The Baetodes complex (Ephemeroptera: Baetidae), phylogeny, biogeography, and new species of Mayobaetis

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The *Baetodes* complex (Ephemeroptera:Baetidae), phylogeny, biogeography, and new species of *Mayobaetis*

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Abstract: The *Baetodes* complex was erected by Lugo-Ortiz and McCafferty based on 2 characters: tarsal claws in the larva with a strong subapical seta and forceps in the male adult with basal segments with a distomedial projection. This complex includes the genera *Baetodes*, *Lugoiops*, *Mayobaetis*, *Moribaetis*, *Prebaetodes*, and *Spiritiops*. It is restricted to the New World, and larvae always live in well-oxygenated streams. A cladistic analysis was conducted for the complex on the basis of a matrix of 16 taxa and 92 morphological characters, all derived from external morphology of adults and larvae. A biogeographic analysis was carried out through Spatial Analysis of Vicariance to establish possible vicariant events that generated this taxonomic complex. The cladistic analysis under implied weights yielded 3 shortest trees, and the *Baetodes* complex was recovered as monophyletic. The biogeographic analysis reconstructed 3 disjunction nodes when no nodes were removed and 2 more when 1 node was removed. The vicariant events cannot be attributed unquestionably to any paleoclimatic or microtectonic event, but they coincide under certain scenarios. *Mayobaetis yala*, new species, from Argentina, was described. It can be distinguished from other species in the genus because segment I of the forceps lacks a projection in the male imago and the dorsal surface of the abdomen lacks a medial dark line in the larva.

Key words: *Baetodes* complex, systematic, biogeography, Neotropical region

The *Baetodes* (Ephemeroptera:Baetidae) complex, a group restricted to the New World, was erected by Lugo-Ortiz and McCafferty (1996) to include 4 genera: *Baetodes* Needham and Murphy (1924), *Mayobaetis* Waltz and McCafferty (1985), *Moribaetis* Waltz and McCafferty (1985), and *Prebaetodes* Lugo-Ortiz and McCafferty (1996). The proposed complex was based on 2 characters: tarsal claws in the larva with a strong subapical seta and forceps of the male adult with basal segments with a distomedial projection (Lugo-Ortiz and McCafferty 1996). Later, McCafferty and Baumgardner (2003) described *Lugoiops* and placed it within the complex. In 2010, Nieto proposed a cladistic hypothesis of the family Baetidae in South America, and the genus *Spiritiops* was recovered as a member of the complex.

The evolutionary radiation responsible for the *Baetodes* complex occurred in the Neotropical region (McCafferty 1998). McCafferty (1998) suggested that this complex originated in South America. Several genera were collected in waterfalls (Mayo 1973), which may represent the ancestral or generalized habitat of the group. The larvae have been collected on the surface of rocks in rapids or in the splash zones (Nieto and Derka 2012) and in fast-flowing water, always in well-oxygenated streams (Salles et al. 2004).

The genus *Baetodes* is one of the most diverse and widely distributed genera in the family and has 44 known species distributed from Arizona and Texas to Argentina (Koss 1972, McCafferty and Provonsha 1993, Nieto 2004, de Souza et al. 2011). *Lugoiops* is a monotypic genus from Guatemala, whereas *Moribaetis* has 3 well-known species from Central America and Mexico (Waltz and McCafferty 1985). *Moribaetis mimbresaurus*, a species from the USA was described by McCafferty (2007) on the basis of adults, so it was not included in the analysis. Three species from South America were transferred to this genus by Lugo-Ortiz and McCafferty (1999), but these species were later transferred to another genus or considered *nomen dubium* (Cruz and Salles 2014). *Prebaetodes* has 2 known species from Colombia, Ecuador, and Venezuela (Chacón et al. 2010). *Spiritiops silvudus* Lugo-Ortiz and McCafferty (1998) was the only species in this widely distributed genus in Brazil, French Guiana, Surinam, and Venezuela, until Nieto and Derka (2012) described a 2nd species from the Tepui region of Venezuela. *Mayobaetis* was originally placed by Waltz and McCafferty (1985) as a subgenus of *Moribaetis* that included 1 species, *Baetis ellenae* (Mayo 1973). However, Lugo-Ortiz and McCafferty (1996) assigned generic rank to *Mayobaetis*. Since then, this genus has been recorded from Argentina, Bolivia, Colombia, Costa Rica, Ecuador, and Peru.

