

A review of *Pseudorygmodus* (Coleoptera: Hydrophilidae), with notes on the classification of the Anacaenini and on distribution of genera endemic to southern South America

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Abstract. The morphology and taxonomy of the genus *Pseudorygmodus* Hansen, 1999 endemic to Chile is reviewed based on freshly collected material and museum specimens. Two species are recognized: *P. flintispangleri* (Moroni, 1985) widespread from Los Lagos Region to Magallanes Region, and *P. versicolor* sp. nov. which is only known from Parque Nacional Nahuelbuta in La Araucanía Region. A phylogenetic analysis is performed to reveal the position of the genus within Hydrophilidae, based on four genes (*coxI*, *cox2*, 18S and 28S). The results reveal that *Pseudorygmodus* is a member of the tribe Anacaenini of the subfamily Chaetarthriinae, which is supported by both adult and larval morphology. Within Anacaenini, it was placed in the *Anacaena* Thomson, 1859 clade, which is supported by the morphology of the nasale of the larva. The phylogenetic analysis performed here as well as the morphological comparison of larvae of the Anacaenini brought additional evidence supporting the internal topology of the tribe, including the polyphyly of *Anacaena* in the current sense. The genus *Crenitulus* Winters, 1926, stat. restit., is hence reestablished for the former *Anacaena suturalis* group, containing the following species: *C. attiguis* (Orchymont, 1942) comb. nov., *C. hirsutus* (Komarek, 2005) comb. nov., *C. nitens* (Gentili, 1993) comb. nov., *C. paleodominicus* (Fikáček & Engel, 2011) comb. nov., *C. perpenus* (Orchymont, 1942) comb. nov., *C. solstitialis* (Kirsch, 1873) comb. nov., *C. schoedli* (Komarek, 2005) comb. nov., and *C. suturalis* (LeConte, 1866). The genus *Gentilina* Hebauer, 2003, syn. nov., is synonymized with *Crenitulus*. A potential distribution is modelled for five hydrophilid genera endemic to southern South America (*Andotypus* Spangler, 1979, *Anticura* Spangler, 1979, *Cylorygmus* Orchymont, 1933, *Hydramara* Knisch, 1925 and *Pseudorygmodus*)

using the high-resolution climatic data and the maximum entropy approach, in order to focus the future collecting effort to the areas where the genera likely occur. Biology and distribution of *Pseudorygmodus* and other endemic austral genera is briefly discussed, as well as problems that should be focused in future phylogenetic studies of the Chaetarthriinae and Anacaenini.

Resumen. La morfología y la taxonomía del género endémico *Pseudorygmodus* Hansen, 1999 de Chile fue revisada, apoyada por recolectas recientes y por material depositado en colecciones. *Pseudorygmodus flintispangleri* (Moroni, 1985), especie que puede ser encontrada desde la Región Los Lagos hasta la Región de Magallanes, y *P. versicolor* sp. nov. presente solamente para el Parque Nacional Nahuelbuta en la Región La Araucanía fueron reconocidas en este estudio. Un análisis filogenético fue realizado para conocer la posición del género dentro de la familia Hydrophilidae, mediante el uso de cuatro genes (*cox1*, *cox2*, 18S y 28S). Los resultados revelaron que *Pseudorygmodus* forma parte de la tribu Anacaenini de la subfamilia Chaetarthriinae, sustentados en los análisis morfológicos realizados en las larvas y los adultos. Dentro de Anacaenini, fue posicionado el clado de *Anacaena* Thomson, 1859, el cual fue apoyado por la morfología del nasale de la larva. El análisis filogenético realizado, así como la comparación morfológica de las larvas de Anacaenini, mostró evidencia adicional que apoya la topología interna de la tribu, incluyendo la polifilia de *Anacaena*. *Crenitulus* Winters, 1926, estatus restituído, fue restablecido para del grupo *Anacaena suturalis*, que contiene las siguientes especies: *C. attiguus* (Orchymont, 1942) nueva combinación, *C. hirsutus* (Komarek, 2005) nueva combinación, *C. nitens* (Gentili, 1993) nueva combinación, *C. paleodomínicus* (Fikáček & Engel, 2011) nueva combinación, *C. perpennus* (Orchymont, 1942) nueva combinación, *C. solstitialis* (Kirsch, 1873) nueva combinación, *C. schoedli* (Komarek, 2005) nueva combinación y *C. suturalis* (LeConte, 1866). *Gentilina* Hebauer, 2003 nuevo sinónimo, fue sinonimizado a *Crenitulus*. La distribución potencial fue modelada para cinco géneros endémicos de la parte sur de Suramérica (*Andotypus* Spangler, 1979, *Anticura* Spangler, 1979, *Cylorygmus* Orchymont, 1933, *Hydramara* Knisch, 1925 y *Pseudorygmodus*) usando datos climáticos de alta resolución y el enfoque de máxima entropía, con el fin de encaminar las recolectas futuras en las áreas donde los géneros probablemente estén presentes. La biología y distribución de *Pseudorygmodus* y otros géneros endémicos australes son discutidos brevemente, así como los problemas que deben ser enfocados en los futuros estudios filogenéticos de Chaetarthriinae y Anacaenini.

Key words. Hydrophilidae, Rygmodinae, Chaetarthriinae, Anacaenini, Hydrophilinae, Hydrobiusini, taxonomy, morphology, DNA, phylogeny, new species, new combination, ecological niche modeling, relict, Argentina, Chile, austral South America, Neotropical Region

Introduction

The hydrophilid fauna of austral South America is relatively species-poor: only 26 species are recorded from Chile (JEREZ & MORONI 2006), and only a dozen additional species are recorded from southern Argentina (OLIVA et al. 2002). Despite of that, the austral Hydrophilidae have always attracted attention due to the occurrence of several, little known, endemic genera. Although originally assigned to several unrelated tribes (HANSEN 1991, 1999a,b), *Andotypus* Spangler, 1979, *Anticura* Spangler, 1979, *Cylorygmus* Orchymont, 1919 and *Pseudorygmus* Hansen, 1999 were recently placed into the subfamily Rygmodinae (SHORT & FIKÁČEK 2013), whereas *Hydracara* Knisch, 1925 is considered as a member of the tribe Hydrobiusini (SHORT & LIEBHERR 2007, SHORT & FIKÁČEK 2013). None of these genera was, however, available in DNA-grade and their subfamily and/or tribal assignment by SHORT & FIKÁČEK (2013) was hence largely based on indirect clues (distribution, phylogenetic position and morphology of supposedly related taxa, larval morphology). To fill in this gap, an expedition to central Chile was organized at the end of 2013 in order to re-collect fresh material of the four aforementioned rygmodine genera. In parallel, material of these genera accumulated during recent expeditions by A. Newton and M. Thayer, as well as additional specimens found in other museums, were examined.

The genus *Pseudorygmus* is a nice example of the scarcity of information about the austral South American Hydrophilidae. It was first discovered by A. Flint, under stones close to the glacier in Fiordo Peel in southern Chile in 1969, and treated rather in detail by SPANGLER (1974), who, however, considered it conspecific with the only Chilean endemic described at that time, *Cylorygmus lineatopunctatus* Orchymont, 1933. Paul Spangler himself, collected the same species along with its larva and pupa in 1978, much further north in the Los Lagos Region, later publishing the description of the immature stages (SPANGLER 1979a). Six years later, MORONI (1985) studied a series of rygmodine hydrophilid from the Valparaíso and Metropolitan Regions and found it not to correspond to SPANGLER's (1974) redescription of *C. lineatopunctatus*. He realized that the specimens in his hands had to be the true *Cylorygmus lineatopunctatus* (as the type locality of the species was in Valparaíso Region), and formally described the southern species as *Cylorygmus flintispangleri* Moroni, 1985. HANSEN (1999a) later reexamined both *C. lineatopunctatus* and *C. flintispangleri* and realized that they differ in several crucial characters (proportions of the gula, size of the maxillary palpi in males, the presence/absence of a basal tooth in the tarsal claws, and presence/absence of metallic coloration) and therefore cannot be congeneric. He placed the southern species into a new genus *Pseudorygmus* Hansen, 1999, assuming it is closely related to the New Zealand endemic genus *Rygmodus* White, 1846. During the 2013 expedition, we succeeded to collect fresh specimens of *Pseudorygmus* in the La Araucanía Region, from where it was never recorded before. Surprisingly, it was revealed to be an undescribed species and its DNA sequences, moreover, indicate that the genus does not belong to the Rygmodinae as supposed by all previous authors.

In the present contribution we summarize all available data on the genus *Pseudorygmus* and transfer the genus from Rygmodinae to Chaetarthriinae: Anacaenini. This transfer also

provided morphological data supporting the internal phylogeny of Anacaenini revealed in previous analyses, including the polyphyly of *Anacaena* Thomson, 1859, which is discussed in detail. In addition, we also summarize all known records of the remaining four genera endemic to austral South America, and provide models of their potential distribution. The results should provide basis for future collecting effort in areas in which occurrence is probable, based on currently available data. We hope it may help to accumulate more precise data about the distribution and biology of the respective genera, as this still remains rather poorly known.

Material and methods

Depositories of examined material.

- BMNH Natural History Museum, London, United Kingdom (M. Barclay);
FMNH Field Museum of Natural History, Chicago, USA (A. F. Newton);
JBCC Juan E. Barriga collection, Curico, Chile;
MNNC Museo Nacional de Historia Natural, Santiago de Chile, Chile (M. Elgueta);
NHMW Naturhistorisches Museum, Wien, Austria (M. A. Jäch);
NMPC National Museum, Praha, Czech Republic (M. Fikáček, J. Hájek);
SEMC University of Kansas, Lawrence, USA (A. E. Z. Short);
USNM Smithsonian Institution, National Museum of Natural History (C. Micheli);
ZMUC Zoological Museum, University of Copenhagen, Denmark (A. Solodovnikov).

Taxonomy and adult morphology of *Pseudorygmus*. The study is based on the majority of known specimens of *P. flintispangleri*, and a series of the recently collected new species. Few specimens of both species were dissected, with genitalia embedded in a drop of alcohol-soluble Euparal resin. Two specimens of the new species were completely dissected, cleaned in KOH solution, bleached in hydrogen peroxide, and examined as permanent Euparal slides. Wings of one dissected specimen were kept in dry condition between a slide and a cover-glass. External morphology of both species was also examined with a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum in Prague (in both cases using uncoated specimens). Habitus photographs were taken using Canon D-550 digital camera with attached Canon MP-E65mm f/2.8 1–5× macrolens, and subsequently adapted in Adobe Photoshop CS2. Drawings were traced from photographs taken using the same equipment. Morphological terminology largely follows KOMAREK (2004) and FIKÁČEK (2010). Higher-level classification follows recent changes introduced by SHORT & FIKÁČEK (2013).

Comparison of larval morphology. We used the following sources of larval morphological data for the comparison of larvae of the Anacaenini:

Published data. *Crenitis morata* (Horn, 1890) (ARCHANGELSKY 1997); *Anacaena suturalis* (LeConte, 1866) (ARCHANGELSKY & FIKÁČEK 2004, described under name *A. cordobana* Knisch, 1924); *Anacaena limbata* (Fabricius, 1792) (RICHMOND 1920, described under name *Paracymus subcupreus* (Say, 1825), see ARCHANGELSKY & FIKÁČEK (2004) for details), *Pseudorygmus flintispangleri* (Moroni, 1985) (SPANGLER 1979a; described under the name *Cylorygmus lineatopunctatus* Orchymont, 1933).

Examined larvae.

Anacaena limbata (Fabricius, 1792): 4 first instar larvae reared from adults (NMPC): **CZECH REPUBLIC: BOHEMIA:** Praha, Prokopské údolí valley, 1.iv.2007, M. Fikáček lgt.; 6 first instar larvae reared from adults (NMPC): **MORAVIA:** Zlín-Jaroslavice, 2.iv.2007, M. Fikáček lgt.

Anacaena lutescens (Stephens, 1892): 7 first instar larvae reared from adults (NMPC): **CZECH REPUBLIC: MORAVIA:** Zlín-Jaroslavice, 2.iv.2007, M. Fikáček lgt.

Anacaena sp.: third instar larva (NMPC): **CZECH REPUBLIC: BOHEMIA:** Soběšice env., from soil sample, 1.vi.1986, J. Vilimová lgt. [The larva corresponds in all characters with above first instar larvae, and most probably belongs to one of the aforementioned species as these are very common in the Czech Republic].

Crenitis punctatostrata (Letzner, 1840): larva of unknown instar (NMPC): **CZECH REPUBLIC: BOHEMIA:** Přebuz env., Rolava, Lieche (= Rolavský rybník), pond with peaty banks, berlesate *Sphagnum*, 7.ix.2011, P. Kment lgt. [the morphology of this larva corresponds with the description of the larva of *C. punctatostrata* by VAN EMDEN (1932) and with that of *C. morata* by ARCHANGELSKY 1997; *C. punctatostrata* is the only species of the genus occurring in Central Europe].

Unidentified species of *A. suturalis* group: 15 larvae (NMPC, SEMC): **COSTA RICA: CARTAGO:** Tapanti National Park, 16.iii.2010, G. Gustafson lgt. (sample CR10-0316-B2A) [the morphology of these larvae closely correspond to the described larvae of *Crenitis morata* and *Anacaena suturalis*, their assignment to *Crenitis* was excluded as no species of that genus is known from Central America].

