Original Article

Taxonomic revision of the genus *Chiloporter* Lestage (Ameletopsidae: Ephemeroptera) with notes on its biology and distribution

MARITZA MERCADO & SIMON ELLIOTT

Instituto de Zoología, Universidad Austral de Chile, Valdivia, Chile

(Received 25 April 2004; accepted 12 April 2005)

Abstract

A taxonomic revision of the genus *Chiloporter* is presented confronting new material collected in Chile and Argentina, with the literature of the genus. Unknown developmental stages are described; association of larvae and winged stages is confirmed here by rearing. The synonymy of the extant species is proposed. Notes on the biology and distribution are also included.

Resumen

Se presenta una revisión del género *Chiloporter* contrastando material nuevo con las descripciones del género en la literatura. Se describen los estados de desarrollo desconocidos y se asocian todos los estados quedan mediante crianzas. Se propone la sinonimía de las especies existentes. Se incluyen también notas acerca de la biología y distribución del género.

Keywords: *Chiloporter*, Ephemeroptera, taxonomy, distribution

Introduction

The amphinotic family Ameletopsidae comprises the New Zealand genus *Ameletopsis* (one species), the Australian *Mirawara* (three species), and the two Neotropical representatives *Chiloporter* and *Chaqui-hua*, with two species each. *Chiloporter* is restricted to southern South America, *Ch. eatoni* and *Ch. penai* are cited for Chile, only *Ch. eatoni* is recorded in Argentina.

The genus *Chiloporter* was erected by Lestage (1931) for a larval exuvia from Chile, no locality specified, which Eaton (1885) had previously described under the heading “Genus and Species undetermined”. Lestage (1931) named this exuvia *Chiloporter eatoni*, which is the type-species of the genus.

Demoulin (1952) compared the Chilean exuvia, which he stated to be incomplete, with the New Zealand genus *Ameletopsis* and found them very similar in spite of the differences in the gills, and synonymized *Chiloporter-Ameletopsis*. The species was then called *Ameletopsis eatoni*. Later on, Demoulin (1955) presented a new larval specimen from Chile, similar to Eaton’s, although not of the same species. Based on a reappraisal of the gill morphology he concluded that the *Chiloporter-Ameletopsis* synonymy no longer held, and took Eaton’s exuvia back to *Chiloporter*. Having reinstated the genus, Demoulin (1955) described his new material as a new species named *Chiloporter penai*. The specimens, a larva and a male imago, had been captured in the Nuble province, Chile.

Therefore, descriptions of the *Chiloporter* species are based on very poor material from one specific locality and one generic locality only, so that the variability of their characters is not known.

It is the aim of this work to present a revision of the genus *Chiloporter* and to document the specific variability along its distributional area. Earlier descriptions will be complemented with new ones of the undescribed stages, as well as remarks on the
variability of the more relevant characters. A contribution to the biology and distribution of the genus is also presented.

Material and methods

Rivers and streams were sampled in numerous localities from the regions Metropolitana to Magallanes and Tierra del Fuego in Chile, and from Bariloche to Ushuaia, along the Andean foothills, in Argentina. Collections were made in spring and summer 1999–2003. This material is labelled with the prefixes “N” for nymph and “A” for the winged stages. Material from the Colección de Macrozoobentos of the Instituto de Zoología of the Universidad Austral de Chile, labelled BAD, collected prior to this study was also revised.

Nymphs were collected using a dipnet with a mesh of 500 μm. Emerging stages were captured by means of a semi-submerged driftnet anchored to the stream bed from early afternoon until the following morning. Flying insects were captured by the watercourses with an aerial net.

Some of the nymphs collected were reared to adults in their native watercourses or at our laboratory. Specimens in all stages of development were preserved in 70% ethanol. This material is deposited in the macrozoobenthos collection at the Instituto de Zoología of the Universidad Austral de Chile in Valdivia.

Microscopic preparations were made of mouthparts, legs and rear abdomen of specimens from different localities. Some nymphal and adult parts were cleared in KOH and mounted in Euparal.

Material examined


Results

Genus Chiloporter Lestage, 1931

Chiloporter Lestage 1931, pp. 50–51; Demoulin 1955, pp. 5–6


Although the genus was established by Lestage (1931), this author made no explicit reference to
diagnostic characters. He used Eaton’s (1885) description and mentioned only what differences and/or similarities he observed between Eaton’s specimen and other Ephemeroptera groups. Eaton’s (1885) original description contains most of the characters relevant to the genus. His Plate 53 presents the incurved claws of the nymph; Figures 10–12 present the gill structure in abdominal segment II, consisting of a large opercular portion covering a smaller dendritic ventral portion (Figure 14); and the first pair of gills in segment I, in which the dendritic portion only is present (Figure 13).

