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Phylogeny and Biogeography of *Nesydemius*, n. gen., and related Afrotropical genera (Insecta : Ephemeroptera : Baetidae)

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ABSTRACT

A cladistic analysis was made of species belonging to a monophyletic Afrotropical clade within the *Cloeodes* complex consisting of *Crassabwa* LUGO-ORTIZ and McCAFFERTY, *Dabulamanzia* LUGO-ORTIZ and McCAFFERTY (Insecta : Ephemeroptera : Baetidae), and a newly discovered species from Madagascar that is not entirely consistent with either *Crassabwa* or *Dabulamanzia*. A revised classification recognizes three gradational lineages within the clade as genera : *Dabulamanzia* [type *D. indusii* (CRASS)] ; *Nesydemius*, n. gen. [type *N. polhemusorum* LUGO-ORTIZ and McCAFFERTY, n. sp.] ; and *Crassabwa* [type *C. flava* (CRASS)]. A first larval key to the four known Afrotropical genera of the *Cloeodes* complex is provided. *Dabulamanzia* retains most larval plesiomorphies, but is also distinguished by an apomorphic long row of small denticles on the tarsal claws. Larvae of *Nesydemius* and *Crassabwa* share an apomorphic apically papillaform maxillary palp and two greatly enlarged subapical denticles on the tarsal claws. *Crassabwa* is distinguished from *Nesydemius* by numerous additional apomorphies involving mandibular and labial morphology. An area cladogram allows a hypothesis that ancestral *Dabulamanzia* was present in the ancient Africa + Madagascar landmass and that the split of Madagascar and Africa was the vicariant event paralleling the dichotomy of a related but more apomorphic lineage into *Nesydemius* in Madagascar and *Crassabwa* in eastern and southern Africa.

Key words : Ephemeroptera, Baetidae, *Crassabwa, Dabulamanzia, Nesydemius polhemusorum*, new genus, new species.

RÉSUMÉ

Phylogénie et Biogéographie de *Nesydemius* n. gen., et des genres Afrotropicaux apparentés (Insecta: Ephemeroptera: Baetidae).

Il a été effectué une analyse cladistique des espèces appartenant à un clade Afrotropical monophylétique à l'intérieur du complexe *Cloeodes*, regroupant *Crassabwa* LUGO-ORTIZ & McCAFFERTY, *Dabulamanzia* LUGO-ORTIZ & McCAFFERTY (Insecta: Ephemeroptera: Baetidae) et une espèce nouvellement découverte de Madagascar qui n'est pas entièrement consistante avec soit *Crassabwa* soit *Dabulamanzia*. Une classification revue reconnaît en tant que genres trois lignées graduelles à l'intérieur du clade: *Dabulamanzia* [type *D. indusii* (CRASS)] ; *Nesydemius*, n. gen. [espèce type *N. polhemusorum* LUGO-ORTIZ & McCAFFERTY, n. sp.] ; et *Crassabwa* [espèce type *C. flava* (CRASS)]. Une première clé des larves des quatre genres Afrotropicaux connus du complexe *Cloeodes* est présentée. *Dabulamanzia* retient la plupart des plésiomorphies larvaires mais se distingue aussi par une longue rangée apomorphique de petits denticules sur les griffes tarsales. Les larves de *Nesydemius* et de *Crassabwa* partagent les apomorphies représentées par un palpe maxillaire en forme de papille à l'apex et par deux denticules subapicaux de grande taille sur les griffes tarsales. *Crassabwa* se distingue de *Nesydemius* par de nombreuses autres apomorphies touchant la morphologie des mandibules et du labium. Un cladogramme autorise l'hypothèse que *Dabulamanzia* ancestral était présent sur l'ancienne plaque Afrique-Madagascar et que la séparation de Madagascar et de l'Afrique a été l'évènement vicariant mettant en parallèle la dichotomie d'une lignée, proche mais plus apomorphe, en *Nesydemius* à Madagascar et *Crassabwa* en Afrique de l'Est et du Sud.

Mots clés : Ephemeroptera, Baetidae, *Crassabwa, Dabulamanzia, Nesydemius polhemusorum*, genre nouveau, espèce nouvelle.

