

INTERNATIONAL JOURNAL
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MYRIAPODOLOGY

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Brooding in *Mecistocephalus togensis* (Geophilomorpha: Placodesmata) and the evolution of parental care in centipedes (Chilopoda)

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Abstract

The only well-documented data on female brooding posture in the geophilomorph family Mecistocephalidae come from *Dicellyphilus carniolensis* (C.L. Koch, 1847), in which the mother coils around the eggs and hatchlings with the dorsal surface outwards. This posture is shared by Craterostigmomorpha and Scolopendromorpha but not by other Geophilomorpha (united as Adesmata), which coil with the ventral surface outwards. The change in brooding behaviour has been thought to coincide with the evolution of ventral glandular pores in Adesmata and defends the basal split of Geophilomorpha into Placodesmata (Mecistocephalidae alone) and Adesmata. However, a brood of another mecistocephalid, *Mecistocephalus togensis* (Cook, 1896), documented *in situ* in Cameroon, shows the mother to guard the hatchlings with the ventral surface outwards, in the manner of Adesmata rather than that seen in *Dicellyphilus*. This observation suggests that the brooding posture may be more subject to convergence or evolutionary reversal than previously expected.

Key words

Placodesmata, parental care, *Mecistocephalus*, Phylactometria

Introduction

Brooding behaviour provides a valuable trait for centipede phylogenetics and systematics. Available data on maternal care in the orders Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha have been summarised by Bonato & Minelli (2002: Ta-

ble 1). These three orders comprise a monophyletic taxon named Phylactometria, the name referring to maternal care as a shared derived character of the group (Edgecombe & Giribet 2004). A common behavioural character of all members of Phylactometria is a prolonged period of maternal care in which the mother coils her body around the eggs and remains in this position, ceasing to feed for several weeks, and continuing to guard even after eclosion. This situation contrasts with the remaining two centipede orders, Scutigermorpha and Lithobiomorpha, which lay single eggs that are usually concealed in soil and invariably abandoned.

Within the brooding clade, two alternative postures are observed. Scolopendromorpha (data for eight species summarised by Bonato & Minelli 2002; see Coscarón & de Ferrariis 1963; Shelley 2002: fig. 1g; Chao 2008: fig. 6; for additional taxa) and Craterostigmomorpha have mothers that coil around the eggs and hatchlings with the dorsal side facing outwards. Members of several families of Geophilomorpha have been observed to brood in an inverted position, with the ventral side outwards (nine species listed by Bonato & Minelli 2002; see also Arthur & Chipman 2005: fig. 1D). This difference had been regarded as a possible evolutionary novelty of Geophilomorpha as a whole (Dohle 1985) until data became available for the family Mecistocephalidae. Bonato & Minelli (2002) demonstrated that the mecistocephalid *Dicelophilus carniolensis* (C.L. Koch, 1847) guards the eggs and hatchlings with the dorsal side outwards, as in scolopendromorphs and *Craterostigmus* Pocock, 1902 rather than like other geophilomorphs.

The distinction between the style of maternal care in Mecistocephalidae, which was interpreted as a plesiomorphic behaviour (shared with non-geophilomorphs) relative to that of other geophilomorph families, is congruent with prevailing views of centipede phylogenetics. As was recognised in the classification of Verhoeff (1908 and 1918 in Verhoeff 1902-1925), Geophilomorpha divide into Placodesmata (composed of Mecistocephalidae alone) and Adesmata, a clade uniting the remaining 14 currently-recognised families. The split between two monophyletic sister groups, Placodesmata and Adesmata, has been retrieved in morphological cladistic analyses (Foddai & Minelli 2000), as well as separate or combined analyses of multi-locus molecular data and morphology (Edgecombe et al. 1999; Edgecombe & Giribet 2002, 2004).

The Placodesmata-Adesmata division corresponds to anatomical differences between these groups, notably with regards to the absence or presence of ventral pores, the openings of the sternal glands. Ventral pores are observed in members of all families of Adesmata apart from the small tropical American family Neogeophilidae, albeit with repeated instances of apparent secondary losses within diverse families (Turcato et al. 1995). Ventral pores are, in contrast, lacking in Mecistocephalidae apart from doubtfully homologous structures in males only of most species in the genus *Tygarrup* Chamberlin, 1914 (see Bonato & Minelli 2002; Bonato et al. 2003: 573-574, for discussion). Given that the secretions of the sternal glands have been observed to harbour noxious chemicals, the broad correlation between presence of ventral pores and brooding with the ventral side away from the eggs and hatchlings invites a scenario in which the two traits are functionally linked in order to avoid the

brood being exposed to the glandular secretions and/or to maintain the pores facing potential predators (Bonato & Minelli 2002).

