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Loss of the sticky harpoon – COI sequences indicate paraphyly of *Stenus* with respect to *Dianous* (Staphylinidae, Steninae)

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ABSTRACT

The speciose staphylinid subfamily Steninae comprises more than 2700 species of the two genera *Stenus* and *Dianous*. Whereas the labium of *Dianous* beetles is short and unspecialized, the members of *Stenus* are characterized by a protruding elongated labium that functions as a prey-capture apparatus. This is considered the derived state and the most prominent apomorphic character for *Stenus*. To elucidate the phylogenetic relationship of *Stenus* and *Dianous*, we analyzed 807 bp of the mitochondrial cytochrome c oxidase I (COI) gene in 30 *Stenus* and 12 *Dianous* species. Our analysis indicates the evolutionary origin of *Dianous* within *Stenus*, suggesting a secondary loss of the specialized prey-capture apparatus. Whereas the derived phylogenetic position of *Dianous* within *Stenus* is supported by maximum parsimony, neighbor joining, maximum likelihood, and Bayesian analyses, the resolution of COI seems to be insufficient to consistently resolve basal relationships of *Stenus* species.

1. Introduction

The Steninae is a subfamily of the staphylinine group (i.e. subfamily groups of Lawrence and Newton, 1982) within the Staphylinidae (rove beetles), containing only two genera, i.e. *Stenus* Latreille 1797 and *Dianous* Leach 1819. The monophyly of Steninae is supported by many larval and adult autapomorphies (Puthz, 1981; Hansen, 1997; Leschen and Newton, 2003; Thayer, 2005; Grebennikov and Newton, 2009; Clarke and Grebennikov, 2009) and suggested also by molecular analysis (Grebennikov and Newton, 2009). The subfamily Steninae might also include a third, as yet undescribed genus possessing a prey-capture apparatus similar to that in *Stenus* (Leschen and Newton, 2003; Betz and Kölsch, 2004; Clarke and Grebennikov, 2009).

With almost 2500 species (Puthz, 2010), *Stenus* is one of the largest beetle genera and, with the exception of New Zealand, is distributed worldwide (Puthz, 1971, 2010). The most obvious autapomorphic character defining *Stenus* is a harpoon-like protruding elongated labium with the paraglossae being modified into sticky (adhesive) pads (Fig. 1A and B; Weinreich, 1968; Puthz, 1981; Betz, 1996, 2006). This prey-capture apparatus can be rapidly protruded toward the potential prey by increased haemolymph pressure (Bauer and Pfeiffer, 1991; Betz, 1996; Kölsch and Betz, 1998; Heethoff et al., 2011a; Heethoff and Raspotnig, 2012; Koerner et al., 2012a,b). In *Dianous* species, the labium is also slightly protrudable but much shorter and does not form an adhesive prey-capture apparatus, i.e. the paraglossae are not modified into adhesive pads (Fig. 1C and D; Weinreich, 1968; Puthz, 1981). Accordingly, *Dianous* beetles catch their prey solely using their mandibles.

The genus *Stenus* is classified into five subgenera, i.e. *Stenus* s.str., *Hemistenus* Motschulsky 1860, *Hypostenus* Rey 1884, *Metatesnus* Adam 1987 and *Tesnus* Rey 1884 (Puthz, 2001, 2008). This classification is based on the morphology of the 4th segments of the metatarsi (simple or bi-lobed), the relative length of the 1st and 5th segment of the metatarsi, the relative length of the metatarsi and metatibiae and the presence or the absence of abdominal paratergites (e.g. Cameron, 1930; Freude et al., 1964; Zhao and Zhou, 2004). This subgeneric classification of *Stenus* seems to be artificial and does probably not reflect the true phylogenetic relationships among species (e.g. Puthz, 1972, 2003). Therefore, a more elaborate classification of *Stenus* species into monophyletic species groups has been suggested (summarized in Puthz, 2008).

Although the genus *Stenus* has been considered monophyletic on the basis of its possession of the labial adhesive capture apparatus and several other adult (mostly related to the prey-capture apparatus) and larval characters, the genus *Dianous* is not defined by any autapomorphies (Puthz, 1981; Clarke and Grebennikov, 2009). Grebennikov and Newton (2009) have suggested three autapomorphic characters for the genus *Dianous*, but their analysis was based only on one *Dianous* species. Since some members of the species groups of *Dianous* greatly differ morphologically (Puthz, 1981, 2000; Shi and Zhou, 2011), they may even represent several