The present biogeographic analysis is an attempt to recognize the barriers separating a biota rather than to propose...
relationships between predefined areas. The method used here follows the approach advocated by Hovenkamp (1997, 2001) because the analysis is focused on taxon history (Arias et al. 2011). Given a phylogeny, taxon history methods are used to explain the distribution of a particular taxon in a geological context. In other words, a Spatial Analysis of Vicariance (SAV; Arias 2010) is an attempt to discover disjunct (allopatric or vicariant) distribution among sister groups. Thus, knowing the phylogeny of the taxa is crucial.

The main goals of the present analysis are to: 1) explore the phylogenetic relationships among the genera of the Baetodes complex, based on a previous cladistic analysis (Nieto 2010) and the new species described since then; 2) perform a Spatial Analysis of Vicariance to establish the possible vicariant events that affected this complex; and 3) describe a new species of Mayobaetis, based on larvae and adults from Argentina.

MATERIAL AND METHODS

Larvae were collected with kick and D-frame nets. Light traps were most efficient for capturing adults, but rearing larvae provided an accurate association of both states. All specimens were conserved in 96% ethyl alcohol. To study morphology, mature larvae and imagos were selected and dissected. Dissected parts of the specimens under study were mounted on microscope slides with Canada balsam. Line drawings were made with a camera lucida attached to a microscope. Photographs of adult and larval specimens were taken with an SMZ-10 stereomicroscope (Nikon, Tokyo, Japan) or a BX-51 microscope; Olympus, Tokyo, Japan, with a Nikon D5000 digital camera. For some of the pictures, a series of partially focused images was processed with the program Combine ZP (Combine Z5; Hadley 2009) to produce final images with enhanced quality. The material examined is housed at the following institutions: IBN (Instituto de Biodiversidad Neotropical), Tucumán, Argentina; IML (Instituto Miguel Lillo), Tucumán, Argentina; ULUMSA (Instituto de Ecología, Universidad de Límnología, Universidad Mayor de San Andrés), La Paz, Bolivia; MEUV (Museo de Entomología de la Universidad del Valle), Cali, Colombia.

Taxa

A matrix of 16 taxa and 80 morphological characters was constructed (Appendix S1). The ingroup taxa belonging to the Baetodes complex that were included in the matrix are: Lugoiops (L. maya), Prebaetodes (P. sitesi and P. meridinensis), Spiritios (S. silvudus and S. tepuenisis), Moribaetis (M. macaferti, M. maculipennis, and M. salvini), and Mayobaetis (M. ellenae and M. yala, new species). Moribaetis mimibresaurus was not included because only the adults are known and lack of information on larvae would have left several gaps in the matrix. Baetodes was included at the generic level because it has 40 species, and their inclusion would have exceeded the scope of this paper. As in a recent analysis by Nieto (2010), 5 species were included as outgroups. Four of them belong to the family Baetidae: Rivudiva minantenna, Rivudiva trichobasis, Cryptonympha copiosa, and Cryptonympha dasilvai. The trees were rooted with Metamonius anceps (Nesametidae), considered closely related to Baetidae (e.g., Staniczek 1997, Kluge 2004). A detailed list of specimens of these species can be found in Nieto (2010). Other species included were S. tepuenisis, scored from type material (IML), and P. meridinensis scored from the literature (Chacón et al. 2010).