DNA sequencing and phylogenetic analysis. DNA was isolated from a single adult specimen (paratype) of *Pseudorygmodus versicolor* sp. nov. and three specimens of *Anticura flinti* Spangler, 1979, each from a different region (PN Nahuelbuta in Coastal Cordillera, PN Villarica and PN Puyehue in the Andes Mts.; these specimens are mentioned in the discussion). Sequences of four genes were amplified for *P. versicolor*, two mitochondrial: cytochrome oxidase I and II (*cox1* and *cox2*), and two ribosomal: 18S and 28S. For *A. flinti*, only *cox1* was amplified for this study. Methods for DNA isolation, contig assembly, sequence editing, and alignment follow SHORT & FIKÁČEK (2013) with modifications as described by FIKÁČEK et al. (2013). Amplified sequences were submitted to GenBank under the accession numbers KM262050-KM262053 for *P. versicolor*, and KM262054-KM2056 for *A. flinti*. A set of phylogenetic analyses were performed to reveal the phylogenetic position of *Pseudorygmodus*, in all cases based on the data and taxon sampling used by SHORT & FIKÁČEK (2013). The first quick analysis, based on *cox1* sequences only, was performed to get the basic idea about the position of the Chilean endemic genera within the Rygmodinae – *Pseudorygmodus* was revealed as sister to the outgroup (*Chasmogenus ruidus* Short, 2005) instead of a member of the Rygmodinae. A quick morphological study was then performed in order to estimate the possible position of *Pseudorygmodus*, and the New Zealand endemic *Horelophus* Orchymont, 1913 was estimated as a possible sister-group. Based on this estimate, a second analysis was performed based on all four genes amplified, containing few representatives of each subfamily and tribe except for the Hydrophilinae (which were excluded as potential placement due to the morphology of the mesofurca: FIKÁČEK et al. 2013, SHORT & FIKÁČEK 2013 for details) – *Pseudorygmodus* was placed within the Anacaenini as expected. Based on this result, a third analysis was performed, focused on revealing the placement of *Pseudorygmodus* within the Anacaenini; results of this analysis are presented in this study. The analysis contains 29 taxa: all taxa of the Chaetarthriinae used by SHORT & FIKÁČEK (2013) (but we kept only a single specimen

of each species), selected representatives of the Acidocerinae and Enochrinae (in all cases those for which all four genes were available, were used), and *Hydrobius fuscipes* as the outgroup (the only representative of the Hydrophilinae in the analysis). The sequences were newly aligned to incorporate the new data, with the final concatenated alignment consisted of 3915 sites. Models of sequence evolution under different partition schemes were compared using PartitionFinder (LANFAR et al. 2012). A phylogenetic tree was constructed under Bayesian inference with MrBayes v. 3.1.2 (HUELSENBECK & RONQUIST 2001) using four chains of 10,000,000 generations and sampling the chain every 1000 generations. Stationarity in Monte Carlo Markov chains was determined using Tracer 1.5.0 (RAMBAUT & DRUMMOND 2007) and burn-in was set appropriately. Genetic distances between sequences of *Anticura flinti* were estimated using maximum composite likelihood model as implemented in MEGA5.1 software (TAMURA et al. 2011)

Modeling of potential distribution. To model the potential distribution of each genus, we used the maximum entropy algorithm (MaxEnt; PHILLIPS et al. 2006, ELITH et al. 2011) for the species distribution modeling. The algorithm uses a set of layers of environmental variables as a source of environmental data, and a list of geo-referenced occurrence records of the taxon. In the first step, the model of ecological niche is created for the taxon by extracting the environmental conditions from all occurrence points and their evaluation and weighting. In the second step, a potential distribution is predicted using that model, i.e. the ecological niche of the taxon is mapped.

As occurrence data, we summarized all available (published and unpublished) records for the five austral endemic genera (*Andotypus*, *Anticura*, *Cylorygmus*, *Hydamara* and *Pseudorygmus*). In *Pseudorygmus* and *Andotypus*, which contain two species each, both species were included in the analysis of the respective genus, as we expect similar climatic requirements for congeneric species (tested recently for *Andotypus* and related taxa by FIKÁČEK et al. (2014), for *Pseudorygmus* we expect the same situation). As environmental data, we used the high-resolution climate data available in Worldclim database downloaded from <http://www.worldclim.org/> (HIJMANS et al. 2005) containing 19 layers summarizing the most important temperature and precipitation data, including their seasonality. As the number of records is very low (<15) in four of the five evaluated genera, we did not divide the occurrence data into training and validation subsets, and did not test discriminative power of the model by the actual occurrence data. The analysis was performed by a R script, using the *maxent* command of the *dismo* package. After mapping the ecological niche of the genus, we converted the prediction values (which are continuous between 0 and 1 and are difficult to interpret) into binary (presence/absence) using the threshold for equal or maximum training sensitivity (i.e. success of predicting presence) and specificity (i.e. success in predicting absence) provided as the output of the particular model. Basic outputs of the model (AUC, main thresholds) are summarized for each genus. The calibration of the model was always done in the area shown in the respective map.

Review of the genus *Pseudorygmus*

Genus *Pseudorygmus* Hansen, 1999

Pseudorygmus Hansen, 1999a: 143.

Pseudorygmus: SHORT & FIKÁČEK (2013): 737 (assigned to subfamily Rygmodinae).

Type species. *Cylorygmus flintispangleri* Moroni, 1985 (original designation).

Diagnosis. Adult. *Pseudorygmus* may be easily distinguished from all other hydrophilid genera by the combination of the following characters: (1) elytra with metallic sheen (Figs 1–2, 5–6), (2) elytron without scutellar stria (Fig. 24), (3) labrum exposed and well sclerotized (Figs 3–4, 7, 57–58), (4) antenna with 9 antennomeres (Fig. 16), (5) antennal club loosely segmented (Fig. 16), (6) gular sutures fused (Figs 35–36), (7) prosternum very short with distinct transverse groove (Figs 35, 37–38), (8) anapleural sutures present, dividing mesoventrite from other parts of mesothorax (Figs 18, 39, 41), (9) mesoventrite without distinct median elevation or projection (Figs 39, 41), (10) first abdominal ventrite without median longitudinal carina (Figs 25, 30), (11) posterior margin of abdominal ventrite 5 without notch (Fig. 26), (12) pro- and mesofemora densely pubescent in basal two thirds, but metafemur bare, (13) legs without swimming hairs on tibiae or tarsi, and (14) basal meso- and metatarsomere much shorter than tarsomere 2 (Figs 27–28).

Adults of *Pseudorygmus* keys out to the Anacaenini using the keys of HANSEN (1991), and to couplet 23 (containing Anacaenini, part of Rygmodinae and *Hybograalius* Orchymont, 1942) in the tribal key by SHORT & FIKÁČEK (2013). It may be distinguished from all genera of the Anacaenini except *Horelophus* (as well as from all Rygmodinae and *Hybograalius*) by the reduced gula and fused gular sutures. In contrast to *Horelophus*, *Pseudorygmus* has the pronotum narrowing anteriorly (subquadrate in *Horelophus*) and its prosternum is extremely short (very long in *Horelophus*), and both genera also never live together (*Horelophus* is endemic to New Zealand: FIKÁČEK et al. 2012).

Larva (based on SPANGLER 1979a). *Pseudorygmus* is easy-to-recognize by the large ligula projecting much further than the labial palps (Fig. 66) and frontal sulci not joining posteriorly into the coronal sulcus (Figs 62–63), both of which assign the larva to the subfamily Chaetarthriinae. Within Chaetarthriinae, it is most similar to *Anacaena* Thomson, 1859 (not to *Crenitulus* Winters, 1926, for details see Internal phylogeny of Anacaenini below) by the presence of the nearly symmetrical nasale with five teeth, of which the medium one is lower than the remaining four (Fig. 69). *Pseudorygmus* is not co-occurring with any member of *Anacaena* in its range nor in the habitat it lives in, and its larva is hence easy-to-identify. In Chile, it may co-occur with larvae of *Anticura* (which differs by the short ligula, nasale bearing only two teeth and frontal sulci converging posteriorly: SPANGLER 1979b, ARCHANGELSKY 1997) and possibly also *Enochrus* (*Hugoscottia*) (which differs by the short ligula, asymmetrical nasale with variable number of small teeth and frontal sulci converging posteriorly: FERNÁNDEZ 1992).

Adult morphology. Body elongate, moderately convex. General coloration of dorsal surface dark brown to black, with greenish or bluish metallic sheen; ventral parts reddish brown to dark brown.

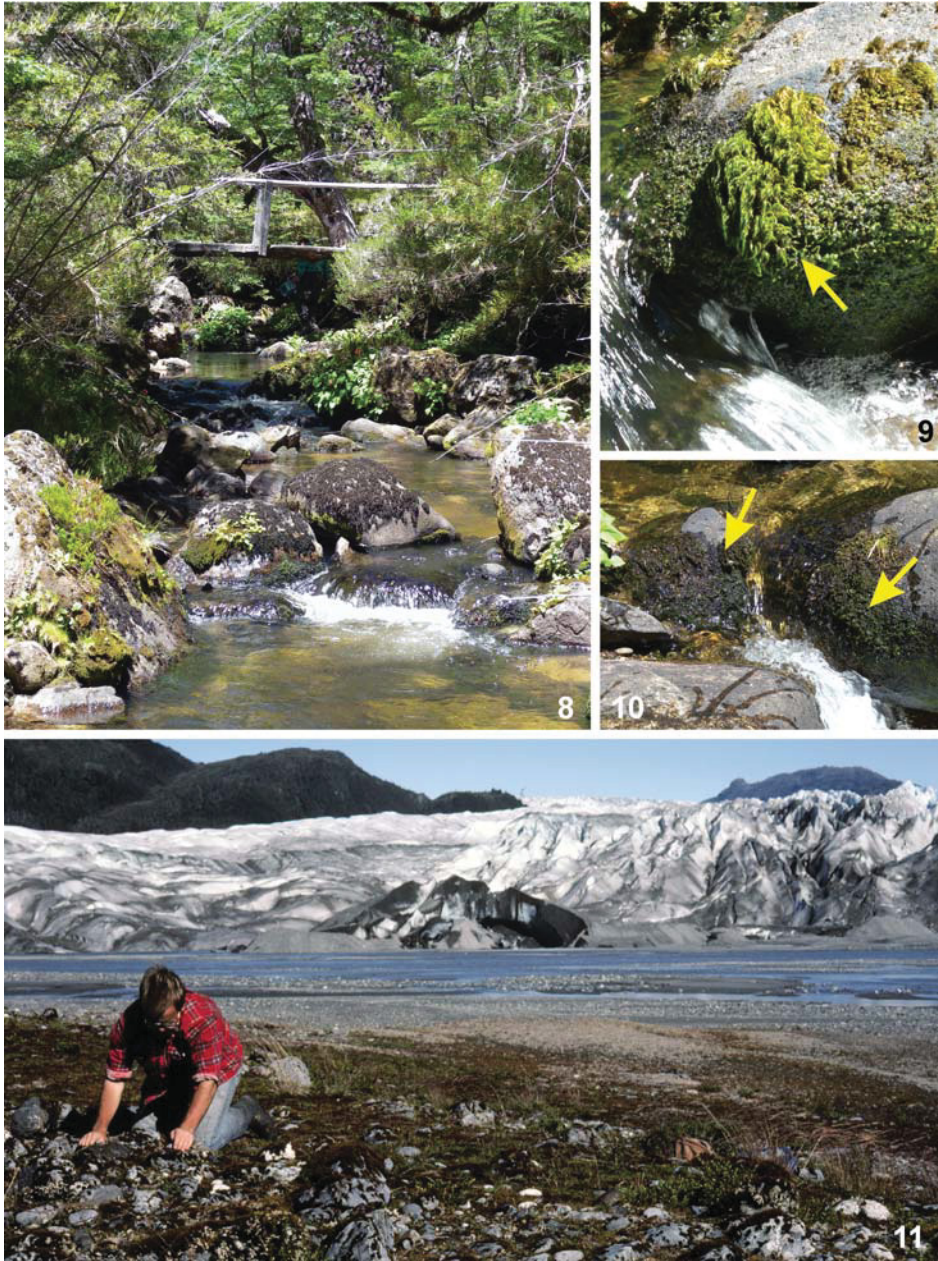
Head. *Clypeus and frons* with sparse punctation, each puncture bearing very short apically widened seta, trichobothria absent on frons and clypeus; frontoclypeal suture indistinct; clypeus covering bases of antennae anterior of eyes, slightly projecting anteriorly sublaterally, shallowly concave on anterior margin, membrane between clypeus and labrum not or only very narrowly exposed. *Eyes* small, slightly protruding from outline of head, separated by 4–5× the width of one eye. *Labrum* largely exposed dorsally, only slightly retracted under clypeus at base, widest subbasally, narrowed basally and arcuately narrowing anteriorly, shallowly bisinuate on anterior margin (Fig. 13); dorsal surface with two long setae anterolaterally and a transverse row of long setae (trichobothria) inbetween (Figs 57–58), ground punctation similar to that on clypeus; epipharynx with a lateral row of 4–5 stout setae on each side, median portion with two vertical rows of long cuticular spines and cone-shaped group of similar spines anteriorly, sublateral portion on each side with oval/circular porose field, basal portion with densely pubescent membranous cone. *Mandibles* (Fig. 12) symmetrical, with distinct mandibular angle, mandibular apex bifid; mediobasal portion with a group of long cuticular projections, medioproximal portion with fine setae, mola moderately large, bearing numerous backwards directed setae on median face. *Maxilla* (Fig. 14) with a simple subtriangular cardo lacking trichobothria; basistipes triangular, bearing few stout setae (some of them with dough-nut socket); mediostipes rather vaguely delimited from lacinia, the latter membranous, bearing fine hair-like setae mesally and few stouter and longer setae distally, distal portion of lacinia subdivided into dorsal and ventral lobe; galea short, rounded apically, with distal setae arranged into well-defined rows; palpifer rather small, with few rather long setae; palpomeres 2–4 enlarged or not, sexually dimorphic or of the same morphology in both sexes (Figs 49–52); base of palpomere 4 with a group of digitiform sensilla on dorsolateral surface (Figs 14 (detail), 32–33). *Labium* (Figs 15, 35–36) with submentum slightly shorter and as wide as mentum, bearing sparsely arranged setae; mentum 1.0–1.3× as wide as long, with continually strongly convex anterior margin, its surface flat, without microsculpture, bearing a few large setae (many of those with dough-nut sockets), lateral margins with sparse rows of long setae; prementum subdivided into two membranous lobes bearing fine long setae, palpifer vaguely sclerotized; labial palpus with three palpomeres, palpomere 1 minute, palpomere 2 subequal in length to palpomere 3; palpomere 2 with two long subapical setae; palpomere 3 with numerous small distal short setae and one digitiform sensillum. *Antenna* (Figs 16, 31) with 9 antennomeres, scapus subcylindrical, ca. 2× longer than pedicel, pedicel widest at midlength, bearing few pore-like sensilla and one tiny seta, antennomeres 3–5 rather long, their combined length ca. 1.5× longer than pedicel, cupula small, antennomeres 7–9 forming a distinct, loosely segmented and densely pubescent antennal club; antennomere 9 slightly longer than antennomere 7 and 8 each. *Gula* (Figs 35–36) completely reduced posteriorly, with gular sutures confluent, extremely narrow to totally reduced anteriorly, tentorial pits closely aggregated or totally confluent. *Temporae* without distinct ridge arising from inner margin of each eye.