INTRODUCTION

LUGO-ORTIZ and McCAFFERTY (1996a) erected the genus *Crassabwa* for certain African species that had been previously placed in *Afroptilum*, and shortly thereafter LUGO-ORTIZ and McCAFFERTY (1996b) erected the genus *Dabulamanzia* for certain other African species that had also been placed in *Afroptilum*. Later, LUGO-ORTIZ and McCAFFERTY (1997) discovered that *Dabulamanzia* also occurred in Madagascar. LUGO-ORTIZ and McCAFFERTY (1996a, b) indicated that *Crassabwa* and *Dabulamanzia* were probably related to the broadly distributed Gondwanan genus *Cloeodes* TRAVER because the three taxa possess a distinctive subproximal arc of setae on the tibiae.

Recently, we discovered a new species from Madagascar that showed a combination of certain characteristics that have been associated with both *Crassabwa* and *Dabulamanzia*. For example, the new species shares with *Dabulamanzia* the cleft incisors and apically setose prostheca of the right mandible (Fig. 5) and labial palps that lack a distomedial process on segment 2 and have a clublike segment 3 (Fig. 7) ; the new species shares with *Crassabwa* an apically papillaform maxillary palp (Fig. 6) and a pair of greatly enlarged subapical denticles on the tarsal claws (Fig. 9). Thus, the new species presented us with the dilemma as to what genus it should reside in. Because the taxa involved appeared to form a monophyletic clade within the *Cloeodes* complex, evidenced by synapomorphies involving the tarsal claws and abdominal gills, and because of the intermediacy of the new species, we undertook a cladistic analysis to determine the phylogenetic relationships of the new species and hence an appropriate phylogenetic classification. The results of the analysis are presented herein. The material examined is housed in the Purdue Entomological Research Collection, West Lafayette, Indiana, USA.

PHYLOGENETIC SYSTEMATICS

1. Phylogeny

The operational taxonomic units analyzed included the species groups associated with *Crassabwa* (CRASSABWA) and *Dabulamanzia* (DABULAMANZIA) and the new species (given the operational name NESYDEMIUS). The outgroup used to determine character state polarities was *Cloeodes*. Standard cladistic methodology was after HENNIG (1966), ROSS (1974), and WILEY (1981). The nine comparative characters used and their plesiomorphic and apomorphic states are given in Table 1. All characters are based on larvae because the adults of the NESYDEMIUS lineage are not known. Only two character states are evident for each character.

Apomorphies 1 and 2 in Table 1 and Fig. 1 distinguish the study group as a monophyletic clade within the *Cloeodes* complex. Within the clade, the DABULAMANZIA lineage is the most primitive, but is further distinguished from NESYDEMIUS and CRASSABWA by the long, well-defined row of tarsal claw denticles (apomorphy 9 in Table 1 and Fig. 1). Apomorphies 3 and 4 (the greatly developed pair of tarsal claw denticles and the apically papillaform maxillary palps) found in NESYDEMIUS and the CRASSABWA lineage show them to be sister lineages. Apomorphies 5, 6, 7, and 8 are unique to the CRASSABWA lineage. Because NESYDEMIUS represents a monobasic lineage, there is no question about the basal origin of the CRASSABWA lineage.

2. Classification

Based on the results of our cladistic analysis (Table 1 and Fig. 1), there are five alternative phylogenetic classificatory schemes that could be used for the DABULAMANZIA, CRASSABWA, and NESYDEMIUS lineages. The inclusion of the new species in DABULAMANZIA is not one of those alternatives because all similarites between DABULAMANZIA and NESYDEMIUS are represented by symplesiomorphies only. Also significantly, as demonstrated in Table 1 and Fig. 1, NESYDEMIUS shares two synapomorphies with the CRASSABWA lineage.

