Systematics of Amphineurus (Rhamphoneurus Alexander) (Diptera: Tipuloidea: Limoniidae)

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http://zoobank.org/62FFB94C-EBF4-4163-9F22-881435EFC37C

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Received 3 March 2022
Accepted 30 June 2022
Published 12 September 2022

Citation: Santos D, Santos RR, Ribeiro GC (2022) Systematics of Amphineurus (Rhamphoneurus Alexander) (Diptera: Tipuloidea: Limoniidae). Arthropod Systematics & Phylogeny 80: 439–494. https://doi.org/10.3897/asp.80.e83035

Abstract

The subgenus Amphineurus (Rhamphoneurus Alexander) (Diptera: Limoniidae), a group of craneflies endemic to southern South America, is revised. The previously described species are redescribed and illustrated, along with fifteen new species: A. (R.) alexanderi sp. nov., A. (R.) amorimi sp. nov., A. (R.) anchoralis sp. nov., A. (R.) anfractus sp. nov., A. (R.) billingkani sp. nov., A. (R.) caleuchus sp. nov., A. (R.) deceptus sp. nov., A. (R.) falcatus sp. nov., A. (R.) immaculatus sp. nov., A. (R.) morphyi sp. nov., A. (R.) oosterbroeki sp. nov., A. (R.) podenasi sp. nov., A. (R.) theischingeri sp. nov., A. (R.) triangularis sp. nov., and A. (R.) stigmaticus sp. nov. In addition, A. (R.) fuscifusus Alexander is considered a nomen dubium. A phylogenetic analysis with a broad taxonomic sampling with all valid species of the subgenus A. (Rhamphoneurus Alexander) and species from all the subgenera of Amphineurus Skuse is performed. The broad outgroup sampling used in the study (including taxa from the entire range of distribution of Amphineurus) suggests that the subgenus A. (Rhamphoneurus) is a monophyletic taxon, that its closest relatives are taxa currently distributed in New Zealand, and that Australasian taxa are paraphyletic with respect to the Neotropical Clade.

Key words

Chioneinae, Chile, crane flies, phylogeny, taxonomy, Tipulomorpha

1. Introduction

The southernmost parts of the Southern Hemisphere contain a rich and unique biota of craneflies (Diptera: Tipuloidea) which is poorly understood, but that nevertheless suggests strong biogeographical links between southern South America and Australasia. In a comprehensive review of the subject, Ribeiro and Eterovic (2011) examined in detail the distributional patterns of over 700 species in 30 genera and subgenera of Tipuloidea endemic to areas that constitute what is known in biogeography as the South Pacific Track (Crisp et al. 1999). One of such groups of craneflies is the genus Amphineurus Skuse.

Amphineurus was erected by Skuse (1890) as a subgenus of Rhypholophus Kolenati to allocate two Australian species with an open discal cell. Edwards (1923), advocating that these Australian species differed considerably from the Holarctic genus Rhypholophus, raised Amphineurus to genus level to allocate them together with some other related New Zealand species.
The genus *Amphineurus* includes four subgenera and over 80 species. *Amphineurus* (*Amphineurus*), with approximately 42 described species, is distributed in southern South America, New Zealand, New Caledonia, Australia and New Guinea. The Australian species of *A. (Amphineurus)* were revised by Theischinger (1994, 1996), but there is no recent taxonomic treatment of the species from the other regions. The subgenera *A. (Ne-or-nosisia Alexander) (four species) and A. (Nothornosisia Alexander) (18 species)* are New Zealand endemics. Alexander (1929a) proposed the subgenus *A. (Rhamphoneurus)* to include a group of Neotropical species with a long rostrum, which now constitutes a southern South American endemic group (10 species in Chile and Argentina) (Oosterbroek 2022).

It is of historical interest that, when reporting for the first time the occurrence of *Amphineurus* in the Neotropical Region, Alexander (1929a) regarded this fact as being of great scientific significance. In his own words: “Although the majority of the Chilean species represent a new subgeneric group, one species, *A. castroensis […]*, belongs to the rather extensive aggregation of forms that are allied to *A. perdecensis* Edwards, and *A. pressus* Alexander, known hitherto only from New Zealand” (Alexander 1929a: 186). These remarks were made in a context in which Alexander (1929a) defended the hypothesis already raised at that time that Antarctica must have played a role as a land connection between South America and Australasia.

As discussed by Ribeiro and Eterovic (2011), detailed taxonomic and phylogenetic studies of this fauna are of paramount importance for testing the primary hypothesis of biogeographical homology they propose, stating that cranefly taxa now disjunct in different sides of the Pacific were integrated into an ancient biota that underwent considerable level of differentiation before the breakup of Gondwana.

In the present contribution, we provide a detailed taxonomic revision and phylogenetic study of the Neotropical subgenus *A. (Rhamphoneurus)*, with the description of 15 new species and an identification key for all its included taxa. Knowledge of the previously described species of the subgenus *A. (Rhamphoneurus)* is virtually limited to the original descriptions. In addition, knowledge of the morphology and biology of immature stages of this subgenus remains unknown.

Testing the monophyly of *A. (Rhamphoneurus)* demanded broad taxonomic sampling including representatives of all subgenera of *Amphineurus* from the entire distribution range of the genus; i.e., from South America, New Zealand, Australia, Tasmania, New Guinea and New Caledonia.

2. Material and methods

The specimens of this study belong to the Alexander Collection of Crane Flies of the National Museum of Natural History, Smithsonian Institution, USA (USNM). The holotype of *A. (R.) sanus* belongs to the Natural History Museum, London, UK (BMNH). C.P. Alexander made preliminary identifications of all examined specimens. Specimens on slides prepared by C.P. Alexander were identified with an asterisk (*).

Descriptive terminology follows McAlpine (1981) for most structures, Schneeberg and Beutel (2011) for head morphology, and Ribeiro (2006) for terms of the structures of the male terminalia. The terminology applied to the wing veins follows, with minor changes, the terminology adopted in the “Manual of Afrotropical Diptera” (Cumming and Wood 2017).

Abbreviations used in the figures are as follows: *ej*, ejaculatory apodeme; *ad sp*, anterodorsal spur; *aed*, aedeagus; *sh*, sheath of aedeagus; *anat*, anatergite; *anep*, anepimeron; *apr*, anepisternum; *arc*, arculus; *sp*, basal spur; *cer*, cercus; *clasper*, branch of gonostylus; *cv*, cervical sclerites; *cx*, coxa; *db*, dorsal branch of clasper of gonostylus; *dg*, dorsal branch of gonocoxite; *dl*, dorsal branch of lobe of gonostylus; *f*, foramen of male tergite X; *gonex*, gonocoxite; *gonst*, gonostylus; *hlt*, halter; *hph*, hypopharynx; *hyp val*, hypogynial valve; *ib*, interbase; *kn*, knob of halter; *kepm*, katepimeron; *keps*, katepisternum; *ktg*, kategaster; *lb*, left mesal lobe of gonocoxite; *lh*, lobe of lobe of gonostylus; *lb clasper*, lateral branch of clasper of gonostylus; *lb lobe*, labellae; *lb sp*, lateral spur; *lb sh*, lateral branch of sheath of aedeagus; *lh*, lateral humps of male tergite IX; *mb c*, medial branch of clasper of gonostylus; *mh*, medial humps of male tergite IX; *mr*, meron; *ms lobe*, mesal lobe of gonocoxite; *mtakeps*, metakatepisternum; *mtapep*, metepimeron; *mtb*, metabasitergite; *mtn*, metanotum; *p*, posterior basalar; *paratg*, paratergite; *pb sh*, posterior branch of sheath of aedeagus; *plp*, palpus; *pm*, paramere; *pprn*, postpronotum; *precs*, prescutum (including prescutal scutum); *r ms*, right mesal lobe of gonocoxite; *rst*, rostrum; *scct*, postscutal scutum; *setl*, scutellum; *st*, sternite; *t r*, tip of rostrum; *tg*, tergite; *t9*, male tergite IX; *t10*, male tergite X; *vb clasper*, ventral branch of clasper of gonostylus; *vb g*, ventral branch of gonocoxite; *vb lobe*, ventral branch of lobe of gonostylus; *vt*, vertex.

When necessary, clarifications of male and female genitalia were made with the method proposed by Santos et al. (2018) using Proteinase K. The genomic material of the clarified specimens was stored. Photographs were taken with a Nikon DS-Ri1 digital camera attached to a Nikon SMZ1000 (stereoscopic) microscope. Deep focus images were stacked with Combine ZP software. Measurements were taken with Carl Zeiss AxioVision (Release 4.8) software. Line drawings were made by camera lucida attached to the microscopes. Described measurements are of the holotypes. Regarding species distribution records, we have included the approximate geographic coordinates of the localities identified on the labels of the studied specimens.

The phylogenetic analysis was made under different criteria: 1) parsimony with equal weights; 2) parsimony
with implied weights; 3) Bayesian inference. This was made in order to test the stability of the results under different analytical protocols.

For the parsimony analysis, we used heuristic searches with tree-bisection reconnection (TBR) branch swapping with 1,000 replicates holding up to 100 trees per replication. All characters were treated as unordered. Cases with the character state unknown were scored with ‘?‘ and cases where a character is inapplicable with ‘—’. The analyses were made using TNT (Goloboff and Catalano 2016) and rooted following the outgroup method revised by Nixon and Carpenter (1993). It must be emphasized here that, according to Nixon and Carpenter (1993), a good definition of character polarity within the ingroup does not only depend on the proper definition of the outgroup taxa, but also on the inclusion of characters selected to provide some resolution within the outgroup. In this paper, we have adopted this protocol as much as possible, including an impressive representation of all subgenera of Amphineurus and its morphological variation.

For Bayesian inference, we used the MK model (Lewis 2001). A log normal distribution was used to account for character rate variation. The analysis was made with two simultaneous runs containing 10 million generations of the mcmc chain, each run had four chains. Trees were sampled every 1000 generations with a burning cutoff of 25 percent. Convergence was checked by examining the trace plots using Tracer 1.7 (Rambaut et al. 2018) and the standard deviation of the sample split. The tracer plots reached stationary and the standard deviation was lesser than 0.01 (0.004).

3. Taxonomic revision of Amphineurus (Rhamphoneurus Alexander)

Family Limoniidae

Subfamily Chioneinae

3.1. Genus Amphineurus Skuse, 1890

Amphineurus Skuse, 1890: 800 (as a subgenus of Rhypholophus).

Type-species: Amphineurus (A.) umbraticus Skuse, 1890 (as Rhypholophus).

Diagnosis. Amphineurus can be diagnosed by the following combination of characters: gonocoxite bifid; wing with R_{2+3+4} aligned with R_{1+3}. When there is an element R_{4+5} (and therefore, no R_{5+}), members of the genus are distinguished from other Chioneinae by the closed discal cell.

Remarks. There is great diversity in the male terminalia of Amphineurus (Figs. 1, 2). There are many variations from the simplified pattern of A. (A.) patya Theischinger (Fig. 1A) to the asymmetric disposition of A. (Nesormia) (Fig. 2D). Therefore, defining a broad diagnosis for Amphineurus is not so easy. Skuse (1890) defined Amphineurus as a subgenus of Rhypholophus. Skuse’s definition fits better to the current subgenus A. (Amphineurus) but does not portray the reality of other species of Amphineurus. His diagnosis included the absence of the discal cell, the radial sector with four branches, “second longitudinal vein angulated”, and hind femora one third longer than the intermediate pair. These features are non-exclusive or variable in the genus.

Alexander (1920) allocated Amphineurus as a subgenus of Ormosia after highlighting the abundant and conspicuous wing macrotrichia (Fig. 5B). Edwards (1923) redefined the genus to support two New Zealand species. Edwards’ diagnosis includes the short mid-leg, short and hairy wing, and radius four-branched. Nevertheless, these features occur in other Chioneinae. Edwards (1923) also referred to the fact that the medial vein forks in M_{3+4} and M_{1+2} and that the anal vein is sinuous. These features are plastic in the genus. Alexander (1929a) used the definition of Edwards (1923) and emphasized the characteristic “abundant trichiation” of the genus. However, in the same article, Alexander (1929a) described the genus Maietta, which has more wing vestiture than Amphineurus. Some species of the Neotropical subgenus A. (Rhamphoneurus) have less macrotrichia than other subgenera. No more inclusive diagnosis was proposed and recent revisions (e.g., Theischinger 1994, 1996) redefined only the diagnosis of the subgenus A. (Amphineurus).

Amphineurus has an 180° rotation of male terminalia (in the words of Edwards: “undergone permanent torsion”). Edwards (1923) also shows that Amphineurus has a long, finger-like gonocoxite process (Fig. 1A). This is evidence of the bifid gonocoxite, a condition present (Fig. 29G) in some Chioneinae with inverted male terminalia. This gonocoxal process forms a protective hood (Kramer 2020) for the appendices of the inverted terminalia.

The Chioneinae genera with inverted terminalia bear great diversity and frequently they have hairy wings similar to Amphineurus. The great amount of wing vestiture resembles Maietta Alexander. The wings of some A. (Amphineurus) (Fig. 32: Node 18) have a distinctive radial sector such as seen in Molophilus Curtis. Some A. (Amphineurus) (Fig. 32: Node 23) resembles Hoplolabis (Parilisia Savchenko). The trifid claspers of A. (Rhamphoneurus) are observed in genera such as Hoplolabis Osten Sacken and Cheirotrichia Rossi. Despite that, in the group of genera with a bifid gonocoxite and inverted terminalia, vein R_{2+3} is normally aligned with R_{2+3+4}. The exception is a clade of A. (Amphineurus) (Fig. 32: Node 18) that shows resemblances in the radial sector with Molophilus (where R_{2+3+4} is lacking), but the former has a closed discal cell among other wing features which places it within Amphineurus.
3.2. **Subgenus Rhamphoneurus**
Alexander, 1929a

*A. (Rhamphoneurus)* Alexander, 1929a: 186. Type-species: *A. (R.) nothofageterorum* Alexander, 1929a.

**Diagnosis.** This subgenus is distinguished by the rostrum at least as long as the remainder of the head. Cell M, open.

**Description.** Habitus of representative species of the subgenus *A. (Rhamphoneurus)* is shown in Fig. 3. Head as long as wide in lateral view (Fig. 4A). Two ventral cervical sclerites of same proportions, longer than wide, while sclerite in middle of neck nearly horizontal; sclerite near head more vertically orientated (Fig. 4A). Neck approximately 2.5× shorter than head. Rostrum as long as remainder of head. In some specimens, dorsal concentration of setae at end of rostrum. End of rostrum with sclerotized bifurcated tips (Fig. 4B) of variable sizes and shapes. Antenna 16-segmented, ca. twice length of head. Scape cylindrical, 2× longer than wide. Pedicel rounded, as long as wide. Pedicel approximately as long as scape. First flagellomere ca. 1.2× longer than pedicel. Pedicel ca. 1.5× wider than first flagellomere. Flagellomeres ca. 2× longer than wide. Flagellomeres vary in pilosity. Terminal flagellomere may be expanded. Palpus with 4 segments and large auxiliary segment at base (Fig. 4A). Palpus ca. 1.4× longer than rostrum. Length of palpal segments variable, but all cylindrical and similar in width. Wings 3–3.5× longer than wide, bearing typical distinctive hairs.
Figure 2. Schematic illustration of the male terminalia of representatives of *Amphineurus* (dorsal view). A *A. (A.) maculosus*; B *A. (Nothormosia) edentulus*; C *A. (A.) perdecorus*; D *A. (Nesormosia) fatuus*. — Abbreviations: **aed**, aedeagus; **aed sh**, sheath of aedeagus; **cgonst**, clasper of gonostylus; **db clasper**, dorsal branch of clasper of gonostylus; **goncx**, gonocoxite; **gonst**, gonostylus; **lb sh**, lateral branch of sheath of aedeagus; **lgonst**, lobe of gonostylus; **ms lobe**, mesal lobe of gonocoxite; **t9**, male tergite IX; **vb clasper**, ventral branch of clasper of gonostylus.

Figure 3. Habitus of some *Amphineurus* (*Rhamphoneurus*) species (lateral view). A *A. (R.) stigmaticus* sp. nov. (female); B *A. (R.) glabristylatus* (female); C *A. (R.) morphyi* sp. nov. (female); D *A. (R.) immaculatus* sp. nov. (male).
Figure 4. Morphology of the head of *Amphineurus (Rhamphoneurus)* (male). A Head of *A. (R.) chiloeanus* (lateral view); B Mouthparts of *A. (R.) nullus* (dorsal view). — Abbreviations: cv, cervical sclerites; hph, hypopharynx; lbl, labella; lbr, labrum; plp, palpus; rst, rostrum; t r, tip rostrum; vt, vertex.

Figure 5. A Wing of *Amphineurus (Rhamphoneurus) caleuchus* sp. nov. (male); B detail of wing of *Amphineurus (Rhamphoneurus) immaculatus* sp. nov. — Abbreviation: arc, arculus.

Figure 6. Male terminalia of *Amphineurus (Rhamphoneurus) insanus*. Dorsal view with some structures in lateral view. — Abbreviations: a ej, ejaculatory apodeme; aed, aedeagus; aed sh, sheath of aedeagus; ap, gonocoxite apodeme; cgonst, clasper of gonostylus; db g, dorsal branch of gonocoxite; goncx, gonocoxite; lb, interbase; l ms, left mesal lobe of gonocoxite; lb, lobule of lobe of gonostylus; lb c, lateral branch of clasper of gonostylus; lgonst, lobe of gonostylus; mb c, medial branch of clasper of gonostylus; pm, paramere; r ms, right mesal lobe of gonocoxite; vb g, ventral branch of gonocoxite.
Wing veins run mostly in parallel (Fig. 5), especially in radial sector. Vein Sc complete. Crossvein sc-r near origin of Rs. Rs complete or faded. Tip of Rs complete or faded. Insertion of m-cu variable: proximal to fork of bM, in fork of bM, or M₃+₄. Discal cell open. Wing markings in shades of brown important taxonomically. Thorax ca. 1.5× longer than wide in lateral view. Tibial spurs absent. Empodium pulvilliform. Two tarsal claws present. Abdomen ca. 2× longer than thorax, 3× longer than head. Male terminalia inverted. Male terminalia with posterior margin of tergite IX usually with median notch (Fig. 23G); posterior margin may bear medial sclerotized projection (Fig. 28G); darkened in most species (Fig. 20F). Gonocoxite bifid (Fig. 6) with long ventral branch and short dorsal branch; additional branch of gonocoxite (= mesal lobe) present in majority of species (Fig. 6), very variable, including asymmetry. If asymmetrical, right and left mesal lobes drawn in corresponding position on plates. Gonostylus bifid (Fig. 6) with medial and lateral branches. Clasper of gonostylus very variable. Lobe of gonostylus ca. as long as clasper. Lobe of gonostylus bifid, smaller pigmented branch termed lobule (Fig. 6). Sheath of aedeagus variable, as in other Chioneinae, projecting ventrally to aedeagus and almost detached form aedeagus. Female terminalia with curved cercus. Hypogynial valve blade-shaped, variable in length. Genital fork (Fig. 7B) without membranous area, posterior region concave similar to other Chioneinae such as Erioptera Meigen. Two oval-shaped spermathecae present, longer than wide (Fig. 7A).

3.3. Species descriptions

3.3.1. Amphineurus (Rhamphoneurus) alexanderi sp. nov.

http://zoobank.org/BEE1DE9C-DAFF-4AE8-9702-76AE6264BB37

Material examined. Holotype: ♂, Chile, Llanquihue, Carelmapu [41°44' S 73°40' W], Coast of Canal de Chacao, 18-III-1957, Peña (USNM)*. Paratypes: 1 ♂, Chile, Chiloé Is., Dalcahue [42°22′ S 73°39′ W], 10/12-II-1954, Peña (USNM)*; 1 ♂, Chile, Chiloé Is., Aulen [42°2′ S 74°1′ W], 8-II-1952, Peña (USNM)*.