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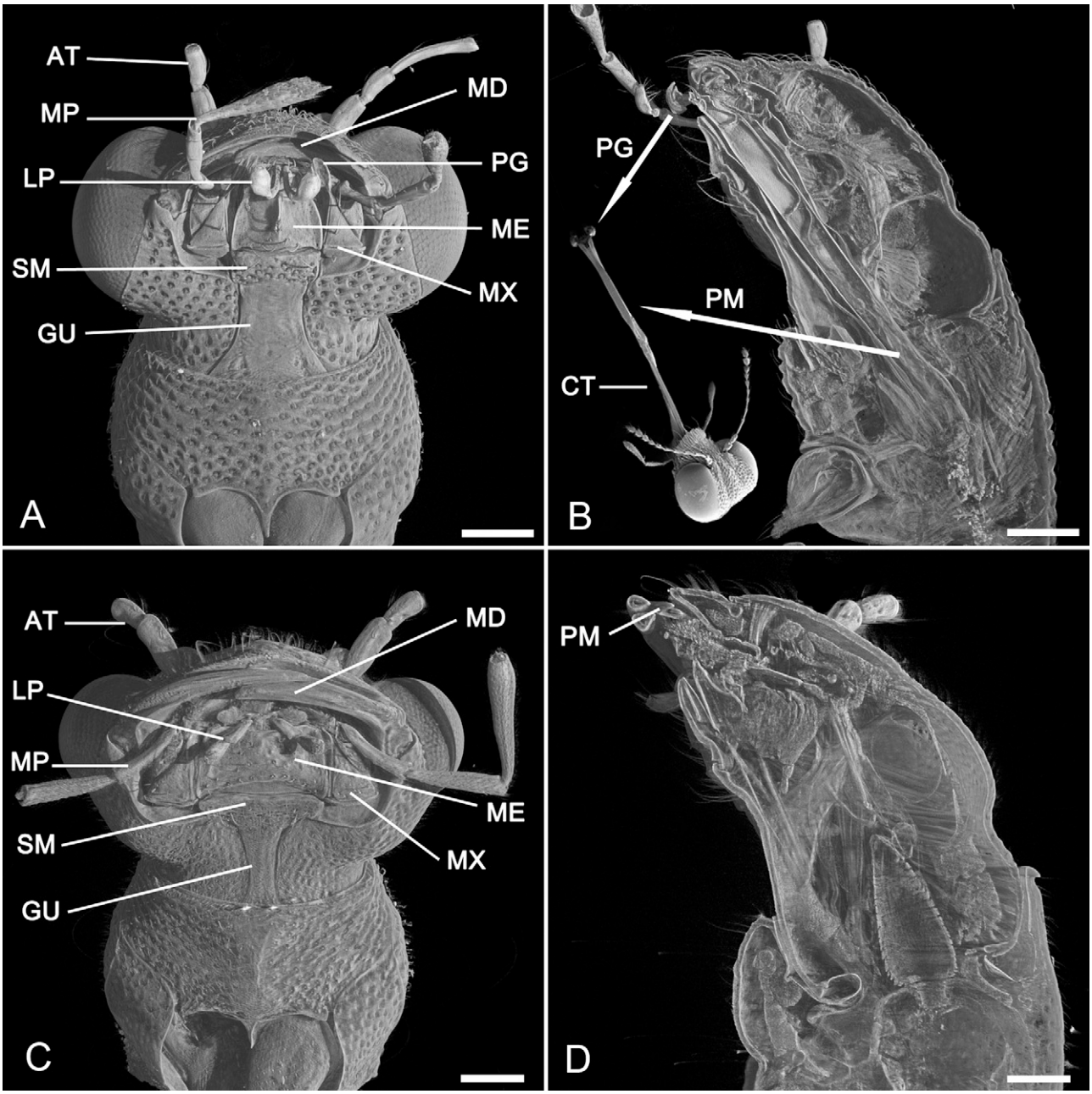

Fig. 1. Head morphology of *Stenus cicindeloides* in the resting position (A, B) and *Dianous coerulescens* (C, D) as investigated by Synchrotron μCT. (A, C) Three-dimensional model of the head (ventral aspect); (B, D) sagittal virtual section through the head. The inset in (B) is a scanning electron micrograph of the head with the protruded labium. Scale bars = 0.2 mm, inset not to scale. *Abbreviations*: AT, antenna; CT, connecting labial tube; GU, gula; LP, labial palp; MD, mandible; ME, mentum; MP, maxillary palp; MX, maxilla; PG, paraglossa modified into adhesive pad; PM, prementum; SM, submentum.

genera (Puthz, 1981). According to Puthz (1981), the genus *Dianous* forms a 'plesiomorphic, perhaps paraphyletic group and continues to represent a taxonomic unit which must be used as long as this genus cannot be defined phylogenetically'.

The genus *Dianous* comprises more than 210 species (e.g. Shi and Zhou, 2009, 2011) and is distributed in the Oriental, the Palaearctic and the Nearctic regions with its main distribution in Asia (India, China and Southeast Asia). According to the morphology of the frons (frontal area of the head), it can be categorized into species groups I and II (Puthz, 1981, 2000; Shi and Zhou, 2011; Tang et al., 2011). In contrast to *Dianous* group II (e.g. Fig. 1C), the members of *Dianous* group I (about 30% of all *Dianous* species) have large "*Stenus*"-like eyes and were traditionally considered to belong to the genus *Stenus*, until it was recognized that they do not possess the typical prey-capture apparatus of this genus (Puthz, 1981).

The aim of the current study was to clarify the phylogenetic relationships of *Stenus* and *Dianous* on the basis of a molecular phylogeny using the barcoding gene cytochrome oxidase I. Our results indicate that *Stenus* is paraphyletic with respect to *Dianous* species group II, suggesting that the labial morphology of *Dianous* reflects a process of secondary reduction of the formerly more complex prey-capture apparatus rather than its precursor.

2. Materials and methods

2.1. Material examined

Molecular analyses were conducted with 21 species of the genus *Stenus* and one representative of the genus *Dianous* (Table 1). The species were collected in Germany and identified according to