The maternal brooding posture documented in the single species *Dicellyphilus carniolensis* has been assumed to be shared by all species of Placodesmata (= Mecistocephalidae) (ca. 170 known species), despite the lack of comparable data for other species. Here we add a new field observation on maternal care in another mecistocephalid species. A mature female of *Mecistocephalus togensis* (Cook, 1896) and her hatchlings were found and photographed *in situ* in a piece of wood in Cameroon. This brood demonstrates that at least some mecistocephalids guard the hatchlings with the ventral side facing outwards, as in Adesmata. This variability between different mecistocephalids opens the question as to whether brooding posture may be more subject to homoplasy – to convergence or reversal – than appeared to be the case in the absence of these data.

Description of brooding in *Mecistocephalus togensis*

The brood documented here was found during fieldwork in the Ototomo forest, near Ngoumou, Central Province, Cameroon, by L. Benavides, G. Giribet, G.N. Legrand, and J. Murienne. The locality is situated at 03°39.717'N 11°18.015'E, at an elevation of 731 m, and the specimens were photographed and collected on 5 June, 2009.

The sample consists of a mature female of *Mecistocephalus togensis*, associated with 20 hatchlings, all of which were collected along with the mother and are housed in the Museum of Comparative Zoology, Harvard University (MCZ DNA105637). All hatchlings represent the same developmental stage, and their association is as typifies all broods in Scolopendromorpha and Geophilomorpha.

The brood chamber was a cavity in a piece of wood in a decaying log, most of the volume of which was occupied by the centipedes (Fig. 1). When found, the adult female was coiled around the hatchlings, though not forming a simple loop (as usual in Craterostigmomorpha and Scolopendromorpha) but instead having at least part of the trunk in an S-curve (as usual in other Geophilomorpha, including the mecistocephalid *Dicellyphilus carniolensis*), with two clear loops visible (Fig. 1a, b). The head of the mother had its dorsal side directed towards the hatchlings (Fig. 1a), and at least the posterior 20 of 49 leg-bearing trunk segments likewise had their dorsal side directed towards the hatchlings (Fig. 1b, d). The anterior part of the trunk (ca segments 5–8) is exposed in one view (Fig. 1a), and is also seen to have its dorsal side directed inwards, as is a section of several segments that apparently lies a short distance anterior to the rearmost 20. Given the total length of the trunk and the confined space of the brood chamber, it appears unlikely that the concealed parts of the trunk could be twisted into a different dorsoventral orientation. The temporal series of photographs, recorded over a span of 30 sec, shows that the mother maintained most of the body in the same stance rather than exhibiting much mobility (Fig. 1). It is thus highly unlikely that the orientation with the dorsal side directed inwards is anything other than the posture that the mother maintained while brooding.