Etymology. The species is named after C.P. Alexander, the remarkable Tipulomorpha expert who described all the species of this subgenus, among many others.

Diagnosis. This species is distinguished by a curved R₂₊₃, large markings only near R₂, r-m longer than basal deflection of R₅, and R₂₊₃₊₄ longer than R₂₊₃. Furthermore, the species has characteristic male terminalia with a trapezoidal-shaped spur and symmetrical tip of left mesal lobe.

Description. Wing length 5.68 mm, width 1.61 mm. — Coloration: General coloration dark brown. Rostrum and palpus dark brown. First segment of antenna yellowish-brown, remaining segments dark brown. Head dark brown. Abdomen brown. — Head (dorsal view Fig. 8B, ventral view Fig. 8A): terminal segments of antenna missing, as indicated by asterisks on Fig. 8B. Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape shorter and thinner than pedicel. Thorax: Wing (Fig. 8C) almost clear of markings, except strong marking covering R₂; veins near fork of bM (Fig. 8D) faded; r-m similar in length to basal deflection of R₄; M₁₂ shorter than basal deflection of M₁; R₂₃+₄ longer than R₂₃, more than twice length of R₅. — Male terminalia (Fig. 8E): Male tergite IX slightly darkened at posterior margin, with wide V-shaped median notch; posterolateral lobes triangular. Ventral branch of gonocoxite with one side with a few long setae, while other side with many short setae. Dorsal branch of gonocoxite half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half length of lobe of gonostylus.

Figure 7. A spermathecae of Amphineurus (Rhamphoneurus) caleuchus sp. nov. (dorsal view); B genital fork of Amphineurus (Rhamphoneurus) glabristylatus Alexander (ventral view).
narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch wide club-shaped. Mesal lobes of gonocoxite asymmetrical; left mesal lobe with flat posterior margin; right mesal lobe elongated and curved. Sheath of aedeagus straight, darkened halfway of length; apex extended into narrowed tip and additional nearly rectangular preapical spur.

Remarks. Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) insanus* Alexander. This species resembles *A. (R.) insanus* but differs mainly in the attachment of m-cu, length of r-m, shape of thorax, mesal lobe and sheath of aedeagus.

3.3.2. **Amphineurus (Rhamphoneurus)** *amorimi* sp. nov.

http://zoobank.org/0FAC83AC-F5B5-40B2-BC5F-D09D0B46B1B9

Material examined. **Holotype:** ♂, Chile, Chiloé Is., Dalcahue [42°22′S 73°39′W], 10/12-II-1954, Peña (USNM)*. **Paratypes:** 2 ♂, Chile, Chiloé Is., Chaiten [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM)*; 1 ♂, Chile, Caramavida [37°40′S 73°20′W], 1000–1300 m, 1-I-1954, Peña (USNM)*. — **Additional material:** CHILE. 3 [sex unknown], Chiloé Is., Dalcahue [42°22′S 73°39′W], 10/12-II-1954, Peña (USNM); 1 [sex unknown], Chiloé Is., Chaiten [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM).
Etymology. The species is named after Dalton de Souza Amorim, a remarkable Brazilian Diptera expert.

Diagnosis. This species is distinguished by only a marking near $R_2$ and $R_{2+3}$ as long as $R_{2+3}$. Furthermore, the species has characteristic male terminalia with a triangular spur and an atrophied tip of the left mesal lobe.

Description. Wing length 5.60 mm, width 1.68 mm. — Coloration: General coloration dark brown. Thorax dark brown, pleura brown. Scutum without stripes. Halter dark brown with knob pale. Coxae light brown and legs brown. — Head (dorsal view Fig. 9B, ventral view Fig. 9A): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape thinner.
than pedicel, terminal flagellomere longer than penultimate. — **Thorax** (lateral view Fig. 9E, dorsal view Fig. 9F): Thorax with long setae, notably on coxae. Anatergite taller than katatergite. Halter with dilated knob. Wing (Fig. 9D) almost clear of markings, except for strong marking covering R₃; veins near fork of bM (Fig. 9C) faded; M₁₂ shorter than basal deflection of M₁; R₂₃₄ similar in length to R₂₃. — **Male terminalia** (Fig. 9G): Male tergite IX slightly darkened at posterior margin, with wide V-shaped median notch; posterolateral lobes nearly triangular. Ventral branch of gonocoxite slender. Dorsal branch of gonocoxite shorter than half length of ventral branch, setose on distal tip. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half-length of lobe of gonostylus, about as wide as stem. Clasper of gonostylus with differently shaped branches: lateral branch long and straight; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical; left mesal lobe straight and narrow, with small bend at distal section; right mesal lobe curved, elongated. Sheath of aedeagus straight; apical half darkened, with short, curved triangular projection.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) insanus* Alexander. This species resembles *A. (R.) morphi* sp. nov. but differs mainly in the chaetotaxy of the thorax and gonocoxite, length of R₂₃₄ and shape of the mesal lobe.

### 3.3.3. Amphineurus (Rhamphoneurus) anchoralis sp. nov.

http://zoobank.org/87DAED38-FF8B-48DC-8957-1F60A208E890

**Material examined.** Holotype: ♂, Chile, Arauco, Nahuelbuta, Con- tulmo, Palo Botado [37°39′S 73°55′W], 12-II-1952, Peña (USNM)*.  
Paratypes: 1 ♂ and 1 [sex unknown], Chile, Arauco, Nahuelbuta [37°46′S 72°59′W], 2-II-1953, Peña (USNM); 1 [sex unknown], Chile, Chiloé Is., Rio Coluco [42°6′S 73°55′W], 30-I-1952, Peña (USNM).

**Etymology.** The word *anchoralis* is Latin for “of the anchor”. The term refers to the shape of the projection of the male 9th tergite, which resembles an anchor.

**Diagnosis.** The species is distinguished by the absence of markings near R₄, and R₂₃ shorter than R₃. Furthermore, this species has a long vertical spur on the sheath of aedeagus, male tergite IX has a distinctive ridge projection, mesal lobes absent and the posterior margin of the male tergite IX is mostly unpigmented.

**Description.** Wing length 6.15 mm, width 1.86 mm. — **Coloration:** General coloration yellowish brown. Rostrum and palpus dark brown. First segments of antenna pale, remaining segments dark yellow. Head brownish-black. Eyes black. Thorax yellowish-brown, pleura pale. Scutum without stripes. Halter pale with knobs light orange. Coxae and legs brownish. — **Head** (dorsal view Fig. 10B, ventral view Fig. 10A): Rostrum bifurcated with short appendices; first palpal segment as long as terminal segment, second palpal segment dilated; scape thinner than pedicel, terminal flagellomere dilated, antenna with several long setae. — **Thorax** (lateral view Fig. 10E, dorsal view Fig. 10F): a few setae on prescutum. Division line of laterotergite almost vertical; anatergite as tall as katatergite. Halter with dilated knob. Wing (Fig. 10D) almost clear of markings, except marking covering R₃; veins near fork of bM (Fig. 10C) faded; M₁₂ longer than basal deflection of M₁; R₂₃₄ at least twice as long as R₂₃. — **Male terminalia** (Fig. 10G): Male tergite IX with posterior margin with irregular ridges; median U-shaped notch with straight projection in middle; tip of projection also ridge shaped; projection and surrounding area darkened. Ventral branch of gonocoxite inclined laterally. Dorsal branch of gonocoxite half-length of ventral branch, atrophied and pointed medially; both branches setose. Lobe of gonostylus with pointed lobule, shaped similar to folded leaf. Clasper of gonostylus with differently shaped branches: lateral branch long, bent near middle; medial branch curved into stub. Mesal lobes absent. Sheath of aedeagus darkened on apical half, angulated, with long pointed projection perpendicular to remainder of sheath.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) sanus* Alexander and *A. (R.) insanus* Alexander. This species resembles *A. (R.) sanus* but differs mainly in M₁₂, shape of projection in male tergite IX, ventral branch of gonocoxite and spur of sheath of aedeagus.

### 3.3.4. Amphineurus (Rhamphoneurus) anfractus sp. nov.

http://zoobank.org/species/B1BD9665-44D9-4EF5-922E-72B470EE85F9

**Material examined.** Holotype: ♂, Chile, Arauco, Nahuelbuta, Butamalal [37°49′S 73°14′W], 1100–1400 m, 23/31-I-1954, Peña (USNM)*.  
Paratypes: 1 [sex unknown], Chile, Arauco, Nahuelbuta [37°46′S 72°59′W], 5/10-II-1953, Peña (USNM); 1 ♂, Chile, Chiloé Is., Rio Coluco [42°6′S 73°55′W], 30-I-1952, Peña (USNM).

**Etymology.** The word *anfractus* in Latin is for “winding”. The term refers to the winding or sinuous aspect of the anal vein and crossvein m-cu.

**Diagnosis.** This species is distinguished by sinuose crossvein m-cu and anal vein. Furthermore, this species is characterized by the male terminalia with a folded medial branch of the clasper of gonostylus and a cylindrical left mesal lobe.

**Description.** Wing length 7.84 mm, width 2.48 mm. — **Coloration:** General coloration dark brown. Thorax dark brown, pleura brown. Scutum with one black stripe.
ter pale with knobs ochreous. Coxae brownish yellow and legs dark brown. — **Head** (dorsal view Fig. 11B, ventral view Fig. 11A): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape as thick as pedicel, pedicel constricted at base; terminal flagellomere shorter than penultimate, antenna with long setae. — **Thorax** (lateral view Fig. 11E, dorsal view Fig. 11F). Division line of laterotergite very sinuous; anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 11D) with several marks, including faint markings on A₁ and near tip of R₃, marking highlighting m-cu, markings on Rs, R₂+₃+₄ and R₂+₃, small, strong marking at tip of R₁ and large, strong marking covering R₂; veins near fork of bM (Fig. 11C) faded; A₁ sinuose; M₁₂ longer than basal deflection of M₁; R₂+₃+₄ longer than R₂+₃. — **Male terminalia** (Fig. 11G): Male
tergite IX darkened along posterior margin; posterior margin flat, with short median U-shaped notch; postero-lateral lobes nearly rectangular with slightly visible shallow emarginations. Ventral branch of gonocoxite wide. Dorsal branch of gonocoxite long, almost as long as ventral branch, with long setae on distal tip. Lobe of gonostylus with rounded lobule; lobule wider than long, shorter than half-length of lobe of gonostylus, twice as wide as stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical, both similarly shaped with flat posterior margins; left mesal lobe narrower. Sheath of aedeagus slightly curved on distal half, with tip narrowed, darkened almost along entire length.

**Remarks.** Some specimens of this new species were previously identified by C.P. Alexander as *A. (R.) glabristylatus* Alexander and some as *A. (R.) nothofagetorum* Alexander. This species resembles *A. (R.) chiloeanus* but
differs mainly in the form of the anal vein, shape of male tergite IX, sheath of aedeagus and mesal lobe.

3.3.5. *Amphineurus (Rhamphoneurus) apiculatus* Alexander, 1968

*Amphineurus (Rhamphoneurus) apiculatus* Alexander, 1968: 29 (description, fig. 15: male terminalia).

Material examined. Holotype: ♂, Chile, Chaihuin [39°56′S 73°34′W], 810 m, 20-III-1955, Peña, Holotype 12206 (USNM) [part of specimen pinned and part on slide prepared by C.P. Alexander].

Diagnosis. This species is distinguished by having vein bM forking into M$_{2+3+4}$ and M$_{1}$, absence of markings on R$_{2}$ and insertion of r-m desclerotized. Furthermore, the species has distinctive male terminalia with a curved sheath of aedeagus and both mesal lobes similar in length with vertically directed tiny tips.

Figure 12. *Amphineurus (Rhamphoneurus) apiculatus* Alexander. A head (dorsal view); B detail of wing; C wing; D thorax (lateral view); E thorax (dorsal view); F male tergite IX (dorsal view) and remainder of male terminalia (lateral view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; egonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hit, halter; k, knob of halter; kepm, katepimeron; kepst, katepisternum; ktg, katatergite; lms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; mtlst, metanepistemum; mtep, metepterygium; mttg, mediotergite; mtkepst, metakatepisternum; mtn, metanotum; p, posterior basalar; patg, paratergite; ppbn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; scctl, scutellum; t9, male tergite IX.
Redescription. Wing length 6.26 mm, width 1.82 mm. — **Coloration:** General coloration yellowish brown. Rostrum and palpus brown. First segment of antenna yellow, remainder segments brown. Head brownish gray. Eyes black. Thorax yellowish-brown, pleura brown. Scutum without stripes. Halter yellow. Coxae light yellow and legs dark yellow. Abdomen yellowish-brown. — **Head** (Fig. 12A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape as thick as pedicel; terminal flagellomere longer than penultimate. — **Thorax** (lateral view Fig. 12D, dorsal view Fig. 12E): Thorax with several long setae. Anatergite shorter than katatergite. Halter with very dilated knob. Wing (Fig. 12C) without distinct markings; veins near fork of bM (Fig. 12B); R₂, partially faded; bM forking into M₁ and M₁₂; R₂₃ shorter than R₂₄. — **Male terminalia** (Fig. 12F): Male tergite IX darkened on posterior margin, with wide V-shaped median notch; posterolateral lobes obtuse. Ventral branch of gonocoxite wide. Dorsal branch of gonocoxite half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half-length of lobe of gonostylus, wider than stem. Clasper of gonostylus with similarly shaped branches: lateral branch rounded; medial branch curved. Mesal lobes of gonostylus asymmetrical both similarly shaped, with pointed tip; right mesal lobe longer and narrower. Sheath of aedeagus elongated, curved, darkened only at tip. — **Remarks.** This species resembles *A. (R.) nonnullus* Alexander but differs mainly in the fork of bM, shape of male tergite IX, clasper of gonostylus and mesal lobe.  

### 3.3.6. *Amphineurus (Rhamphoneurus) billinghami* sp. nov.

http://zoobank.org/2ECE6B5C-0149-47B9-AAAC-02BA5AC-D4E93

**Material examined. Holotype:** ♂, Chile, Chiloé Is., Osorno, Pucatrihue [40°32′S 73°42′W], 10/12-IV-1968, Peña (USNM)*. **Paratype:** 1 ♂, Osorno, Pucatrihue [40°32′S 73°42′W], 10/12-IV-1968, Peña (USNM)*.  

**Etymology.** The species is named after Zacariah D. Billingham, a great expert of Australian craneflies.  

**Diagnosis.** This species is characterized by crossevein m-cu uniformly inserted at the fork of bM. Furthermore, this species is characterized by the male terminalia with a curved sheath of aedeagus, a small right mesal lobe and the most setose ventral branch of gonocoxite. The thorax is also distinguishable by a narrow knob of the halter and katepisternum longer than the meron.  

**Description.** Wing length 6.45 mm, width 1.66 mm. — **Coloration:** General coloration dark brown. Rostrum and palpus dark brown. First segments of the antenna yellow, remainder dark yellow. Head dark brown. Eyes blackish gray. Thorax dark brown, pleura pale. Scutum without stripes. Halter pale with knob dark yellow. Coxae brownish yellow and legs yellowish-brown. — **Head** (dorsal view Fig. 13B, ventral view Fig. 13A): Rostrum bifurcated with short appendices; first palpal segment as long as terminal segment; scape thicker than pedicel, terminal flagellomere as long as penultimate. — **Thorax** (lateral view Fig. 13E, dorsal view Fig. 13F): Thorax with long setae, particularly on scutum. Anatergite as tall as katatergite. Halter with narrow knob. Wing (Fig. 13D) without clear markings; veins near fork of bM (Fig. 13C) visible; m-cu inserted at fork of bM; M₁₂ longer than basal deflection of M₁; R₂, faded; R₂₃ shorter than R₂₄. — **Male terminalia** (Fig. 13G): Male tergite IX with small V-shaped median notch; posterolateral lobes rounded. Ventral branch of gonocoxite expanded on distal tip. Dorsal branch of gonocoxite nearly half-length of ventral branch; both branches extremely setose. Lobe of gonostylus rounded, longer than wide; longer than half-length of lobe of gonostylus; lobule wider than stem. Clasper of gonostylus with similarly shaped branches; lateral branch rounded; medial branch obtuse. Mesal lobes of gonocoxite asymmetrical, both pointed, with several setae on posterior margin; right mesal lobe shorter. Sheath of aedeagus claw-shaped, curved halfway, darkened only on tip.  

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) nullus* Alexander. This species resembles *A. (R.) theischingeri* sp. nov. but differs mainly in attachment of m-cu, setae concentration in gonocoxite, shape of male tergite IX, and mesal lobe.  

### 3.3.7. *Amphineurus (Rhamphoneurus) caleuchus* sp. nov.

http://zoobank.org/20726C16-A333-4FB5-A226-BC73116D14FF

**Material examined. Holotype:** ♂, Chile, Chiloé Is., Ancud [41°52′S 73°48′W], 23-1-1932, Peña (USNM)*. **Paratypes:** 1 ♂, Chiloé Is., Auxar [42°9′S 73°30′W], 6/15-1-1952, Peña (USNM); 2 ♂, Chile, Chiloé Is., Chaiten [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM)*.  

**Additional material: CHILE.** 1 ♂, Chiloé Is., Auxar [42°9′S 73°30′W], 6/15-1-1952, Peña (USNM); 1 ♂, Chiloé Is., Nahuelbuta [37°46′S 72°59′W], 5/10-II-1953, Peña (USNM) [slide mounted specimen prepared by the authors].  

**Etymology.** The word *caleuchus* refers to the Chilean myth of Caleuche, a sentient ghost ship of the Chiloé islands (Febles 2009). The species is named after this myth due to holotype and the majority of specimens being from the Chiloé islands.  

**Diagnosis.** The species is distinguished by a darkened distal quarter of the wing, R₂₃ shorter than the basal deflection of M₁. Furthermore, the species is characterized by the distinctive clasper of
gonostylus with setae on medial branch, curved lateral branch and male tergite IX with a very shallow notch.

**Description.** Wing length 6.50 mm, width 2.05 mm. — **Coloration:** General coloration dark brown. Rostrum and palpus dark brown. First segments of antenna yellow, remaining segments brownish-yellow. Head brown. Eyes black. Thorax yellowish-brown, pleura yellowish brown. Scutum with three dark brown stripes. Halter pale with knob ochreous. Coxae yellow and legs brown. Abdomen dark brown. — **Head** (dorsal view Fig. 14B, ventral view Fig. 14A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape as thick as pedicel; terminal flagellomere as long as penultimate; antenna with long setae. — **Thorax** (lateral view Fig. 14E, dorsal view Fig. 14F): Thorax with short setae, some organized in rows on prescutum. Division line of laterotergite almost vertical; anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 14D) almost clear of markings, except for faint markings on R2 and tip of R1; distal quarter of wing darkened; veins near fork of bM (Fig. 14C) faded; M1,2 shorter than basal de-
Figure 14. Amphineurus (Rhamphoneurus) calechus sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; cer, cercus; cgonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kep, kephemeron; kept, katepisternum; ktg, katatergite; lms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; ms lobe, mesal lobe of gonocoxite; mtnepst, metanepisternum; mtep, metepimeron; mtg, mediatergite; mtkept, metatokastergite; mta, metanotum; p, posterior basalar; patg, paratergite; prpn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; scatl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
flection of M\textsubscript{1}; R\textsubscript{2+3+4} as long as R\textsubscript{2+3}. — **Female terminalia** (Fig. 14H): Female tergite IX longer and narrower than tergite X; cercus thin and bent at right angle. — **Male terminalia** (Fig. 14G): Male tergite IX with sinuose posterior margin. Ventral branch of gonocoxite slightly inclined laterally, with long setae on lateral margin. Dorsal branch of gonocoxite reduced. Lobe of gonostylus with rounded lobule; lobule longer than wide, shorter than half-length of lobe of gonostylus, and narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straightened, slightly bent towards tip; medial branch curved, club-shaped with concentration of setae. Mesal lobes symmetrical, rounded at posterior margin with bump on side. Sheath of aedeagus angulated with two bends; darkened almost along entire length.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) nothofagetorum* Alexander. This species resembles *A. (R.) stigmaticus* sp. nov. but differs mainly in markings on the sheath of aedeagus, length of R\textsubscript{2+3+4}, and shape of lobe of gonostylus, cercus and mediatergite.