Prothorax. *Pronotum* weakly and evenly convex, subtrapezoid in shape, widest basally, narrowing anteriorly, anterior corners strongly projecting; lateral margins not forming continuous curve with lateral margins of elytra, anterior margin deeply bisinuate, posterior margin weakly bisinuate; ground punctation sparse and rather fine, trichobothria missing; complete anterior, lateral and posterior margins with fine marginal bead (Fig. 46). *Hypomeron* without distinctly

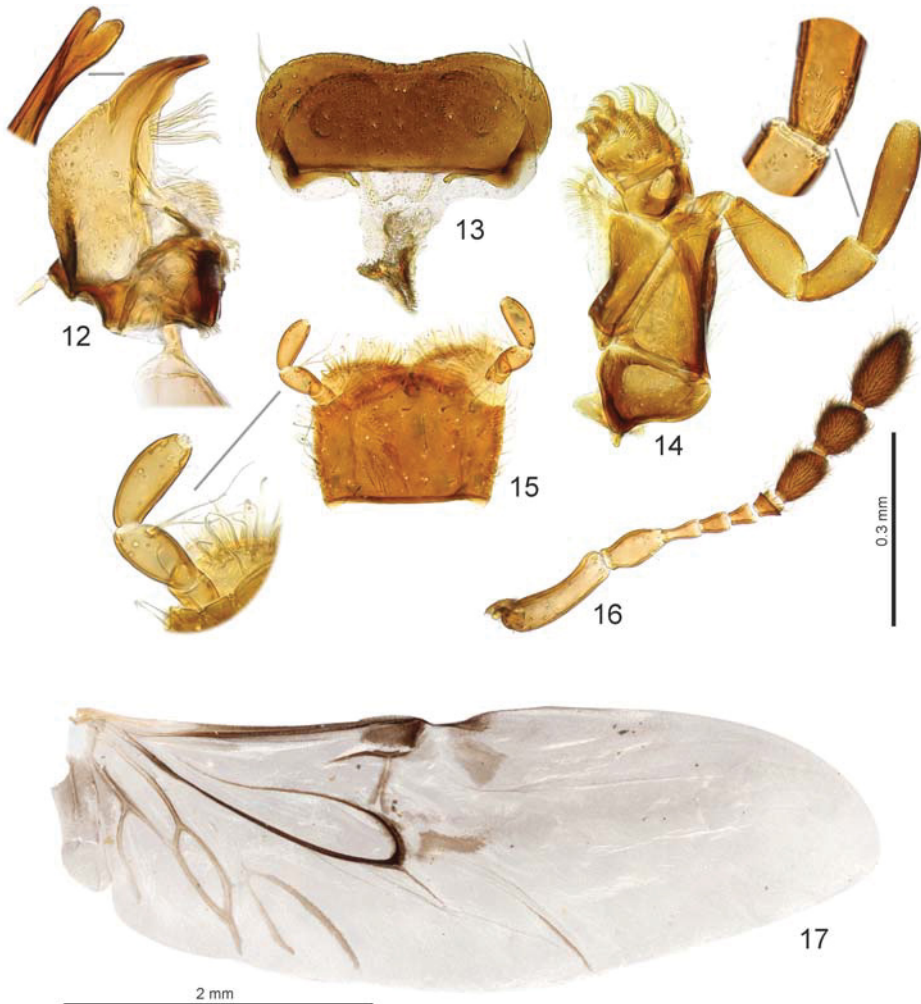
defined lateral glabrous portion, only the lateralmost portion without pubescence, median portion densely pubescent; border between pronotum and hypomeron with series of pits with dough-nut sockets, without distinctly projecting sensilla; hypomerical process large, triangular, rounded mesally. **Prosternum** (Figs 21, 35, 37–38) very short anterior to procoxae, ca. 0.3×



Figs 1–7. Habitus of the species of *Pseudorygmodus* Hansen, 1999. 1–3 – *P. flintispangleri* (Moroni, 1985), male from Magellanes: Fiordo Eyre (1 – dorsal, 2 – lateral, 3 – frontal); 4 – same species, female from PN Puyehue. 5–7 – *P. versicolor* sp. nov., female from PN Nahuelbuta, Estero Agua de los Gringos (5 – dorsal, 6 – lateral, 7 – frontal).

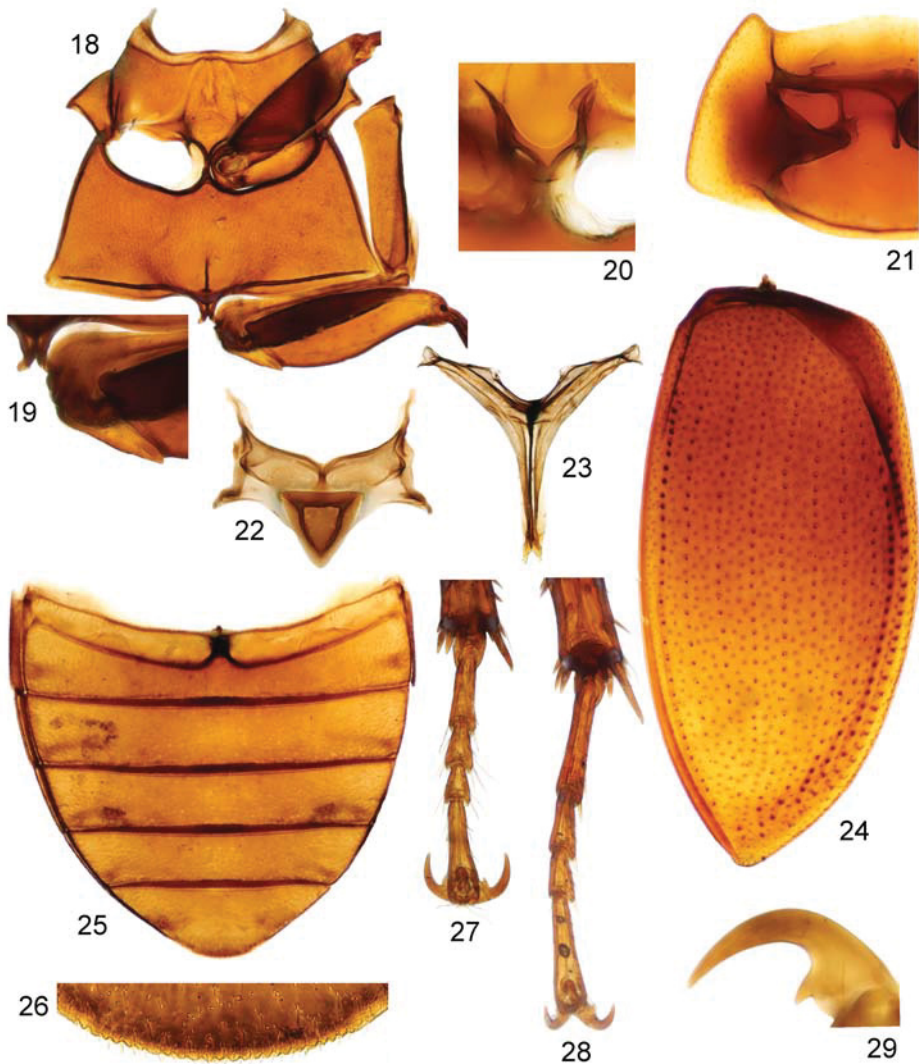


Figs 8–11. Habitats of *Pseudorygmodus* species. 8–10 – type locality and habitat of *P. versicolor* sp. nov. (8 – general view of Estero Agua de Los Gringos, PN Nahuelbuta, Chile. 9–10 – details of microhabitat: wet mosses in the splash zone above the water level which were collected and from which the specimens were subsequently floated). 11 – M. J. Gunderson collecting *P. flintispangleri* (Moroni, 1985) at glacier margin on moraine at Fiordo Bernardo, Aysén Region, Chile, 4.ii.1985 (photo by A. C. Ashworth).



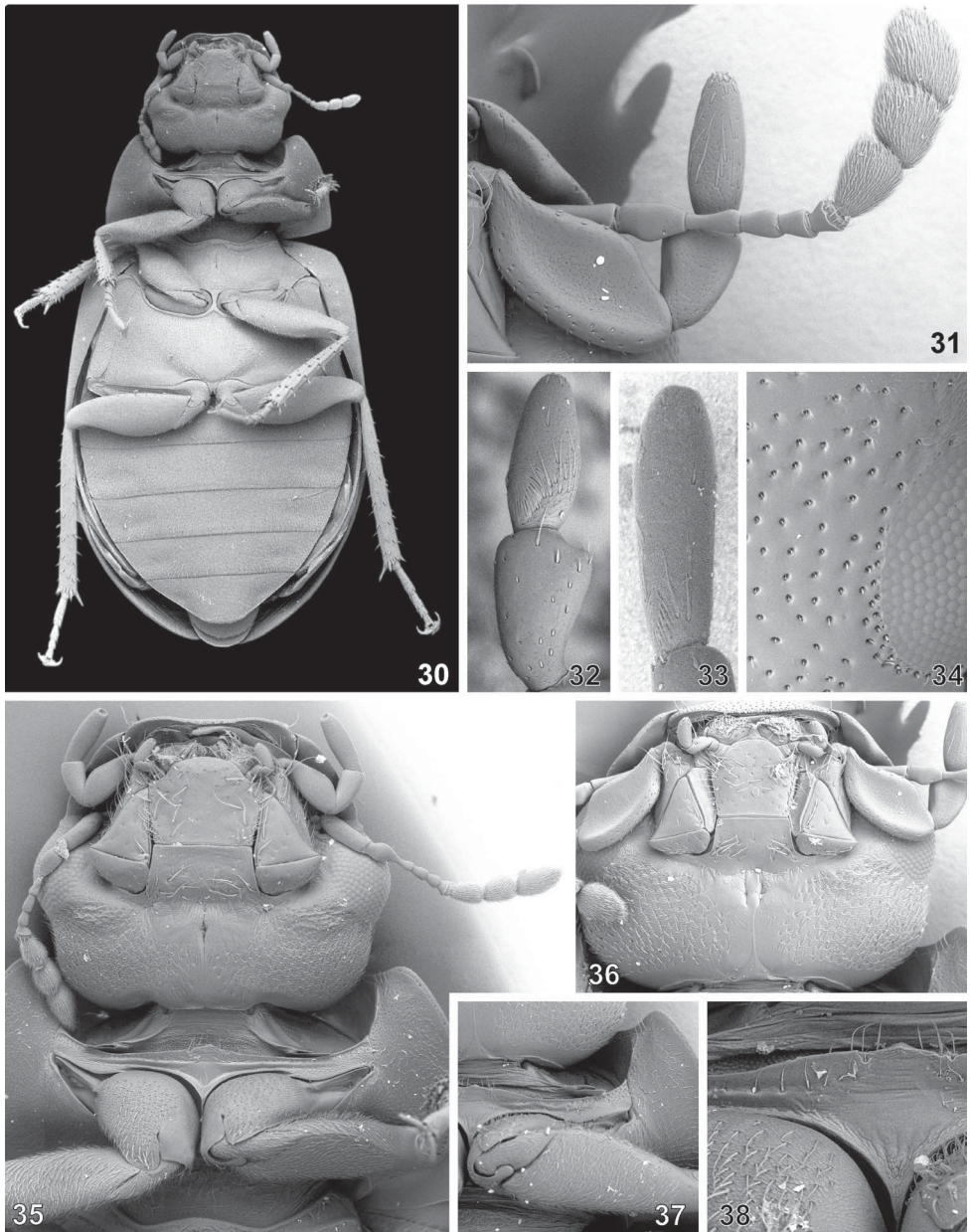
Figs 12–17. *Pseudorygmodus versicolor* sp. nov., slide-mounted male paratype: morphology of head appendages (12–16) and metathoracic wing (17). 12 – mandible, ventral view (detail = mandibular apex in ventromesal view); 13 – labrum, ventral view; 14 – maxilla, ventral view (detail = digitiform sensilla on base of palpomere 4); 15 – mentum and prementum, ventral view (detail = labial palp); 16 – antenna; 17 – wing.

as long as procoxal cavity, with transverse ridge at least submedially, anterior margin slightly projecting mesally, with irregularly serrate shape and series of long setae, prosternal process very narrow, concealed between procoxae. **Coxal cavity** closed internally, open posteriorly, coxal fissure widely open and not distinguished from coxal cavity, notopleural suture distinct. Accessory ridge below posterior pronotal margin laterally obliterated, recognizable as short and indistinct ‘transverse fold’. **Profurca** consisting of two widely separated projections directed posteromesally at base, bent laterad and slightly widened into narrowly asymmetrical apically.

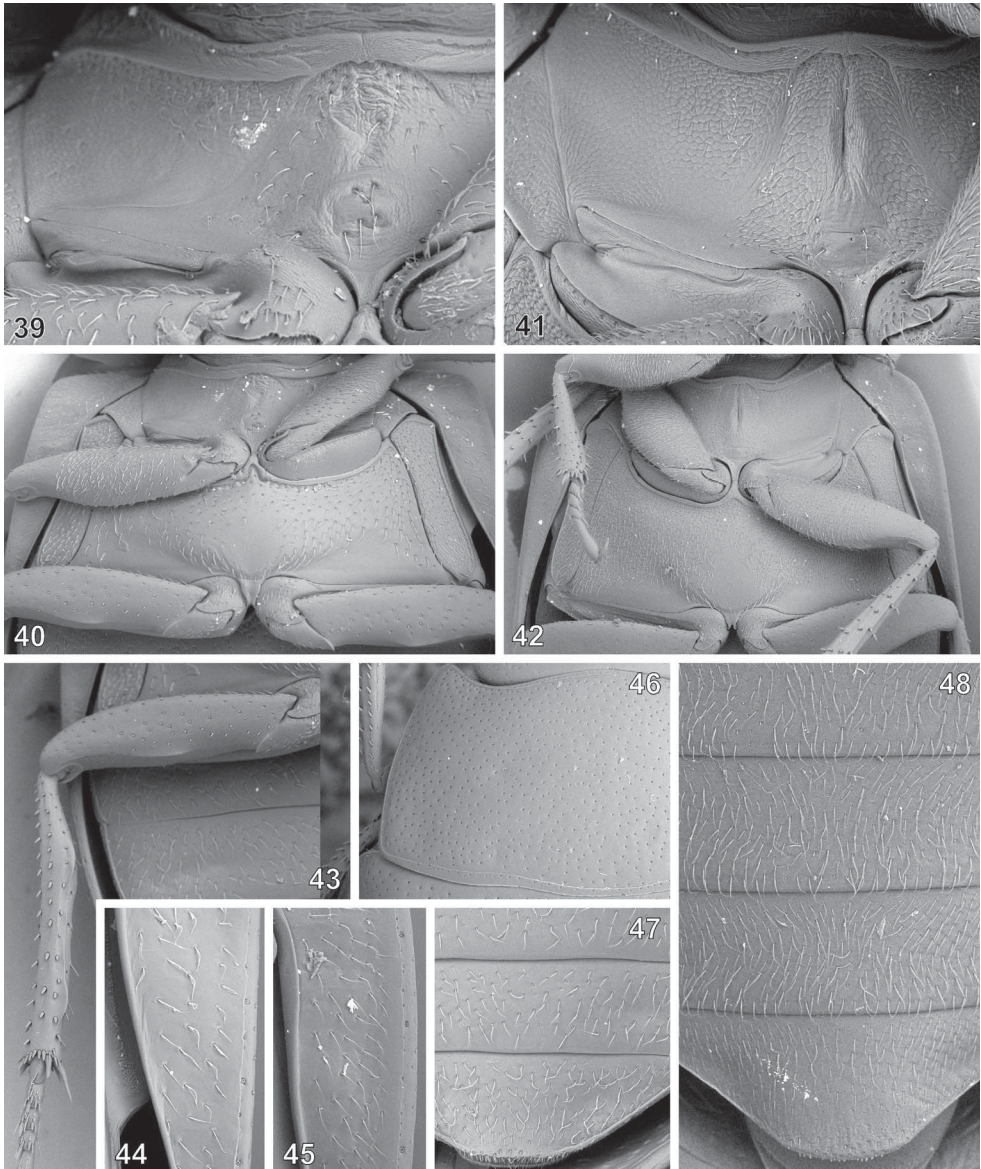


Figs. 18–29. Morphology of *Pseudorygmodes versicolor* sp. nov., slide-mounted male paratype. 18 – meso- and metathorax, ventral view; 19 – detail of metatrochanter; 20 – mesofurca; 21 – half of prothorax in ventral view; 22 – mesoscutellum, dorsal view; 23 – metafurca; 24 – elytron, ventral view; 25 – abdominal ventrites, ventral view; 26 – detail of posterior margin of abdominal ventrite 5; 27 – mesotarsus; 28 – metatarsus; 29 – protarsal claw. Not to scale.