One classificatory alternative would be the recognition of two genera, *Dabulamanzia* and *Crassabwa*. In this alternati-

Character	Plesiomorphy	Apomorphy
1. Tarsal claw denticles	Absent	Present
2. Gill margin	Smooth	Serrate
3. Tarsal claw denticles	Without enlarged subapical pair of denticles	With enlarged subapical pair of denticles
4. Maxillary palp segment 2	Unmodified	Apically papillaform
5. Right mandibular incisors	Fused nearly two-third of length	Entirely fused
6. Right prostheca	Apically setose	Apically denticulate
7. Labial palp segment 2	Without distomedial process	With thumblike distomedial process
8. Labial palp segment 3	Clublike	Somewhat narrow-elongate
9. Tarsal claw denticles	Short, poorly defined row	Long, well-defined row

Table 1. Structural characters and character state polarities used to formulate the cladogram of the *Dabulamanzia, Nesydemius,* and *Crassabwa* lineages in Fig. 12. Numbered characters correspond to the numbered apomorphies distributed on the cladogram.

Tableau 1. Caractères structuraux et polarités utilisés pour l'obtention du cladogramme des lignées *Dabulamanzia, Nesydemius* et *Crassabwa* sur la fig. 12. La numérotation des caractères correspond à celles des apomorphies distribuées sur le cladogramme.

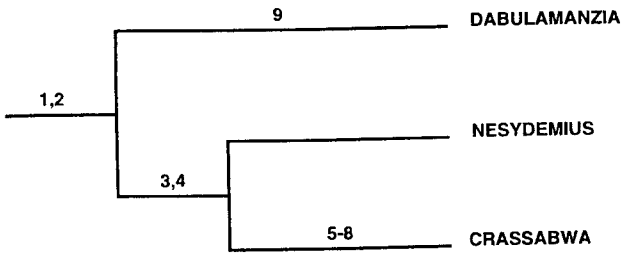

Fig. 1. Cladogram of selected Afrotropical *Cloeodes* complex lineages. Numbered apomorphies correspond to the numbered apomorphies in Table 1.

Fig. 1. Cladogramme des lignées Afrotropicales du complexe *Cloeodes* prises en compte. La numérotation des apomorphies correspond à celle du Tableau 1.

ve, the new species would be assigned to *Crassabwa* based on phylogenetic relationships. A second alternative would recognize only one genus, without subgenera, and all species in the clade would be included in *Crassabwa*. A third alternative would recognize two subgenera, *Dabulamanzia* and *Crassabwa* s.s., within *Crassabwa*. Similar to the first alternative, the new species would be assigned to *Crassabwa* s.s. based on phylogenetic relationships. A fourth alternative would recognize three genera, with the new species representing a new genus. A final alternative would recognize *Dabulamanzia*, *Crassabwa* s.s., and the new species as three subgenera of *Crassabwa*.

We consider the recognition of three genera (including *Nesydemius*, n. gen., for the new species) to be the most appropriate classificatory scheme at this time. This alternative would not obscure the distinctiveness of the *Dabulamanzia* from *Crassabwa* lineages as either larvae or adults, and requires only a minor revision of their conceptual limits. The more conservative approach of recognizing only one genus, with or without subgenera, may be called for in the future if more intermediate species are discovered.

3. Biogeography

An area cladogram (Fig. 2) (ROSEN 1975, NELSON and PLATNIK 1981) is derived from our distributional data and the cladogram in Fig. 1. It reveals the role of vicariance in the evolution and biogeography of the clade. *Dabulamanzia* is widespread in Africa south of the Sahel and also occurs in Madagascar. *Nesydemius* only occurs in Madagascar. *Crassabwa* occurs in eastern and southern Africa. We hypothesize that the *Dabulamanzia* lineage and a *Nesydemius*-like ancestor to the *Nesydemius* + *Crassabwa* lineage were present in the Africa + Madagascar landmass. Approximately 100 million years ago (middle Cretaceous), Africa and Madagascar separated (e.g., PIELOU 1979), providing a vicariant event that led to the isolation of the *Nesydemius* lineage in Madagascar and the *Crassabwa* lineage in Africa, the latter of which has undergone considerable additional evolution since that time.