### 3.3.8. *Amphineurus (Rhamphoneurus) chiloanus* Alexander, 1969

*Amphineurus (Rhamphoneurus) chiloanus* Alexander, 1969: 374 (description, fig. 37: wing, fig. 38: male terminalia).

**Material examined.** Holotype: ♂, Chile, Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1954, Peña, Holotype 12553 (USNM) [part of specimen pinned and part in slide prepared by C.P. Alexander]. **Paratypes:** 1 ♂, Chile, Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1954, Peña (USNM). **Additional material:** CHILE. 1 [sex unknown], Chile, Chiloé Is. Ancud [41°52′S 73°48′W], 23-1-1952, L. Guzman (USNM); 1 ♂, Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1954, Peña (USNM)*.

**Diagnosis.** The species is distinguished by having m-cu strongly sinuous, straight anal vein and beginning of M\textsubscript{1+2} retains sclerotized section. Furthermore, this species has a characteristic sheath of aedeagus with a long basal spur, mesal lobe is very reduced and male tergite IX is remarkable by its rounded posteralateral lobes.

**Redescription.** Wing length 7.37 mm, width 2.14 mm. — **Coloration:** General coloration light brown, Rostrum and palpus dark brown. First segment of antenna light yellow, remaining segments dark yellow. Head dark brown. Eyes black. Thorax light brown, pleura dark yellow. Scutum with three brown stripes. Halter brownish yellow with knob ochreous. Coxae brownish yellow and legs yellowish-brown. — **Head** (dorsal view Fig. 15B, ventral view 15A): terminal segments of antennae missing, as indicated by asterisks. Rostrum bifurcated with short appendices; first palpal segment longer than terminal segment; scape as thick as pedicel, pedicel constricted at base. — **Thorax** (lateral view Fig. 15E, dorsal view Fig. 15F): Division line of laterotergite very sinuous; Anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 15D) with some markings, including faint markings on A\textsubscript{1} and Rs; markings highlighting m-cu, r-m, fork of Rs and R\textsubscript{2+3+4}; distal quarter of wing slightly darkened, with large, strong marking covering R\textsubscript{2} and last segment of R\textsubscript{1}; veins near fork of bM (Fig. 15C) faded; R\textsubscript{2+3+4} longer than R\textsubscript{2+3}. — **Male terminalia** (Fig. 15G): Male tergite IX faintly darkened at posterior margin, with wide, shallow U-shaped median notch; posterolateral lobes rounded. Dorsal branch of gonocoxite poorly developed, shorter than half-length of ventral branch. Lobe of gonostylus with elongate lobule, longer than wide, longer than half-length of lobe of gonostylus, but narrower than stem. Clasper with differently shaped branches: lateral branch straight and long; medial branch curved, wide club-shaped. Mesal lobes atrophied, similar in shape to dorsal branch of gonocoxite. Sheath of aedeagus long and sinuose, darkened almost entire length, with pointed perpendicular spur projecting at end of straight section.

**Remarks.** Some specimens of this species were misidentified by C.P. Alexander as *A. (R.) nothofagetorum* Alexander. This species resembles *A. (R.) glabristylatus* Alexander but differs mainly in attachment of m-cu, length of cercus, shape of male tergite IX, sheath of aedeagus and mesal lobe.

### 3.3.9. *Amphineurus (Rhamphoneurus) extraordinarius* Alexander

*Amphineurus (Rhamphoneurus) extraordinarius* Alexander, 1939: 280 (description); Alexander, 1947 (fig. 18: wing).

**Remarks.** The species *Amphineurus extraordinarius* was originally included in the subgenus *Amphineurus*. In all the phylogenetic analysis we performed (see below in this paper), this species is the sister-group of the other species of *Rhamphoneurus*, and we think it should be transferred to this subgenus. This new subgenus placement is therefore based on the phylogenetic analysis, but specimens of *A. extraordinarius* were not available when the analysis was finalized. Consequently, a redescription of the species is not possible at this time.

### 3.3.10. *Amphineurus (Rhamphoneurus) deceps* sp. nov.

http://zoobank.org/CE7F253C-DC89-4DAC-95B7-1C4D89095BB9

**Material examined.** Holotype: ♂, Chile, Chiloé Is. Ancud [41°52′S 73°48′W], 23-1-1952, Peña (USNM)*. **Paratypes:** 1 ♂, Chile, Arauco, Nahuelbuta, Butamalal [37°29′S 73°14′W], 1100–1400 m, 23/31-I-1954, Peña (USNM); 1 ♀, Chile, Chiloé Is., Castro [42°28′S 73°46′W], 5/8-II-1954, Peña (USNM)*. — **Additional material:** CHILE. 1 [sex unknown], Chiloé Is. Ancud [41°52′S 73°48′W],
The word *deceptus* is Latin for “deceived”. The term refers to the fact that specimens of this new species were misidentified by Alexander as two different species.

**Diagnosis.** This species is distinguished by the darkened distal quarter of the wing, and bM is uniform. Furthermore, the species is characterized by the distinctive male terminalia with clasper of gonostylus with setae on medial branch and straightened base of sheath of aedeagus.

**Description.** Wing length 6.50 mm, width 2.06 mm. — **Coloration:** General coloration dark brown. Rostrum and palpus brownish-black. First segments of the antenna yellow, remaining segments dark yellow. Head dark brown. Eyes gray. Thorax dark brown, pleura yellowish-brown. Scutum with three dark brown stripes. Halter brownish-yellow. Coxae brownish yellow and legs yellowish-brown. Abdomen dark brown. — **Head** (dorsal view Fig. 16B, ventral view Fig. 16A): Rostrum bifurcated with long appendices; first palpal segment shorter than...
**Figure 16.** Amphineurus (Rhamphoneurus) deceptus sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; cer, cercus; cgonst, clasper of gonostylus; cx, coxa; gnx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kepm, katepimeron; kepst, katepisternum; ktg, katatergite; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; mtsnst, metanepisternum; mtepm, metepimeron; mttg, mediotergite; mtkpepst, metakatepisternum; mtn, metanotum; p, posterior basalar; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; scctl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
terminal segment; scape as thick as pedicel; terminal flagellomere as long as penultimate; antenna with long setae.

— **Thorax** (lateral view Fig. 16E, dorsal view Fig. 16F): Prescutum with short setae. Division line of laterial tegron almost vertical; anatergite as tall as katatergite. Halter with dilated knob. Wing (Fig. 16D) with several markings, including faint markings on A1 and Rs, marking at tip of R1, markings highlighting m-cu, R2+3+4 and R2+3, and strong marking covering R4; distal quarter of wing darkened, veins near fork of bM (Fig. 16C) faded; M1+2 shorter than basal deflection of M1; R2+3 shorter than half-length of R2+3, — **Female terminalia** (Fig. 16H): Female tergite IX longer and as wide as tergite X; cercus slightly curved dorsad. — **Male terminalia** (Fig. 16G): Male tergite IX with V-shaped median notch. Ventral branch of gonocoxite with long setae on lateral margin. Dorsal branch of gonocoxite half-length of ventral branch. Lobe of gonostylus with rounded lobe; lobule longer than wide, shorter than half-length of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch long and straight, bent near tip; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical; left mesal lobe with more rectangular posterior projection; right mesal lobe rounded with bump on side. Sheath of aedeagus straightened, bent towards tip, darkened almost along entire length.

**Remarks.** Some specimens of this new species were previously identified by C.P. Alexander as *A. (R.) glabri-stylatus* Alexander and some as *A. (R.) nothofagetorum* Alexander. This species resembles *A. (R.) nothofageto-rum* but differs mainly in the shape of the branches of the clasper, male tergite IX, mesal lobes and sheath of aedeagus.

### 3.3.11. Amphineurus (Rhamphoneurus) *falcatus* sp. nov.

http://zoobank.org/571A228A-E186-439F-AD46-342D236F-3B4A

**Material examined.** Holotype: ♂, Chile, Osorno, Bahia Mansa {40°35′S 73°44′W}, South of Pucotrihue, 12-IV-1968, Peña (USNM)*.

**Paratypes:** 1 {sex unknown}; Chile, Chiloé Is., Aulen {42°2′S 74°1′W}, 8-II-1952, L.P. Guzman (USNM); 1, ♂, Chile, Chiloé Is., Aulen {42°2′S 74°1′W}, 8-II-1952, Peña (USNM)*; 1 {sex unknown}; Chile, Chiloé Is., Aulen, Duhatao {41°58′S 74°02′W}, 6-8-11-1952, Peña (USNM)*.

**Etymology.** The word *falcatus* is Latin for “armed with scythes”. This name is in reference to the sheath of aedeagus, which resembles a scythe.

**Diagnosis.** This species is distinguished by absence of markings near R2 and R2+3+4 longer than R2+3. Furthermore, this species has distinctive male terminalia with a curved sheath of aedeagus, only the right mesal lobe folded, and the longest lobule of the subgenus, as long as the remainder of the lobe of gonostylus.

**Description.** Wing length 6.08 mm, width 1.86 mm. — **Coloration:** General coloration blackish brown. Thorax blackish brown, pleura gray. Scutum without stripes. Halter ochreous. Coxae brownish yellow and legs dark brown. — **Head** (dorsal view Fig. 17B, ventral view Fig. 17A): Rostrum bifurcated with short appendices; first palpal segment as long as terminal segment; scape as thick as pedicel; last flagellomere as long as penultimate.

— **Thorax** (lateral view Fig. 17E, dorsal view Fig. 17F): Division line of laterotergite sinuous and almost vertical; anatergite as tall as katatergite. Halter with long dilated knob; length of knob half-length of stem of halter. Wing (Fig. 17D) without distinctive markings; veins near fork of bM (Fig. 17C) visible; R2 faded; r-m shorter than M2+3; R5+6+7 at least 2.3× longer than half deflection of R2+3; R2+3+4 longer than R2+3, — **Male terminalia** (Fig. 17G): Male tergite IX darkened along posterior margin, with wide V-shaped median notch; posterolateral lobes nearly triangular, obtuse at apex. Ventral branch of gonocoxite expanded on distal tip. Dorsal branch of gonocoxite shorter than half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wide, shorter than half-length of lobe of gonostylus and wider than stem. Clasper of gonostylus with similarly shaped branches: lateral branch rounded; medial branch oblong. Mesal lobes of gonocoxite asymmetrical; left mesal lobe straightened and pointed; right mesal lobe bent at right angle. Sheath of aedeagus curved, darkened for most of length.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) nullus* Alexander. This species resembles *A. (R.) nullus* but differs mainly in the attachment of m-cu, shape of male tergite IX, prescutum and left mesal lobe.

### 3.3.12. Amphineurus (Rhamphoneurus) *fuscifusus* Alexander, 1929a, nomen dubium

*Amphineurus (Rhamphoneurus) fuscifusus* Alexander, 1929a: 190 (description).

**Remarks.** *Amphineurus (R.) fuscifusus* Alexander is the only species of the genus in which the male is unknown. Additionally, the only identified specimen is the female holotype, currently housed in the Natural History Museum (BMNH). The absence of an associated male specimen and its terminalia is problematic because this is an important source of characters and taxonomic data. Lacking a well-defined diagnosis in the description, the erection of the new species was proposed mostly due to subtle differences in coloration. The only considerable difference in coloration in *A. (R.) fuscifusus* is the pale halter, which is unlike the yellowish brown halter of *A. (R.) nothofageto-rum* Alexander.
Some morphological data described by Alexander (1929a) suggest this specimen shares similar features with clade 33 (Fig. 32). The presence of long setae on the antenna, “weak branches” in medial veins, three stripes on the scutum, and a marking near the fork of Rs are features shared between the holotype and this group. The holotype was collected in the same location as the holotype of *A. (R.)* nothofagetorum Alexander. However, the absence of males added to the fact that there is only a single known specimen makes the synonymization or identity confirmation of the species problematic. For these reasons, we define *Amphineurus (Rhamphoneurus)* fuscifusus Alexander as nomen dubium.

### 3.3.13. *Amphineurus (Rhamphoneurus)* glabristylatus Alexander, 1929a

*Amphineurus (Rhamphoneurus) glabristylatus* Alexander, 1929a: 188 (description, fig. 224: male terminalia).
Figure 18. *Amphineurus* (*Rhamphoneurus*) *glabristylatus* Alexander. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: **aed sh**, sheath of aedeagus; **anatg**, anatergite; **anepm**, anepimeron; **anepst**, anepisternum; **apr**, anteropronotum; **cer**, cercus; **cgonst**, clasper of gonostylus; **cx**, coxa; **goncx**, gonocoxite; **hlt**, halter; **hyp val**, hypogynial valve; **k**, knob of halter; **kepm**, katepimeron; **kepst**, katepisternum; **ktg**, katatergite; **l ms**, left mesal lobe of gonocoxite; **lgonst**, lobe of gonostylus; **mr**, meron; **mtanepst**, metanepisternum; **mtepm**, metepimeron; **mt**-**kepst**, metakatepisternum; **mtn**, metanotum; **p**, posterior basalar; **patg**, paratergite; **pprn**, postpronotum; **presct**, prescutum; **r ms**, right mesal lobe of gonocoxite; **sct**, scutum; **sctl**, scutellum; **st**, sternite; **tg**, tergite; **t9**, male tergite IX.
Material examined. Paratypes: 1 ♂, Chile, Chiloé Is., Mechuque Is. [42°18′S 73°16′W], 23-XII-1926, F. & M. Edwards (USNM); 1 ♂, Chile, Peulla [41°55′S 72°1′W], 12/13-XII-1926, F. & M. Edwards (USNM); 1 ♂, Chile, Chiloé Is., Mechuque Is. [42°18′S 73°16′W], 23/26-XII-1926, F. & M. Edwards (USNM)*. — Additional material: ARGENTINA. 1 ♂, Bariloche, Rio Negro [41°7′S 71°24′W], XI-1926, R. & E. Shannon (USNM). CHILE. 1 ♂, 1 ♀ and 4 [sex unknown], Arauco, Nahuelbuta, Butamalal [37°49′S 73°14′W], 1100–1400 m, 23/31-I-1954, Peña (USNM); 2 ♂ and 1 ♂, Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 200–1400 m, 23/31-I-1954, Peña (USNM); 1 ♂ and 1 ♂ [sex unknown], Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 200–1400 m, 23/31-I-1954, Peña (USNM); 1 ♂ and 1 ♂ [sex unknown], Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 12/20-II-1954, Peña (USNM); 1 [sex unknown], Chiloé Is., Chepu [42°2′S 74°1′W], 4/6-IV-1968, Peña (USNM); 1 [sex unknown], Arauco, Nahuelbuta, Butamalal [37°49′S 73°14′W], 1400 m, 23/31-I-1954, Peña (USNM); 1 ♂ and 1 ♂ [sex unknown], Arauco, Nahuelbuta, Butamalal [37°49′S 73°14′W], 1400 m, 23/31-I-1954, Peña (USNM); 1 ♂ and 1 ♂ [sex unknown], Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 1200–1400 m, 23/31-I-1954, Peña (USNM); 1 ♂, Chiloé Is., Aulen [42°2′S 74°1′W], 4/II-1952, L. P. Guzman (USNM); 1 ♂, Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 21/25-II-1958, Peña (USNM); 1 [sex unknown], Malleco, Rio Blanco [38°23′S 71°48′W], 27-II-1951, Peña (USNM); 1 [sex unknown], Arauco, Nahuelbuta, Butamalal [37°46′S 72°59′W], 1200–1400 m, 23/31-I-1954, Peña (USNM); 1 ♂, Malleco, Rio Blanco [38°23′S 71°48′W], 27-II-1951, Peña (USNM); 1 ♂, Malleco, Rio Blanco [38°23′S 71°48′W], 15-I-1952, L. P. Guzman (USNM); 1 [sex unknown], Osorno, Pucotrihue [40°32′S 73°42′W], 10/12-I-1948, Peña (USNM); 2 ♂ and 1 ♂ [sex unknown], Arauco, Nahuelbuta, Pichinahuel [37°48′S 73°02′W], 1400–1600 m, 21/25-II-1953, Peña (USNM)*; 2 ♂, Arauco, Nahuelbuta, Butamalal [37°49′S 73°14′W], 1100–1400 m, 23/31-I-1954, Peña (USNM)*; 1 ♂, Arauco, Nahuelbuta, Caramavida [37°40′S 73°20′W], 1200–1400 m, 9-I-1954, Peña (USNM); 1 ♂, Chiloé Is., Aucar [42°9′S 73°30′W], 15-I-1952, L. P. Guzman (USNM); 1 [sex unknown], Osorno, Pucotrihue [40°32′S 73°42′W], 10/12-I-1948, Peña (USNM)*; 1 ♂, Chile, Chiloé Is., Mechuque Is. [42°18′S 73°16′W], 27-II-1951, Peña (USNM); 1 [sex unknown], Malleco, Rio Blanco, Nahuelbuta [38°23′S 71°48′W], 14/20-II-1954, Peña (USNM); 1 ♂, Chile, Chiloé Is., Mechuque Is. [42°18′S 73°16′W], 27-II-1951, Peña (USNM); 1 ♂, Chile, Osorno, Pucochihue [42°2′S 74°1′W], 1-II-1952, Peña (USNM); 2 ♂, Chile, Chaihuin [39°5′S 73°34′W], 810 m, 20-III-1955, Peña (USNM). — Additional material: ARGENTINA. 1 ♂, R. & E. Shannon (USNM). — Remarks. We could not examine the holotype, but the paratypes were examined. This species resembles A. (R.) chiloaeus Alexander but differs mainly in the attachment of m-cu, length of female cercus, shape of male tergite IX, sheath of aedeagus and mesal lobe.

3.3.14. Amphineurus (Rhamphoneurus) immaculatus sp. nov.

Material examined. Holotype: ♂, Chile, Osorno, Pucotrihue [40°32′S 73°42′W], 10/12-IV-1968, Peña (USNM)*. Paratypes: 1 ♂, Chile, Osorno, Bahia Mansa [40°35′S 73°44′W], South of Pucotrihue, 12-IV-1968, Peña (USNM); 2 ♂, Chile, Chaihuin [39°5′S 73°34′W], 810 m, 20-III-1955, Peña (USNM). — Additional material: CHILE. 2 ♂ and 1 ♂ [sex unknown], Chiloé Is., Chepu [42°2′S 74°1′W], 1-3-II-1952, Peña (USNM)*; 2 [sex unknown], Chiloé Is., Aulen [42°2′S 74°1′W], 1-II-1952, Peña (USNM)*; 1 ♂, Malleco, Rio Blanco [38°23′S 71°48′W], 1050 m, 27-III-1951, Peña (USNM)*.

Diagnosis. This species is distinguished by the sinuous anal vein and straight m-cu. Furthermore, this species has characteristic male terminalia with a folded medial branch of the clasper of gonostylus without setae, an unpigmented male tergite IX, sinuous sheath of aedeagus, and the right mesal lobe is longer than the left mesal lobe, with a cylindrical apical tip.