Mesothorax. Scutellum (Fig. 22) with finely microsculptured median portion, bearing sparsely arranged setae; scutellar shield exposed, triangular, pointed posteriorly, slightly longer than wide, with a few fine setae present on its surface. **Elytron** (Fig. 24) elongate, evenly convex; sutural stria present, reaching ca. apical third to half of elytral length; elytral series more or less regular, formed of punctures of only slightly larger size and slightly more densely



Figs 30–38. Morphology of *Pseudorygmodus* Hansen, 1999, SEM micrographs. 30, 33, 35 – *P. versicolor* sp. nov.; 31–32, 34, 36–38 – *P. flintispangleri* (Moroni, 1985), male. 30 – ventral morphology; 31 – detail of antenna and male maxillary palpus, ventral view; 32 – maxillary palpomeres 3–4 in dorsal view, with digitiform sensilla; 33 – maxillary palpomere 4 in dorsal view, with digitiform sensilla; 34 – punctuation of frons next to eyes; 35 – head and prothorax in ventral view; 36 – head in ventral view; 37–38 – prothorax.



Figs. 39–48. Ventral morphology of *Pseudorygmodus* Hansen, 1999, SEM micrographs. 39–40, 43–44, 46–47 – *P. flintispangleri* (Moroni, 1985), male; 41–42, 45, 48 – *P. versicolor* sp. nov. 39, 41 – mesoventrite; 40, 42 – meso- and metaventrite; 43 – male metafemur and metatibia; 44–45 – detail of epipleuron; 46 – detail of pronotum; 47–48 – detail of abdominal ventrites.

arranged than interval punctation; scutellary stria absent, not visible even in slide-mounted elytron; elytral trichobothria absent, punctures of elytral series and intervals each bearing a very short apically slightly widened seta; lateral edge with a narrow bead, straight; epipleuron moderately wide anteriorly, gradually narrowing posteriad, very narrow in posterior half of elytral length, but reaching elytral apex; lateral bare portion of epipleuron very narrow, divided from median pubescent portion by a fine ridge with series of pit-like dough-nut sockets without projecting setae (Figs 44–45); ventral surface without any elevated ridges, only with a narrow longitudinal field of fine spines situated sublaterally between anterior fourth and midlength. **Mesoventrite** (Figs 18, 39, 41) distinctly divided from mesanepisternum by distinct anapleural suture; subtrapezoid in shape in anterior two thirds, widely extended laterad in posterior third, coxal lobes of lateral extensions rather small; mesoventrite only very slightly bulged mesally, without distinct protuberances or ridges, bearing very sparse pubescence, medially with few trichobothria; mesoventral process narrow. **Mesanepisterna** meeting only at anterior margin of mesothorax; anterior collar well-defined, moderately wide; mesal portion of each mesanepisternum pubescent, large lateral portions bare. **Mesepimeron** with large ventral portion, not reaching anterior collar or mesanepisternum anteriorly, forming lateral margin of coxal cavity; its whole surface sparsely pubescent. **Coxal cavities** obliquely transverse, ca. $2.5\times$ wider than long, very narrowly separated from each other by mesoventral and metaventral processes. **Mesofurca** (Fig. 20) well-developed, consisting only of the basal portion, furcal arms absent; basal portions arising as two widely separate projections from posterior wall of coxal cavities, apically widened into lance-like extensions.

Metathorax. Metanotum weakly sclerotized, ca. $2.2\times$ wider than long, with rather wide anterior membranous area, alacristae slightly diverging posteriad. **Metaventrite** (Figs 40, 42) ca. $1.5\times$ longer than mesoventrite, evenly convex, without defined median portion, whole surface (except for a small posteromedian area) bearing more or less dense pubescence; metaventral process narrow, contacting mesoventral process; metacoxal process short but distinctly exposed. Postcoxal ridge very narrow but well-defined, continuous medially. **Metanepisternum** ca. $4.5\text{--}6.0\times$ longer than wide, oblique transverse strengthened anterior ridge present only laterally, mesally reaching anterior margin; whole surface pubescent. **Metepimeron** not exposed ventrally. **Metafurca** (Fig. 23) rather large, Y-shaped; stalk grooved medially, without basal extensions; lateral arms rather long, with large anterobasal extensions, apical portions roundly plate-like. **Hind wing** (Fig. 17) well developed, ca. $2\times$ longer than elytron, venation well-developed in basal half, absent in distal half; anal lobe rather large, well-defined by anal notch; venation nearly identical as that of *Horelophus walkeri* (see FIKÁČEK et al. 2012), only with the following differences: RP very long, reaching subbasally; median spur longer; RP_{3+4} pigmented near posterior margin.

Legs. Coxae – procoxae subglobular, narrowly transverse, pubescent ventrally; mesocoxae transverse, rather robust mesally, narrowly separated, finely pubescent ventrally; metacoxae narrowly transverse, subrectangular in ventral view, sparsely pubescent on whole ventral surface. **Trochanters** with proximal parts concealed by coxae, distal subtriangular parts exposed ventrally, pubescent; meso- and metatrochanter projecting into a small wide spine postero-distally, not forming continuous curve with posterior face of femora, protrochanter without

such spine. **Femora** attached to trochanters by their posteromesal (meso- and metafemora) or anteromesal (profemora) portions only, anteromesal (meso- and metafemora) or posteromesal bases (profemora) free, angulate; pro- and mesofemora densely pubescent in their basal 0.65, metafemora lacking such pubescence except on extremely anterobasal portion, most of their surface bearing sparsely arranged spine-like setae; tibial grooves not defined or very slightly defined (male of *P. flintispangleri*, Fig. 43). **Tibiae** slightly longer than femora, cylindrical, slightly widening distad; each tibia with several rather irregular series of spines, distal portion with a group of enlarged spines and two rather short but stout tibial spurs; protibia oblique distally, with 2–3 large closely associated spines subdistally on outer margin closely associated with the outermost series of spines. **Tarsi** (Figs 27–28) with 5 tarsomeres, basal tarsomere short, shorter than tarsomeres 2–5 each, tarsomere 2 longest, slightly longer than tarsomere 5, tarsomeres 3–4 subequal in length. Ventral setae of all tarsomeres short, spine-like in both sexes; claws rather large, arcuate, bearing a sharp subbasal tooth (Fig. 29), shape sexually dimorphic (in *P. flintispangleri*) or identical in both sexes (*P. versicolor* sp. nov.); empodium moderately large, bearing a pair of stout subapical setae.

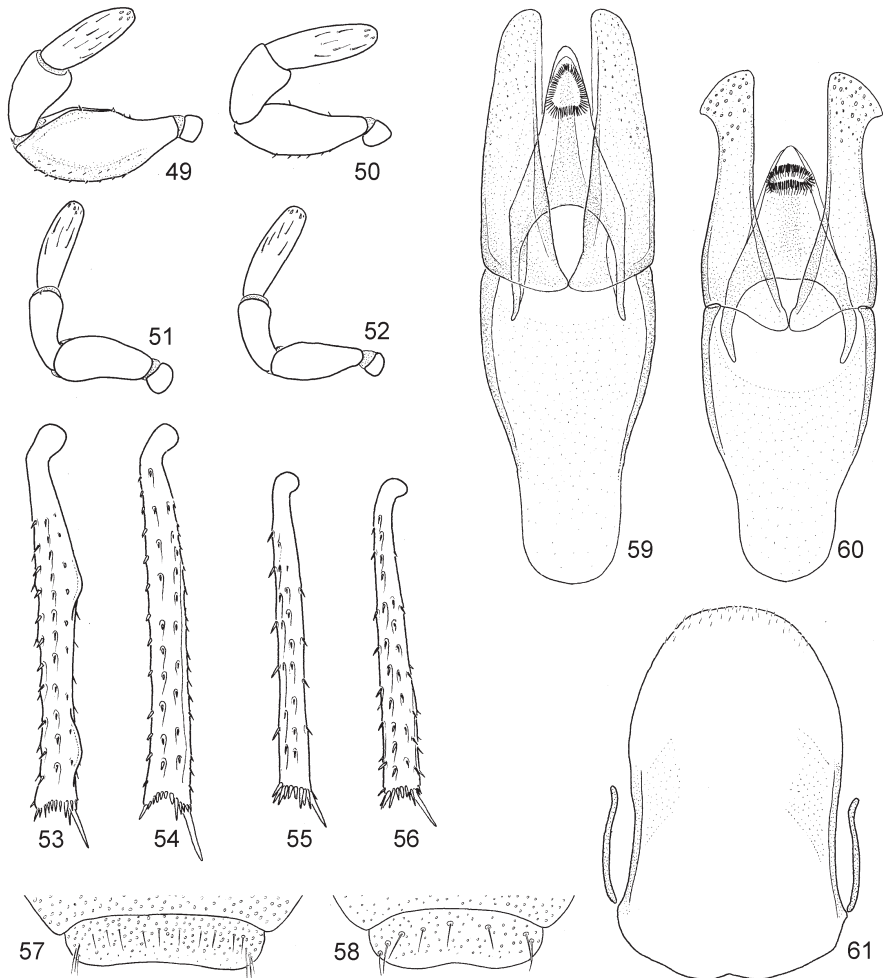
Abdomen (Figs 25, 46, 48) with five exposed ventrites; ventrite 1 with moderately large bare coxal grooves, remaining portion more or less densely pubescent, median portion without longitudinal carina; ventrites 2–5 subequal in length, more or less densely pubescent on whole surface, posterior margin of ventrites 1–4 smooth, lateral margins of ventrites 1–5 with a narrow bead; posterior margin of ventrite 5 without median emargination or group of enlarged setae, finely serrate with series of small spine-like setae; laterotergite 3 simple, dorsal portion not divided from ventral one by a ridge, bearing an area of goose-head-shaped cuticular projections, without any kind of organized stridulatory file; tergites weakly sclerotized.

Genitalia. Male genitalia (Figs 59–61). Aedeagus of simply trilobed type; parameres ca. as long as or indistinctly shorter than phallobase, bearing numerous pore-like sensilla in apical portion; median lobe ca. as long as parameres, with subtriangular apical part, basal apodemes rather long, gonopore large, well defined, apical to subapical; phallobase symmetrical, rounded basally, without distinctly defined manubrium. Sternite 9 widely tongue-like, with very short subbasal lateral struts. Sternite 8 crescent-like, smooth (i.e. not serrate) on posterior margin, densely pubescent, without anterior projection. **Female genitalia** examined only externally, with long peg-like gonocoxites 9 and gonostyli 9.

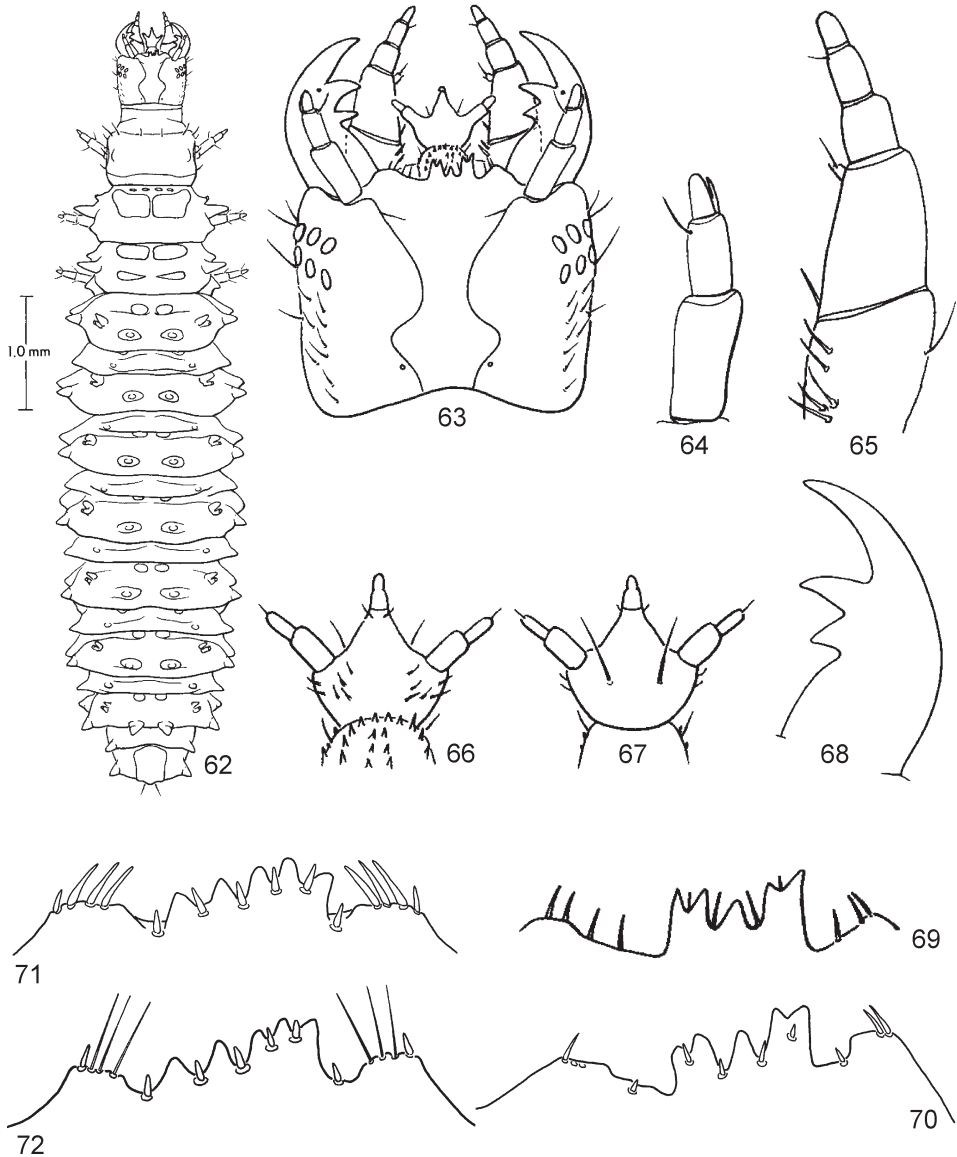
Key to species of *Pseudorygmodus*

1. Whole dorsal surface uniformly dark, at most with indistinctly defined paler coloration along lateral margins of elytra and pronotum (Figs 1–2). Maxillary palpi tickened in both sexes, moderately so in females, extremely so in males (Figs 49–50). Metaventricle and abdominal ventrites with very sparse long pubescence (Figs 40, 47). Male metatibiae with a pair of flat buldges on inner face, male femur with one such bulge on posterior margin, female without such bulges (Figs 43, 53–54). Elytral punctuation coarse (Figs 1–2). Parameres not widened apically, apex simply rounded (Fig. 59). Body larger (3.9–4.4 mm). *Pseudorygmodus flintispangleri* (Moroni, 1985)
- Dorsal surface bicolored, with wide, sharply defined, yellow lateral portions of elytra and pronotum (Figs 5–7). Maxillary palpi not thickened, of the same shape in both sexes

(Figs 51–52). Metaventrite and abdominal ventrites with dense pubescence (Figs 42, 48). Metafemora and metatibiae of both sexes simple, without flat bulges on inner or posterior margins (Figs 55–56). Elytral punctation fine (Figs 5–6). Parameres widened apically (Fig. 60). Body smaller (3.2–4.1 mm). *Pseudorygmodus versicolor* sp. nov.



