Psectrotanypus* are other Macropelopiini collected in the Parque Nacional Nahuel Huapi (Donato *et al.* 2008). *Macropelopia*, like *Alotanypus*, is included within the "Group A5", but  $S_7$  and  $S_8$  are not aligned with DP, and  $S_9$  and  $S_{10}$  are vertically aligned. The line connecting  $S_9$ - $S_{10}$  also intersects close to the middle of the line  $SS_m$ -VP but with an angle of 45 degrees. *Apsectrotanypus* is included within "Group A6" because the  $SS_m$  and VP are below the  $S_{10}$ . In this genus,  $S_7$  and  $S_8$  are not arranged in a line with DP, and the line connecting  $S_9$ - $S_{10}$  intersects the line connecting  $SS_m$ -VP close to  $SS_m$ . *Psectrotanypus* belongs to "Group A4", since the  $SS_m$ ,  $S_{10}$  and VP are almost lined up.

## Acknowledgments

The authors wish to thank the Willi Hennig Society for the free availability of the TNT program, to the NHM by the loan of the type material of *Alotanypus vittigera* used in this study and to Mónica Caviglia for improvement of the English. The paper is a Scientific Contribution N° 886 of the Institute of Limnology “Dr. R.A. Ringuelet” (ILPLA, CCT-La Plata, CONICET, UNLP). This paper is supported by CONICET and Darwin Initiative “Capacity Building for Biodiversity Studies in Freshwater Insects” (Ref. 15025).

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