Redescription. Wing length 7.07 mm, width 2.22 mm. — Coloration: General coloration brown. Rostrum and palpus dark brown. First segments of antenna light yellow, remaining segments dark yellow. Head dark brown. Eyes gray. Thorax brown, pleura yellowish brown. Three reddish-brown stripes on scutum. Halter dark yellow with knob ochreous. Coxae yellowish-brown and legs brown. Abdomen brown. — Head (ventral view Fig. 18A, dorsal view Fig. 18B): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape as broad as pedicle, terminal flagellomere as long as penultimate; antenna with several long setae. — Thorax (lateral view Fig. 18E, dorsal view Fig. 18F). Anatergite taller than katatergite; prescutum with long setae (Fig. 29B); mediostergite with notch on posterior margin (Fig. 18F). Halter with dilated knob. Wing (Fig. 18D) with several markings, including subtle markings on A4; slightly darkened areas along medial veins; markings on Rs, R2-5, and m-cu; strong markings on R2 and near end of R1; veins near fork of bm (Fig. 18C) faded; M3, longer than basal deflection of M1, R2-5 longer than R2-5. — Female terminalia (Fig. 18H): Female tergite IX shorter, narrower than tergite X. Hypogynial valves slender, longer than cercus. Cercus strongly curved dorsal. — Male terminalia (Fig. 18G): Male tergite IX unpigmented, with shallow median U-shaped notch, with additional shallow sublateral notch on either side creating sinuous appearance. Ventral branch of gonocoxite wide. Dorsal branch of gonocoxite long, almost as long as ventral branch. Lobe of gonostylus with rounded lobule; lobule as long as wide, shorter than half-length of lobe of gonostylus, wider than stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical, both elongated and slightly rounded at posterior margin; left mesal lobe wider than right. Sheath of aedeagus straight, dark almost entire length.

Etymology. The word immaculatus is Latin for “unstained”. The term refers to the fact that the wing has no pterostigma or markings.

Diagnosis. This species is characterized by having sinuous cross-vein m-cu and no markings near R2. Furthermore, the species is characterized by male terminalia with a curved sheath of aedeagus and right mesal lobe similar in shape, but longer than left one, and scutellum rounded in lateral view.

Description. Wing length 6.22 mm, width 1.74 mm. — Coloration: General coloration brownish-yellow. Rostrum and palpus dark brown. First segments of antenna
Figure 19. Amphineurus (Rhamphoneurus) immaculatus sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteroprnotum; cer, cercus; cgonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kepm, katepimeron; kepst, katepisternum; ktg, katepisternum; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; ms lobe, mesal lobe of gonocoxite; mtanepst, metanepisternum; mtepm, metepimeron; mtg, mediotergite; mtkepst, metakatepisternum; mtn, metanotum; p, posterior basalare; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; scl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
yellow, remaining segments dark yellow. Head dark brown. Eye black. Thorax brownish yellow, pleura pale. Scutum without stripes. Halter brownish-yellow. Coxae brownish yellow and legs brown. Abdomen blackish brown. — **Head** (dorsal view Fig. 19B, ventral view Fig. 19A): Rostrum bifurcated with short appendices; first palpal segment as long as terminal segment; scape as thick as pedicel; terminal flagellomere as long as penultimate. — **Thorax** (lateral view Fig. 19E, dorsal view Fig. 19F): Short setae on prescutum. Division line of laterotergite almost vertical; anatergite taller than katatergite. Halter with dilated knob. Wing (Fig. 19D) without markings; veins near fork of bM (Fig. 19C) visible; M₁+₂ as long as M₁; R₂+₃+₄ longer than R₂+₃; wing very light on pigmentation, almost translucent. — **Female terminalia** (Fig. 19H): Female tergite IX shorter and as wide as tergite X; cercus slightly curved dorsad. — **Male terminalia** (Fig. 19G): Male tergite IX slightly darkened along posterior margin, with deep V-shaped median notch; posterolateral lobes of triangular shape with rounded tips. Ventral branch of gonocoxite expanded in distal tip. Dorsal branch of gonocoxite half-length of ventral branch, curved ventrally. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half-length of lobe of gonostylus, wider than stem. Clasper of gonostylus with similarly shaped branches: lateral branch rounded, narrow; medial branch wider, oblong. Mesal lobes of gonocoxite symmetrical; both straight with slightly bent pointed tip. Sheath of aedeagus curved halfway and darkened only near tip.

**Remarks.** Some specimens of this new species were previously identified by C.P. Alexander as *A. (R.) sanus* Alexander, some as *A. (R.) nullus* Alexander and some as *A. (R.) billighami* Alexander. This species resembles *A. (R.) alexanderi* sp. nov. but differs mainly in attachment of m-cu, setae concentration in gonocoxite, shape of male tergite IX and right mesal lobe.

### 3.3.15. Amphineurus (Rhamphoneurus) insanus Alexander, 1952

*Amphineurus (Rhamphoneurus) insanus* Alexander, 1952: 111 (description, fig. 9: male terminalia).

**Material examined.** Holotype: ♂, Chile, Malleco, Rio Blanco [38°23′S 71°48′W], 5/27-III-1951, Peña, Holotype 9362 (USNM) [part of specimen pinned and part on slide prepared by C.P. Alexander]. — **Additional material: CHILE.** 3 [sex unknown], Llanquihue, Carelmapu [41°44′S 73°40′W], Coast North of Canal de Chacao, 18-III-1957, Peña (USNM); 2 [sex unknown], Chiloé Is., Chiloe [42°28′S 72°32′W], 5/8-II-1954, Peña (USNM); 1 [sex unknown], Chiloe Is., Chepu [42°2′S 74°1′W], 10/14-III-1952, Peña (USNM); 1 ♂, Llanquihue, Carelmapu [41°44′S 73°40′W], Coast North of Canal de Chacao, 18-III-1957, Peña (USNM); 1 ♂, Chiloe Is., Aulen [42°2′S 74°1′W], 8-II-1952, Peña (USNM)*.

**Diagnosis.** This species is distinguished by only a dark spot near R₂ and a curved m-cu. Furthermore, this species has a remarkable thorax which is as long as tall and characteristic male terminalia with the sheath of aedeagus with a rectangular spur and the tip of left mesal lobe curved.

**Redescription.** Wing length 6.75 mm, width 2.04 mm. — **Coloration:** General coloration brown. Rostrum and palpus brown. First segment of antenna yellow, remaining segments dark yellow. Head brown. Eyes black. Thorax brown, pleura yellowish brown. Scutum with one black stripe. Halter pale with knob ochreous. Coxae and legs yellowish-brown. — **Head** (dorsal view Fig. 20A): Rostrum bifurcated with short appendices; first palpal segment slightly shorter than terminal segment; scape thinner than pedicel, terminal flagellomere longer than penultimate. Thorax (lateral view Fig. 20D, dorsal view Fig. 20E): Thorax wider than long, with compressed aspect, with larger membranous area. Anepisternum and anepimerum short; prothorax wide. Anatergite as tall as katatergite. Halter with dilated knob. Wing (Fig. 20C) almost clear of markings, except for strong marking covering R₂; veins near bM fork faded (Fig. 20D); M₁+₂ shorter than basal deflection of M₁; r-m at least 1.25× longer than combined length of M₁₁ and basal deflection of M₁; R₂+₃ longer than R₂+₃+₄. — **Male terminalia** (Fig. 20F): Male tergite IX faintly darkened on posterior margin, with wide V-shaped median notch; posterolateral lobes nearly triangular. Dorsal branch of gonocoxite poorly developed. Lobe of gonostylus with rounded lobule, longer than wide; lobule longer than half-length of lobe of gonostylus, as wide as stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch ovoid. Mesal lobes of gonocoxite asymmetrical; left mesal lobe elongated, curved; right mesal lobe with sharp turn. Sheath of aedeagus straight, darkened on distal portion, narrowed at tip with preapical, nearly rectangular extension.

**Remarks.** This species resembles *A. (R.) alexanderi* sp. nov. but differs mainly in attachment of m-cu, length of r-m, shape of thorax, mesal lobe and sheath of aedeagus.

### 3.3.16. Amphineurus (Rhamphoneurus) morphyi sp. nov.

http://zoobank.org/3200E7A9-C1D2-4CE0-9A73-BD-C7F670061B

**Material examined.** Holotype: ♂, Chile, Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1968, Peña (USNM)*. — **Paratypes:** 1 ♂, Chile, Osorno, Pucotrihue [40°32′S 72°32′W], 60 m, 10-III-1958, Peña (USNM)*; 1 ♂, Chile, Chiloé Is., Dalcahue [42°2′S 73°39′W], 10/12-II-1954, Peña (USNM)*; 1 ♂, Chile, Arauco, Nahuelbuta, Butamal [37°49′S 73°14′W], 1100–1400 m, 23/31-I-1954, Peña (USNM)*. — **Additional material: CHILE.** 1 ♂ and 1 [sex unknown], Chiloé Is., Chiloe [42°28′S 72°32′W], 5/8-II-1954, Peña (USNM); 1 [sex unknown], Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1968, Peña (USNM).
Etymology. The species is named after Charles Morphy D. dos Santos, a Brazilian entomologist who studied the taxonomy and biogeography of South American Diptera.

Diagnosis. This species is distinguished by only a marking near R₂, and basal deflection of R₃ shorter than half-length of R₂₊₃₊₄. Furthermore, the species is characterized by male terminalia with a triangular spur, tip of left mesal lobe bent, tip of right mesal lobe slightly curved and cercus thin and abruptly curved.

Description. Wing length 5.63 mm, width 1.74 mm. — Coloration: General coloration yellowish brown. Rostrum and palpus dark brown. First segments of antenna yellow,
Figure 21. *Amphineurus (Rhamphoneurus) morphyi* sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropreronotum; cer, cercus; cgont, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kepm, katepimeron; kepst, katepisternum; ktg, katatergite; l ms, left mesal lobe of gonocoxite; lgont; lobe of gonostylus; mr, meron; ms lobe, mesal lobe of gonocoxite; mtnepst, metanepternum; mtep, metepimeron; mtep, metepisternum; mtkp, metakatepisternum; mtn, metanotum; p, posterior basalar; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sc, scutum; scl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
remaining segments dark yellow. Head blackish brown. Eyes black. Thorax yellowish-brown, pleura yellow. Scutum with one reddish-brown stripe. Halter dark yellow with knob pale. Rostrum and legs brownish yellow. Abdome dark brown. — **Head** (dorsal view Fig. 21B, ventral view Fig. 21A): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape thinner than pedicel; terminal flagellomere as long as penultimate. — **Thorax** (lateral view Fig. 22E, dorsal view Fig. 22F). Laterotergite almost triangular, anatergite taller than katatergite. Halter with dilated knob. Wing (Fig. 22D) without distinctive markings; veins near fork of bM (Fig. 22C) faded; m-cu inserted distal to fork of bM; M_{2+3} shorter than basal deflection of M_{1+2}; R_{2+3} longer than R_{3+4}. — **Male terminalia** (Fig. 22G): Male tergite IX slightly darkened on distal margin, with wide median U-shaped notch; posterolateral lobes rounded. Dorsal branch of gonocoxite half-length of ventral branch; both branches setose. Lobe of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical; both mesal lobes with sharp, 90° turn on posterior end; right mesal lobe significantly longer than left. Sheath of aedeagus curved, darkened only at distal portion.

**Remarks.** This species resembles *A. (R.) apiculatus* Alexander but differs mainly in the fork of bM, shape of male tergite IX, clasper of gonostylus and mesal lobe.

### 3.3.17. Amphineurus (Rhamphoneurus) nonnullus Alexander, 1967

*Amphineurus* (*Rhamphoneurus*) *nonnullus* Alexander, 1967: 491 (description); Alexander, 1968: fig. 17 (male terminalia).

**Material examined.** Holotype: ♂, Chile, Chiloé Is., Aucar [42°9'S 73°30'W], 6/15-I-1952, Peña, Holotype 9619 (USNM); *Additional material:* CHILE. 1 [sex unknown], Chiloé Is., Chaiten [42°58'S 72°32'W], 5/8-II-1954, Peña (USNM)*; 1 [sex unknown], Chiloé Is., Chepu [42°2'S 74°1'W], 1/3-II-1952, Peña (USNM)*.

**Diagnosis.** This species is distinguished by R_{3} without a dark spot and the beginning of M_{1} desclerotized. Furthermore, the species has a distinctive male terminalia with a curved sheath of aedeagus with the branches of the clasper of different sizes.

**Redescription.** Wing length 5.58 mm, width 1.71 mm. — **Coloration:** General coloration brownish-yellow. Rostrum and palpus dark brown. First segment of antennae yellow, remaining segments brownish-yellow. Head brown. Eyes grayish black. Thorax brownish yellow, pleura grayish-yellow. Scutum with one brownish-black stripe. Halter light yellow. Coxae light yellow; legs yellow-brown. Abdome yellowish brown. — **Head** (dorsal view Fig. 22B, ventral view Fig. 22A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape thinner than pedicel, terminal flagellomere as long as penultimate. — **Thorax** (lateral view Fig. 22E, dorsal view Fig. 22F). Laterotergite almost triangular, anatergite taller than katatergite. Halter with dilated knob. Wing (Fig. 22D) without distinctive markings; veins near fork of bM (Fig. 22C) faded; m-cu inserted distal to fork of bM; M_{2+3} shorter than basal deflection of M_{1+2}; R_{2+3} longer than R_{3+4}. — **Male terminalia** (Fig. 22G): Male tergite IX slightly darkened on distal margin, with wide median U-shaped notch; posterolateral lobes rounded. Dorsal branch of gonocoxite half-length of ventral branch; both branches setose. Lobe of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, club-shaped. Mesal lobes of gonocoxite asymmetrical; both mesal lobes with sharp, 90° turn on posterior end; right mesal lobe significantly longer than left. Sheath of aedeagus curved, darkened only at distal portion.

**Remarks.** This species resembles *A. (R.) apiculatus* Alexander but differs mainly in the fork of bM, shape of male tergite IX, clasper of gonostylus and mesal lobe.

### 3.3.18. Amphineurus (Rhamphoneurus) nothofagetorum Alexander, 1929a

*Amphineurus* (*Rhamphoneurus*) *nothofagetorum* Alexander, 1929a: 187 (description, fig. 90; wing, fig. 223: male terminalia).

**Material examined.** Paratypes: 1 ♂, Argentina, Nahuel Huapi, Lago Correntoso [40°42'S 71°39'W], 2-XXI-1926, R.C. Shannon (USNM)*; 1 ♂, Chile, Puerto Varas [41°19’S 72°59’W], 16-XII-1926, F. & M. Edwards (USNM)*. — **Additional material:** CHILE. 1 ♂, 1 ♀ and 2 [sex unknown], Arauco, Nahuelbuta [37°49’S 72°59’W], 5/II-1953; Peña (USNM)*; 2 [sex unknown], Cautin, Villarica [39°27’S 71°54’W], 30 Km. NE, 1/30-I-1965, Peña (USNM)*; 2 ♀ and 1 [sex unknown], Chiloé Is., Ancud [41°52’S 73°48’W], 23-I-1952, L.P. Guzman (USNM)*; 1 ♀ and 1 [sex unknown], Chiloé Is., Chaiten [42°58’S 72°32’W], 5/8-II-1954, Peña (USNM)*; 1 [sex unknown], Arauco, Nahuelbuta, Butamalal [37°49’S 73°14’W], 1100–1400 m, 23/31-I-1954, Peña (USNM)*; 1 [sex unknown], Cordillera las Raices [38°31’S 71°28’W], West of Lonquimay, 1500 m, 28-XII-1967, Peña (USNM).

**Material examined.** Holotype: ♂, Argentina, Nahuel Huapi, Lago Correntoso [40°42’S 71°39’W], 2-XXI-1926, R.C. Shannon (USNM)*; 1 ♂, Chile, Puerto Varas [41°19’S 72°59’W], 16-XII-1926, F. & M. Edwards (USNM)*. — **Additional material:** CHILE. 1 ♂, 1 ♀ and 2 [sex unknown], Arauco, Nahuelbuta [37°49’S 72°59’W], 5/II-1953; Peña (USNM)*; 2 [sex unknown], Cautin, Villarica [39°27’S 71°54’W], 30 Km. NE, 1/30-I-1965, Peña (USNM)*; 2 ♀ and 1 [sex unknown], Chiloé Is., Ancud [41°52’S 73°48’W], 23-I-1952, L.P. Guzman (USNM)*; 1 ♀ and 1 [sex unknown], Chiloé Is., Chaiten [42°58’S 72°32’W], 5/8-II-1954, Peña (USNM)*; 1 [sex unknown], Arauco, Nahuelbuta, Butamalal [37°49’S 73°14’W], 1100–1400 m, 23/31-I-1954, Peña (USNM)*; 1 [sex unknown], Cordillera las Raices [38°31’S 71°28’W], West of Lonquimay, 1500 m, 28-XII-1967, Peña (USNM).
Diagnosis. The species is distinguished by the darkened distal quarter of the wings and \( M_{1+2} \) longer than half the length of the basal deflection of \( M_1 \). Furthermore, the species has a distinctive clasper of gonostylus with setae on medial branch and straightened lateral branch.

Redescription. Wing length 6.10 mm, width 1.92 mm.

— Coloration: General coloration brown. Rostrum and palpus dark brown. First segments of antenna brownish yellow, remaining segments brown. Head dark brown. Eyes black. Thorax reddish-brown, pleura brown. Three brown stripes on scutum. Halter yellowish brown. Coxae and legs brownish yellow. Abdomen brown. — Head (ventral view Fig. 23A, dorsal view Fig. 23B): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape narrower than pedicel, terminal flagellomere as long as penultimate; antenna with several long setae. — Thorax (lateral view Fig. 23E, dorsal view Fig. 23F): Anatergite as tall as katatergite. Halter with dilated knob. Wing (Fig. 23D) with several

Figure 22. Amphineurus (Rhamphoneurus) nonnullus Alexander. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; cgonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hlt, halter; k, knob of halter; kepml, katepimeron; kepst, katepisternum; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; mtanepst, metanepisternum; mtepm, metepimeron; mttg, metatergite; mtkepst, metakatepisternum; mtn, metanotum; p, posterior basalar; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; sctl, scutellum; t9, male tergite IX.
Figure 23. Amphineurus (Rhamphoneurus) nothofagetorum Alexander. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; cer, cercus; cgonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; halter; hyp val, hypogynial valve; k, knob of halter; kep, katepimeron; kepst, katepisternum; ktg, katatergite; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; mtanepst, metanepisternum; mtepm, metepimeron; mtg, mediatergite; mtkepst, metakatepisternum; mtn, metanotum; p, posterior basalarc; patg, paratergite; ppnt, postpronotum; presct, prescutum; rms, right mesal lobe of gonocoxite; sc, scutum; scl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
markings, including faint markings on A₁ and beginning of Rs; markings highlighting m-cu and R₁,₂,₃,₄; stronger markings on R₁ and near tip of R₂; distal quarter of wing darkened; veins near fork of bM (Fig. 23C) faded; M₁,₂ longer in length than half-length of basal deflection of M₁; R₁,₂,₃,₄ about same length as R₂,₃.

— Female terminalia (Fig. 23H): Female tergite IX longer and wider than tergite X. Hypogynial valve slender, longer than cercus. Cercus strongly curved dorsad. — Male terminalia (Fig. 23G): Male tergite IX unpigmented, with shallow curved median U-shaped notch. Dorsal branch of gonocoxite long, ca. 0.75 times length of ventral branch. Lobe of gonostylus with rounded lobule, lobule as long as wide, shorter than half-length of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches; lateral branch straight, medial branch curved, club-shaped, with concentration of setae. Mesal lobes of gonocoxite asymmetrical, both with posterior margin rounded with bump on side; right mesal lobe wider. Sheath of aedeagus angulated, darkened through half its length.

Remarks. We could not observe the holotype, but the paratypes were examined. This species resembles A. (R.) deceptus sp. nov. but differs mainly in shape of branches of the clasper, male tergite IX, mesal lobes and the sheath of the aedeagus.

3.3.19. Amphineurus (Rhamphoneurus) nullus Alexander, 1967

Amphineurus (Rhamphoneurus) nullus Alexander, 1967: 492 (description); Alexander, 1968: fig. 11 (wing), fig. 16 (male terminalia).

Material examined. Holotype: ♀, Chile, Chiloé Is., Aulen, Duhatao [41°58′S 74°02′W], 6/8-II-1952, Peña, Holotype 9620 (USNM) [part of specimen pinned and part in slide prepared by C.P. Alexander].