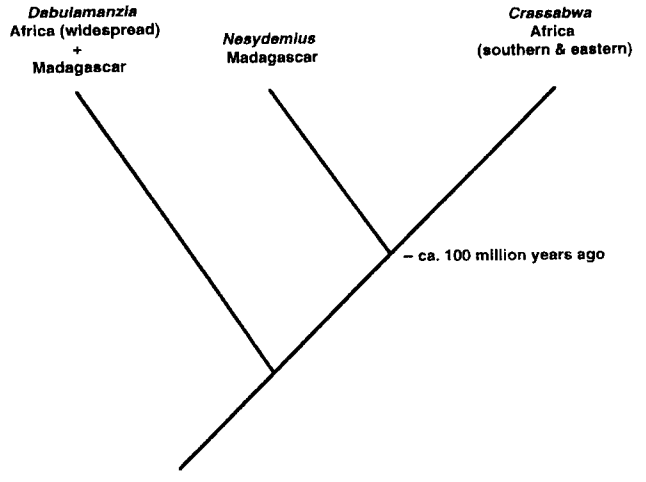

Fig. 2. Area cladogram of *Dabulamanzia*, *Nesydemius*, and *Crassabwa*.

Fig. 2. Cladogramme de *Dabulamanzia*, *Nesydemius* et *Crassabwa*.

DESCRIPTIVE TAXONOMY

4. *Nesydemius* LUGO-ORTIZ and McCAFFERTY, n. gen.

— Description

Larva

Head : Labrum (Fig. 3) broadly rounded anteriorly, with deep anteromedial notch. Left mandible (Fig. 4) with 1 set of incisors ; incisors base broad ; prostheca robust, apically denticulate ; few short, fine, simple setae between prostheca and mola. Right mandible (Fig. 5) with 1 set of incisors ; incisors deeply cleft ; prostheca slender, apically setose ; few long, robust, simple setae between prostheca and mola ; tuft of short, fine, simple setae at base of mola. Maxillae (Fig. 6) with galealaciniae with 4 short, acute denticles ; palps 2-segmented, slightly extending beyond galealaciniae ; palp segment 2 with papillaform apex. Labium (Fig. 7) with glossae subequal in length to paraglossae ; glossae basally broad, apically narrow ; paraglossae subrectangular ; palps 3-segmented ; palp segment 2 with small distomediall protuberance ; palp segment clublike.

Thorax : Legs (Figs. 8) held close to body ; femora, tibiae, and tarsi with row long, fine, simple setae dorsally ; tibiae with subproximal arc of long, fine, simple setae. Tarsal claws (Fig. 9) with 1 row of denticles and 2 greatly enlarged denticles subapically.

Abdomen : Terga (Fig. 10) with scale bases and triangular spination on posterior margin. Gills (Figs. 11, 12) on abdominal segments 1-7, platelike, held dorsolaterally, well-tracheated, marginally serrate and with minute, fine, simple setae. Paraprocts (Fig. 13) with marginal spines and scale bases and minute, fine, simple setae ventrally. Medial caudal filaments well developed.

Adult

Unknown.

— Etymology

The generic name is masculine and is a combination of the Greek words *nesos* (island) and *endemos* (native).

— Type species

Nesydemius polhemusorum LUGO-ORTIZ and McCAFFERTY, n. sp. (type species).

— Included species

Nesydemius polhemusorum LUGO-ORTIZ and McCAFFERTY, n. sp. (type species).

— Distribution

Madagascar.

5. *Nesydemius polhemusorum* LUGO-ORTIZ and McCAFFERTY, n. sp.

— Description

Larva

Body length : 6.0-7.0 mm ; caudal filaments length : unknown.

Head : Coloration pale to medium yellow-brown, with few vermiform markings on frons and vertex. Antennae approximately 2.5 x length of head capsule. Labrum (Fig. 3) with submedial pair of long, fine, simple setae and submarginal row of 4-5 long, fine, simple setae ; minute, fine, simple setae scattered over dorsal surface in posterior 1/3. Left mandible (Fig. 4) with 4 poorly defined denticles. Right mandible (Fig. 5) with outer incisors consisting of 1 blunt denticle and inner incisors with 3 poorly defined denticles. Maxillae (Fig. 6) with galealaciniae with 4 short, acute denticles ; row of 5-6 minute, fine, simple setae near medial hump ; palp segments 1 and 2 with minute, fine, simple setae scattered over surface ; palp segment 1 approximately 0.51 x length of segment 2. Labium (Fig. 7) with palp segment 2 with row of 3-4 minute, fine, simple setae dorsally ; palp segment 3 clublike, with abundant minute, thick, simple setae over surface.