Figs 49–61. Morphological details of adults of *Pseudorygmodus* Hansen, 1999. 49–52 – maxillary palpus, ventral view (49 – *P. flintispangleri* (Moroni, 1985), male; 50 – *P. flintispangleri*, female; 51 – *P. versicolor* sp. nov., male; 52 – *P. versicolor*, female). 53–56 – metatibia, ventral view (53 – *P. flintispangleri*, male; 54 – *P. flintispangleri*, female; 55 – *P. versicolor*, male; 56 – *P. versicolor*, female). 57–58 – labrum, dorsal view (57 – *P. flintispangleri*, 58 – *P. versicolor*). 59 – aedeagus of *P. flintispangleri*. 60–61 – male genitalia of *P. versicolor* (60 – aedeagus, 61 – sternite 9).



Figs. 62–72. Larval morphology of *Pseudorygmodus* Hansen, 1999 and its comparison with other genera of Anacaenini. 62–69 – larval morphology of *P. flintispangleri* (Moroni, 1985) according to SPANGLER (1979a) (62 – general habitus; 63 – head in dorsal view; 64 – antenna; 65 – maxilla; 66 – labium, dorsal view; 67 – labium, ventral view; 68 – right mandible, dorsal view; 69 – detail of clypeolabrum). 70–72 – morphology of clypeolabrum of third instar larvae of other Anacaenini (70 – *Anacaena* sp. from the Czech Republic; 71 – *Crenitis morata* (Horn, 1890), redrawn from ARCHANGELSKY (1997); 72 – *Anacaena suturalis* (LeConte, 1866), redrawn from ARCHANGELSKY & FIKÁČEK 2004).

***Pseudorygmus flintispangleri* (Moroni, 1985)**

(Figs 1–4, 31–32, 34, 36–40, 43–44, 46–47, 49–50, 53–54, 57, 59, 62–69, 74)

Cylorygmus lineatopunctatus Orchymont, 1933 (misidentification); SPANGLER (1974: 246, description of adult, notes on biology); SPANGLER (1979a: 745, description of larva and pupa).*Cylorygmus flintispangleri* Moroni, 1985: 150 (original description).*Cylorygmus flintispangleri*: ARCHANGELSKY (1997: 67, 174–176, redescription of larva and pupa).*Pseudorygmus flintispangleri* (Moroni): HANSEN (1999a: 146, transferred from *Cylorygmus*); HANSEN (1999b: 235, catalogue).**Type locality.** Chile, Magallanes Region, Fiordo Peel near glacier, ca. 50°57'S 73°45.5'W.**Type material examined.** HOLOTYPE: ♂ (USNM): '♂ // CHILE:Magal. / Fiordo Peel / nr. glacier / 1 Oct. 1969 / O.S.Flint,Jr. // NEOHOLOTYPE / Cylorygmus / lineatopunctatus / d'Orchymont [red label] // TypeNo / 72520 / USNM [red label]'. ALLOTYPE: ♀ (USNM): same locality label as holotype plus '♀ // NEOALLOTYPE / Cylorygmus / lineatopunctatus / d'Orchymont [red label] // TypeNo / 72520 / USNM [red label]'. PARATYPES: 4 ♂♂ 1 ♀ (USNM): same locality data as the holotype plus 'NEOPARATYPE / Cylorygmus / lineatopunctatus / d'Orchymont [blue label]'; 2 ♂♂ 2 ♀♀ (USNM): 'CHILE:Magal. / I.Desolacion / Pto. Churruca / 5 Oct. 1969 / O.S.Flint,Jr. // NEOPARATYPE / Cylorygmus / lineatopunctatus / d'Orchymont [blue label]' [GPS data ca. 53°2'S 73°56'W]. We labelled each specimen with label 'HOLOTYPE [respectively ALLOTYPE or PARATYPE] / CYLORYGMUS / flintispangleri / Moroni, 1985 / M. Fikáček labelled' and also attached the identification label 'PSEUDORYGMODUS / flintispangleri / (Moroni, 1985) / M. Fikáček det. 2014'.**Additional material examined:** CHILE: Los LAGOS: 3 ♂♂ 3 ♀♀ (USNM): P. N. Puyehue, Anticura, elev. 350–460 m [40°40.3'S 72°10.2'W], 12.ii.1978, P. J. Spangler lgt; 1 spec. (torso without head, prothorax and legs, NMPC): PN Puyehue, Anticura, Río Anticura between Salto Pudú and confluence with Río Golgol, floating: mosses from the stones in the river (submerged+just above water) and the flood debris accumulated in logjam, 40°40.0–40.5'S 72°9.9–10.6'W, 350–460 m, 6.–9.xii.2013, Fikáček, Kment & Vondráček lgt. LLANQUIHUE: 1 spec. (MNNC): Lago Chapo [41°27'S 72°30'W], ii.1985, J. Zuniga lgt. AYSÉN: 11 spec. (NMPC, NHMW, SEMC): Provincia Capitan Prat, Fiordo Bernardo, northern margin of Glacier Bernardo, 48°31'S 73°55'W, Magellanic Moorland: under rocks, sparse vegetation of mosses, by a river on outwash plain, 4.ii.1985, A. C. Ashworth & M. J. Gunderson lgt. MAGALLANES: 2 spec. (MNNC): Fiordo Calém, elev. 150 m [48°22'S 73°33'W], 15.xii.1960, J. Ever lgt.; 5 spec. (BMNH, NMPC): Ultima Esperanza, Fiordo Eyre, Ana Maria, northern margin of Glacier Pio XI, 49°14'S 74°5'W, Magellanic Moorland, glacier margin on recently deglaciated moraine, with sparse vegetation of mosses, 10.ii.1985, A. C. Ashworth & M. J. Gunderson lgt.; 8 spec. (NMPC, NHWM, SEMC): Provincia Capitan Prat, Fiordo Tempanos (Iceberg), northern side of Glacier Tempanos, 48°44'S 74°03'W, Magellanic Moorland: under rock on open, well drained grass-covered moraine, 31.i.1985, A. C. Ashworth & M. J. Gunderson lgt.; 5 spec. (NMPC): Provincia Ultima Esperanza, Fiordo Tempanos (Iceberg), southern side of Glacier Tempanos, 48°45'S 74°03'W, Magellanic Moorland: under rocks, sparse vegetation of grasses and mosses on fiord shore, 30.i.1985, A. C. Ashworth & M. J. Gunderson lgt.; 1 spec. (MNNC): Puerto Bellavista [51°28'S 73°17'W], 12.xii.1979, S. & C. Manrilla lgt.; 1 spec. (ZMUC): Tierra del Fuego, Cordillera Darwin, 25.ii.1962, E. Shipton lgt., forest litter [precise locality unknown, not included into the analysis of potential distribution].**Larva.** Not examined. The specimen described by SPANGLER (1979a) was not found in the collection of USNM (C. Micheli, pers. comm.) and the data on larval morphology used here are hence, based purely on the description by SPANGLER (1979a).**Redescription. Body.** Body elongate oval, moderately convex. Body length 3.9–4.4 mm (4.0 mm in the holotype), body width 2.4–2.7 mm (2.5 mm in the holotype). **Coloration.** Dorsal surface brown to dark brown, metallic, with very indistinctly lightened lateral margins of pronotum and elytra, epipleuron reddish-brown to dark brown. Ventral portion of head black, remaining ventral portions brown to dark brown. Maxillary palps reddish with darker palpomere 4, remaining head appendages and all parts of legs brown to dark brown. **Head.** Frons and clypeus with rather coarse, sharply impressed and rather dense punctation, interstices without microsculpture. Eyes weakly protruding, separated by ca. 4.0–4.4× the width of one eye. Labrum with punctation slightly finer and denser than on disc of clypeus, bearing a transverse series of many trichobothria with sockets as large

as surrounding punctation. Maxillary palpi sexually dimorphic, widened in both sexes, extremely so in males in which palpomere 2 is compressed, slightly concave and with numerous disc-like fields on ventral surface. Posterior tentorial pits situated very close to each other, but still distinctly separated from each other. **Thorax.** Pronotum with punctation similar to that on head, interstices without microsculpture. Elytral series rather distinct, consisting of punctures which are slightly larger but much more closely aggregated than interval punctation; interval punctation coarse and dense, slightly coarser and denser than on pronotum; interstices without microsculpture. Prosternum with medially widely interrupted transverse ridge. Mesoventrite with slightly bulged posteromedian portion bearing few setae, anteromedian portion of metaventrite without any impression; anterior portion of mesoventrite does not subdivide the posterior portion of the mesothoracic collar. Metaventrite with very sparse hydrofuge pubescence except posteromesal area and anterior of metacoxae, interstices without microsculpture, shiny; postcoxal ridge of metaventrite crenulate. **Abdomen.** Abdominal ventrites completely covered with sparse pubescence. **Legs.** Metafemur and metatibia sexually dimorphic: male femur with a pair of projecting wide low lobes at midlength, weakly defining the tibial groove at least at midlength, female femur without such lobes; male tibia deeply sinuate on inner margin, widened subbasally and subapically; female tibia subcylindrical; claws sexually dimorphic, slightly sinuate in males, arcuate in females. **Male genitalia.** Aedeagus with parameres evenly rounded apically, without apical widening; median lobe narrowly triangular, gonopore nearly circular. **Biology.** In southern Chile, repeatedly found at ocean shore close to the glaciers (once in October, five times in January/February). All specimens from southern Chile were found outside of water, usually under stones and among mosses and roots of grasses (SPANGLER 1974; A. C. Ashworth, pers. comm.; Fig. 11), one specimen was also collected from forest litter. In the north, SPANGLER (1979a) reported the finding of adults, single larva and pupae from debris and loam among grass roots caught up in logjam and driftwood, in the midstream of Río Anticura (PN Puyehue) in February. The intensive collecting in Río Anticura and surrounding rivers and streams performed by the authors between December 5–9 2013 resulted only in the discovery of one dead torso of the species floated from loam and flood debris caught up in logjams, but no living specimens were found. See Discussion for more comments on supposed habitat requirements of this species.

Distribution. Widely distributed in southern Chile, from the Los Lagos Region south to the southernmost parts of the Magallanes Region (Cordillera Darwin).

Pseudorygmodus versicolor sp. nov.

(Figs 5–7, 12–30, 33, 35, 41–42, 45, 48, 51–52, 55–56, 58, 60–61, 74)

Type locality. Chile, La Araucanía Region, Parque Nacional Nahuelbuta, 2.2 km north of Pehuenco, Estero Agua de Los Gringos stream at the place where it is crossed by Sendero Estero Los Gringos track, 37°48.5'S 73°0.7'W, 1160 m a.s.l.

Type material. HOLOTYPE: ♂ (MNNC), 'CHILE: IX. La Araucanía Region / PN Nahuelbuta, 2.2 km N of / Pehuenco, Estero Agua de Los / Gringos, 37°48.5'S 73°0.7'W / 1160m, 11–12.xii.2013 / Fikáček, Kment & Vondráček / CH37 // floated from mosses at water / level or in the splash zone at / stones at sides and in the middle / of a mountain stream'. PARATYPES: 29 spec. (NMPC, BMNH, FMNH, JBCC, MNNC, SEMC, USNM, ZMUC): same label data as the holotype.

Description. Body. Body elongate oval, moderately convex. Body length 3.2–4.1 mm (3.4 mm in the holotype), body width 1.9–2.3 mm (2.0 mm in the holotype). **Coloration.** Dorsal surface very dark brown to black, elytra with weak bluish metallic sheen; lateral parts of pronotum widely yellow and rather sharply defined from dark pronotal disc; lateral margin of elytra with a narrow yellow stripe which is rather sharply defined anteriorly but rather vaguely posteriorly, epipleuron yellow. Ventral portion of head black, mouthparts brown; prosternum brown, prothoracic hypomeron yellowish; ventral portions of meso- and metathorax dark brown, abdominal ventrites brown to dark brown. Head appendages yellowish proximally, brown to dark brown distally; femora reddish, tibiae and tarsi slightly darker, brown. **Head.** Frons and clypeus with fine but sharply impressed rather sparse punctation, interstices without microsculpture. Eyes weakly protruding, separated by ca. $5.3\times$ the width of one eye. Labrum with punctation similar to that on clypeus, bearing a transverse series of few trichobothria with sockets larger than surrounding punctation. Maxillary palpi not widened, of same morphology in male and female. Posterior tentorial pits fused together. **Thorax.** Pronotum with punctation similar to that on head, interstices without microsculpture. Elytral series rather indistinct anteromesally, more distinct posteriorly and laterally; interval punctation fine, rather sparse but sharply impressed, punctures only slightly smaller than serial ones; interstices without microsculpture. Prosternum with nearly complete transverse ridge. Mesoventrite nearly flat, only with slightly elevated posteromedian portion, bearing a longitudinal impression anteromedially, anteriorly dividing the posterior portion of the mesothoracic collar. Metaventrite with dense hydrofuge pubescence except posteromesally and anterior of metacoxae; postcoxal ridge of metaventrite straight, not crenulate. **Abdomen.** Abdominal ventrites completely covered by dense pubescence. **Legs.** Metafemur and metatibia of the same morphology in male and female; femur slender, subcylindrical, without tibial groove, tibia subcylindrical; claws not sexually dimorphic, arcuate in both sexes. **Male genitalia.** Aedeagus with parameres widened apically (chopper-like); median lobe widely triangular, gonopore narrowly transverse.

Etymology. The species name *versicolor* (Latin, colorful) reflects the dorsal coloration of this species, combining yellow, black and metallic bluish, in which it differs from *P. flinti-spangleri*.