Allotype: 1 ♂, Chile, Chiloé Is., Aulen, Duhatao [41°58′S 74°02′W], 6/8-II-1952, Peña (USNM). — Additional material: CHILE. 1 ♂ and 2 [sex unknown], Osorno, Bahia Mansa [40°35′S 73°44′W], South of Pucotrihue, 12-IV-1968, Peña (USNM); 1 ♂, Pucotrihue [40°32′S 73°42′W], 10-60 m, 12-III-1955, Peña (USNM); 1 ♂, Chiloé Is., Aulen [42°2′S 74°1′W], 15-1-1952, Peña (USNM)*; 1 ♂, Chiloé Is., Aulen [42°2′S 74°1′W], 8-II-1952, L.P. Guzman (USNM)*; 1 ♂, Pucotrihue [40°35′S 73°44′W], 10-60 m, 12-III-1955, Peña (USNM)*; 1 [sex unknown], Chiloé Is., Aulen, Duhatao [42°2′S 74°1′W], 14-II-1952, Peña (USNM)*; 1 [sex unknown], Chiloé Is., Chepu [42°2′S 74°1′W], 4/6-IV-1952, Peña (USNM)*; 1 ♂, Osorno, Bahia Mansa [40°35′S 73°44′W], South of Pucotrihue, 12-IV-1968, Peña (USNM)*.

Diagnosis. The species is distinguished by absence of markings near R₁, cross-vein m-cu attached to M₁,₂ and length of r-m twice length of basal deflection of R₁. Furthermore, the species has distinctive male terminalia with a curved sheath of aedeagus, both mesal lobes with folded tips and branches of clasper of gonostylus of similar sizes. The species further distinguished also by the combination of sheath of aedeagus with small markings and male tergite IX pigmented. Furthermore, females of this species have the thickest cercus of the subgenus.

Redescription. Wing length 6.32 mm, width 1.76 mm. — Coloration: General coloration brownish-yellow. Rostrum and palpus dark brown. First segment of antenna yellow, remaining segments dark yellow. Head grayish brown. Eyes black. Thorax brownish yellow, pleura brownish-yellow. Scutum without stripes. Halter yellow. Coxae and legs yellow. Abdomen brown. — Head (dorsal view Fig. 24B, ventral view Fig. 24A): Head wide, rostrum bifurcated with long appendices, first palpal segment longer than dilated terminal segment; scape as thick as pedicel, terminal flagellomere longer than penultimate.

— Thorax (lateral view Fig. 24E, dorsal view Fig. 24F): Anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 24D) clear, without distinct markings; veins near fork of bM (Fig. 24C) visible; R₁ partially faded; crossvein r-m longer than basal deflection of R₁; M₁,₂ about same length of M₁,₂; R₁,₂,₃,₄ longer than R₂,₃.

— Female terminalia (Fig. 24H): Female tergite X longer than tergite IX, tergite IX wider. Cercus thick, longer than hypogynial valves, slightly curved dorsad. — Male terminalia (Fig. 24G): Male tergite IX darkened on posterior margin, with V-shaped median notch. Ventral branch of gonocoxite expanded in distal section. Dorsal branch of gonocoxite half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wider, than half length of lobe of gonostylus, wider than stem. Clasper of gonostylus with similarly shaped branches: lateral branch nearly oval: medial branch distally flattened, narrowed at margin. Mesal lobes of gonocoxite asymmetrical, both hook-shaped; left mesal lobe narrower. Sheath of aedeagus angulated, darkened only at tip.

Remarks. This species resembles A. (R.) falcatus sp. nov. but differs mainly in the attachment of m-cu, shape of male tergite IX, prescutum and left mesal lobe.

3.3.20. Amphineurus (Rhamphoneurus) oosterbroekii sp. nov.

http://zoobank.org/E2E9C3EF-604A-4BA3-A41C-A3B3F-0B75A38

Material examined. Holotype: ♀, Chile, Chiloé Is., Chaiten [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM)*. Paratypes: 1 ♂, Chile, Chiloé Is., Chaiten [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM)*; 1 ♂, Chile, Llanquihue, Carelmapu [41°44′S 73°40′W], Coast of Canal de Chacao, 18-III-1957, Peña (USNM)*; 1 ♂, Chile, Osorno, Bahia Mansa [40°35′S 73°44′W], South of Pucotrihue, 12-IV-1968, Peña (USNM)*.

Etymology. The species is named after Pjotr Oosterbroek, an important Tipulomorpha expert.

Diagnosis. This species is distinguished by only a dark spot on R₁, basal deflection of R₁ as long as r-m, and M₁,₂ longer than basal deflection of M₁. Furthermore, this species is characterized by male terminalia with sheath of
Figure 24. Amphineurus (Rhamphoneurus) nullus Alexander. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, antero pronotum; cer, cercus; cgonst, clasper of gonostylus; coxa, coxa; goncx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kepm, katepimeron; kepst, katepisternum; ktg, katatergite; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; mtnanepst, metanepistemum; mtep, metepimeron; mti, mediotergite; mk, metakatepisternum; mtn, metanotum; p, posterior basalare; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; sctl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
aedeagus with a triangular spur and the tip of sheath inclined.

**Description.** Wing length 5.47 mm, width 1.68 mm. — **Coloration:** General coloration brown. Rostrum and palpus brown. First segments of antenna yellow, remaining segments yellowish brown. Head brown. Abdomen yellowish brown. — **Head** (dorsal view Fig. 25B, ventral view Fig. 25A): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape narrower than pedicel; terminal flagellomere dilated. — **Thorax:** Wing (Fig. 25D) almost clear of markings,
except for marking on R5; veins near fork of bM (Fig. 25C) faded; M1+2 2.5× longer than basal deflection of M1; R2+3+4 longer than R3+3. — Male terminalia (Fig. 25E): Male tergite IX slightly darkened along posterior margin, with deep median U-shaped notch. Ventral branch of gonocoxite slender, very long, setose on distal tip. Lobe of gonostylus with rounded lobe; lobule longer than wide, shorter than half of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch curved. Mesal lobes of gonocoxite asymmetrical; left mesal lobe curved; right mesal lobe short with sharp turn. Sheath of aedeagus straightened, with wide rectangular projection; darkened only near tip.

Remarks. Specimens of this new species were previously identified by C.P. Alexander as A. (R.) insanus Alexander. This species resembles A. (R) podenaspi sp. nov. but differs mainly in the length of r-m, concentration of setae on gonocoxite, shape of male tergite IX and right mesal lobe.

3.3.21. Amphineurus (Rhamphoneurus) podenaspi sp. nov.

http://zoobank.org/species/BFE444EF-6A92-4F3E-9F39-A74E7D4483EE

Material examined. Holotype. ♂, Chile, Arauco, Nahuelbuta, Pichinau [37°48′S 73°02′W], 1400–1600 m, 12-20-II-1953, Peña (USNM)*. Paratypes: 1 ♂, Chile, Chiloé Is., Rio Coloco [42°6′S 73°55′W], 30-I-1952, Peña (USNM)*; 1 ♂, Chile, Llanquihue, Carelmapu [41°44′S 73°40′W], Coast North of Canal de Chacao, 18-III-1957, Peña (USNM)*. Additional material: CHILE. 1♀ and 1 [sex unknown], Chiloé Is., Dalcahue [42°22′S 73°39′W], II-1954, Peña (USNM); 1 [sex unknown], Chiloé Is., Aulen [42°2′S 74°1′W], 8-II-1952, L.P. Guzman (USNM); 1 [sex unknown], Chiloé Is., Chaiten [42°58′S 72°32′W], 5-8-II-1954, Peña (USNM).

Etymology. The species is named after Sigitas Podenas, a skilled Tipulomorpha expert.

Diagnosis. This species is distinguished by only a dark spot on R3 and basal deflection of R5 longer than r-m. Furthermore, this species is characterized by male terminalia with sheath of aedeagus with a spur, tip of right mesal lobe curved downwards and sheath of aedeagus with rounded spur.

Description. Wing length 5.73 mm, width 1.83 mm. — Coloration: General coloration brownish-yellow. Ros- trum and palpus brown. First segment of antenna yellow, remaining segments dark yellow. Head dark brown. Eyes black. Thorax brownish yellow, pleura pale. Contrasting golden setae on prescutum. Scutum without stripes. Halter brownish-yellow. Coxae and legs brownish yellow. Abdomen dark brown. — Head (dorsal view Fig. 26B, ventral view Fig. 26A): Rostrum bifurcated with long appendices; first palpal segment shorter than terminal segment; scape thinner than pedicel; flagellomeres gradually reducing in length, resulting in shorter terminal flagellomeres. — Thorax (lateral view Fig. 26E, dorsal view Fig. 26F): Thorax with several setae, including long setae on prescutum. Anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 26D) almost clear of markings, except for strong marking covering R3; veins near fork of bM (Fig. 26C) faded; M1+2 longer than basal deflection of M1; R2+3+4 shorter than both R3+3, and basal deflection of R5. — Female terminalia (Fig. 26H): Female tergite IX longer and wider than tergite X; cercus shorter than hypogynial valves, curved dorsad. Both cercus and hypogynial valve very slender. — Male terminalia (Fig. 26G): Male tergite IX slightly darkened along posterior margin, with wide V-shaped median notch. Ventral branch of gonocoxite inclined medially in distal tip. Dorsal branch of gonocoxite nearly half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half-length of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, club shaped. Mesal lobes of gonocoxite asymmetrical; left mesal lobe short with sideways projection; right mesal lobe curved. Sheath of aedeagus straightened, with rounded projection; darkened only on tip.

Remarks. Specimens of this new species were previously identified by C.P. Alexander as A. (R.) insanus Alexander. This species resembles A. (R) oosterbroekii sp. nov. but differs mainly in the length of r-m, concentration of setae on the gonocoxite, shape of male tergite IX and right mesal lobe.

3.3.22. Amphineurus (Rhamphoneurus) rutristylus Alexander, 1968

Amphineurus (Rhamphoneurus) rutristylus Alexander, 1968: 30 (description, fig. 18: male terminalia).

Material examined. Holotype: ♂, Chile, Valdivia, Enco [39°53′S 72°8′W], 1400–1600 m, 6-III-1955, Peña, Holotype 12226 (USNM) [part of specimen pinned and part in slide prepared by C.P. Alexander]. Additional material: CHILE. 1♀ and 1 [sex unknown], Arauco, Nahuelbuta [37°46′S 72°59′W], 13/20-II-1958, Peña (USNM)*; 1 [sex unknown], Caramavida [37°40′S 73°20′W], 1000–1300 m, 1/6-I-1954, Peña (USNM). Caramuvida [37°40′S 73°20′W], 1000–1300 m, 1/6-I-1954, Peña (USNM)*; 1 [sex unknown], Lonquimay West, Cordillera las Raices [38°31′S 71°28′W], 1500 m, 25-XII-1968, Peña (USNM); 1 ♂, Chile, Llanquihue, Carelmapu [42°58′S 72°32′W], 5/8-II-1954, Peña (USNM)*.

Diagnosis. This species is distinguished by a dark spot near R3 and m-cu inserted at fork of bM. Furthermore this species is distinguished by the male terminalia with the lobule with two rounded margins forming heart shape, sheath of aedeagus is straight but without spurs and the mesal lobes are symmetrical, with slender, bare and slightly curved tips.
Figure 26. *Amphineurus* (*Rhamphoneurus*) *podenasi* sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: **aed sh**, sheath of aedeagus; **anatg**, anatergite; **anepm**, anepimeron; **anepst**, anepisternum; **aprn**, anteropronotum; **cer**, cercus; **cgonst**, clasper of gonostylus; **cx**, coxa; **goncx**, gonocoxite; **hlt**, halter; **hyp val**, hypogynial valve; **k**, knob of halter; **kepm**, katepimeron; **kepst**, katepisternum; **ktg**, katatergite; **l ms**, left mesal lobe of gonocoxite; **lgonst**, lobe of gonostylus; **mr**, meron; **ms lobe**, mesal lobe of gonocoxite; **mtanepst**, metanepisternum; **mtepm**, metepimeron; **mtg**, mediotergite; **mtkepst**, metakatepisternum; **mnt**, metanotum; **p**, posterior basalare; **patg**, paratergite; **pprn**, postpronotum; **presct**, prescutum; **r ms**, right mesal lobe of gonocoxite; **sct**, scutum; **sctl**, scutellum; **st**, sternite; **tg**, tergite; **t9**, male tergite IX.
Redescription. Wing length 6.87 mm, width 2.00 mm.

**Coloration:** General coloration dark brown. Rostrum and palpus dark brown. First segment of antenna light yellow, remaining segments dark yellow. Head brown. Eyes black. Thorax yellowish-brown, pleura light brown. Scutum without stripes. Halter brownish-yellow. Coxae brownish yellow and legs dark brown. Abdomen dark brown. — **Head** (Fig. 27A): Rostrum bifurcated with long appendices; first palpal segment slightly shorter than terminal segment; scape thicker than pedicel, terminal flagellomere as long as penultimate, antenna with numerous setae. — **Thorax** (lateral view Fig. 27D, dorsal view Fig. 27E): Thorax with several long setae. Anatergite taller than katatergite. Halter with dilated knob. Wing (Fig. 27C) almost clear of markings, except for marking covering R_2_; veins near bM (Fig. 27B) faded; m-cu inserted at fork of bM; M_{1+2} shorter than basal deflection of M_1; R_{2+3+4} longer than R_{2+3}. — **Male terminalia** (Fig. 27F):
Male tergite IX faintly darkened at posterior margin, with wide V-shaped median notch; posterolateral lobes nearly triangular; ventral branch slender, with concentration of setae on distal tip. Dorsal branch of gonocoxite shorter than half length of ventral branch. Lobe of gonostylus with heart-shaped lobule, more than twice as wide as lobe of gonostylus. Clasper of gonostylus with differently shaped branches: lateral branch straight; medial branch curved, oblong-shaped. Mesal lobes of gonocoxite symmetrical, both with narrow, elongate, straight extremity. Sheath of aedeagus straight, slightly bent near tip, darkened at distal one-third.

Remarks. Some specimens of this species were misidentified by C.P. Alexander as A. (R.) insanus Alexander. This species resembles A. (R.) glabristylatus Alexander but differs mainly in the attachment of m-cu, wing markings, shape of male tergite IX and mesal lobe.

3.3.23. Amphineurus (Rhamphoneurus) sanus Alexander, 1929a

Amphineurus (Rhamphoneurus) sanus Alexander, 1929a: 189 (description, fig. 90: wing, fig. 225: male terminalia).

Material examined. Holotype: 1 ♂, Chile, Chiloé Is., Ancud [41°52′S 73°48′W], 10/12-IV-1968, Peña (USNM); 1 ♂, Chiloé Is., Dalcahue [42°22′S 73°39′W], II-1954, Peña (USNM); 1 ♂, Chiloé Is., Chepu [42°2′S 74°1′W], 4/6-IV-1968, Peña (USNM); 1 ♂, Chiloé Is., Aulen [42°2′S 74°1′W], 8-II-1952, Peña (USNM)*.

Diagnosis. This species is distinguished by a subtle spot on R₂. Furthermore, this species has a remarkable sheath of aedeagus with a long horizontal spur, male tergite IX with a distinctive rectangular projection, mesal lobes absent and posterior margin of male tergite IX pigmented.

Redescription. Wing length 5.86 mm, width 1.90 mm. — Coloration: General coloration dark brown. Rostrum and palpus dark brown. Antenna yellow, with apical segments slightly darker. Head brown. Eyes black. Thorax brown dark, pleura brown. Scutum without stripes. Halter brownish-yellow. Coxae brownish yellow and legs dark brown. Abdomen dark brown. — Head (dorsal view Fig. 28B, ventral view Fig. 28A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment, terminal palpal segment dilated; scape narrower than pedicel; terminal flagellomere shorter and thicker than penultimate; antenna with several long setae. — Thorax (lateral view Fig. 28E, dorsal view Fig. 28F): Anatergite taller than katatergite. Prothorax wide, prescutum with a few short setae. Halter with dilated knob. Wing (Fig. 28D) almost clear of markings, except subtle marking on R₂; veins around fork of bM (Fig. 28C) faded; M₁,₂ longer than basal deflection of M₁; R₂,₃,₄ longer than R₂,₃,₄.

— Male terminalia (Fig. 28G): Male tergite IX darkened on posterior margin, with wide median U-shaped notch; rectangular projection in two points on either side of extension; posterior margin with projection flat. Dorsal branch of gonocoxite very reduced. Lobe of gonostylus with pointed lobule shaped similar to folded leaf. Clasper of gonostylus with differently shaped branches: lateral branch long, bent around middle; medial branch curved into short stub. Mesal lobes absent. Sheath of aedeagus dark along almost entire length, angulated with smooth curvature, with setae on distal portion of lateral margin, as well as large distal horizontal lateral projection.

Remarks. Some specimens were misidentified by C.P. Alexander as A. (R.) nullus Alexander. The rostrum of the holotype is longer than in the other species of this subgenus. This species resembles A. (R.) anchoralis sp. nov. but differs mainly in M₁,₂ shape of projection on male tergite IX, ventral branch of gonocoxite and spur of sheath of aedeagus.

3.3.24. Amphineurus (Rhamphoneurus) stigmaticus sp. nov.

http://zoobank.org/species/9AD-19D8-E-C3EE-46E1-9298-4AAEA89CAEDAC

Material examined. Holotype: 1 ♂, Chile, Llanquihue, Hornohuina [41°25′S 72°37′W], XII-1968, Peña (USNM)*. Paratypes: 1 ♀ and 1 [sex unknown], Chile, Arauco, Nahuelbuta [37°46′S 72°59′W], 5/10-II-1953, Peña (USNM); 1 ♀, Chile, Chiloé Is., Chepu [42°2′S 74°1′W], 4/6-IV-1968, Peña (USNM)*. — Additional material: CHILE. 2 ♂, Pucoritrihue [40°32′S 73°42′W], 60 m, 10-III-1955, Peña (USNM); 1 male and 1 ♀, Chiloé Is. Ancud [41°52′S 73°48′W], 17-XII-1926, Peña (USNM); 1 ♀, Chiloé Is., Aulen [42°2′S 74°1′W], 8-II-1952, Peña (USNM)*.

Diagnosis. This species is distinguished by a subtle spot on R₂. Furthermore, this species has a remarkable sheath of aedeagus with a long horizontal spur, male tergite IX with a distinctive rectangular projection, mesal lobes absent and posterior margin of male tergite IX pigmented.

Redescription. Wing length 5.86 mm, width 1.90 mm. — Coloration: General coloration brown. Rostrum and palpus dark brown. Antenna yellow, with apical segments slightly darker. Head brown. Eyes black. Thorax brown dark, pleura brown. Scutum without stripes. Halter brownish-yellow. Coxae brownish yellow and legs dark brown. Abdomen dark brown. — Head (dorsal view Fig. 28B, ventral view Fig. 28A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment, terminal palpal segment dilated; scape narrower than pedicel; terminal flagellomere shorter and thicker than penultimate; antenna with several long setae. — Thorax (lateral view Fig. 28F, dorsal view Fig. 28F): Anatergite taller than katatergite. Prothorax wide, prescutum with a few short setae. Halter with dilated knob. Wing (Fig. 28D) almost clear of markings, except subtle marking on R₂; veins around fork of bM (Fig. 28C) faded; M₁,₂ longer than basal deflection of M₁; R₂,₃,₄ longer than R₂,₃,₄.

— Male terminalia (Fig. 28G): Male tergite IX darkened on posterior margin, with wide median U-shaped notch; rectangular projection in two points on either side of extension; posterior margin with projection flat. Dorsal branch of gonocoxite very reduced. Lobe of gonostylus with pointed lobule shaped similar to folded leaf. Clasper of gonostylus with differently shaped branches: lateral branch long, bent around middle; medial branch curved into short stub. Mesal lobes absent. Sheath of aedeagus dark along almost entire length, angulated with smooth curvature, with setae on distal portion of lateral margin, as well as large distal horizontal lateral projection.

Remarks. Some specimens were misidentified by C.P. Alexander as A. (R.) nullus Alexander. The rostrum of the holotype is longer than in the other species of this subgenus. This species resembles A. (R.) anchoralis sp. nov. but differs mainly in M₁,₂ shape of projection on male tergite IX, ventral branch of gonocoxite and spur of sheath of aedeagus.