Thorax : Coloration medium yellow-brown, with no distinct markings. Hindwingpads present. Legs (Fig. 8) pale yellow-brown ; femora with faint medium brown subrectangular marking anteriorly, row of 13-15 long, thick, simple setae dorsally, and numerous minute, thick, simple setae ventrally ; tibiae with numerous minute, thick, simple setae dorsally and ventrally, dorsal apical seta longer and thicker than rest; tarsi with ventral row of 10-12 thick, simple setae, increasing in length apically ; tarsal claws (Fig. 9) with 4-5 poorly defined denticles basally.

Abdomen : Coloration medium brown to medium yellow-brown ; tergum 1 medium yellow-brown, with no distinct markings, posterior margin dark brown ; terga 2-6 generally medium brown, anterolaterally medium yellow-brown, with 3 submedial round to elliptical spots anteriorly, posterior margin dark brown ; terga 7-9 pale brown to medium yellow-brown, with no distinct markings, posterior margin dark brown ; tergum 10 pale brown to medium yellow-brown, with no distinct markings, posterior margin pale brown to medium yellow-brown. Terga (Fig. 10) with abundant scale bases over surface and posterior marginal spines approximately 1.5 x as long as basally wide. Sterna pale brown to pale yellow-brown, middle segments sometimes with dark brown posterior margin. Gills as in Figs. 11, 12. Paraprocts (Fig. 13) with 12-14 marginal spines, increasing in size apically, and with 4-5 small spines apically. Caudal filaments medium yellow-brown.

Adult

Unknown.

— Material examined

Holotype : Larva, Madagascar, Antananarivo (= Tananarive) Prov, Manankazo R, at Manankazo Forest Station, 1417 m, 7-XI-1986, J. T. and D. A. Polhemus. *Paratype* : Larva, same data as holotype [mouthparts, forelegs, tergum 4, gill 4, and paraproct of 1 larva mounted on slide (medium: Euparal)]. *Other material* : Three larvae, same data as holotype.

— Etymology

The species is named after John T. and Dan A. Polhemus, who collected it.

6. Larval key to the genera of the Afrotropical Cloeodes complex (see also Table 1 and Fig. 1).

1. Tarsal claws adenticulate : gill margin smooth ..... *Cloeodes*

1'. Tarsal claws denticulate ; gill margin serrate (Fig. 12) 2

2. Labial palp segment 2 with thumblike distomedial process and segment 3 somewhat narrow-elongate ..... *Crassabwa*

2'. Labial palp segment 2 without thumblike distomedial process and segment 3 clublike (Fig. 7) 3

3. Maxillary palp segment 2 apically papillaform (Fig. 6) ; tarsal claws with subapical pair of greatly enlarged denticles (Fig. 9) ..... *Nesydemius*

3'. Maxillary palp segment 2 apically rounded ; tarsal claws without subapical pair of greatly enlarged denticles ..... *Dabulamanzia*