Biology. All specimens were floated from the wet moss collected on stones in and along the mountain stream, in the splash zone just above the water-line (Figs 8–10). They co-occurred in this habitat with *Anticura flinti* Spangler, 1979 and *Enochrus (Hugoscottia) variegatus* (Steinheil, 1869) (small male specimen corresponding with those from Argentina: Junín de Los Andes identified by L. Fernández, all specimens deposited in NMPC).

Distribution. Only known from the type locality in Parque Nacional Nahuelbuta.

Phylogeny and generic classification of the Anacaenini

Results of the phylogenetic analysis. Division of the concatenated dataset into 8 partitions (each position of *cox1* and *cox2* separately, 18S and 28S) was selected as the best partition scheme. GTR with invariable sites (+I) and rate variation among sites (+G) was selected as the substitution model for the first and second positions of *cox1* and *cox2* and for 28S,

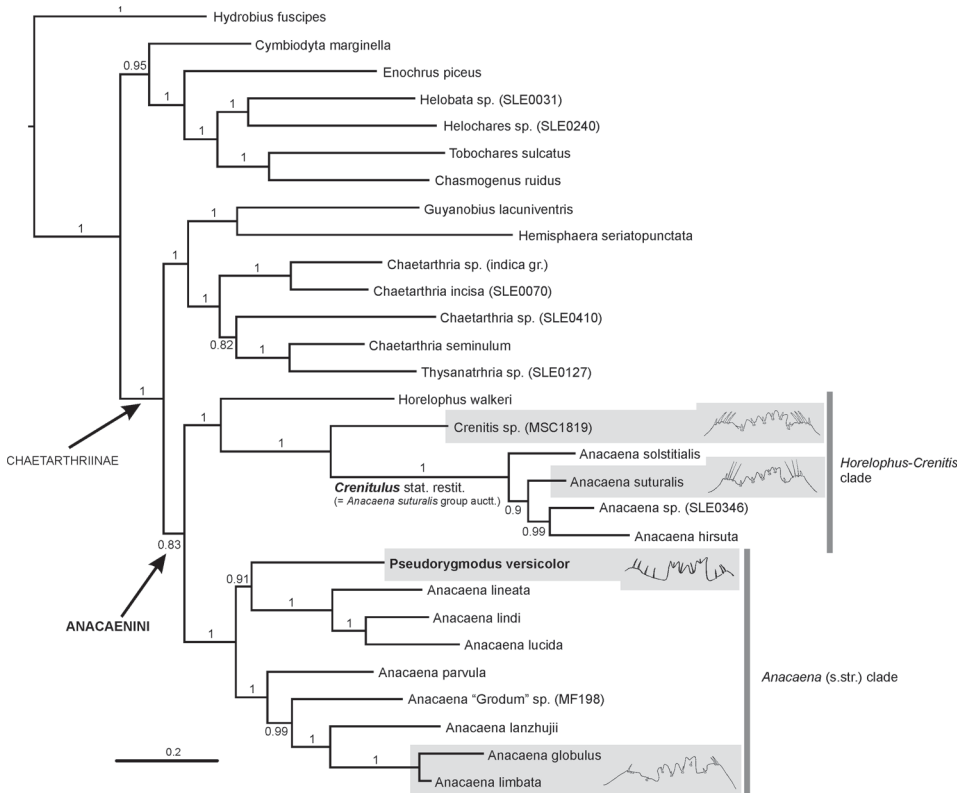


Fig. 73. Bayesian tree based on four genes concatenate (branches with posterior probability values). Clades discussed in the text are marked. *Pseudorygmus* highlighted by bold letters, morphology of the larval nasale is shown for anacaenine taxa for which larvae are known.

HKY+I+G for third positions of *cox1* and *cox2*, and K80+I+G for 18S. In the resulting tree (Fig. 73), the monophyly of the Chaetarthriinae including *Pseudorygmus* is strongly supported, as well as its three internal clades: the Chaetarthriini, the *Horelophus*+*Crenitis* clade, and the *Pseudorygmus*+*Anacaena* s.str. clade. The Anacaenini (i.e. the clade consisting of the two latter ones) is resolved as monophyletic but weakly supported. *Pseudorygmus* is resolved as the sister-group to the clade of Australian/New Guinean species of *Anacaena* with moderate support.

Position of *Pseudorygmus*. Although the placement of *Pseudorygmus* in the Anacaenini was rather unexpected, its adult and larval morphology corresponds with this position very well. The larval morphology agrees with other representatives of the Anacaenini in the large protruding ligula, nasale with five teeth, frontal sulci not converging posteriad, and maxilla with short stipes and long palpomere 1. The adult morphology of *Pseudorygmus* is very close to *Horelophus* (a member of the Anacaenini) in many aspects, e.g. in the morphology

of mouthparts, reduced gula, nine-segmented antenna with elongate antennomere 9, maxillary palpomere 4 with a group of basal digitiform sensilla dorsally, more or less flat mesoventrite with lateral wing-like projections, protibia with a group of two/three strong spines subapically, abdominal ventrite 1 without median carina, abdominal ventrite 5 without apical notch, wide male sternite 9 and very similar hind wing venation. Many of these characters seem to be present in most/all Anacaenini, but the completely reduced gula is unique for *Horelophus* and *Pseudorygmodus* within Anacaenini. Besides that, *Pseudorygmodus* also closely resembles *Horelophus* in general coloration (metallic, with yellow margination of the pronotum both in *P. versicolor* sp. nov. and *H. walkeri* Orchymont, 1913) and both genera are relicts in the southern temperate zone. It was hence surprising when *Pseudorygmodus* was not revealed as a member of the *Horelophus*+*Crenitis* clade, but as an early-branching member of the *Anacaena* s. str. clade. This position is, however, strongly supported by larval morphology (see below under Internal phylogeny of Anacaenini). Hence, the position of *Pseudorygmodus* in the *Anacaena* s. str. clade seems to be well supported, and the similarities with *Horelophus* are secondary. Based on all this evidence, we are transferring *Pseudorygmodus* from the subfamily Rygmodinae to the tribe Anacaenini of the subfamily Chaetarthriinae.

Internal phylogeny of Anacaenini. Two principal clades were already revealed within the Anacaenini in the Bayesian and maximum parsimony analyses by SHORT & FIKÁČEK (2013): the *Horelophus*+*Crenitis* clade also containing the *Anacaena suturalis* group, and the *Anacaena* s.str. clade containing all the remaining *Anacaena*. Both clades were strongly supported in all subsequent analyses based either on the same data but different software and priors/model settings (BLOOM et al. 2014) or on taxonomically more limited dataset with four genes only (this study). The inclusion of *Pseudorygmodus* into the *Anacaena* s.str. clade reveals that members of both clades largely differ in the morphology of the larval nasale: it bears a large median tooth and a couple of less defined (smaller) lateral teeth on each side in *Anacaena* s. str. and *Pseudorygmodus* (i.e. in the *Anacaena* s. str. clade, Figs 69–70, 73), whereas it consists of an oblique series of five large teeth in *Crenitis* and *Anacaena suturalis* (i.e. members of the *Horelophus*+*Crenitis* clade, Figs 71–72, 73). Within the *Anacaena* s.str. clade, the morphology of the nasale is identical in an early branching taxon (*Pseudorygmodus*) and one supposedly derived one (European *Anacaena*¹⁾), and we may hence suppose that it is shared by all members of that clade. Within the *Horelophus*+*Crenitis* clade, the larva of *Horelophus* remains unknown, but the morphology of the nasale is identical in *Crenitis* (both species with known larva) and in *Anacaena suturalis* group (*A. suturalis* and Costa Rican larvae examined for this study, see Material and methods). The *Crenitis*-like shape of the nasale (Figs 72–73) is therefore clearly a synapomorphy of at

¹⁾ European *Anacaena* otherwise correspond with other known Anacaenini in the long ligula, short maxillary stipes and long maxillary palpomere 1, both bearing numerous cuticular spines. It also agrees with larvae of *Anacaena suturalis* and *Crenitis* (and differs from *Pseudorygmodus*) in the presence of lateral lobes on the pronotum (these are similar in shape to those of *A. suturalis*, see ARCHANGELSKY & FIKÁČEK (2004)) and trifurcate posterior margin of abdominal tergite VIII (but the projections are wide and much shorter than those in *A. suturalis* and *Crenitis*). In contrast to *A. suturalis* and *Crenitis*, the antennal sensorium of European *Anacaena* is slightly shorter than antennomere 3 – the same character state is probably found in *Pseudorygmodus* (Fig. 64) and the shortened antennal sensorium may therefore represent an additional synapomorphy of the *Anacaena* (s.str.) clade.

least *Crenitis* and *Anacaena suturalis* group, but it is probable that it will also represent a synapomorphy of the whole *Horelophus*+*Crenitis* clade.

The shape of the larval nasale provides additional support for the internal topology within the Anacaenini revealed by molecular studies, and also brings additional proof of the polyphyly of *Anacaena* in current sense. The *Anacaena suturalis* group was considered likely monophyletic and was already well defined by morphological characters by KOMAREK (2005), but was not treated as a separate taxon as it would violate the monophyly of *Anacaena*. SHORT & FIKÁČEK (2013) revealed that the *A. suturalis* group is not closely related to the remaining *Anacaena*, but refrained from any taxonomic changes, as no morphological evidence supporting these molecules-based results was available. At the moment, there is strong molecular evidence for the monophyly of the *Anacaena suturalis* group, corresponding with a set of morphological adult characters diagnosing the group (see below), and there is strong molecular evidence, supported by larval morphology, that the *Anacaena suturalis* group belongs to a different clade than *Anacaena* s. str. The *Anacaena suturalis* group hence does not violate the monophyly of *Anacaena* s.str., and both taxa (*Anacaena* s. str. and *Anacaena suturalis* group) are easily distinguishable from each other both in adult and larval form. For all these reasons, we consider it unsustainable to continue to treat members of the *Anacaena suturalis* group as being within *Anacaena*. We here resurrect the genus *Crenitulus* Winters, 1926, which was previously erected for *Anacaena suturalis*, but later synonymized with *Anacaena* by ORCHYMONT (1933).

Crenitulus Winters, 1926, **stat. restit.**

Crenitulus Winters, 1926: 54. Type species: *Limnebius suturalis* LeConte, 1866 (original designation).

Crenitulus: ORCHYMONT (1933: 202, synonymized with *Anacaena*).

Gentilina Hebauer, 2003: 112, **syn. nov.** Type species: *Paranacaena nitens* Gentili, 1993 (original designation).

Gentilina: KOMAREK & BEUTEL (2007: 225, synonymized with *Anacaena*).

Anacaena suturalis group: KOMAREK (2005: 288), KOMAREK (2007: 162), FIKÁČEK & ENGEL (2011: 625); SHORT & FIKÁČEK (2013: 729).

Species included (all species are transferred to *Crenitulus* from *Anacaena*):

Crenitulus attiguus (Orchymont, 1942), **comb. nov.** – Peru

Crenitulus hirsutus (Komarek, 2005), **comb. nov.** – Costa Rica, Guatemala

Crenitulus nitens (Gentili, 1993), **comb. nov.** – Australia: Queensland

Crenitulus paleodomincicus (Fikáček & Engel, 2011), **comb. nov.** – Dominican amber

Crenitulus perpennus (Orchymont, 1942), **comb. nov.** – Costa Rica

Crenitulus solstitialis (Kirsch, 1873), **comb. nov.** – Central and northern South America

Crenitulus schoedli (Komarek, 2005), **comb. nov.** – Costa Rica

Crenitulus suturalis (LeConte, 1866), **comb. restit.** – widespread in North, Central and South Americas

Diagnosis. Adults (partly based on KOMAREK 2005, 2007): Body attenuated posteriad; eyes anteriorly not emarginated by a canthus of frons, remnants of frontoclypeal suture not bent along anterior margin of eye; antenna always with 9 antennomeres; procoxae in many species with apparent strong spines (absent in *C. solstitialis*, weakly developed on some *C. suturalis*); gula very narrow; mesoventrite only narrowly reaching anterior margin of mesothorax;

elytron with subserially arranged punctures; meso- and metatarsi with few long swimming hairs on dorsal face (except in *C. attiguus*); aedeagus very similar in all species of *Crenitulus*: phallobase ca. as long as parameres, without or with very weakly defined broad manubrium; parameres acute apically, regularly convex on outer margin; median lobe slightly narrowing apicad, cut off apically, with very short apodemes; gonopore apical or subapical.

Larvae (partly based on ARCHANGELSKY & FIKÁČEK 2004): Nasale with five teeth, all of more or less the same size, the right one reaching furthest, the left one least projecting; epistomal lobes present, rather small, nearly symmetrical; antenna with rather long antennomere 3, sensorium thin and as long as antennomere 3; maxilla with short stipes and very long palpomere 1; mandibles symmetrical, with two large and one very small basal tooth; labium with long ligula, projecting further than labial palps; seta on inner margin of antennal socket brush-like apically; pronotum with lateral projections; each segment of thorax dorsally with complex set of sclerites, some of which bear sclerotized projections; tergite of abdominal segment 8 trifold posteriorly.

Comments. The most apparent shared character of all species of *Crenitulus* is the morphology of the aedeagus, which is extremely similar in all species included here in the genus. KOMAREK (2005) did not include *A. perpenna* into the *Anacaena suturalis* group (i.e. what is now *Crenitulus*), but mentioned the resemblance of its aedeagus with members of the group. The same is true for *A. nitens*, which KOMAREK (2007) only commented as showing morphological affinities to *A. suturalis* group. Neither of these two species was included in the molecular analyses as DNA-grade material is not available at the moment. It is true that both aforementioned species differ in several aspect from the remaining species of *Crenitulus*: *C. perpennus* e.g. in the short terminal antennomere and transverse ridge of the mesoventrite; *C. nitens* in the mesoventrite without a median protuberance and the pubescence of the metafemur extending slightly further distad than in Neotropical species. However, both species share the aedeagal morphology, which is very characteristic for the genus, and also completely match the generic diagnosis provided above. For these reasons, we include them into *Crenitulus*.

During routine identification, both the Neotropical and Australian species may only be confused with the genus *Anacaena*. In the Neotropics, they may be easily distinguished from *Anacaena* by the metafemoral pubescence confined solely to the base and anterior margin (see KOMAREK 2005: Figs 51, 55–57, 59) whereas the *Anacaena* species have the pubescence much more extending distad (less so in *A. parvula*, which may be easily distinguished from *Crenitulus* by the antenna having 7 antennomeres). The only Australian species of *Crenitulus* may be easily distinguished from *Anacaena* by the narrowly elongate, darkly-colored body (more globular, and at least in some species, pale-colored in *Anacaena*) and by the antenna with 9 antennomeres (8 antennomeres in all Australian *Anacaena*). In all cases, species of *Crenitulus* may be easily distinguished from *Anacaena* by the morphology of the aedeagus: parameres are apically pointed and the phallobase does not have a distinctly constricted basal portion (manubrium) in *Crenitulus*, whereas the parameres are apically more or less widely rounded in all New World and Australian *Anacaena*, and the phallobase bears a narrowly projecting manubrium in all Australian *Anacaena*.