Etyymology. The word stigmaticus is Latin for “marked”. The term refers to the darkened mark near the tip of the wing of this new species.

Diagnosis. This species is distinguished by the darkened distal quarter of the wings and basal deflection of M₁ shorter than M₁,₂. Furthermore, the species is characterized by the male terminalia with setae on the median
branch of clasper of gonostylus and small marking on sheath of aedeagus.

**Description.** Wing length 7.48 mm, width 2.57 mm. — **Coloration:** General coloration dark brown. Rostrum and palpus dark brown. First segment of the antenna yellow, remaining segments dark yellow. Head dark brown. Eye gray. Thorax dark brown, pleura brown. Scutum with three brownish black stripes. Halter pale. Coxae and legs brownish yellow. Abdomen dark brown. — **Head** (dorsal view Fig. 29B, ventral view Fig. 29A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; palpus with several setae; scape thicker than pedicel; terminal flagellomere as long as penultimate. — **Thorax** (lateral view Fig. 29E, dorsal view Fig. 29F): Scutum with two rows of short setae; anatergite shorter than katatergite. Halter with dilated knob. Wing (Fig. 29D) with several markings including faint marking on A1; markings highlighting m-cu, r-m, part of R5, and R2+3; marking on Rs, darkened distal quarter of wing and strong markings on R1 and at tip of R2; veins near fork of bm (Fig. 29C) faded; M1-2 longer than basal deflection of
Figure 29. *Amphineurus* (*Rhamphoneurus*) *stigamticus* sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: aed sh, sheath of aedeagus; anatg, anatergite; anepm, anepimeron; anepst, anepisternum; aprn, anteropronotum; cer, cercus; cgonst, clasper of gonostylus; cx, coxa; goncx, gonocoxite; hlt, halter; hyp val, hypogynial valve; k, knob of halter; kepn, katepimeron; kepst, katepisternum; kg, katatergite; l ms, left mesal lobe of gonocoxite; lgonst, lobe of gonostylus; mr, meron; ms lobe, mesal lobe of gonocoxite; mtanepst, metanepisternum; mtepm, metepimeron; mtg, mediatergite; mtkepst, metakatepisternum; mtn, metanotum; p, posterior basalar; patg, paratergite; pprn, postpronotum; presct, prescutum; r ms, right mesal lobe of gonocoxite; sct, scutum; sctl, scutellum; st, sternite; tg, tergite; t9, male tergite IX.
M₁; R₂+3+4 shorter than half-length of R₂+3. — **Female terminalia** (Fig. 29H): Female tergite IX as wide and longer than tergite X; hypogynial valve slender; cercus bent at right angle, expanded in base; cercus shorter than hypogynial valve. — **Male terminalia** (Fig. 29G): Male tergite IX with shallow median U-shaped notch. Dorsal branch of gonocoxite longer than half-length of ventral branch, well separated from ventral branch. Lobe of the gonostylus rounded; lobule longer than wider, shorter than half-length of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straightened; medial branch curved, round club shaped, with concentration of setae. Mesal lobes of gonostylus symmetrical; both rounded with bump on side. Sheath of aedeagus angulated, darkened only near tip.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) nothofagetorum* Alexander. This species resembles *A. (R.) caleuchus* sp. nov. but differs mainly in marking in the sheath of aedeagus, length of R₂+3+4, shape of lobe of gonostylus, cercus and mediotergite.

### 3.3.25. *Amphineurus (Rhamphoneurus)* *theischingeri* sp. nov.

http://zoobank.org/species/A63932FB-5A55-4323-A10E-5E6F257A0C8F

**Material examined.** Holotype: ♂, Chile, Osorno, Pucotrehue [40°32′S 73°42′W], 10/12-IV-1968, Peña (USNM)*. **Paratypes:** 2 ♂ and 1 ♀, Chile, Osorno, Bahia Mansa [40°35′S 73°44′W], South of Pucotrihue, 12-IV-1968, Peña (USNM).

**Etymology.** The species is named after Gunther Theischinger, an expert on Tipulomorpha who revised the Australian *Amphineurus*.

**Diagnosis.** This species is distinguished by an absence of markings near R₁, r m as long as basal deflection of R₁, and cross-vein m-cu straight and inserted at bm. Furthermore, this species is characterized by male terminalia with curved sheath of aedeagus, straight medial branch of clasper of gonostylus and mesal lobes with slender, vertical tips. The thorax is also distinguishable by narrow knob of halter and katepisternum as long as meron.

**Description.** Wing length 6.30 mm, width 1.77 mm. — **Coloration:** General coloration dark brown. Rostrum and palpus brownish black. First segment of antenna yellow, remaining segments dark yellow. Head brownish gray. Eye black. Thorax dark-brown, pleura light brown. Scutum without stripes. Halter brownish-yellow. Coxae brownish-yellow, legs dark brown. Abdomen brownish black. — **Head** (dorsal view Fig. 30B, ventral view Fig. 30A): Rostrum bifurcated with short appendices; first palpal segment shorter than terminal segment; scape thinner than pedicel; terminal flagellomere longer than penultimate. — **Thorax** (lateral view Fig. 30E, dorsal view Fig. 30F): Anatergite shorter than katatergite. Halter with narrow knob. Wing (Fig. 30D) clear of distinctive markings; veins near fork of bm (Fig. 30C) visible; M₁₂ longer than basal deflection of M₁; R₂ faded; R₂+3+4 longer than R₂+3. — **Female terminalia** (Fig. 30H): Female tergite IX shorter and wider than tergite X; hypogynial valve very slender; cercus longer than hypogynial valve, thick, and slightly curved dorsal. — **Male terminalia** (Fig. 30G): Male tergite IX with V-shaped median notch. Distal tip of ventral branch of gonocoxite expanded, setose, with slight curve ventrally. Dorsal branch of gonocoxite shorter than half-length of ventral branch. Lobe of gonostylus with rounded lobule; lobule longer than wider, more than half as long as lobe of gonostylus, wider than stem. Clasper of gonostylus with similarly shaped branches: lateral branch rounded; medial branch conical. Mesal lobes of gonocoxite asymmetrical; both with long, narrow, straight distal projection; right mesal lobe wider. Sheath of the aedeagus curved halfway along length, darkened only on tip.

**Remarks.** Specimens of this new species were previously identified by C.P. Alexander as *A. (R.) nullus* Alexander. This species resembles *A. (R.) billighami* sp. nov. but differs mainly in the attachment of m-cu, setae concentration in gonocoxite, shape of male tergite IX and mesal lobe.

### 3.3.26. *Amphineurus (Rhamphoneurus)* *triangularis* sp. nov.

http://zoobank.org/species/F3B376D0-C8CE-4145-AD33-A1BA5DDF5AAB

**Material examined.** Holotype: ♂, Chile, Chiloé Is., Chepu [42°2′S 74°1′W], 8-II-1952, Peña (USNM)*. **Paratypes:** 1 ♂, Chile, Chiloé Is., Dalcahue [42°22′S 73°39′W], 1/4-IV-1968, Peña (USNM); 1 ♂, Chile, Chiloé Is., Chepu [42°22′S 74°1′W], 10/14-II-1952, Peña (USNM)*. — **Additional material:** CHILE. 2 ♂ and 1 [sex unknown], Pucotrehue [40°32′S 73°42′W], 60 m, 10-III-1955, Peña (USNM); 1 ♂, [sex unknown], Llanquihue, Carelmapu [41°44′S 73°40′W], Canal Chacao, 18-III-1957, Peña (USNM); 1 [sex unknown], Chiloé Is., Chepu [42°2′S 74°1′W], 8-II-1952, Peña (USNM).

**Etymology.** The word *triangularis* is Latin for “triangular”. This name references the triangular shape of the spur of sheath of aedeagus.

**Diagnosis.** This species is distinguished by only a dark spot near R₁ and M₁₂ as long as the basal deflection of M₁. Furthermore, this species is characterized by male terminalia with sheath of aedeagus with a triangular spur, tip of both mesal lobes bent horizontally, straightened lateral branch of clasper of gonostylus and cercus uniformly wide and abruptly angled dorsal.

**Description.** Wing length 5.76 mm, width 1.74 mm. — **Coloration:** General coloration brownish yellow. Rostrum and palpus dark brown. First segment of antenna yellowish brown, remaining segments brown. Head brown. Eye black. Thorax brownish yellow, pleura pale. Scutum
Figure 30. Amphineurus (Rhamphoneurus) theischingeri sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: **aed sh**, sheath of aedeagus; **anatg**, anatergite; **anepm**, anepimeron; **anepst**, anepisternum; **aprn**, anteropronotum; **cer**, cercus; **cgonst**, clasper of gonostylius; **cx**, coxa; **goncx**, gonocoxite; **hlt**, halter; **hyp val**, hypogynial valve; **k**, knob of halter; **kepm**, katepimeron; **kepst**, katepisternum; **ktg**, katatergite; **l ms**, left mesal lobe of gonocoxite; **lgonst**, lobe of gonostylius; **mr**, meron; **ms lobe**, mesal lobe of gonocoxite; **mtanepst**, metanepisternum; **mtepm**, metepimeron; **mtg**, mediotergite; **mtkepst**, metakatepisternum; **mtu**, metanotum; **p**, posterior basalar; **patg**, paratergite; **pprn**, postpronotum; **presct**, prescutum; **r ms**, right mesal lobe of gonocoxite; **sct**, scutum; **sctl**, scutellum; **st**, sternite; **tg**, tergite; **tg IX**, male tergite IX.
Figure 31. *Amphineurus (Rhamphoneurus) triangularis* sp. nov. A head (ventral view); B head (dorsal view); C detail of wing; D wing; E thorax (lateral view); F thorax (dorsal view); G male tergite IX (dorsal view) and remainder of male terminalia (lateral view); H female terminalia (dorsal view). — Abbreviations: *aed sh*, sheath of aedeagus; *anatg*, anatergite; *ane pm*, anepimeron; *ane pst*, anepisternum; *aprn*, anteropronotum; *cer*, cercus; *cgonst*, clasper of gonostylus; *cx*, coxa; *goncx*, gonocoxite; *hlt*, halter; *hyp val*, hypogynial valve; *k*, knob of halter; *kepm*, katepimeron; *kepst*, katepisternum; *ktg*, katatergite; *l ms*, left mesal lobe of gonocoxite; *lgonst*, lobe of gonostylus; *mr*, meron; *mt ane pst*, metanepisternum; *mt epm*, metepimeron; *mtg*, mediatergite; *mt kepst*, meta katepisternum; *mt n*, metanotum; *p*, posterior basalare; *patg*, paratergite; *pprn*, postpronotum; *presct*, prescutum; *r ms*, right mesal lobe of gonocoxite; *sct*, scutum; *sctl*, scutellum; *st*, sternite; *tg*, tergite; *t9*, male tergite IX.
with one black stripe. Halter dark yellow with knob yellowish brown. Coxae yellow and legs brown. Abdomen yellowish brown. — **Head** (dorsal view Fig. 31B, ventral view Fig. 31A): Rostrum bifurcated with long appendices; first palp segment shorter than terminal segment; scape thiner than pedicel; terminal flagellomere longer than penultimate. — **Thorax** (dorsal view Fig. 31E, dorso lateral view Fig. 31F): Division line of laterotergite almost vertical, anatergite as tall as katatergite. Halter with dilated knobs. Wing (Fig. 31D) almost clear of markings, except marking on R; veins near fork of bM (Fig. 31C) faded; M₁,₂ as long as basal deflection of M₁, R₂,₃,₄ longer than R₂,₅; basal deflection of R₃ shorter than R₂,₃. — **Female terminalia** (Fig. 31H): Female tergite IX shorter, wider than tergite X; cercus bent at right angle. Hypopygium valve slender and longer than cercus. — **Male terminalia** (Fig. 31G): Male tergite IX slightly darkened along posterior margin, with wide V-shaped median notch. Ventral branch of gonocoxite slightly sinuous, with concentration of setae on distal tip. Dorsal branch of gonocoxite shorter than half-length of ventral branch, slightly inclined medially. Lobe of gonostylus with rounded lobule; lobule longer than wide, longer than half-length of lobe of gonostylus, narrower than stem. Clasper of gonostylus with differently shaped branches: lateral branch straight, medial branch curved. Mesal lobes of gonocoxite asymmetrical; left mesal lobe curved; right mesal lobe short with sideways projection. Sheath of aedeagus straight with triangular projection, darkened near tip.

**Remarks.** Some specimens of this new species were previously identified by C.P. Alexander as *A. (R.) insanus* Alexander and some as *A. (R.) glabristylatus* Alexander. This species resembles *A. (R.) podenasi* sp. nov. but differs mainly in the length of M₁,₂ and R₂,₃,₄ shape of cercus and ventral branch of gonocoxite.

### 3.4. Identification key to species of Amphineurus (Rhamphoneurus)

| 1 | Dark spot on R₁ (Fig. 31D); sheath of aedeagus straight (Fig. 26G) | 2 |
| 1' | Faint cloudings or without markings on R₁ (Fig. 19D); sheath of aedeagus curved (Fig. 30G) | 18 |
| 2 | Distal quarter of wing clear (Fig. 26D); without setae on clasper of gonostylus (Fig. 25E) | 3 |
| 2' | Distal quarter of wing darkened (Fig. 29D); with setae on clasper of gonostylus (Fig. 16G) | 15 |
| 3 | No markings at end of R₁ (Fig. 31D); sheath of aedeagus with distal spur (Fig. 21G) | 4 |
| 3' | Dark distal spot to end of R₁ (Fig. 29D); sheath of aedeagus without distal spur (Fig. 11G) | 13 |
| 4 | Antenna hairy (Fig. 16B); medial branch of clasper bent, shorter than half-length of distal branch (Fig. 27F) | 5 |
| 4' | Antenna with few setae (Fig. 25B); medial branch of clasper straight, at least half-length of distal branch (Fig. 9G) | 7 |
| 5 | Mesal lobe of gonocoxite well-developed (Fig. 27F); m-cu inserted at fork of bM; male tergite IX without sclerotized projections (Fig. 28G) | *A. (R.) nutristylus* Alexander |
| 5' | Mesal lobe of gonocoxite absent (Fig. 28G); m-cu inserted in bM; male tergite IX with sclerotized projections (Fig. 28G) | *A. (R.) nutristylus* Alexander |
| 6 | Spur of sheath of aedeagus projecting horizontally (Fig. 28G); R₂,₃,₄ longer than R₁,₂; katepisternum as long as meron (Fig. 28E) | *A. (R.) sanus* Alexander |
| 6' | Spur of sheath of aedeagus projecting vertically (Fig. 10G); R₂,₃,₄ shorter than R₁,₂; katepisternum longer than meron (Fig. 10E) | *A. (R.) anchoralis* sp. nov. |
| 7 | M₁,₂ shorter than basal deflection of M₁ | 8 |
| 7' | M₁,₂ longer than or equal to basal deflection of M₁ | 11 |
| 8 | Tip of left mesal lobe of gonocoxite symmetrical (Fig. 8E); r-m shorter than basal deflection of R₃ | *A. (R.) alexanderi* sp. nov. |
| 8' | Tip of left mesal lobe of gonocoxite asymmetrical (Fig. 21G); r-m as long as basal deflection of R₃ | 9 |
| 9 | Thorax as long as tall (Fig. 20D); m-cu curved (Fig. 20B) | *A. (R.) insanus* Alexander |
| 9' | Thorax longer than tall (Fig. 9E); m-cu straight (Fig. 9D) | 10 |
| 10 | Distal portion of left mesal lobe well-developed (Fig. 21G); prescutum without setae (Fig. 21E); R₂,₃,₄ shorter than R₁,₂,₃ | *A. (R.) morphyphi* sp. nov. |
| 10' | Distal portion of left mesal lobe atrophied (Fig. 9G); prescutum with long setae (Fig. 9F); R₂,₃,₄ as long as R₁,₂,₃ | *A. (R.) amorimi* sp. nov. |
| 11 | R₂,₃,₄ longer than R₁,₂,₃; M₁,₂ as long as basal deflection of M₁ | *A. (R.) triangularis* sp. nov. |
| 11' | R₂,₃,₄ shorter than R₁,₂,₃; M₁,₂ longer than basal deflection of M₁ | 12 |
| 12 | Tip of right mesal lobe projecting horizontally (Fig. 25E); basal deflection of R₃ as long as r-m | *A. (R.) oosterbroeki* sp. nov. |
| 12' | Tip of right mesal lobe curved down (Fig. 26G); basal deflection of R₃ longer than r-m | *A. (R.) insanus* Alexander |
| 13 | R₂,₃,₄ shorter than R₁,₂,₃; male tergite IX unpigmented (Fig. 18G) | *A. (R.) glabristylatus* Alexander |
| 13' | R₂,₃,₄ shorter than R₁,₂,₃; male tergite IX dark (Fig. 15G) | 14 |
4. Phylogenetic analysis

Alexander (1929a) related the Neotropical genus Maietta with Amphineurus due to the presence of vestiture on the wings. A recent revision of Maietta (Santos et al. 2019) reinforced the link between Maietta and Amphineurus. The species M. dextra Santos et al. and M. edwardsi Santos et al. were, therefore, included in the phylogenetic analysis as outgroup taxa, along with one species of the genus Aphrophila Edwards (i.e., A. neozelandica Edwards).

A proper understanding of the phylogenetic relationships within the subgenus A. (Rhamphoneurus) depends on a broad taxonomic sampling including representatives of all subgenera of Amphineurus. With that in mind, we included in the analysis representative species of all the subgenera of Amphineurus from the Neotropical and Australasian regions (26 species in total).

4.1. List of characters

Here the characters and their states are defined (the number of steps of each character as they were optimized in the chosen tree is shown within square brackets). In some cases, the understanding of the morphological features under description requires examination of the accompanying illustrations. The data matrix, with a total of 54 terminal taxa and 112 characters, is shown in Supplementary Material 1.