Recently, the following diagnostic characters for the genus were gathered from the literature by Dominguez et al. (1994): nymph: head wider than thorax, abdominal gills with a fringed ventral portion and a subcircular pigmented dorsal portion covering the terga. Additionally, we observed that the nymphs present feathered caudal filaments (Figure 1) and large eyes covering approximately 1/3 of each hemi-head. Adult stages: transverse veins of forewings without anastomosis, costal projection of hindwings rounded; genitalia as in his Plate IV, Figure 3; tarsal claws different within a pair. Regarding the forewings, we disagree with the above since our material presented anastomosis in the stigmatic area (Figure 2a). This anastomosis is not abundant but proved to be a constant character amongst our specimens.

**Chiloporter eatoni** Lestage, 1931

“Genus and Species undetermined” Eaton 1885, pp. 229–230, Pl. 53, Figures 1—14

**Chiloporter eatoni** Lestage 1931, pp. 50–51

**Ameletopsis eatoni** Demoulin 1952, pp. 170–172

**Chiloporter penai** Demoulin 1955; NEW SYNONYMY

The original description of the species *Ch. eatoni* is based on an obviously incomplete nympha1 exuvia from Chile, and apart from the holotype no author has ever mentioned it again for Chile. It has been recorded in Argentina, where no *Ch. penai* has been recorded. We found no differences between Eaton’s (1885) description of this species and the material so far determined as *Ch. penai*.

The descriptions by Eaton (1885) and Demoulin (1955) are quite accurate and closely correspond to our new material. Therefore, we shall add here only new observations and mention discrepancies with these former descriptions.

**Larvae (Figure 1)**

Body dorsoventrally flattened; pigmentation variable and sometimes uneven, most frequently dark brown or reddish brown, occasionally bright yellow. When present, the yellow pigment is completely lost in alcohol, other colors also fade to some extent in alcohol.

Prognathous head with large eyes. Antennae multisegmented filiform, as are maxillary and labial palps. Demoulin (1955) mentioned 17, 13 and 11 articles for the flagellum antennal, maxillary and labial palpi, respectively. We found that the number of articles is extremely variable and related to the nymph’s development. We have found that nymphs 5 mm long present a combination of 12, 7 and 9 articles, respectively, and large nymphs up to 26 mm long a combination of 20, 14 and 14 articles. The above seem to be minimum and maximum combination numbers. Irregularities were sometimes found in these combinations, both as unequal pairs and as unexpectedly low numbers in a large specimen. Observations through a 100x magnification microscope could not always clarify whether the segments had been amputated or not, though in some cases amputation was clearly apparent.

The mandibles (Figure 2c) present at the apex a trifid canine (incisor) and another one transversally oriented, in a subapical position very near the molar area, which if bifid (kinetodontium). The molar

![Figure 1. Chiloporter eatoni, dorsal view of nymph and (a) detail of gill, ventral view.](image-url)
Figure 2. *Chiloporter eatoni*. (a) Forewing, male imago; (b) Genitalia, male imago, ventral view; (c) Nymph, right mandible; (d) Nymph, labium, ventral view; (e) Nymph, left maxilla.
portian is represented by a rectangular projection almost perpendicular to the mandible, the distal free end of which presents another tooth-like projection, in an anterior position. Following this tooth in a proximal direction along the inner surface of the molar projection, abundant setae can be observed. Maxillae wide (Figure 2e) and triangular in shape, with five teeth at the apex, the four at the front long and incurved, the inner one almost straight and half as long as the others. Labium (Figure 2d) with glossa and paraglossa subrectangular. As was remarked by Putz (1998), the paraglossae are not segmented as in other Ameletopsidae. The submentum presents lateral expansions on both sides; these are lamellar in shape as mentioned by Kluge (2004). We have found similar structures in the genus Chaquihua, but different in shape from Chiloporter in that they present a pointed anterior apex. Putz (1998) also mentions such structures for Mirawara. Kluge lists these lamellae amongst the autopomorphies of Ameletopsis/fg1 (Kluge 2004).

All Chiloporter legs with a mid-dorsal line of hair from femur to tarsus. The inside of the tarsi with strong setae, as in tibia but less numerous. Each leg segment with a reddish-brown transversal band. Legs of subequal length, the posterior ones being the longest. In the first two pairs of legs, the femur is subequal to the tibia and tarsi combined, the third pair with the femur longer than tibia and tarsi. Incurved claws without denticles.