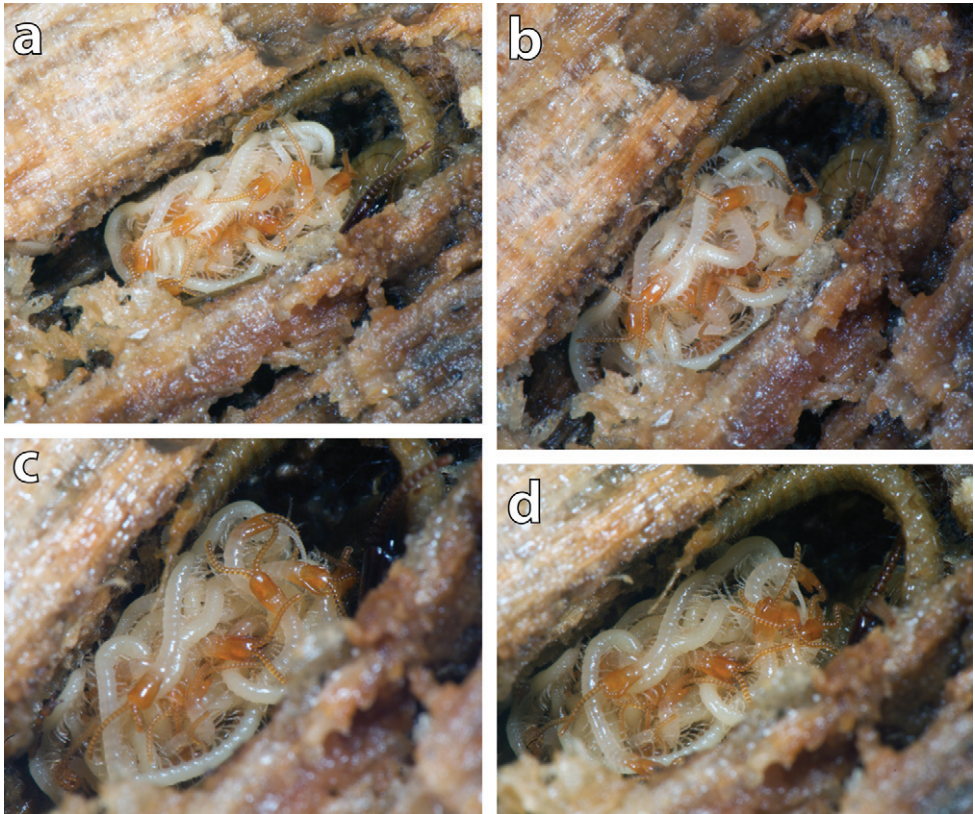


Figure 1. Brooding female of *Mecistocephalus togensis* with 20 hatchlings in a hollow cavity inside a piece of decaying wood (Ototomo forest, Cameroon, 5 June 2009) taken during a 30 second interval (a-d).

Taxonomic assignment

Various species names are applied in the literature to tropical West African *Mecistocephalus*, among them such classical names as *M. maxillaris* (Gervais, 1837), *M. punctifrons* Newport, 1843, and *M. insularis* (Lucas, 1863). However, observations on collections and literature surveyed by L.B. indicate that a single morphologically recognisable species of *Mecistocephalus* is widely distributed throughout most parts of the Afrotropics, including Cameroon, and it is correctly identified as *Mecistocephalus togensis* (Cook, 1896). The morphology of this species has been well illustrated (as *Lamnonyx punctifrons*) by Ribaut (1914).

The following characters detected in the adult specimen allowed us to confidently assign it to *Mecistocephalus togensis*: cephalic plate 1.55 times as long as wide; areolate part of the clypeus about as long as the plagulae; cephalic pleurites bearing setae only on their posterior part; forcipular coxosternal cerrus featuring as a pair of broad bands of setae; no dark patches along the trunk; and a total number of 49 pairs of legs. The combination of these characters permits distinction of *M. togensis* from all other species with which it has been repeatedly misunderstood (including *M. maxillaris*, *M. puncti-*

frons and *M. insularis*; see Bonato & Minelli 2004 and Bonato et al. 2009, for revised descriptions and discussions on the identity of these species), as well as from other congeneric species known to occur in other parts of the African continent (especially *M. guildingii* Newport, 1843 from western coastal regions; Bonato et al. 2009).

Discussion

Unlike the situation in *Dicellyphilus carniolensis* in which multiple observations have been made on broods and the same posture is seen by different mothers when guarding either eggs or hatchlings (Bonato & Minelli 2002 and a few other subsequent records by L.B.), brooding in *Mecistocephalus togensis* is known from a single instance, and is limited to knowledge of post-embryonic guarding only. We do not yet know whether or not *M. togensis* maintains this posture through the full period of parental care; the data for *D. carniolensis* allow a reasonably confident inference that brooding posture does not change. Likewise, we cannot evaluate whether or not the behaviour of the Cameroon brood of *Mecistocephalus togensis* is typical for the species, or instead variable between specimens, nor whether it is more broadly shared with other members of *Mecistocephalus* or other mecistocephalid genera.

Those caveats noted, the fact stands that for at least some part of the brooding phase in some mecistocephalids, a posture otherwise known only in Adesmata is seen. This is the first indication of homoplasy in this character in Phylactometria; brooding posture had previously fit the widely accepted cladogram with complete consistency, with the dorsal surface inward orientation having a single evolutionary gain in Adesmata from ancestors that brooded with the ventral surface inwards. Assuming the sister group relationship between Placodesmata and Adesmata (as had been defended by both morphological and molecular data before and independently of the discovery of *Dicellyphilus* broods), and the monophyly of Mecistocephalidae (a result supported in published analyses; Bonato et al. 2003), the new data from *Mecistocephalus* allow for the possibility that “dorsal surface inwards” could be convergent in *Mecistocephalus* and Adesmata, or that the general condition in Geophilomorpha is brooding with the dorsal surface inwards and *Dicellyphilus* exhibits a reversal to the primitive state for Phylactometria as a whole. The data at hand do not permit a choice between these equally parsimonious optimisations. Additional observations on brooding posture in Mecistocephalidae, and indeed more geophilomorph diversity, are needed.

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