Potential distribution of southern South American endemic genera

Additional, focused collecting is clearly necessary in order to understand the distribution, as well the biology, of the five hydrophilid genera endemic to austral South America (*Andotypus*, *Anticura*, *Cylorygmus*, *Hydramarara* and *Pseudorygmodes*). To facilitate this task, we analyzed the known records and modeled the potential distribution of each genus – the main aim of this analysis is to identify areas in which focused collecting effort may produce additional records of each taxon. However, it is necessary to keep in mind that the models are based purely on climatic data, and do not take into consideration potential historical or biotic factors which may restrict or expand the real range of each taxon. Also, suitable microhabitats have to be inspected in the potential areas of distribution, which is why we also add the basic description of the microhabitats in which the available specimens were collected. Potential distribution and actual records of all genera and species are summarized in Fig. 74.

Subfamily Hydrophilinae

Hydramarara Knisch, 1925

Known distribution. The genus contains a single species, *H. argentina* (Knisch, 1925). It is known from the following localities: **ARGENTINA:** CATAMARCA: El Rodeo [28°12'25"S 65°52'42"W] (SPANGLER 1979b). **CORDOBA:** without precise locality (SPANGLER 1979b; not included into the dataset). **LA RIOJA:** Departamento General Lamadrid, Río del Peñon [28°52'43.3"S 68°34'24.3"W] (ARCHANGELSKY 2000); Departamento Sanagasta, Arroyo Tambito, 29°09'47"S 67°4'47"W (ARCHANGELSKY 2000); Departamento Chilecito, road to Mina de Oro [29°6'25"S 67°36'17.4"W] (ARCHANGELSKY 2000). **MENDOZA:** Punta del Agua [35°31'7.4"S 68°5'0.3"W] (KNISCH 1925); Tala (KNISCH 1925, not localized and not included into the dataset). **SALTA:** Angastaco [25°37'49"S 66°9'39.3"W] (SPANGLER 1979); Cafayate [26°4'49"S 65°58'58.3"W] (SPANGLER 1979b); Cañada la Gotera, Rt. 59, km 23.5 [24°56'33.8"S 68°6'37.4"W] (SPANGLER 1979b); Depto. Rosario de la Frontera, El Morenillo [26°12'1.5"S 64°50'6"W] (SPANGLER 1979b); La Zanja, west of Chicoana [= Las Zanjas, 25°8'20"S 65°44'29"W] (SPANGLER 1979b). **SAN LUIS:** Merlo [32°20'17.8"S 64°59'54.4"W] (SPANGLER 1979). **TUCUMAN:** Hotco Molle [26°47'28.6"S 65°19'49.1"W] (SPANGLER 1979b); Tipas [= Las Tipas, 26°40'0.7"S 65°24'3.7"W] (SPANGLER 1979b).

Results of the model of the potential distribution. Number of occurrence points analyzed: 14. Training AUC: 0.979. Treshhold for equal training sensitivity and specificity: 0.248. Most contributing climatic layers: bio6 – minimum temperature of the coldest month (50.2 %), bio19 – precipitation of the coldest quarter of the year (27.1 %).

Potential distribution. The potential distribution covers a large area of mostly semiarid to arid montane and sub-montane regions in central and northwest Argentina (where actual records are known), but also includes dry parts of the Andean altiplano in Chilean regions Atacama, Antofagasta, Tarapaca and Arica y Parinacota, the dry high-altitude areas in southwestern and western Bolivia, and a narrow isolated belt of dry Andean foothills in southern Peru between the provinces of Lima and Arequipa. A very isolated area of suitable climatic conditions is also present in the southern part of the Argentinian province of Santa Cruz.

Biology. Based on the published records, *Hydramarara argentina* inhabits the montane or sub-montane rivers and streams, often those which are highly seasonal, and dry up for the larger part of the year (SPANGLER 1979b, ARCHANGELSKY 2000).

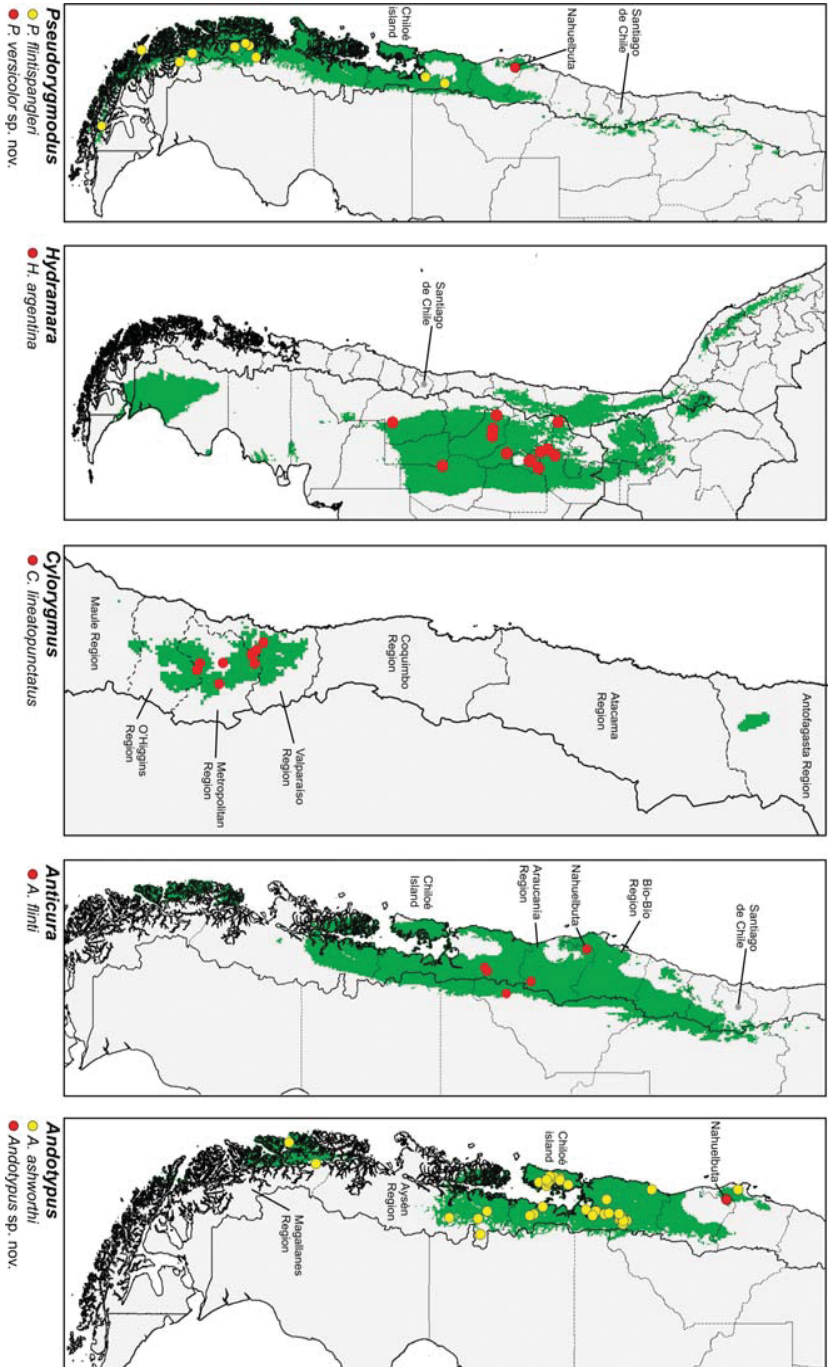


Fig. 74. Potential distribution (green) of the five hydrophilid genera endemic to southern South America. The southernmost record of *Pseudorygmopus flintspangleri* (Moroni, 1985) was not used for the analysis, but is shown here to provide complete data on known distribution of the species.

Subfamily Chaetarthriinae

Pseudorygmodus Hansen, 1999

Known distribution. The genus contains two species – the widespread *P. flintispangleri* (Moroni, 1985) and *P. versicolor* sp. nov., known from a single locality in Parque Nacional Nahuelbuta (La Araucanía Region). The complete list of known specimens and localities is provided above in the review of the genus; same data were used for the model of the potential distribution of the genus.

Results of the model of the potential distribution. Number of occurrence points analyzed: 11. Training AUC: 0.922. Treshold for equal training sensitivity and specificity: 0.448. Most contributing climatic layers: bio19 – precipitation in coldest quarter of the year (75 %).

Potential distribution. In the north, the genus may potentially reach the Bío-Bío Region along the Andes Mts. and the northern border of the Los Lagos Region (incl. whole Chiloé island) along the coastal mountain range. In the coastal mountain range, an isolated spot of potential distribution is predicted for the Cordillera de Nahuelbuta, from where *P. versicolor* is here described. South of the Los Lagos Region, the potential distribution includes coastal areas reaching the southernmost parts of the Magellanes Region. Climatically suitable conditions are also predicted in small isolated spots at high altitudes along the Chilean-Argentinian border north of Region Maule, but these regions were massively affected by glaciation during the Pleistocene, hence, actual distribution there seems less probable. In the northern part of the continual potential distribution, it generally corresponds with the distribution of Valvidian/*Nothofagus* forests.

Biology. Associated with streams and rivers, most likely to be found in mosses on stones above water, in flood debris accumulated in logjam and on humid places on the banks of the streams. In the south, also likely inhabiting humid places far from streams/rivers. See above for details for each species, and Discussion for more details on supposed habitat differences between species.

Subfamily Rygmodinae

Andotypus Spangler, 1979

Known distribution. The genus contains two species – the widespread *Andotypus ashworthi* Spangler, 1979, and *Andotypus* sp. nov. (to be described by FIKÁČEK et al. 2014) known from a single female from Parque Nacional Nahuelbuta (La Araucanía Region). The complete list of known specimens and localities was provided by FIKÁČEK et al. (2014) and these data were used here for estimating the potential distribution of the genus.

Results of the model of the potential distribution. Number of occurrence points analyzed: 44. Training AUC: 0.980. Treshold for equal training sensitivity and specificity: 0.086. Treshold for maximum sensitivity and specificity: 0.063. Most contributing climatic layers: bio19 – precipitation in coldest quarter of the year (58 %), bio15 – precipitation seasonality (18.5 %), bio17 – precipitation of driest quarter of the year (17.3 %). The maximum sensitivity/specificity treshold was used for the prediction, as the area of potential distribution predicted using equal sensitivity/specificity did not cover all actual records of the genus.

Potential distribution. Four isolated regions were predicted as potential distribution for the genus: the coastal area in southern Bío-Bío and northern Araucanía Regions (ca. between Concepción and Carahue), a large area ranging from southernmost Bío-Bío in the Andes Mts. (ca. Reserva Nacional Ralco and volcan Callaqui) through the whole width of Chile south to ca. 46°S, coastal areas south of Golfo de Penas between ca. 47.5–51°S, and a small coastal

area between ca. 52–54°S. The species was actually recorded in all these regions except the southernmost one.

Biology. Usually collected using meat/cheese-baited pitfall traps in forested areas, also found by sifting leaf-litter and accumulations of decaying plant matter, probably including beach drift (SPANGLER 1979c, FIKÁČEK et al. 2014).

Anticura Spangler, 1979

Known distribution. The genus contains a single species, *A. flinti* Spangler, 1979. It is known from the following localities: **ARGENTINA: NEUQUÉN:** San Martin de los Andes, Arroyo Rosales [40°6'56"S 71°18'25"W] (SPANGLER 1979d). **CHILE: LA ARAUCANÍA:** Parque Nacional Nahuelbuta, 2.2 km N of Pehuenco, Estero Agua de Los Gringos, 37°48.5'S 73°0.7'W, 1160 m (Fikáček, unpubl. data); 21.8 km SE of Pucón, Rio Palguín at Ruta S-941 km 9, 39°24.6'S 71°46.4'W, 650 m (Fikáček, unpubl. data); Villarica (Fikáček, unpubl. data, not included into the analysis). **LOS LAGOS:** Parque Nacional Puyehue, Anticura, in Rio Anticura, 350–460 m, 40°40.3'S 72°10.2'W (SPANGLER 1979d; Fikáček, unpubl. data); Parque Nacional Puyehue, Anticura, in Rio Gol Gol, 380 m [40°39'43"S 72°10'16"W] (SPANGLER 1979d); Parque Nacional Puyehue, Aguas Calientes, in Rio Chanlefu [40°44'S 72°18'42"W] (SPANGLER 1979d).

Results of the model of the potential distribution. Number of occurrence points analyzed: 6. Training AUC: 0.972. Treshholds for equal and maximum sensitivity and specificity: 0.269. Most contributing climatic layers: bio19 – precipitation in coldest quarter of the year (78.3 %).

Potential distribution. A wide continual potential distribution was predicted for this genus, ranging from high altitude places in the Metropolitan Region Santiago de Chile through the Andes Mts. southwards to ca. Puerto Aysén (45.5°S), and south of ca. Concepción extending also to large regions in the coastal mountain range. An isolated smaller region of potential distribution is also predicted along the coast between Golfo de Penas and Isla Duque de York. The potential range also includes the forested areas on eastern slopes of Andes Mts. in Argentinian provinces Mendoza, Neuquén, Río Negro and Chubut. The potential distribution is actually much wider than the distribution currently known from available records.

Biology. To be collected in mountain streams and rivers, most frequently from mosses growing at water level or just above on the stones at sides or even directly in the stream; also collected from flood debris accumulated in river logjams.

Cylorygmus Orchymont, 1933

Known distribution. In South America, the genus contains a single species, *C. lineatopunctatus* Orchymont, 1933. It is known from the following localities: **CHILE: SANTIAGO:** Lo Águila (or Hospital Lo Águila) [33°54'S 70°46'W] (MORONI 1985; Fikáček, unpubl. data); Peñalolén, 14 km SE of Santiago de Chile [33°33'21"S 70°31'41.3"W] (Newton & Thayer, unpubl. data); Rungua [33°0'24.12"S 70°53'20.4"W] (Fikáček, unpubl. data); Quebrada La Plata [33°29'38"S 70°53'23"W] (Fikáček, unpubl. data); Rangué [33°51'19"S 70°53'11"W] (Fikáček, unpubl. data). **VALPARAÍSO:** 4 km E of Quebrada Alvarado, 500 m, 33°3'S 71°3'W (Newton & Thayer, unpubl. data); La Vega vicinity, 940 m, 33°2.71'S 71°1.63'W (Newton & Thayer, unpubl. data); Parque Nacional La Campana, Sector Granizo, Cajón La Opositora, 685 m, 32°58.78'S 71°6.93'W (Newton & Thayer, unpubl. data); Parque Nacional La Campana, Sector Ocoa, 4.75 km SE of park entrance, "La Cascada", 870 m, 32°57.7'S 71°3.2'W (Fikáček, unpubl. data); Parque Nacional La Campana, Sector Ocoa, vicinity of Quebrada Buitrera, 415 m, 32°55.89'S 71°5.1'W (Newton & Thayer, unpubl. data); Quillota [32°52'S 71°15'0"W] (ORCHYMONT 1933, MORONI 1985, Fikáček, unpubl. data).