Phylogenetic analysis

The matrix was analyzed with the program TNT (Goloboff et al. 2008) under an implied weights assumption (Goloboff 1993) with k values ranging from 2 to 6. The shortest trees were obtained under Analyze/TraditionalSearch commands; i.e., 500 replicates of random addition sequences followed by tree bisection–reconnection, saving 10 trees/replcation. Group support was obtained by applying frequency differences (Goloboff et al. 2003), which were calculated with 500 jackknifing replicates (Farris et al. 1996) by symmetrical resampling of the original matrix (each character presents the same probability of being positively or negatively reweighted; Goloboff et al. 2003). Each jackknifing replicate was calculated by 10 random-addition sequences plus tree bisection–reconnection, saving 10 trees/replcation.

Biogeographic analysis

All available geographical records of the Baetodes complex were mapped with DIVA-GIS (Hijmans et al. 2012) based on the limits of the freshwater ecoregions of the world by Abell et al. (2008). Water lines and water bodies were provided on the DIVA website (http://www.diva-gis.org/Data). The biogeographic analysis was carried out through SAV (Arias et al. 2011), a method that uses observed distributions as data. SAV does not assume predefined areas or a hierarchical relationship between them. The main purpose of this method is to discover disjunct (allopatric or vicariant) distributions among sister groups. The analysis was implemented in the Vicariance Inference Program (VIP; Arias 2010). Distributions were represented as absence/presence data in 1° × 1° cells in a latitudinal–longitudinal grid.
RESULTS AND DISCUSSION

Phylogeny

The analysis under implied weights yielded 3 shortest trees (length = 168 steps, fit = 53.45). Figure 1 shows the strict consensus of the shortest trees with *Metamonius anceps* as the outgroup. The topology of the consensus tree is similar to that in fig. 73 by Nieto (2010).

The *Baetodes* complex was obtained as monophyletic group (Node A; Fig. 1, Appendix S3). Four synapomorphies in the larvae and good support values under jackknifing sustained this result: the glossae overlapping to paraglossae (character 29), tibiae longer than tarsi (character 43), tarsal claws with strong subapical setae (character 48), and abdominal terga with covers (character 50). The *Baetodes* complex originally did not include *Spiritiops*. Nieto (2010) showed that this genus must be included in the complex to support its monophyly. This result was confirmed in this analysis. The strong subapical seta in the tarsal claws, which is the main synapomorphy for this group, is present in other genera, such as *Echinobaetis*, *Indobaetis*, and *Papuanatula*, outside the New World. However, a preliminary analysis of the family Baetidae suggests that these genera are not related to this complex (J.-L. Gattollati, Musée cantonal de zoologie, Lausanne, and CN, unpublished data).

The inclusion of *Mayobaetis yala*, new species, *P. meridinensis*, and *S. tepuensis*, 3 genera previously considered monospecific, confirmed the monophyly of the *Baetodes* complex. *Mayobaetis* (Node F; Fig. 1, Appendix S3) was recovered with 8 synapomorphies, among which pedicel of the antennae with scale-like tuberculations (character 3), dorsoventrally flattened scape (character 4), long scape (>3× the pedicel) (character 6), and cerci (Fig. 6L) with spines on external margins (character 60), were particularly important. *Prebaetodes* (Node D; Fig. 1, Appendix S3) displayed 6 synapomorphies, such as lingua without projection (character 21), long and slender teeth at the apex of the maxilla crown (character 27), and absence of gill tracheation (character 55). *Spiritiops* (Node B; Fig. 1, Appendix S3) was recovered with 4 synapomorphies: crenelated lateral margin of superlinguae (character 22), segment III of the labial palp (character 35) showing length subequal to width, length of gill/length of tergum ratio 2.0 to 2.9 (character 52) and forewings with pterostigma 3–5 cross-veins (character 69).

*Spiritiops* was recovered as a sister group of *Lugoiops* (Node G). In turn, *Mayobaetis* was recovered as a sister group of both *Baetodes* and *Lugoiops* (Node G). *Prebaetodes* was placed as sister to all the former (Node H), followed by *Moribaetis* (Node I), and last, *Spiritiops*, as a sister group of the rest of the complex.

