A taxonomic revision of the genus *Daedalma* Hewitson with the descriptions of twenty new taxa and the immature stages of two species (Lepidoptera: Nymphalidae: Satyrinae)

TOMASZ W. PYRCZ*, HAROLD F. GREENEY**, KEITH R. WILLMOTT*** & JANUSZ WOJTUSIAK****

*Zoological Museum of the Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland. pyrcztomasz@hotmail.com
**Yanayacu Biological Station & Center for Creative Studies, Cosanga, Napo, c/o Foch 721 y Amazonas, Quito, Ecuador: revm-moss@yahoo.com
***McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA. kwillmott@flmnh.ufl.edu
****Zoological Museum of the Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland. wojt@zuk.iz.uj.edu.pl

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TOMASZ W. PYRCZ, HAROLD F. GREENEY, KEITH R. WILLMOTT & JANUSZ WOJTUSIAK

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Abstract

The taxonomy of the Andean butterfly genus Daedalma (Nymphalidae, Satyrinae) is discussed. Generic synapomorphies based on adult morphology are proposed, and the relationships with allied genera of the subtribe Pronophilina are evaluated. The status of Junea as the sister-genus of Daedalma is reconsidered, particularly in light of new data on the larval stages. The genus Daedalma is divided into two presumed monophyletic groups distinguished by a series of morphological and ecological characters. Three species, D. eliza n. sp., D. dognini n. sp. and D. rubroreducta n. sp., and seventeen new subspecies are described, one new status is proposed, and three lectotypes are designated. Female genitalia of Daedalma are described for the first time and their taxonomical value is assessed. The early stages of D. rubroreducta and D.
dinias are described, the first larval descriptions for any species of Daedalma. Distribution and diversity patterns of Daedalma are discussed. Distribution maps, illustrations of male and female genitalia, and figures of adult butterflies of both sexes are provided for all taxa where possible, with comments on bionomics and adult behaviour for all taxa in the genus.

**Key words:** altitudinal distribution, Andes, Chusquea, genitalia, gregarious larvae, Junea, new taxa

**Introduction**

The genus *Daedalma* Hewitson (1858) belongs to the subtribe Pronophilina Miller (Harvey, 1991; Lamas et al., 2004; Viloria, 2007), an entirely neotropical and mostly montane section of the cosmopolitan nymphalid subfamily Satyrinae. Recent years have witnessed a considerable number of publications concerning the Pronophilina. Three decades ago it was one of the least known groups of butterflies world-wide, but thanks to the articles of Adams & Bernard (1977, 1979, 1981), Adams (1985, 1986), and numerous subsequent contributions, knowledge of the pronophilines has been greatly improved. In addition to a two-fold increase in the number of described taxa, our understanding of the subtribe's taxonomy, ecology, and biogeography has also improved significantly.

Despite this progress, the extremely high diversity and inaccessible, remote Andean habitats of the Pronophilina leave much work to be done. Although altitudinal distribution patterns and some ecological data are described by Pyrcz & Wojtusiak (1999, 2002), Pyrcz (2004) and Pyrcz et al. (2009), the area where our knowledge of the Pronophilina is perhaps most deficient is that of their immature stage biology. Since Schultze (1929) first published incomplete life histories for *Pedaliodes phoenissa* (Hewitson), *Lymanopoda samius* Westwood, and *Junea doraete* (Hewitson), there has been very little progress in this area. Several authors report oviposition, in most cases on *Chusquea* (Poaceae) or other woody bamboos (Adams, 1986; Pyrcz et al., 1999), but the only important recent contributions to the immature stage biology of Pronophilina are data on the early stages of several species found in Costa Rica, published by DeVries (1987), Pelz’s (1997) paper on the biology of *Parapedaliodes parepa* (Hewitson) in Ecuador, Heredia & Viloria’s (2004) data on *Pedaliodes zingara* Viloria & Heredia in Colombia, and Greeney et al.’s papers (2009, 2010) on *Pedaliodes poesia* (Hewitson) and *Corades medeba* Doubleday in Ecuador.

**History of research**

The genus *Daedalma* was described by Hewitson (1858), a British naturalist who was also the author of most descriptions of Andean Satyrinae in the 19th century. Although he placed the vast majority of pronophiline species that he described in the genus *Pronophila* Doubleday, including species from such diverse genera as *Pedaliodes* Butler, *Steroma* Westwood and *Pseudomaniola* Röber, he immediately recognised *Daedalma* as standing apart from other Andean satyrines, emphasizing the distinctiveness of this genus. His description of *Daedalma* was however very concise: "Head and eyes densely covered with long hair. Palpi long and projecting. Anterior wing with the sub-costal nervure four-branched; the first and second branches before the end of the cell. Posterior wing usually tailed, the costal margin projecting.” None of the specified characters of head morphology, venation and wing shape distinguish *Daedalma* from all other genera of Pronophilina. Hewitson originally recognised four species of *Daedalma*, *D. dinia* and *D. drusilla*, as well as two other species now placed in different genera. The latter two species are, surprisingly, *Panyapedaliodes drymaea*, a species not even related to *Daedalma*, and *Junea doraete*, which was later placed in the genus *Polymastor* by Thieme (1907), a junior homonym replaced with *Junea* by Hemming (1964). Butler (1867) designated *D. dinia* Hewitson as the type species of *Daedalma*. Three further taxa of *Daedalma* were described before the end of 19th century: *palacio* Dognin (1891), *boliviana*, and *dora* Staudinger (1897). The entire 20th century witnessed the description of only four more taxa, *adamsi* d’Abrera (1988), *parvomaculata* Krüger (1924), and *rhomboidea* and *oenotria* Weymer (1912), the latter two now treated as junior synonyms. Two new species, *D. fraudata* and *D. vertex*, as well as one subspecies, *D. boliviana peruviana*, were recently described by Pyrcz (2004). Vargas & Salazar (2004) published a short synopsis of the genus *Daedalma* in Colombia. Several other species, now placed in the genera *Pseudomaniola* Röber (1889) and *Thiemeia* Weymer (1912), have also been associated with *Daedalma*. Currently, the genus *Daedalma* is restricted to a small group of butterflies distinguished by the unique combination of characters discussed below. Compared to other genera of Pronophilina the systematics of *Daedalma*, thought not to be a very diverse genus, have remained largely