Results of the model of the potential distribution. Number of occurrence points analyzed: 10. Training AUC: 0.995. Treshholds for equal and maximum sensitivity and specificity: 0.328. Most contributing climatic layers: bio18 – precipitation of warmest quarter of the year (35.7 %), bio19 – precipitation of coldest quarter of the year (24.7 %), bio14 – precipitation of driest month (15.7 %).

Potential distribution. Compared to other hydrophilid endemic genera, a very small area of potential distribution was predicted for *Cylorygmus lineatopunctatus*. It includes the small part of the Coastal Cordillera from northern Valparaíso Region southwards to the central/southern O'Higgins Region (i.e. Vizcachas Mts. and the Altos de Cantillana range) and the adjacent foothills. Actual records are known from both these ranges. An additional small area of climatically suitable conditions is predicted in the coastal mountain range of the southernmost Antofagasta province, but actual occurrence there does not seem probable due to large isolation of this area from the southern range of the species and the lack of forests in this area (it is part of the Atacama Desert).

Biology. Collected in leaf accumulations at sides of the streams, either in forested areas or even in small remnants of forests e.g. in deep ravines (Newton & Fikáček, unpubl. data).

Discussion

Biology of *Pseudorygmus*. Habitat preference of *Pseudorygmus versicolor* sp. nov. seems to be clear – a long series of specimens was floated from mosses in the splash-zone of a mountain stream (Figs 8–10) in December 2013, together with specimens of another austral endemic hydrophilid, *Anticura flinti*. The habitat requirements of *P. flintispangleri* are less clear. Adults, larva and pupae were found in the loam and flood debris in the midstream of Río Anticura in February 1978 (SPANGLER 1979a), which seems to be in agreement with the habitat of *P. versicolor*. However, we failed to collect a single specimen in that river during a four-day effort in December 2013, despite the fact that we focused our collecting effort on mosses in splash zones, submerged ones, as well as on flood debris accumulated in logjam, in which we found numerous *Anticura* adults and larvae. We only succeeded in collecting one dead torso of *P. flintispangleri* by floating flood debris accumulated in logjams on the side of the river. This confirms that the species still lives along Río Anticura, but suggests that the aforementioned habitats may not be the preferred ones. This would correspond with the fact that the type series of *P. flintispangleri* was originally found under stones, in a deforested area along sea coast, in southern Chile (SPANGLER 1974). As the type specimens were found in October (i.e. spring), SPANGLER (1979a) supposed that they were overwintering, and hence found far from water. However, longer series of *P. flintispangleri* was repeatedly found under similar conditions in January/February 1985 by A. C. Ashworth and M. J. Gunderson (Fig. 11), and one specimen was collected in forest litter in Cordillera Darwin (southernmost Chile) in February 1965 (i.e., in both cases in summer). The records outside of water are hence more frequent, likely not accidental, and cannot represent overwintering specimens. Therefore, *Pseudorygmus flintispangleri* seems to actually be a hygropetric species, not requiring direct association with water courses, in contrast to *P. versicolor*. Morphology corresponds with this hypothesis, as the ventral pubescence of *P. flintispangleri* is sparse and partly reduced – this is possible for non-aquatic species in which the pubescence does not need to hold the air bubble during submersion (see e.g. FIKÁČEK et al. 2012 for details). In contrast, the ventral pubescence of *P. versicolor* is dense and corresponds with that of the majority of aquatic Hydrophilidae. It hence seems rather likely that the finding of adults, larva and pupae in midstream of Río Anticura, as reported by SPANGLER (1979a), had been

accidental, possibly following floods after heavier rains, bringing the specimens with flood debris from humid sites along the river.

Distribution of endemic austral South American genera. All five hydrophilid genera endemic to austral South America (*Andotypus*, *Anticura*, *Cylorygmus*, *Hydramara* and *Pseudorygmus*) are very rare in collections – all but one are known from less than 15 localities, with the only exception being *Andotypus* whose distribution is better known, based on recent collecting effort (FIKÁČEK et al. 2014). Our experience in November–December 2013 showed that the species may also be rare in the areas and habitats where they do occur. For example, collecting effort for *Anticura flinti* in the Parque Nacional (PN) Puyehue (where the type locality is situated) and in PN Villarica (from where we knew of one previous record) resulted in the discovery of several micro-spots (mosses on stones in rivers, submerged or in splash zone, and flood debris accumulated in logjam) from which numerous adults and larvae were collected, while several similar-looking spots in the same rivers gained only singletons, and the majority of samples taken from these, and several surrounding rivers nearby, with similar microhabitats, completely lacked specimens of *A. flinti*. In case of *Andotypus ashworthi*, which is supposedly common in the areas we visited (A. Newton, pers. comm.), we failed to collect a single individual in most localities despite several dozens of pitfall traps set up in each area. About 30 specimens were collected only at the last night in PN Puyehue – the night was warmer than previous ones experienced during the expedition, and followed a rainy afternoon. Few specimens of *A. ashworthi* were collected in almost every pitfall trap that night, which confirms that the species is rather common in the area, and its absence at previous nights was likely caused by unsuitable (probably too cold) weather. Based on this experience, it seems probable that the rarity of austral-endemic hydrophilids is likely caused by a combination of preference for particular microhabitat and seasonality. This motivated us to model the potential distribution of each genus (Fig. 74), to facilitate future collecting effort by focusing on areas in which the occurrence of the particular taxon is probable.

The potential distribution largely corresponds with known records for three genera (*Pseudorygmus*, *Cylorygmus* and *Andotypus*), whereas much larger than known distribution is predicted for *Hydramara argentina* and *Anticura flinti* (Fig. 74). The models show that climatic conditions themselves may explain the absence of *Pseudorygmus*, *Cylorygmus*, *Anticura* and *Andotypus* from Argentina (except its westernmost border) as well as apparent gaps observed in the known range of some taxa (*Andotypus*, *Pseudorygmus*).

Available distribution data as well as presented models showed the exceptional position of Cordillera de Nahuelbuta, which is the part of the Chilean Coastal Cordillera. Three hydrophilid species were found in PN Nahuelbuta, two of which are endemic to this national park (*Pseudorygmus versicolor* sp. nov. described above, and *Andotypus* sp. nov. which will be described by FIKÁČEK et al. 2014) and one more widely distributed (*Anticura flinti*). The high local endemism in Nahuelbuta is exceptional as most austral-endemic species are rather widely distributed. Nahuelbuta region is notable for its climate and geoclimatic history. Parts of PN Nahuelbuta belong to the coldest areas in Coastal Cordillera and are comparable to much more southern regions in mean temperature (6–8°C based on Worldclim data; HIJMANS et al. 2005). Historically, Cordillera de Nahuelbuta is situated in the part of the Coastal Cordillera,

which was not glaciated neither during the Last Glacial Maximum (so-called Llanquihue glaciation, ca. 26.5–19 thousand years before present; EHLERS & GIBBARD 2004, CLARK et al. 2009, MOREIRA-MUÑOZ 2011), nor during the older and more extensive Pleistocene glaciations (EHLERS & GIBBARD 2004). The glaciation was extensive only in the Andes Mts. at the latitude of Nahuelbuta and more in the north, and reached the coast and the Coastal Cordillera only in southern Chiloé and more in the south (HEUSSER 2004). The glaciated areas of the Coastal Cordillera hence started only ca. 450 km south of Nahuelbuta.

The effect of the glaciation on species diversity may be twofold: (1) the complete depletion of the fauna and flora from the glaciated areas, and (2) splitting up the continuous populations, promoting speciation. Populations may be divided either by the glaciers themselves during the glacial period, or by uphill shift of populations from lowland glacial refugia during interglacials. The latter is supposed to be the case of several taxa in Cordillera de Nahuelbuta (e.g. araucaria trees, HEUSSER 2004): the treeline went lower and the Central Valley served as continuous ice-free refugium during the glacial periods, but the population split up and moved to higher altitudes in Cordillera Nahuelbuta and in the Andes Mts. during interglacials when temperature rose and made the conditions of Central Valley unsuitable. In hydrophilids, this process may have been the reason for the presence of isolated populations of *Pseudorygmodus* and *Andotypus* in Cordillera de Nahuelbuta, but cannot be responsible for the origin of both species endemic to Nahuelbuta. Both endemic species are morphologically very distinct from their respective sister species and are very likely of much older origin than the Pleistocene glaciation. This is well illustrated by *Andotypus*, as both its species (the widespread *A. ashworthi* as well as the locally endemic *Andotypus* sp. nov.) inhabit Cordillera de Nahuelbuta. These indirect clues suggest that the reason for high endemism in Nahuelbuta is rather the fact that the diversity present before the Pleistocene (i.e. species of Cenozoic origin) was not depleted by glaciation in this area, and at the same time, the proximity of the much warmer Central Valley (serving as refugium during the glacial periods), and the much colder but always ice-free Cordillera de Nahuelbuta (serving as refugium during interglacials), serving as an ideal setting for survival of cold-temperate forest species. In contrast to that, the fauna and flora of the Andes Mts. and of regions south of Chiloé Island was completely and repeatedly depleted by glaciations and its origin has to be very recent (following the Last Glacial Maximum), based either on the species which survived north of the glaciation or in the small ice-free areas on the periphery of glaciers in the otherwise completely glaciated southern regions (e.g. PALMA et al. 2012, VERA-ESCALONA et al. 2012, MARÍN et al. 2013). Current distribution of endemic hydrophilids corresponds with this view, as the formerly glaciated areas are inhabited by widely distributed species only, and the local endemics all occur more in the north. The repeated finding of *Pseudorygmodus flintispangleri* very close to glaciers (e.g., Fig. 11) also illustrates that at least some of the hydrophilid taxa were capable to survive the glaciations in close proximity of glaciers.

In contrast to *Pseudorygmodus* and *Andotypus*, the model of potential distribution of *Anticura flinti* suggests that in this species, the populations from Nahuelbuta region should be connected with those in the Andes Mts. This may look surprising as the Coastal Cordillera is currently divided from the Andes Mts. by a wide largely deforested Central Valley (SMITH-RAMÍREZ 2004). However, the quick check of the *cox1* sequences of one *Anticura* specimen

from each locality sampled in 2013 (PN Nahuelbuta in Coastal Cordillera, PN Villarica and PN Puyehue in Andes Mts., see Material and methods for GenBank accession numbers) seem to confirm the results of the model. The genetic distances between all three specimens are low (0.3–1.1 %) and the Nahuelbuta specimen is genetically closer to those from the Andes Mts. than both Andean specimens to each other. Moreover, the deforestation of the Central Valley is very recent – continuous forests connecting the Coastal Cordillera and the Andes Mts. were still present in 1850 and forested areas of both mountain ranges became completely disconnected from each other only between 1850 and 1950 (HEUSSER 2004).

Phylogeny of the Chaetarthriinae/Anacaenini. When the results of molecular analyses performed within last two years are compared, it is evident that several results are common for all analyses, despite the different algorithm, taxon and gene sampling, and model/prior settings used: (1) the monophyly of the subfamily Chaetarthriinae is always strongly supported, and (2) four strongly supported clades are recognized within the subfamily: *Guyanobius*+*Hemisphaera* clade, *Chaetarthria*+*Thysanarthria* clade, *Horelophus*+*Crenitis* clade and *Anacaena* s. str. clade (in the current analysis also including *Pseudorygmodus*). The relationships of these clades differ between different analyses performed (SHORT & FIKÁČEK 2013, BLOOM et al. 2014, this paper). Still, Anacaenini and Chaetarthriini were resolved as reciprocally monophyletic several times, and their monophyly is also supported by morphological characters: members of Chaetarthriini share the series of long setae at the base on abdomen (unique within Hydrophilidae), Anacaenini are unique by short stipes and rather long palpomere 1 in the larval maxilla (present in all four anacaenine genera in which larvae are known at the moment, see e.g. Fig. 65). Additional studies are necessary to find the synapomorphies of the Chaetarthriinae as a subfamily, as it may be currently defined only by the combination of characters (see SHORT & FIKÁČEK 2013). A possible candidate for the synapomorphy of Chaetarthriinae is a set of digitiform sensilla on the fourth maxillary palpomere. SEM studies confirmed their presence in *Horelophus walkeri* (FIKÁČEK et al. 2011), *Hemisphaera socotrana* Fikáček, Delgado & Gentili, 2012 (FIKÁČEK et al. 2012) and *Pseudorygmodus* (this study, Figs 32–33), and they were also found in *Chaetarthria pallida* (LeConte, 1861) and *Notohydrus montanus* (Blackburn, 1891) by examination of microscopic slides (Newton & Fikáček, unpubl. data). The character does not seem to be exclusive for the Chaetarthriinae, as one or two sensilla are also present e.g. in *Micramphiops* Short, 2008 (Hydrophilinae: Amphiopini), *Notionotus* Spangler, 1972 (Enochrinae) and *Eurygmus* Hansen, 1990 (Rygmodynae). The sensilla are however absent in the majority of hydrophilid taxa examined for this character and the number of sensilla is lower (usually one or two sensilla only) in aforementioned non-anacaenine genera than in members of the Anacaenini.

Within the Anacaenini, the basal split into two main clades (Fig. 73) is well supported by molecular data as well as by larval morphology. Still, additional studies are necessary to understand the genus-level phylogeny of the tribe. Two Australian genera (*Notohydrus* Balfour-Browne, 1939 and *Phelea* Hansen, 1999) are still not available in DNA-grade and their larval morphology is unknown, and it is hence unclear which of the principal anacaenine clades they belong to. Additional problems may be expected in *Crenitis* which is morphologically quite diverse but was so far represented by a single species in the analyses. The morphology

of the supposed larvae of *Crenitulus* from Costa Rica are moreover extremely similar to the known larvae of *Crenitis* (they also bear highly lobate pronota and lateral portions of meso- and metathorax, and of abdominal segments) and both genera may hence be more difficult to define from each other than currently expected. In the *Anacaena* clade, *Pseudorygmodus* makes *Anacaena* paraphyletic in our analysis and divides it into two clades: the Australian-New Guinean clade (corresponding with former genus *Paranacaena* Blackburn, 1888) and the Afro-Asian-American clade (corresponding with true *Anacaena*). The species sampling used in current analyses is however not sufficient to reliably reveal the internal phylogeny of *Anacaena*, as this may be more complex than we can see at the moment. The first step would be to include a wider spectrum of species into the molecular analysis. Inclusion of New Caledonian species would be interesting to test the monophyly of *Paranacaena*, and the addition of more Oriental, European, Afrotropical and Neotropical species is necessary to understand the position of the ‘true *Anacaena*’.

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