Some characters showed a tendency to diminish in size or number inside the complex. For instance, the basal state in the tarsal claw (character 47) in *Spiritiops* displays 2 rows of denticles, a feature that is reduced to 1 in the rest of the complex. The antennae (character 5) are fairly long in *Spiritiops*, *Moribaetis*, and *Prebaetodes*, whereas they are short in *Mayobaetis*, *Lugoiops*, and *Baetodes*. A similar pattern can be observed in the length of the terminal filament (character 59).

Biogeographic analysis

The complex is distributed throughout North, Central, and South America. It appears mainly in the freshwaters of the ecoregions Papaloapan, Chiapas, San Juan, and Chiriquí.
(Abell et al. 2008) in North and Central America. These ecoregions are characterized by tropical and subcoastal rivers with tropical climate featuring a dry season followed by a rainy season (Abell et al. 2008). In South America, the complex is distributed in 2 areas. Some genera, such as *Mayobaetis* or *Prebaetodes*, are distributed mainly in the west side in the Amazonas High Andes, Amazonas Lowlands, and in the North Andean and Central Pacific slopes. These freshwater ecoregions are composed of many independent short rivers in small watersheds. These

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Figure 3. Hypothetical barriers generated by the Vicariance Inference Program (VIP). A.—Vicariant node 1, showing the split of *Spiritiops* (red dots) and the other genera of the complex (blue dots). B.—Vicariant node 2, showing the split of *Moribaetis* (red dots) and the other genera of the complex (blue dots). C.—Vicariant node 3, showing the split of *Prebaetodes meridinensis* (red dots) and *Prebaetodes sitesi* (blue dots). D.—Vicariant node 4, showing the split of *Mayobaetis yala* (red dots) and *Mayobaetis ellenae* (blue dots). E.—Vicariant node 5, showing the split of *Baetodes* (red dots) and *Lugoios maya* (blue dots). Open squares, species not considered in this node.
rivers are narrow and high-gradient with a climate that varies from cool to cold and temperatures inversely proportional to increasing altitude. In eastern South America, some genera, such as *Baetodes* or *Spiritiops*, are distributed in the Upper and Lower Paraná, lower Uruguay, the Amazonas Guiana Shield and Orinoco Guiana Shield, and Maracaibo, among other freshwater ecoregions. The climate is humid subtropical with warm summers. The habitats range from large low-gradient rivers to steep headwater streams with fast waters.

In the biogeographic analysis, without removing nodes (Fig. 2), VIP recovered 1 reconstruction with a cost of 9.00 and 3 disjunction pairs (nodes 3–5). However, *Baetodes* was removed in most of the 175 VIP possible reconstructions in which some nodes were removed, as expected. This outcome creates a challenge in attempts to find a biogeographical explanation because this genus is widely distributed. Two more disjunct pairs were recovered (nodes 1 and 2) from 1 reconstruction in which the node (*Baetodes + L. maya*) (*M. yala + M. ellenae*) was removed.