**Head**

| Character | State | Description |
|-----------|-------|-------------|
| 0 | 0 | Size of rostrum: (0) shorter than remainder of the head; (1) longer or equal to remainder of the head. [1] |
| 1 | 0 | Shape of rostrum: (0) bifurcated (Fig. 4B); (1) non-bifurcated. [2] |
| 2 | 0 | Shape of bifurcation: (0) short appendices, shorter than half-length of labrum (Fig. 20A); (1) long appendices, near half-length of labrum (Fig. 4B). [1] |
Size of labrum: (0) longer than half the size of the hypopharynx (Fig. 4); (1) shorter or equal to half the size of the hypopharynx. [1]

Setae of antennae: (0) few setae (Fig. 17B); (1) many long and thin setae (Fig. 16B). [2]

Width of scape: (0) wider or equal to pedicel; (1) thinner than pedicel. [4]

Width of terminal flagellomere: (0) as wide as penultimate flagellomere; (1) 1.5× wider than the penultimate flagellomere. [2]

Thorax

Long setae on anterior region of prescutum: (0) absent; (1) present (Fig. 26F). [4]

Two rows of short setae on dorsal prescutum: (0) absent; (1) present (Fig. 14F). [2]

Width of prescutum (including presutural scutum): (0) as wide as postsutural scutum; (1) shorter than postsutural scutum. [2]

Central dark line on dorsal scutum: (0) absent; (1) present. [3]

Lateral dark lines on dorsal scutum: (0) absent; (1) present. [4]

Protuberance on scutum: (0) absent; (1) present (Fig. 23B). [3]

Shape of scutellum in lateral view: (0) with a notch (Fig. 30E); (1) aligned with scutum (Fig. 22E). [1]

Long setae on anteropronotum: (0) absent; (1) present (Fig. 26E). [6]

Long setae on aepimeron: (0) absent; (1) present (Fig. 11E). [3]

Height of aepisternum: (0) less than katepisternum (Fig. 12D); (1) broader than katepisternum (Fig. 18E). [1]

Notch on margin of aepisternum: (0) present (Fig. 10E); (1) fused (Fig. 17E). [2]

Anterodorsal margin of aepisternum: (0) at level or below posterodorsal margin (Fig. 20D); (1) above posterodorsal margin (Fig. 30E). [1]

Shape of posterior basalar sclerite: (0) less than 2× longer than wide; (1) more than 3× longer than wide. [1]

Laterotergite: (0) divided; (1) undivided. [1]

Long setae on mediocoxa: (0) absent; (1) present (Fig. 14E). [4]

Fissure in dorsal mediocoxa: (0) absent; (1) present (Fig. 15F). [1]

Mediocoxa: without membranous opening (Fig. 29E); (1) with membranous opening (Fig. 31E). [1]

Knob of halter: (0) less than 2× longer than wide (Fig. 9E); (1) more than 2.5× longer than wide (Fig. 13E). [1]

Wing

Dense vestiture on wing: (0) absent; (1) present. [1]

Flattened scales on wing: (0) absent; (1) present. [1]

Dense concentration of setae on distal region of wing: (0) present (Fig. 5B); (1) absent (Fig. 14D). [2]

Markings at tip of wing: (0) absent (Fig. 19D); (1) completely darkened (Fig. 16D); (2) along radial veins (Fig. 18D). [2]

Marking near apex of vein R₁: (0) absent; (1) present (Fig. 23D). [1]

Markings at forks of radial veins: (0) absent; (1) present (Fig. 23D). [1]

Pterostigma (marking near vein R₁): (0) absent; (1) present (Fig. 31D). [3]

Marking at vein R₅: (0) absent; (1) present (Fig. 23D). [2]

Marking at crossvein m-cu: (0) absent; (1) present (Fig. 23D). [2]

Marking on anal vein: (0) absent; (1) present (Fig. 23D). [2]

Tip of distal region of vein R₅: (0) darker than other veins (Fig. 31D); (1) as dark as other veins (Fig. 27C). [4]

Tip of vein R₅: (0) complete (Fig. 24D); (1) desclerotized (Fig. 16D). [2]

Base of vein R₅: (0) without spur; (1) with long spur. [1]

Tip of crossvein r-m: (0) complete (Fig. 24C); (1) desclerotized (Fig. 16D). [1]

Vein M₁₃: (0) complete (Fig. 17C); (1) desclerotized (Fig. 16D). [1]

Tip of vein bM: (0) complete (Fig. 18C); (1) desclerotized (Fig. 14C). [1]

Tip of crossvein m-cu: (0) complete (Fig. 24D); (1) desclerotized (Fig. 14C). [1]

Bifurcation of vein R₅: (0) R₅,₃₋₄ and R₅ (Fig. 5A); (1) R₅₋₃ and R₅₋₄. [1]

Vein R₅: (0) desclerotized (Fig. 19D); (1) present (Fig. 16D). [1]

Length of vein R₅,₃₋₄: (0) less than 2× longer than R₅₋₃₋₄; (1) at least 2× longer than R₅₋₃₋₄. [1]

Length of crossvein r-m: (0) longer than basal deflection of R₅; (1) shorter or equal to basal deflection of R₅. [5]

Cell d: (0) closed; (1) open. [4]

Length of discal cell: (0) at least 2× longer than wide; (1) less than 2× longer than wide. [2]

Vein M₃₋₄: (0) bifurcated; (1) non-bifurcated. [2]

Shape of crossvein m-cu: (0) straight (Fig. 27B); (1) strongly angulated (Fig. 15D). [1]

Position of crossvein m-cu: (0) inserted more distal than fork of Rs; (1) inserted at level of fork of Rs; (2) inserted more proximal than fork of Rs. [6]

Shape of anal vein: (0) straight (Fig. 8D); (1) strongly sinuous (Fig. 11D). [2]

Female terminalia

Cercus: (0) without membranous projection; (1) with membranous projection. [1]

Shape of cercus: (0) slightly curved dorsad (Fig. 19H); (1) strongly curved dorsad (Fig. 14H). [3]
Male tergite IX

54 Shape of male tergite IX: (0) wider than long; (1) longer than wide. [2]
55 Distal half of male tergite IX: (0) dark (Fig. 21G); (1) unpigmented (Fig. 23G). [2]
56 Sclerotized projection at apex of male tergite IX anchor-shaped: (0) absent; (1) present (Fig. 10G). [1]
57 Caudal projection in dorsal margin of male tergite IX: (0) absent; (1) present. [1]
58 Number of humps in dorsal margin of male tergite IX: (0) 0; (1) 2; (2) 3; (3) 4. [8]
59 Height of two medial humps in dorsal margin of male tergite IX: (0) tall; (1) short. [3]
60 Height of two lateral humps in dorsal margin of male tergite IX: (0) tall; (1) short. [1]
61 Shape of median notch of male tergite IX: (0) V-shaped (Fig. 30G); (1) U-shaped (Fig. 25E). [2]
62 Size of median notch of male tergite IX: (0) at least 2× wider than deep (Fig. 12F); (1) less than 1.3× wider than deep (Fig. 16G). [1]

Male terminalia

63 Foramen in tergite X: (0) absent; (1) present. [1]
64 Gonostylus: (0) non-bifurcated; (1) bifurcated in lobe and clasper. [1]
65 Symmetry of claspers of gonostylus: (0) symmetrical; (1) asymmetrical. [1]
66 Base of clasper of gonostylus: (0) pedunculated; (1) wide. [1]
67 Basal spur in clasper of gonostylus: (0) absent; (1) present. [1]
68 Lateroapical spur in clasper of gonostylus: (0) absent; (1) present. [1]
69 Dorsoapical spur in clasper of gonostylus: (0) absent; (1) present. [1]
70 Dense concentration of setae in clasper of gonostylus: (0) absent; (1) present (Fig. 16G). [1]
71 Clasper of gonostylus: (0) non-bifurcated; (1) bifid. [1]
72 Position of fork of clasper of gonostylus: (0) very proximal; (1) in more distal half. [1]
73 Shape of medial branch of clasper of gonostylus: (0) straight (Fig. 19G); (1) curved internally (Fig. 23G); (2) curved externally. [3]
74 Size of branches of clasper of gonostylus: (0) branches of same length (Fig. 19G); (1) branches of different lengths (Fig. 14G). [2]
75 Size of curved branch of clasper of gonostylus: (0) not surpassing straight branch (Fig. 16G); (1) surpassing the straight branch (Fig. 14G). [1]
76 Shape of lateral branch of clasper of gonostylus: (0) straight (Fig. 15G); (1) angulated in middle (Fig. 49G); (2) angulated at apex (Fig. 14G). [2]
77 Lobe of gonostylus: (0) non-bifurcated; (1) bifid. [2]
78 Position of fork of lobe of gonostylus: (0) very proximal; (1) in more distal half. [1]
79 Protuberance in stem of lobe of gonostylus: (0) absent; (1) present (Fig. 28G). [1]
80 Length of lobe: (0) shorter than half-length of stem of lobe of gonostylus (Fig. 12F); (1) longer or equal to half-length of stem of lobe of gonostylus (Fig. 15G). [3]
81 Width of lobe: (0) wider than stem of lobe of gonostylus (Fig. 13G); (1) thinner than stem of lobe of gonostylus (Fig. 20F). [3]
82 Shape of lobe: (0) longer but less than 4× longer than wide (Fig. 21G); (1) more than 4× longer than wide (Fig. 31G); (2) as long as wide (Fig. 23G). [4]
83 Tip of lobe: (0) rounded (Fig. 18G); (1) pointed (Fig. 28G). [1]
84 Gonocoxite: (0) non-bifurcated; (1) bifid. [1]
85 Mesal lobe: (0) absent; (1) present. [2]
86 Height of mesal lobe: (0) tall; (1) short. [1]
87 Color of mesal lobe: (0) unpigmented (Fig. 18G); (1) dark (Fig. 21G). [2]
88 Setae in mesal lobe: (0) lateral rows (Fig. 30G); (1) concentrated at apex (Fig. 21G); (2) uniformly distributed (Fig. 14G). [3]
89 Lateral non-sclerotized bulge in mesal lobe: (0) absent; (1) present (Fig. 29G). [1]
90 Sclerotized tip of mesal lobe: (0) absent; (1) present (Fig. 12F). [1]
91 Shape of sclerotized tip of left mesal lobe: (0) straight (Fig. 13G); (1) folded (Fig. 6). [3]
92 Shape of sclerotized tip of right mesal lobe: (0) straight (Fig. 17G); (1) curved (Fig. 6). [3]
93 Base of right mesal lobe: (0) asymmetrical (Fig. 6); (1) symmetrical (Fig. 12F). [1]
94 Lateral process of sheath of aedeagus: (0) well-developed; (1) absent. [1]
95 Protuberance in sheath of aedeagus: (0) absent; (1) present (Fig. 27F). [1]
96 Position of lateral process of sheath of aedeagus: (0) fused laterally with aedeagus; (1) detached from aedeagus. [1]
97 Coloration on detached sheath of aedeagus: (0) absent (Fig. 2D); (1) present (Fig. 11G). [1]
98 Size of coloration on detached sheath of aedeagus: (0) only at apex (Fig. 17G); (1) on half of sheath (Fig. 29G). [3]
99 Setae on detached sheath of aedeagus: (0) absent; (1) present (Fig. 10G). [1]
100 Shape of detached sheath of aedeagus: (0) straight; (1) angulated (Fig. 23G); (2) curved (Fig. 17G). [4]
101 Shape of angulated sheath of aedeagus: (0) one-folded (Fig. 21G); (1) two-folded (Fig. 16G). [1]
102 Spur of sheath of aedeagus: (0) absent; (1) present (Fig. 28G). [2]
103 Size of spur of sheath of aedeagus: (0) short (Fig. 31G); (1) long (Fig. 28G). [1]
104 Shape of spur of sheath of aedeagus: (0) triangular (Fig. 31G); (1) quadrangular (Fig. 25G). [1]
105 Height of spur of sheath of aedeagus: (0) short (Fig. 21G); (1) tall (Fig. 26G). [1]
106 Lateral branches in sheath of aedeagus: (0) absent; (1) present. [2]
107 Shape of lateral branches: (0) straight; (1) curved. [1]
108 Length of lateral branches: (0) not surpassing aedeagus; (1) surpassing aedeagus. [1]
109 Orientation of lateral branches: (0) divergent and surpassing axis of sheath of aedeagus; (1) vertical and not surpassing axis of sheath of aedeagus. [1]
110 Tips of lateral branches: (0) unipigmented; (1) dark. [1]
111 Posterior lateral branches on sheath of aedeagus: (0) absent; (1) present. [2]

4.2. Phylogenetic results

The parsimony analysis with equal weights resulted in one most parsimonious tree of 209 steps, Consistency Index (CI) = 0.58 and Retention Index (RI) = 0.86. The analyses with implied weighting (k ranging 1–6) resulted in only one most parsimonious tree with the same topology, shown in Figs. 32 and 33. The Bayesian analysis provided a tree very similar to that of the parsimony analysis, and it is depicted here in Fig. 34. The main difference is a less resolved tree in the Bayesian analysis, especially regarding the relationships within the outgroups. Within the ingroup, there are minimal topological differences; i.e., the collapse of a single node and the position of one species.

To discuss the distribution of the characters in the tree, we use the result of the analysis with implied weighting (with k=3), focusing on the more relevant characters. We believe that our extended outgroup sampling has an enormous heuristic value for future research on the genus Amphineurus, and although we will not discuss here the synapomorphies of the clades recovered in the outgroup, we have numbered all the nodes of the cladogram for future reference. In the lines below, we discuss the synapomorphies and the relationships recovered for the subgenus A. (Rhamphoneurus) (Node 25, Fig. 33).

The synapomorphies of each clade (as provided by the analysis with implied weighting with k=3) are listed within square brackets in the discussion of each node in a standardized way: [number of character: plesiomorphic state – synapomorphic state]. Homoplasic apomorphic states are indicated by an asterisk (*).

Node 25 — subgenus A. (Rhamphoneurus). Synapomorphies: [50: 2-1*]; [77: 0-1*]; [78: 0-1]. The clade is supported by the bifurcated lobe of gonostylus [77: 1]. This feature is present also in clade 9 (outgroup), but there are differences. In A. (Rhamphoneurus), the bifurcation of the lobe is a lobule [78: 1]. Besides, the position of crossvein m-cu [50: 1] reinforces this clade.

In our analysis, the species A. extraordinarius is the sister group of all the other species of A. (Rhamphoneurus). Alexander (1939) commented that this Chilean species is very different from the rest of the Neotropical fauna, justifying the choice of the species epithet (meaning "extraordinary"). Many features are discordant with the other Neotropical Amphineurus. Its rostrum is short, tergite IX is trilobate, the apex of the sheath of aedeagus is serrated and the verticils of the antennae are unilaterally distributed.

Amphineurus extraordinarius has M3+4 bifurcated, as in the Neotropical A. castroensis. However, this resemblance in the medial sector is a synapomorphy. A considerable difference between them is the open discal cell of A. extraordinarius as opposed to a closed one in A. castroensis. The very short M3+4 of A. extraordinarius is a necessary step to the probable capture of M3 in Node 26. In our view, this species is a representative of a short-rostrum lineage of A. (Rhamphoneurus), and we expand the diagnosis of the subgenus to include it.

Node 26. Synapomorphies: [0: 0-1]; [1: 1-0*]; [5: 0-1*]; [48: 0-1*]; [55: 0-1*]; [87: 0-1*]; [88: 2-0*]; [98: 1-0*]; [100: 0-2*].

The subgenus A. (Rhamphoneurus) was erected by Alexander (1929a) to allocate the Neotropical species with rostrum equal or longer than the remainder of the head [0: 1] (Fig. 4A). The bifurcated distal margin of the rostrum [1: 0] (Fig. 4B) and the shape thinner than the pedicel [5: 1] are presented here as synapomorphies of this clade, despite the absence of data for these structures in A. extraordinarius. The wings of A. (Rhamphoneurus) contrast with the usual mottled pattern seen in many Amphineurus. More apomorphic groups of A. (Rhamphoneurus) show more markings on the wings but in general A. (Rhamphoneurus) species have fewer markings than other Amphineurus.

The terminalia in this clade is very different from that of other Amphineurus. The distal half of the male tergite IX is dark [55: 0] (Fig. 17G). The sheath of aedeagus is curved [100: 2], with a single marking near to its apex [98: 0] (Fig. 17G). However, the shape of the sheath of aedeagus changes sometimes in the group. Another relevant feature in this clade is the mesal lobe. The mesal lobe of Node 26 has a dark end [87: 1], in contrast with other mesal lobes. Alexander (1925) cited the mesal lobe of A. pulchripes as “abruptly paler” compared with that of A. (Rhamphoneurus) species. Furthermore, the mesal lobe in Node 26 has typical lateral rows of setae [88: 0] (Fig. 20F). The shape of the mesal lobes varies considerably in derived clades in this group, even disappearing in Node 42.

Node 27. Synapomorphies: [31: 1-0*]; [37: 1-0]; [45: 1-0]; [73: 1-0*].

This clade is supported by wing features such as crossvein r-m longer than the basal deflection of R4 [45: 0] and vein R4 faded on the clade (Fig. 13G). Wings of this clade have a notable absence of markings, even the pterostigma [31: 0]. The maximum of this reduction is in A. (R.) immaculatus sp. nov. (Fig. 19G). Also, the species of this group show a characteristic clasper of gonostylus (Fig. 13G), with branches of the same length [73: 0]. Despite the shared similarities in the wings and gonostylus, the mesal lobes vary in this group.

Node 28. Synapomorphies: [9: 0-1*]; [11: 0-1*]; [91: 0-1*].

This clade groups the species A. (R.) nullus and A. (R.) falcatus.
metrical sclerotized tips of the mesal lobes [91: 1]. Asymmetrical structures are not uncommon in *Amphineurus*. These species show one tip of the mesal lobe straight and the other bent (Fig. 17G). In addition, the node is supported by the shorter prescutum [9: 1] (Fig. 17F) and by characteristic lateral dark lines in the dorsal scutum [11: 1].

**Node 29.** Synapomorphies: [10: 1-0*]; [50: 1-0*].

This clade is supported by a simple scutum, without dorsal markings [10: 0]. Also, these species do not show other thoracic markings, an uncommon condition for this subgenus. This clade has species with translucent wings with great concentration of setae (Fig. 13G). Furthermore, the insertion of crossvein m-cu distal to the fork of Rs [50: 0] is another synapomorphy of this node (Fig. 13G) that is only observed in the outgroup as a homoplasy.

**Figure 32.** Most parsimonious tree (part) yielded by parsimony analysis with implied weighting (K=3), depicting recovered relationships among outgroup taxa. Numbers at tree branches designate nodes (see 4.2.). — Abbreviations: Aus, Australia; NC, New Caledonia; NG, New Guinea; NZ, New Zealand, SAm, South America; Tas, Tasmania.
Node 30. Synapomorphies: [3: 0-1]; [14: 1-0*]; [18: 0-1]; [19: 0-1]; [24: 0-1]; [31: 0-1*]; [35: 0-1*]. *Amphineurus (R.) theischingeri* sp. nov. and *A. (A.) billinghami* sp. nov. are species with high morphological similarity. These species have very similar wings and male terminalia, although the length of the mesal lobes is crucially different. The node is supported by the labrum shorter or equal to half the size of the hypopharynx [3: 1] (Fig. 13B). Also, the wings of this clade have the vein R₅ as dark as the other veins [35: 1] (Fig. 13D).

Other synapomorphies are seen in the thorax: notably long setae on the anepisternum [14: 0], the anterodorsal margin of the anepisternum above the posterodorsal margin [18: 1], and the posterior basalar sclerite more than 3× longer than wide [19: 1] (Fig. 13E). The knobs of the halteres in both species also have the characteristic shape of being more than 2.5× longer than wide [24: 1].

Node 31. Synapomorphies: [11: 0-1*]; [36: 0-1*]; [38: 0-1]; [39: 0-1]; [41: 0-1]; [74: 0-1*].

This clade is defined by the presence of faded veins in the middle of the wing (Fig. 16C). There are not only faded veins, but also a lack of pigmentation in their vicinity, giving this section a lighter appearance. Alexander (1929a) points out “weak branches” near to the fork of bM. It may be related to the thyridium, a desclerotization of the medial vein before the fork (Shcherbakov et al. 1995). In some species, this desclerotization of the nodal flexion line extends beyond the fork and affects crossvein m-cu and vein M₁+₂.

Despite the co-occurrence, these faded sections are independent events in unrelated veins such as the tip of vein R₁ [36: 1], vein M₁+₂ [39: 1], the insertion of m-cu [41: 1], and the distal section of r-m [38: 1]. Other evidence to the independence of these evolutive novelties is the reversion of some of them independently. The descler-
rotization of the tip of R$_1$ is reversed in Node 44. These transformations are common in the subgenus. In Node 27, independently, there are species with vein R$_2$ faded.

In addition, this clade is characterized by a distinct clasper of gonostylus (Fig. 16G), with the medial branch shorter than the lateral branch [74: 1]. It is reversed only in A. (R.) apiculatus (Fig. 12F). Besides that, the dorsal scutum has lateral dark lines [11: 1]. These lines are present also in Node 28 and reversed in Node 40.

**Node 32.** Synapomorphies: [13: 0-1]; [17: 0-1*].

In the description of A. (R.) apiculatus, Alexander (1968) already commented on the high similarity of this species with A. (R.) nonnullus. These species share apomorphic thoracic features: the scutellum at the same level laterally [13: 1] and the fused margin of the anepisternum [17: 1]. The fused anepisternum is also seen in A. (R.) falcatus sp. nov. (Fig. 17E). Despite the resemblances, the male terminalia of both species are different. The main difference is a reversion of Ch. 74 in A. (R.) apiculatus (Fig. 12F). In this species, the claspers have branches of the same length [74: 0].