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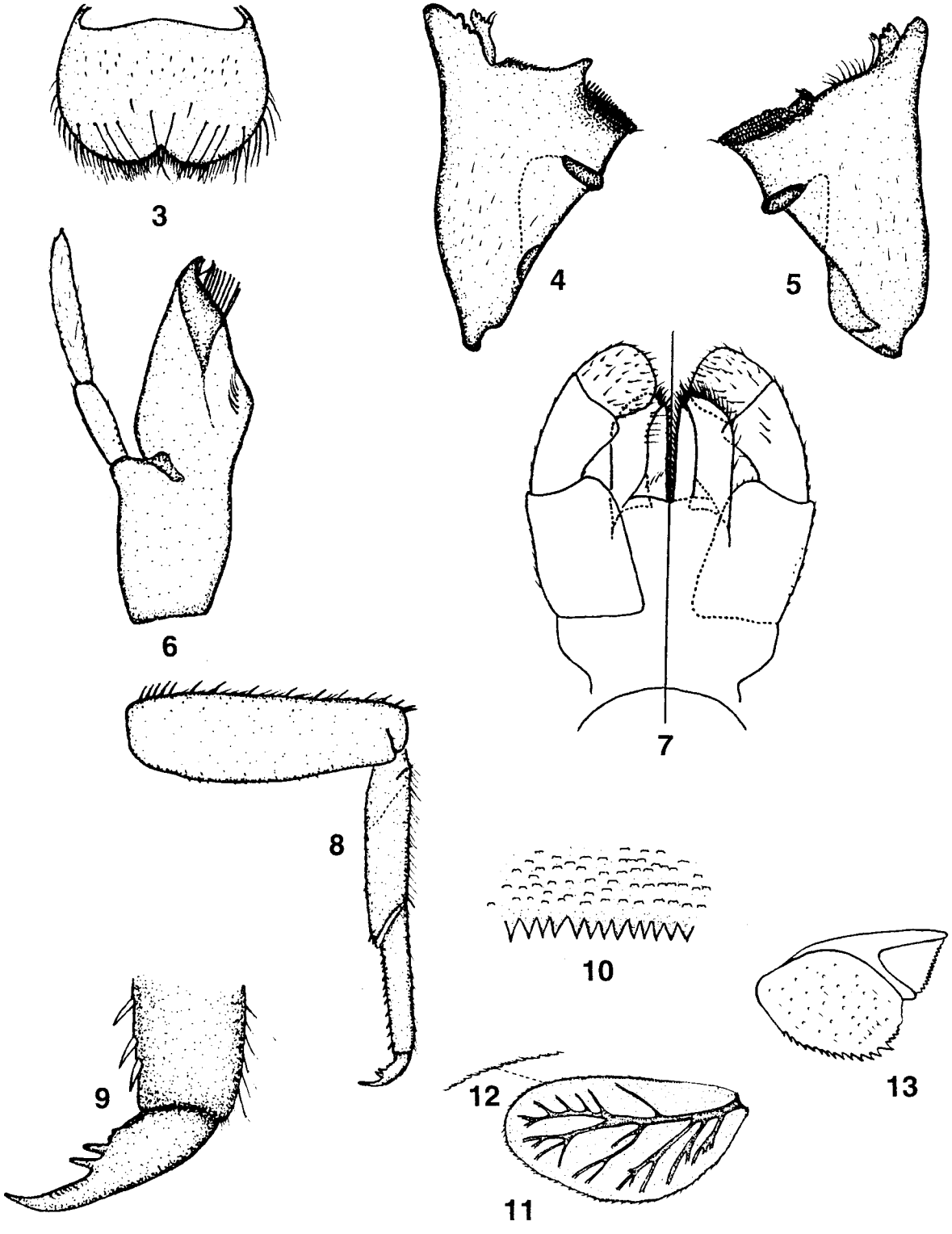

Figs. 3-13. *Nesydemius polhemusorum* LUGO-ORTIZ and McCAFFERTY, n. gen., n. sp.
Fig. 3 : Labrum. Fig. 4 : Left mandible. Fig. 5 : Right mandible. Fig. 6 : Right maxilla. Fig. 7 : Labium (left-ventral; right-dorsal). Fig. 8 : Left foreleg. Fig. 9 : Tarsal claw. Fig. 10 : Detail of tergum 4. Fig. 11 : Gill 4. Fig. 12 : Detail of gill margin. Fig. 13 : Paraproct.

Figs. 3-13. *Nesydemius polhemusorum* LUGO-ORTIZ et McCAFFERTY, n. gen., n. sp.
Fig. 3 : Labre. Fig 4 : Mandibule gauche. Fig. 5 : Mandible droite. Fig. 6 : Maxille droite. Fig. 7 : Labium (à gauche : vue ventrale ; à droite : vue dorsale). Fig. 8 : Patte antérieure gauche. Fig. 9 : Griffe tarsale. Fig. 10 : Détail de la surface tergale. Fig. 11 : 4e branchie. Fig. 12 : Détail du bord branchial. Fig. 13 : Paraprocte.

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