A brief description of tectonic background is necessary to explain the possible coincidence between vicariant events of this complex and tectonic events. During the middle and late Miocene, 3 successive Atlantic marine transgressions, all informally known as the Paranaean Sea, were recorded in South America. The northwestern part of the Paranaean Sea was connected with the so-called “Tethys Waterspout”. During this time, an open seaway separated terrestrial environments or, in this case, freshwater ecosystems. During the middle Miocene, a great increase of thermal gradient occurred from the equator toward both poles. In addition, the uplifting Andes constituted a major barrier to moisture-laden South Pacific winds (Ortiz-Jaureguizar and Cladera 2006). All of these elements could have concurred with the split between *Spiritiops* and the rest of the complex (Fig. 3A), i.e., node 1. Concurrently, the absence of the
Isthmus of Panama, which was finally closed during the late Pliocene, coincided with the split of *Moribaetis* from the rest of the genera (Fig. 3B), i.e., node 2. Unlike most of the South American Andes, which were formed by convergence across a conventional type-B subduction, the Merida Andes (MA) have some special traits that are worth considering. The MA do not have a direct historical relationship with the rest of the range (Audemard 2003). In addition, together with the eastern mountain ranges, they are separated by the southern termination of the left-lateral strike-slip Santa Marta–Bucaramanga fault and the northwest–southeast trending Santander Massif (Audemard 2003). This striking difference would explain the vicariant event that *P. meridinensis* and *P. sitesi* (node 3; Fig. 3C) do not share the same geographical distribution even though both inhabit Andean regions at high altitude. *Prebaetodes meridinensis* occurs in the MA, whereas *P. sitesi* occurs in the Ecuadorian and Colombian Andes. Another interesting vicariant event took place probably as the result of combined action of the Andean uplift and the western Antarctic glaciation during the middle Miocene. These 2 events caused an increase in the thermal gradient from the equator to the poles (Ortiz-Jaureguizar and Cladera 2006). As a consequence, 2 species, *M. yala* and *M. ellenae* (node 4; Fig. 3D), may have appeared on either side of the mountain. A similar result was obtained for the genus *Cyriocosmus* (Araneae:Theraphosidae) (fig. 11 by Ferretti et al. 2012). The last vicariant event (node 5; Fig. 3E) to be considered was caused by the extreme geological complexity of Central America where, in effect, tectonic and volcanic processes operate in tandem (Mann et al. 2007). Central America encompasses an intricate mosaic of dynamic landscapes shaped by a wide range of Earth surface processes, and the resulting physiography of each landscape features a distinctive landform assemblage that preserves a unique history of landscape evolution (Marshall 2007).

**TAXONOMY**

*Mayobaetis* Waltz and McCafferty

*Moribaetis* (*Mayobaetis*) Waltz and McCafferty 1985:240.


(Type-species: *Baetis ellenae* Mayo, original designation)

*Mayobaetis yala* Nieto, sp. nov. (Figs 4A–C, 5A–C, 6A–L)

**Diagnostic characters** *Mayobaetis yala* sp. nov. can be distinguished from the other species of the genus by the following combination of characters. In the male imago: 1) segment I of the forceps without projection (Fig. 5C). In the larva: 1) dorsal surface of abdomen without a medial dark line (Fig. 4C), 2) lingua narrow and pointed apically (Fig. 6E), 3) body length, short, <8 mm.

**Male imago** (Fig. 4A) Length, body: 8.8–9.0 mm; fore wings: 9.4–9.5 mm; hind wings: 1.4 mm. Head yellowish brown, antennae orange brown. Compound eye oval and orange. Height of stalk subequal to eye diameter, ocelli black. Thorax yellowish brown. Mesoscutum orange brown, metascutum brownish. Pleurae dark brownish. Pro, meso, and metasternum orange brown. Legs yellowish. Leg I: tibia 1.5× the length of femur, tarsus subequal to tibia. Legs II and III: tibiae 1.5× the length of femora, tarsi ½ the length of femora. Wings hyaline, except costal and subcostal space of forewings opaque. Marginal intercalary veins longer than the space between longitudinal veins (Fig. 5A). Hind wings with 2 longitudinal veins (Figs. 5Ba, Bb). Abdomen orange brown, posterior and lateral margin of terga brownish. Sterna yellowish. Genitalia orange brown, forceps 3-segmented, segment I without medial projection, segment III short (Fig. 5C). Cerci orange brown.

**Female imago** (Fig. 4B) Length, body: 9.7–9.8 mm; fore wings: 10.6–10.7 mm; hind wings: 1.2–1.3 mm. Head reddish brown. Compound eyes grayish. Thorax reddish brown. Mesocutelum orange brown. Pro-, meso-, and metasternum reddish brown. Legs yellowish brown. Abdomen reddish brown.