As already described by Demoulin (1955) Chiloporter presents seven pairs of double gills, each with a discoidal dorsal portion and a smaller ventral one (Figure 1a), profusely forked or fibrillous. Demoulin (1955) also mentions that the protective dorsal lamella, in all gills except in the first pair, have a ciliated reinforcement. We have observed this reinforcement in the first pair also, though it is less notorious. Gills vary remarkably along nymphal development. Juvenile nymphs have oval shaped elongated dorsal lamellae, with a filamentous projection at the centre of the distal portion. As the nymphp grows these tend to become circular and the filament is lost. The shape of this lamella will regenerate in the shape corresponding to its developmental phase: smaller nymphs will regenerate elongated gills and larger ones a rounded gill. This is noticeable even as the minute new gill sprouts from the former stump. The superior protective lamellae are pigmented, most frequently in dark reddish-brown, but the colouration can vary all the way down to a creamy-pink tone, and occasionally yellow-green in life. The inferior gill is nearly white.

Abdominal segments I – IX of Chiloporter, with small posterolateral projections; those in X are blunt. Segment X with sexual dimorphism: in male nymphs a bi-segmented structure corresponding to the future forceps are apparent and curved towards the free margin of the segment, which in turn has a “V”-shaped cleft of medium depth; in the female this same margin is rounded.

Demoulin (1955, Figure 2k) mentions that the three cerci are “feather-like” and of equal length. We found the terminal filament to be subequal to the cerci and, although they are feathered, the setae on the external margin of lateral cerci are shorter than those on the internal margin or on the terminal filament.

Male imago

Body length 17.5 – 18 mm; cerci 15 mm; forewing 17.3 mm long and 5.8 mm wide; hindwing 8.2 mm long and 4.8 mm wide. Colour in life: body reddish-brown, wings hyaline with a yellow-green tinge. Colour is lost in alcohol to a creamy tone all over.

Head: eyes large, the inner margins meet. Three white ocelli encircled by a dark band at their base. Antennae short, flagellum width three times the ocelli diameter. Thorax: colour in alcohol, bone white. Wing venation as represented by Demoulin (1955, Figure 2a). Our observations indicate that some Anastomosis is present in the stigmatic area, although not dense and varying from 1 to 3 only (Figure 2a). This character as well as all transverse veins are difficult to see because of their translucent quality. Sigmoidal veins as well as most transverse veins may vary in numbers. Claws dissimilar, one obtuse, one hooked. Leg I as long as forewing, femur and tibia of equal length; tarsus almost twice as long as femur or tibia, the inner margins of tarsal segments 1 and 2 with short blunt spines; tarsal formula 2 = 3, 4, 1, 5. Legs II and III identical; femur longer than tibia and tibia longer than tarsus; distal inner margins of segments 1 – 4 with small spines; tarsal formula 1 = 2 = 3 = 5, 4. Abdomen: colour in alcohol, bone white with dusty-rose oblique lateral lines. Stylinger plate elongated (Figure 2b) with a deep, wide “U” shaped cleft; forceps four-segmented, segment I ring shaped, segment II incurved and longer than all three other segments combined; in length, segment III is 1/3 of II, and IV subequal to II; penis lobes cylindric and long, fused all along except at the distal end where a slight constriction of the lobes marks the beginning of a free, wider terminal portion. Three long cerci covered with fine setae approximately as long as the cerci diameter.

Male subimago

Body length 16.2 – 18.8 mm; cerci 17 mm; forewing length 17.2 mm, width 5.6 mm; hindwing length 8 mm, width 4.6 mm. Colour in life bright yellow-green all over, including the eyes, with a grey
diagonal band across the forewing. In alcohol the colour is lost to a bone-white tone. Further references to colour depict specimens in alcohol.

Head: eyes smaller than in imago, they do not meet. The rest is just like the imago. Thorax: bone white with a longitudinal mid-dorsal reddish brown line. Wings of milky appearance, opaque and translucent, margins fringed with setae, venation as in imago except in stigmatic area which is more anastomosed. On the whole, all wing venation is more readily apparent in the subimaginal stage. Legs with a double row of setae on the inner face of the tarsi, culminating in a prominent pair of spines at the distal end of each tarsal segment. Leg I half as long as forewing; femur subequal to tarsus and tibia subequal to femur, tarsal formula 3 = 4, 5, 1 = 2; leg II subequal to I and III subequal to II in length; in legs II and III tarsus subequal to tibia, which is in turn subequal to femur, tarsal formula for both legs 1 = 5, 2 = 3, 4. Abdomen: same as imago.

