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 papilliform 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.

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 already 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.

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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 *Clooedes* 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 *Clooedes*. Standard cladistic methodology was after **HENNING** (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 NERYDEMIEUS 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 *Clooedes* complex. Within the clade, the DABULAMANZIA lineage is the most primitive, but is further distinguished from NERYDEMIUS 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 NERYDEMIUS and the CRASSABWA lineage show them to be sister lineages. Apomorphies 5, 6, 7, and 8 are unique to the CRASSABWA lineage. Because NERYDEMIUS 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 NERYDEMIUS lineages. The inclusion of the new species in DABULAMANZIA is not one of these alternatives because all similarities between DABULAMANZIA and NERYDEMIUS are represented by sympleiomorphies only. Also significantly, as demonstrated in Table 1 and Fig. 1, NERYDEMIUS shares two synapomorphies with the CRASSABWA lineage.

One classificatory alternative would be the recognition of two genera, DABULAMANZIA and CRASSABWA. In this alternati-

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

Table 1. Structural characters and character state polarities used to formulate the cladogram of the DABULAMANZIA, NERYDEMIUS, 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, NERYDEMIUS et CRASSABWA sur la fig. 12. La numérotation des caractères correspond à celles des apomorphies distribuées sur le cladogramme.
**Phylogeny and Biogeography of Nesydemius, N. Gen., and Related Afrotropical Genera**

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

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 PLATNJK 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.

**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 papilliform 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 distomedially protuberant; 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-chaetotomed, marginally serrate and with minute, fine, simple setae. Paraprocts (Fig. 13) with marginal spines and scale bases of 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 vermiciform 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 dorsal surface; palp segment 2 approximately 0.51 x length of segment 2. Labium (Fig. 7) with palp segment 2 with row of 3-4 minute, thick, 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 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. Gill as in Figs. 4, 5, and paraprosternum 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 thumlike distomedical process and segment 3 somewhat narrow-elongate ................................................................. *Crassabwa*

2'. Labial palp segment 2 without thumlike distomedical process and segment 3 clublike (Fig. 7) ....................... 3

3. Maxillary palp segment 2 apically papilliform (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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**References**

PHYLOGENY AND BIOGEOGRAPHY OF NESYDEMIUS, N. GEN., AND RELATED AFROTROPICAL GENERA

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: Mandibule 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.