**Larva** (Fig. 4C) Length, body: 7.7–8.0 mm; cerci: 63 mm; terminal filament: 1.9 mm. Antennae: 1.8–1.9 mm. General coloration yellowish brown. Head yellowish brown,
compound eyes of male brownish. Antennae (Fig. 6A) pale yellow, pedicel of the antennae with scale-like tuberculations. Mouthparts yellowish brown. Labrum (Fig. 6Ba) wider than long, dorsal surface with a row of subapical setae, ventrally lateral margin sclerotized and with a row of 3–4 short spine-like setae, apical setae bifid (Fig. 6Bb). Mandibles (Fig. 6C, D) with incisors fused apically, without setae between prostheca and mola. Left mandible (Fig. 6C) with prostheca robust and with denticles apically. Right prostheca bifid (Fig. 6D). Hypopharynx with lingua longer than superlinguae (Fig. 6E). Maxillae (Fig. 6F) with palpi subequal in length to galea-lacinia, with 2 segments, segment II with a distal constriction. Labium (Fig. 6G) with glossae subequal in length to paraglossae, truncate apically and with 2–3 pectinated setae. Paraglossae with 3 rows of pectinated setae. Labial palpi with segment II without medial projection, segment III oval and with short spines.

Thorax yellowish brown. Anterior margin of metathorax brownish. Pleurae brownish. Sterna pale yellow. Legs (Fig. 6H) yellowish brown, femora with a pale longitudinal band on dorsal surface, tarsi brownish apically. Tarsal claws (Fig. 6I) with 8 denticles, and with strong subapical setae. Abdomen orange brown (Fig. 4C), posterior margin of terga smooth and brownish (Fig. 6J). Sterna yellowish brown. Gills (Fig. 6K) whitish, main trachea weak pigmented. Caudal filaments yellowish. Cerci (Fig. 6L) with spines on external margins.

**Etymology** Yala is the name of one of the rivers where this species was collected.

**Distribution** Argentina, Jujuy.


**Mayobaetis ellenae Mayo**

*Baetis* sp. 1 Roback 1966:137.


*Moribaetides (Mayobaetis) ellenae*; Waltz and McCafferty 1985:240.


**Remarks** This species was originally described as *Baetis ellenae* (Mayo 1973). Its classification has shifted between different statuses, in a subgenus of *Moribaetides* or in its own genus, *Mayobaetides*, but it has never been described again. New material assignable to this species was reviewed, and in the case of adults, the distinctive CuP veins are strongly curved, a character that was omitted in the original description.

**Distribution** Bolivia, Colombia, Costa Rica, Ecuador, Perú, and Venezuela.

**Material examined** 15 larvae, BOLIVIA, Depto. La Paz, San Pedro abajo, cascada camino a Coroico, S 16°15′12″, W 67°47′08″, 2250 m, 25.XI.2000, Dominguez, Molineri y Nieto cols. 30 larvae, San Pedro arriba, cascada camino a Coroico, S 16°16′15″, W 67°47′05″, 2400 m, same date and collectors. 4 larvae, COLOMBIA, Valle del Cauca, Municipio de Riofrío, río La Cristalina, 2 km al Occidente de Salónica, Cuenca alta del río Riofrío, N 04°07′39″, W 76°24′13″, 1240 m, 26.VIII.2000, Zuñiga, Gri sales, R. J. Cardoso-Zuñiga cols, 2 ♀ imagos same locality: 17.IX.2001, Zuñiga, Echeverri, Cardoso-Zuñiga. One larva, Municipio de Cali, Corregimiento de Pance, Vereda El Pato, Cuenca alta Río Pance, 1600 m, N 3°19′52″, W 76°38′48″, 2.VI.2007, Zuñiga, Cardona, López, Montaña, col. 12 larvae from Bolivia housed at IBN, the rest of the material housed at ULUMSA. 2 larvae and 1 ♂ image from Colombia housed at IBN, the other material from the same country housed at MEUV.

**CONCLUSION**

The hypothesis that *Spiritiops* belongs to the *Baetodes* complex is reinforced. Three previously monospecific genera, *Mayobaetides*, *Prebaetodes* and *Spiritiops*, were recovered each as monophyletic. The biogeographic analysis reconstructed 3 disjunction nodes without removing nodes, and 2 more if 1 node is removed. Although some vicariant events and corresponding geological phenomena cannot be proved to have taken place at the same time, some striking coincidences may suggest that in effect they took place simultaneously.

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**LITERATURE CITED**