Female imago

Body size 18 – 22 mm; cerci 17 mm; forewing length 20 mm, width 7 mm; hindwing length 9.4 mm, width 5.2 mm. Colour in life, same as male imago. Further references to colour depict specimens in alcohol. Head: eyes small and separated. Ocelli as in male imago. Antennae shorter than in the male, flagellum twice as thick as ocelli diameter. Thorax: thorax and wings as in male imago; anastomosis in the stigmatic area as in male subimago. Claws as male. Leg I half as long as forewing, femur subequal to tarsus and tibia subequal to femur, tarsal formula 3 = 4, 5, 1 = 2; leg II subequal to I and III subequal to II in length; in legs II and III tarsus subequal to tibia, which is in turn subequal to femur, tarsal formula for both legs 1 = 5, 2 = 3, 4. Abdomen: same as male subimago, but for a reddish mark which may be present at the distal margin of each segment, on the dorsal side. Gonobase rounded.

Female subimago

Body size 15.6 – 20.8 mm. Same as female imago, except colour which is identical to the male imago.

Diagnosis

The nymphs of Chiloporter present the following group of characters: body slightly depressed dorsoventrally; head prognathous and wider than thorax, labrum expanded and with a deep, wide “U”-shaped cleft in the anteromedian position, non-segmented paraglossa, submenton with lateral expansions as lamellae of rounded contours all over (Figure 2d), the antennal flagellum may develop as much as 20 segments, the maxillary palp 14 and the labial palp 14; legs rather wide, with strongly incurved claws; seven pairs of bilamellate abdominal gills (Figure 1a), with a dorsal portion discoidal covering a smaller fibrilllous one; cerci with setae on internal and external margin, those on the external margin shorter; caudal filament slightly shorter than cerci, with setae of equal length on both sides.

The winged stage of the genus present the following character assemblage: moderate anastomosis on the stigmatic area of the forewing (Figure 2a), and rounded costal projections on the hindwing. Claws different within a pair. Male genitalia as in Figure 2b. Terminal filament and cerci long, terminal filament subequal to cerci in length.

Biology

All members of the Ameletopsidae family are among the few non-facultatively carnivorous Ephemeroptera in the world. Of features peculiar to carnivores, the Ameletopsidae nymphs have in common: similar mouth structure with strong masticators and shredding parts, such as the prominent incisors on their maxillae and mandibles; maxillary and labial palpi as multisegmented filiform appendages with sensory functions; dorsoventrally flattened, wide heads with large eyes. Apparently other structures such as the strong setae on the inside of the nymph's forelegs might be associated to the predatory activities of the species: Putz (1998) observed such setae in Mirawara and hypothesized that they would be used for drawing prey into the mouth cavity. Other carnivorous insects use leg spines in a similar way.

Our revision of Chiloporter stomach contents showed remains of other Ephemeroptera larvae, noticeable Baetidae. Trictoptera and Chironomidae (Orthocladius sp.) larvae were also frequently found. We found similar combinations of food items in Chaquihua and they have also been reported for other Ameletopsidae: Phillips (1930, p. 333 in Needham et al. 1935) mentioned that Ameletopsis “feeds on small specimens of Leptophlebiid nymphs and other organisms”; Putz (1998) mentioned a predominance of Atalopylebioides in the stomach contents of Mirawara megaloprepia but also pointed out that the selectivity of the nymphs has not been demonstrated.

Hatching of subimagines have been observed from December to mid-January, lasting for one hour approximately, at dusk and well into the night. Nuptial flights take place at the same time. They have the usual up and down pattern, with a dozen or so insects flying actively in both phases. We observed them flying low above the watercourse, in a wide, open stretch of the Río Quinchilca.
Within the family, the nymph of *Chiloporter* presents the largest eyes in the proportionally largest head, and the shortest maxillary palpi, with less segments (16 segments in *Chaquihua*, 15 in *Amele-topsis* (Needham et al. 1935), and 14 in *Mirawara megaloprepia* (Putz 1998). This points to a possible compensation in the respective sensory functions, with a heavier reliance on the vision in this case, possibly connected with nocturnal activity.

The nymph has mixed locomotion capabilities as it usually crawls among the bottom stones but is also capable of short bursts of fast swimming. This is accomplished by wiggling the abdomen to use the cerci as a fish would use its caudal fin.