**Node 33.** Synapomorphies: [4: 0-1*]; [61: 0-1*]; [82: 0-2*]; [98: 0-1*]; [100: 2-1*].
This clade represents the major radiation of the subgenus. The main synapomorphy is the angulated sheath of aedeagus [100: 1]. The shape of the sheath (Fig. 16G) is variable in the clade, but it differs drastically from the other sheaths found in the subgenus which are normally curved or straight. Also, the sheath of aedeagus is characterized by the presence of dark markings along most of its length [98: 1] (Fig. 16G).

The male terminalia is also characterized by the U-shaped tergite IX [61: 1] (Fig. 25E) and by the lobes of the gonostylus with wide lobules [82: 2]. Another synapomorphy of this clade is the presence of long and thin setae on the antenna [4: 1]. This feature (Fig. 14) is reversed in Node 43.

Node 34. Synapomorphies: [29: 0-1]; [30: 0-1]; [32: 0-1*]; [33: 0-1*]; [34: 0-1*]; [62: 0-1]; [80: 0-1*]; [88: 0-2*]; [90: 0-1]; [101: 0-1].

This clade is supported by the presence of dark markings on the wing (Fig. 29D): a marking near the anal vein [34: 1], another at the tip of vein R5 [29: 1], one in the crossvein m-cu [33: 1], a marking around the forks of the radial veins [30: 1], and another marking on vein Rs [32: 1]. The co-occurrence of such markings is independent. The wing markings of this node resemble the subgenus A. (Nesormosia), but with important differences.

The clade is also sustained by synapomorphies in the male terminalia: the curved shape of median notch of tergite IX [62: 1] and the long lobule [80: 1] (Fig. 14G). The mesal lobes are also characteristic with uniformly distributed setae [88: 2] and without sclerotized tips [90: 1] (Fig. 14G). The main feature of the male terminalia in this group is the long angulated extremity of the sheath of aedeagus [101: 1]. It gives a two-folded shape to the sheath of aedeagus (Fig. 29G), as noticed by Alexander (1929a, 1969). Although the dimensions vary in this clade, it retains the shape of the angulated sheath.

Node 35. Synapomorphies: [5: 1-0*]; [12: 0-1*]; [14: 1-0*]; [15: 0-1*]; [28: 0-2*]; [49: 0-1*]; [51: 0-1*].

This clade is defined by the tip of the wing with markings around the radial veins [28: 2]. The three species of this clade have crossvein m-cu angulated [49: 1]. The strongly sinuous anal vein [51: 1] is a synapomorphy of this clade (Fig. 18D) despite its absence in A. (R.) chiloeanus (Fig. 15D). Other synapomorphies which support this group include a scape wider than the pedicel [5: 0]. This feature (Fig. 18B) is a reversion of the condition of Node 26 and appears again in Node 39 (Fig. 29B).

Another synapomorphy is the scutum with a protuberance [12: 1] (Fig. 18F). This lateral protuberance is also observable in A. (R.) apiculatus (Fig. 12E). The clade is defined by the presence of two sets of long thoracic setae (Fig. 15A): one on the anteropronotum [14: 0] and another on the anepimeron [15: 1]. These setae are homoplasic too. The anteropronotal setae are present in A. (R.) calectus sp. nov. (Fig. 14F) and the anepimeron setae are present in A. (R.) rutristylus (Fig. 27E).

Node 36. Synapomorphies: [16: 0-1*]; [22: 0-1*]; [44: 0-1*]; [45: 1-0*]; [50: 1-2*].

This clade groups together A. (R.) glabristylatus and A. (R.) chiloeanus. These two species have different sheaths of the aedeagus, but very similar wings. Both wings have vein R5-3 at least 2× longer than R5-4 [44: 1], crossvein r-m shorter than the basal deflection of R5 [45: 0] and crossvein m-cu inserted more proximal than the fork of Rs [50: 2]. Besides wing features, the clade is supported by the anepisternum higher than the katepisternum [16: 1] and by the presence of a fissure in the dorsal mediobasal tergite [22: 1] (Fig. 18F).

In the description of A. (R.) chiloeanus, Alexander (1969) suggested similarities between this species with others such as A. (R.) sanus (placed in Node 41) due to the presence of a spur in the sheath of aedeagus. However, when compared with other morphological traits, it becomes clear that the proximal spur of A. (R.) chiloeanus (Fig. 15G) is not the same as the distal spur of the species of Node 41 (Fig. 28G). Amphineurus (R.) chiloeanus is a very modified species with many reversions (Ch. 11, 15, 51, 82, and 87). This fact creates difficulties in the position of this species and may explain the uncertainties of the affinities raised by Alexander (1969).

Node 37. Synapomorphies: [27: 0-1*]; [28: 0-1*]; [55: 0-1*]; [70: 0-1*]; [76: 0-2*]; [81: 0-1*]; [89: 0-1*].

All specimens of the species of this clade were originally identified as A. (R.) nothofagetorum by C.P. Alexander. However, detailed morphological study uncovered a higher diversity, and three new species are placed in this clade along with A. (R.) nothofagetorum. Node 37 groups the species with darkened distal quarters of the wings [28: 1] (Fig. 29D). The wings of these species have fewer setae than what is normally found in the subgenus [27: 1].

Another important synapomorphy is the dorsal margin of the male tergite IX without a dark region [55: 1]. The tergite (Fig. 29G) resembles the groundplan of the genus, but this is likely a reversion. The clade is also supported by the thin lobule [81: 1]. This feature is also present in Node 46. The clade is also defined by a lateral non-sclerotized bulge on the mesal lobe [89: 1] (Fig. 16G). The clasper of gonostylus is characteristic of these species with a concentration of setae in the clasper [70: 1] and lateral branch of the clasper of gonostylus is angled at the apex [76: 2] (Fig. 16G).

Node 38. Synapomorphies: [21: 0-1*]; [40: 0-1*].

This clade is supported by faded veins near the fork of bM [40: 1] (Fig. 14C). This fact highlights other faded veins, such as in Node 33, has occurred independently. The presence of faded sections in veins was shown in the original description of the type-species (Alexander 1929a). This node is also characterized by the presence of setae in the mediobasal tergite [21: 1] (Fig. 14E). These mediobasal tergite setae are also seen in A. (R.) morphyi sp. nov. (Fig. 21E).
Node 39. Synapomorphies: [5: 1-0*]; [53: 0-1*]; [75: 0-1].
This node groups A. (R.) stigmaticus sp. nov. and A. (R.) caleuchus sp. nov. The main synapomorphy is the long medial branch of the clasper of gonostylus [75: 1] (Fig. 14D). Another synapomorphy is the strongly upcurved shaped cercus [53: 1] (Fig. 14C). It is similar with the upcurved cercus of Node 43 (Fig. 21H). Also, the clade is defined by the scape wider than or as wide as the pedicel [5: 0].

Node 40. Synapomorphies: [7: 0-1*]; [11: 1-0*]; [95: 0-1].
This node represents a major branch of the subgenus. The defining synapomorphy of this node is a protuberance in the sheath of aedeagus [95: 1] (Fig. 27G). The clade is also supported by a loss of dark lateral lines in the scutum [11: 0], present in Node 31. The clade is also defined by long setae on the anterior margin of the prescutum [7: 1]. These characteristic setae (Fig. 27E) are absent in Node 47 (Fig. 20E).

Node 41. Synapomorphies: [14: 1-0*]; [82: 2-1*]; [102: 0-1].
This clade is defined by a distinctive spur in the sheath of aedeagus [102: 1]. This distal spur of the sheath of aedeagus (Fig. 31G) is different from the proximal spur in A. (R.) chilosanus (Fig. 15G). This spur varies in shape and size and it is important taxonomically. The clade is also supported by long setae on the anteropronotum [14: 0]. The anteropronotal setae (Fig. 31E) are also seen in Node 44 (Fig. 33). Another synapomorphy for this clade is a long lobule of the gonostylus [82: 1].

Node 42. Synapomorphies: [54: 0-1]; [56: 0-1]; [76: 0-1]; [79: 0-1]; [80: 0-1*]; [83: 0-1]; [85: 1-0*]; [99: 0-1]; [103: 0-1].
This clade groups A. (R.) sanus and A. (R.) anchoralis sp. nov. These two species are very similar to each other and share many apomorphies. The most distinguishable synapomorphy is the anchor-shaped sclerotized projection on male tergite IX [56: 1] (Fig. 10G). The tergite of these species is also unusually longer than wide [54: 1]. The mesal lobe is absent in this clade [85: 0].

The detached sheath of aedeagus of these species is peculiar (Fig. 28G). The most remarkable feature of the sheath is the presence of a very long spur [103: 1]. In addition, the sheath of aedeagus of these species has few or no setae [99: 1]. Another modified structure for these species is the lobe of gonostylus (Fig. 28G). The lobe of this clade has a protuberance in the stem [79: 1]. The lobe is longer than the stem [80: 1]. A more evident feature is the pointed tip of the lobe [83: 1]. The clade is also supported by the lateral branch of the clasper of gonostylus angulated at the apex [76: 1] (Fig. 28G).

Node 43. Synapomorphies: [4: 1-0*]; [53: 0-1*]; [73: 1-0*]; [88: 0-1*]; [91: 0-1*]; [92: 0-1*].
This clade shows great morphological variability, especially in the male terminalia. Of the seven species in this group, however, only A. (R.) insanus has been previously described.

The main characteristic of this clade is the strong asymmetry of the mesal lobes. In this clade, the left mesal lobe has a folded tip [91: 1], while the right one is curved [92: 1] (Fig. 6). The left mesal lobe folded is also found in Node 28 (Fig. 17D) and the curved right mesal lobe is also observable in A. (R.) nonnullus (Fig. 22G). Despite this, the combination of both is a very diagnostic feature of this clade.

The asymmetry in the male terminalia is not uncommon in Amphineurus (e.g., A. (Nesormosia)) nor in the related genus, Maietta (Santos et al. 2019). The mesal lobes of these species also have setae concentrated at their apices [88: 1]. Although the distribution of setae is variable in the genus, these apex-centered setae are unique.

In addition, the medial branch of the clasper of gonostylus is straight [73: 0]. This feature is observable also in Node 27 (Fig. 17G). However, the species of Node 43 (Fig. 6) have the medial branch shorter than the lateral branch. This clade is supported by a cerasus strongly curved dorsad [53: 1] (Fig. 21H). This characteristic is also present also in Node 39 (Fig. 29H). Contrastingly with the pattern of Node 33, the antennae of these species have few setae [4: 0] (Fig. 21B).

Node 44. Synapomorphies: [2: 0-1]; [14: 0-1*]; [23: 0-1]; [36: 1-0*]; [105: 0-1].
This clade is represented by species with a tall spur on the sheath of aedeagus [105: 1] (Fig. 25E). Besides, the rostrum of these species has long appendices [2: 1] (Fig. 26B). Another synapomorphy of Node 44 is that mid coxa has a membranous opening [23: 1] (Fig. 26E). The clade also has two reversions: the tip of vein R₃ is not faded [36: 0] (Fig. 25D), reversing the state of Node 31; the anteropronotal setae has long setae [14: 1] (Fig. 31E), reversing the state of Node 41.

Node 45. Synapomorphies: [6: 0-1*]; [21: 0-1*].
This node groups A. (R.) podenasii sp. nov. and A. (R.) oosterbroekii sp. nov. These species are notable for the dilated last flagellomere [6: 1] (Fig. 25B). The dilated flagellomere is also present in A. (R.) anchoralis sp. nov. (Fig. 10B). These two species are grouped also by the presence of long setae on the mediosternite [21: 1] (Fig. 26E). This feature is also observable in Node 38 (Fig. 14E).

Node 46. Synapomorphy: [81: 0-1*].
This node is supported by the lobule thinner than the stem of the lobe of gonostylus [81: 1] (Fig. 21G). This is also present in Node 37 (Fig. 14G).

Node 47. Synapomorphies: [7: 1-0*]; [104: 0-1].
This node is supported by the quadrangular shape of the spur of the sheath of aedeagus [104: 1] (Fig. 8E). Furthermore, the clade is defined by the loss of long setae in the prescutum [7: 0] (Fig. 21F), reversing the state of Node 40.

Node 48. Synapomorphy: [93: 0-1].
This node groups *A. (R.) insanus* and *A. (R.) alexanderi* sp. nov. These species are so similar that all specimens of *A. (R.) alexanderi* sp. nov. were misidentified by C.P. Alexander as *A. (R.) insanus*. The defining synapomorphy of this clade is the right mesal lobe with symmetrical sides in the base [93: 1] (Fig. 6).

5. Biology

The label data of the *Amphineurus* specimens suggest a univoltine development. The adults are found from the end of November to April, but the majority of species occur from December to January. There is a wide range of tolerated altitude, from sea-level to 1600 m. Most specimens and species were collected in humid environments. *Amphineurus* (*A.*) *submolophilinus* is suggested to be found near streams (Alexander 1923).

The larvae of *A. (A.) hudsoni* have been found in wet decayed fallen leaves of Nikau (*Rhopalostylis sapida* Wendl and Drude), an endemic New Zealand palm (Edwards 1923). *Amphineurus* are frequently associated with plants. *Amphineurus* (*A.*) *bickeli* are found in montane forest (Theischinger 1996), and *A. (A.) molophilinus* in scrub (Alexander 1922a). *Amphineurus* (*A.*) *breviclavus* Alexander, 1924 and *A. (N.) otagensis* Alexander, 1922a are found among the undergrowth ferns in beech forests. The lower vegetation in beech forests is the environment where *A. (A.) campbelli* Alexander, 1922b and *A. (N.) nothofagi* Alexander, 1925 also are found.

In South America, data is more scarce. However, *A. extraordinarius* is associated with trees of Araucaria Kuntze (Alexander 1939). In New Zealand, *A. (N.) longi* and *A. (A.) kingi* are collected near kauri trees (*Agathis australis* Loudon), an endemic Araucariaceae (Alexander 1950). As evidenced by a recent revision of long-proboscid limoniids (Oosterbroek and Lukashevich 2021), *Nothofagus* forests bear genera with long rostrums but without direct evidence of pollination in angiosperms. There is an evolutionary scenario of long rostrum cranifly groups associated with ancient gymnosperm forests that may have eventually adapted to angiosperms. This change has occurred independently in many lineages (Ribeiro 2008; Oosterbroek and Lukashevich 2021).

Alexander (1929b) noticed some *Amphineurus* species in grass steppe and low scrubs of upper montane regions. The most direct association between *Amphineurus* and angiosperms is with *A. (A.) operculatus*, found in shrubs of dogwood (*Cassinia aculeata* Labill.: family Asteraceae) (Alexander 1924). Some *Amphineurus* (mainly the subgenera *A. (Amphineurus)* and *A. (Nothornosia)*) have spotted wings and striped legs. Pritchard (1983) observed that cranefly species with patterned wings are generally found in open woodland. According to Edwards (1923), some *Amphineurus* species may be mimetic of spiders, as in *A. (A.) perdecorus*, when resting, assumes a “decidedly spider-like appearance”. It may suggest a possible mimetic behavior of this species.

6. Biogeography

The biogeography of the genus *Amphineurus* is an old topic. Alexander (1929a) identified Neotropical species of the genus and argued that the presence of the genus in both South America and New Zealand were evidence of past Antarctic land connections. The biogeographical affinities of the cranefly fauna of southern South America and Australasia is reinforced by Ribeiro and Eterovic (2011) and Santos and Ribeiro (2018).

Although the focus of our study is the subgenus *Amphineurus* (*Rhamphoneurus*) (Fig. 35), we used a broad outgroup sampling. These outgroup species embrace the entire range of distribution of *Amphineurus*. Based on the outgroup method (Nixon and Carpenter 1993), our analysis is a step forward in resolving the relationships within the outgroups. The outgroup relationships indicated, with some confidence, that the closest relatives of *A. (Rhamphoneurus)* are in New Zealand.

Ribeiro and Eterovic (2011) criticized the simplistic labeling of the austral distributions of Tipuloidea within the South Pacific Track as Gondwanan, in the sense that the final breakup of Gondwana may have not been the event responsible for the differentiation of the lineages. If the final breakup of Gondwana was the reason behind the diversification of the taxa, we should expect monophyletic groups in each of the resultant landmasses.

Concerning taxa distributed in Australasia and South America, there is a recurrent asymmetry, also not expected by vicariance driven by the fragmentation of Gondwana, in which Australasian taxa (notably, New Zealand taxa) constitute a grade (i.e., are paraphyletic) relative to South American taxa. This asymmetry has been found, for instance, in phylogenetic studies of other components of this Trans-Pacific Biota (such as the genus *Aphrophila* recently revised by Santos and Ribeiro (2018)) where the New Zealand taxa correspond to a grade, with some Zealandia (the continental landmass sensu Mortimer et al. 2017) endemics more closely related to South American groups. Once again, as in the case of *Amphineurus* dealt with in this study, we have observed the same pattern.

The asymmetry just mentioned, and other general distributional patterns non-congruent with the sequence of breakup of Gondwana can be interpreted as evidence of a heterogeneous set of ancient, pre-rift distribution ranges in the area. Recent phylogenetic studies including both fossil and recent representatives of Tipuloidea (Lukaschevich and Ribeiro 2019) indicate that the main Tipuloidea lineages (family level clades) have differentiated, at least, from the Triassic (stem lineages) to Upper Jurassic times (more derived families). During this time interval, a lot of pre-rift differentiation must have occurred before the final continental divisions. The separation of continental landmasses is the only final result of long-lasting tectonic events, which caused a lot of in situ differentiation by altering the local landscapes.

One alternative explanation could be by a posteriori dispersal from Australasia to South America, but the poor dispersal capabilities of some (if not all) of the groups
in question and their very particular habitat needs (for instance, larvae of *Aphrophila* craneflies are restricted to fast-flowing waters in mountainous areas) does not support such views. In addition, assuming independent trans-oceanic dispersal seems odd with a unifying view of biogeography as the result of an evolving geological setting (Nelson and Platnick 1981; Heads 2015), and, unfortunately, such ideas became so uncritically accepted in recent times, linked with naïve interpretations of minimum ages of clades as provided by molecular clock estimates (Heads 2015).

In the words of Heads (2013: 85): “If a group is in Australia, New Zealand and South America, but the groups in each area are not monophyletic, as in craneflies […], the phylogeny cannot have been caused simply by the rifting of a homogeneous population. Instead, the pattern suggests that differentiation developed in a long phase of intracontinental rifting that was a precursor to Gondwana breakup with seafloor spreading. The whole breakup process was drawn out and included early phases of “failed” rifting; […] This suggests that the break seen in craneflies […] – between New Zealand + South American groups, and Australia + South American groups – was associated with Jurassic-Cretaceous extension in the West Antarctic Rift System, not seafloor spreading that later broke Gondwana.”

Lukashevich and Ribeiro (2018) estimated that Tipuloidea must have existed at least since the Middle Triassic (ca. 242–247 m.y.a.), and therefore, the group is old enough to have undergone major pre-rift differentiation and cladogenesis. The alternative hypothesis, i.e., assuming post-rift trans-oceanic dispersal, is not only at odds with the biology and ecological constraints of the groups in question, but with an entire biogeographic research agenda that seeks to understand biogeographic patterns in terms of large integrated processes capable of explaining a plethora of biological phenomena under a unifying view, i.e., that the Earth and life evolve together.

8. Acknowledgments

We are very grateful to Dr. Wayne Mathis, for the loan of the specimens used in this study (as well as for his unconditional support to the work of GCR for many years) when he was still working as curator of Diptera at the NMNH, Washington. We also thank one anonymous reviewer, Dr. Levente-Péter Kolcsár, and subject editor, Dr. Bradley Sinclair, for detailed reviews and corrections that greatly contributed to the final version of this paper. We thank Daniel Dias Dornelas do Carmo for assistance in the Bayesian analysis. This study was financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001 (RRS) and by FAPESP (grant 2017/16305-6 to DS; grant 2010/00557-7 and 2020/02844-5 to GCR).

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Supplementary material 1

Morphological matrix

Authors: Santos D, Santos RR, Ribeiro GC (2022)
Data type: .ss
Explanation note: The file contains the matrix used in the phylogenetic analysis.
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