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Phylogenetic relationships and comparative larval morphology of epigean and stygobitic species of *Limbodessus* Guignot, 1939 (Coleoptera: Dytiscidae: Bidessini), with a key of identification

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Abstract

The larvae of five epigean and 25 stygobitic species of the diving beetle genus *Limbodessus* Guignot, 1939 are described and illustrated for the first time, with special emphasis on morphometry and chaetotaxy of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. Those of the following five epigean species are described: *L. amabilis* (Clark, 1862), *L. compactus* (Clark, 1862), *L. inornatus* (Sharp, 1882), *L. praelargus* (Lea, 1899), *L. shuckardii* (Clark, 1862). The 25 stygobitic larvae described are: *L. barwidgeeensis* Watts & Humphreys, 2006, *L. bigbellensis* (Watts & Humphreys, 2000), *L. challaensis* (Watts & Humphreys, 2001), *L. cooperi* Watts & Humphreys, 2006, *L. eberhardi* (Watts & Humphreys, 1999), *L. exilis* Watts & Humphreys, 2006, *L. fridaywellensis* (Watts & Humphreys, 2001), *L. hillviewensis* (Watts & Humphreys, 2004), *L. hinkleri* (Watts & Humphreys, 2000), *L. leysi* Watts & Humphreys, 2006, *L. macrohinkleri* Watts & Humphreys, 2006, *L. masonensis* (Watts & Humphreys, 2001), *L. millbilliensis* Watts & Humphreys, 2006, *L. mirandae* Watts & Humphreys, 2006, *L. morgani* (Watts & Humphreys, 2000), *L. nambiensis* Watts & Humphreys, 2006, *L. ordinarius* Watts & Humphreys, 2009, *L. palmulaoides* Watts & Humphreys, 2006, *L. pulpa* (Watts & Humphreys, 1999), *L. raeae* Watts & Humphreys, 2006, *L. raesideensis* (Watts & Humphreys, 2001), *L. windarraensis* (Watts & Humphreys, 1999), *L. yandalensis* Watts & Humphreys, 2006, *L. yarrabubbaensis* Watts & Humphreys, 2009, *L. yuimmeryensis* (Watts & Humphreys, 2003). The morphology and chaetotaxy of epigean vs.

stygobitic species are compared, and a key for the identification of the species is presented. Contrary to their epigeal counterparts, larvae of stygobitic *Limbodessus* have turned out to be very divergent morphologically. In addition to the common characteristics associated with an underground living (i.e., absence of stemmata, reduced pigmentation, and thin or soft exoskeleton), larvae of these species have undergone a variable modification of the frontoclypeus and have evolved relatively shorter tarsal claws. Two morphological groups of stygobitic species are evident, one including species less deviated from the ancestral (epigeal) condition and another group comprising more modified species that typically have a larger size, a more or less pyriform head with a digitiform nasale, and a strongly reduced occipital foramen. Primary chaetotaxy of the species has remained a very conservative expression of the phenotype. Secondary chaetotaxy shows variation among the species, the most obvious being the variable number of lamellae clypeales and the presence or absence of secondary setae on the urogomphus. The phylogenetic relationships of *Limbodessus* are analyzed cladistically. Larvae of this genus lack the primary pore ABC, which is a synapomorphy of the tribe Bidessini. As presently defined, *Limbodessus* is probably paraphyletic with respect to *Allodessus* Guignot, 1953.

Key words: Coleoptera, Dytiscidae, Bidessini, *Limbodessus*, larva, groundwater, morphometry, chaetotaxy, phylogeny

Introduction

Limbodessus Guignot, 1939 is a genus of 70 known species primarily found in Australia. Indeed, except for *L. compactus* (Clark, 1862) and *L. curviplicatus* (Zimmermann, 1927), which are distributed in the Palaearctic-Oriental-Australian and Pacific regions respectively, all other species are endemic to the Australian region (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006). The most recent revision of the genus recognizes nine epigeal species, which are often abundant in still to slightly moving, shallow water (Watts & Leys 2005). Recently, however, many species of *Limbodessus* have been found living underground, in what represents the most extensive radiation of subterranean diving beetles known so far (see Watts & Humphreys 2009 and references therein). Within the last 15 years about 60 species of obligate groundwater (stygobitic) *Limbodessus* (many of them previously included in the genera *Tjirtudessus* Watts & Humphreys, 1999 and *Nirridessus* Watts & Humphreys, 1999) have been described, associated with calcrete (terrestrial limestone) aquifers in the Yilgarn region of Western Australia and the Ngalia basin in the Northern Territory (Watts & Humphreys 2009). The species of stygobitic *Limbodessus* have all been found in calcretes of ancient palaeodrainage channels in arid and semiarid areas of western and central Australia (Watts & Humphreys 2006). The calcretes form by precipitation of carbonates from shallow groundwater flow paths in palaeodrainage channels, and are the only permanent freshwater habitats for macro- and mesofauna through much of the arid zone of inland Australia (Leys *et al.* 2003).

Limbodessus is one of the more than 40 genera of the hydrophiline tribe Bidessini (ca. 600 species worldwide), which includes most of the smaller species of diving beetles or Dytiscidae (generally smaller than 5 mm long) (Nilsson 2001). All the species of *Limbodessus* are postulated to share a monophyletic origin (Balke & Ribera 2004). Sequence data for members of this genus and other bidessine relatives were presented by Leys *et al.* (2003), Balke and Ribera (2004), Hendrich and Balke (2009), and Hendrich *et al.* (2009) and have confirmed a close relationship between *Limbodessus* and the genus *Allodessus* Guignot, 1953. A recent phylogenetic analysis based on molecular data suggested that the majority of stygobitic *Limbodessus* species independently evolved from a small number of widespread surface species approximately five million years ago (Leys *et al.* 2003).

Despite the Bidessini representing one of the most significant radiations of diving beetles (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006), larval morphology of members of this tribe remains imperfectly known. So far, the larvae of only 16 genera have been described (Meuche 1937; Watts 1963; Bertrand 1972; Perkins 1980; Richoux 1982; Matta 1983; Nilsson 1985; Alarie & Wewalka 2001; Alarie *et al.* 2007; Michat & Alarie 2006, 2008; Michat & Torres 2006; Michat *et al.* 2010, 2011), some of them very superficially, and the larvae of several genera are unknown. Regarding *Limbodessus*, only brief descriptions of the larvae of the epigeal *L. amabilis* (Clark, 1862) and the stygobitic *L. eberhardi* (Watts & Humphreys, 1999) and *L. pulpa* (Watts & Humphreys, 1999) have been published (Watts 1963; Watts & Humphreys 1999).

Larval morphology is important in the study of the phylogenetic relationships among Holometabola. As different expressions of the same genotype, larval characters help to complement adult characters that have been traditionally the primary basis for classification. As demonstrated recently, larval chaetotaxy is a significant source of characters both for diagnosis of the genera and species and for the study of the phylogenetic relationships within the Dytiscidae (e.g., Alarie *et al.* 2009a, 2009b, 2011), in particular within the Bidessini (Alarie *et al.* 2007; Michat