The characteristic streambed habitat in the Río Biobío (Chile) was described by Arenas (1995): in the higher reaches where the river runs through the Andean plateau, it consists of large cobbles, rough volcanic sand or gravel, and medium to large boulder armour in the Andean foothills and central depression reaches. Miserendino (2001) reported *Chiloporter* in the Río Esquel (Argentina) in stony bottom mountain reaches, whether these were running through sparsely or thickly wooden areas, and also in open prairie reaches. Our findings are consistent with the above: the nymph of *Chiloporter* is rheophilous and usually found under medium to large stones in fast to moderately fast, well-oxygenated waters, both in large and small streams and occasionally in small creeks. It can be present in the higher reaches of the Andean foothills as well as in lower reaches of the Central Depression of Chile or the Argentine prairie, as long as rhithric conditions persist. *Chiloporter* also inhabits rivers receiving untreated domestic and agricultural discharges such as the Río Toltén, where it thrives.

*Chiloporter* is a common enough aquatic insect within its distributional area, though not really abundant, as the predatory nymphs are sparsely distributed along the streambed.

**Geographic distribution (Figure 3)**

New records extend the distributional area of *Chiloporter* in Chile to the north as far as Río Toro at Radal (35°24'52"S; 71°03'13"W) VII Region, and down to Río Simpson (45°34'S) in the XI Region, to the south. *Chiloporter* is found mostly in rivers and streams of Andean origin, but south of 35°S it also becomes frequent in the Chilean coastal ranges. In Argentina it has has been recorded from the Río Chimehuín (40°02'S), Province of Neuquén, to the Río Esquel (42°53'S), Province of Chubut (Miserendino & Pizzolon 2000). Camousseight (2001) mentions Ushuaia (Tierra del Fuego) as an Argentinean locality for *Chiloporter* but this is probably a mistake since it is not mentioned in the Argentinean
Discussion

Even though Demoulin (1955), with the scant material available at the time, tentatively proposed diagnostic characters for the nymphs of the two species, our ample material supply has permitted us to establish that all these characters lie within the variability of one species.

Based on Eaton’s (1885) description, Demoulin (1955) proposed the following diagnostic characters for *Ch. eatoni* different from *Ch. penai*: 20 articles to the antennae (17 for *Ch. penai*), 11 articles to the maxillary palp (13 for *Ch. penai*), 14 to the labial palp (11 for *Ch. penai*), and also the absence of the protective lamellae in the first pair of gills of *Ch. eatoni* (seven pairs of bilaminate gills in *Ch. penai*).

Amongst our new material we found the number of articles of the antennal flagellum, maxillary and labial palps to be extremely variable, related to the nymphs’ development, not even stable for the terminal nymphs, and therefore of no use as a diagnostic character differentiating species.

The alleged absence of the superior lamellae on the first pair of abdominal gills in *Ch. eatoni* would stand as an important character capable of differentiating species in this genus if more material was available to support it. The fact is that the only specimen described as lacking those lamellae is the one incomplete exuvia that Eaton (1885) described, which lacked most of its gills altogether; Eaton himself (1885) remarked that he expected all gills of this nymph to be of the bilamellate type. We must state at this point that these lamellae break off easily, this often happened to us while manipulating the nymphs and many of our captured specimens lacked a number of their protective gills, while new ones could frequently be seen sprouting in their place.

Our material from Argentina (Río Epyúen) turned out to be completely consistent with the old descriptions of *Ch. penai*. It is most interesting to remark that Argentinean investigators, having diagnosed *Ch. eatoni*, invariably represent it in their drawings with the old *Ch. penai* seven pairs of bilamellate gills, disregarding even their own written descriptions (Wais 1985, Figure 5; Wais 1987, Figure 27a, 27b; Domínguez et al. 1994, plate IV, Figure 4). Because of all the above and, having found no evidence whatsoever among the material studied or described in literature capable of sustaining different species in this genus, we propose the synonymy of *Ch. eatoni* and *Ch. penai*, the name of *Ch. eatoni* prevailing by right of priority. The genus is therefore monospecific.

Acknowledgments

We wish to thank Nikita Kluge and Tomas Soldán who provided us with literature indispensable for this work, Eduardo Domínguez who kindly revised and commented this work, Janet Elliott and Anne Zillikens who revised the English version of this text. Vicente Irarrázaval who contributed most effectively in our fieldwork, and Rolando Carrasco who translated for us Putz’s work from Czech.

References