

Morphological structures in some Neotropical *Myrmecodesmus* species (Diplopoda: Polydesmida: Pyrgodesmidae) reveal the ability for plastron respiration

Морфологические структуры у некоторых неотропических видов *Myrmecodesmus* (Diplopoda: Polydesmida: Pyrgodesmidae) обнаруживают способность к пластронному дыханию

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КЛЮЧЕВЫЕ СЛОВА: Diplopoda, морфология, церотегумент, погружение в воду, воздушный чехол, Амазонка, Бразилия.

ABSTRACT: Plastron respiration in submerged *Myrmecodesmus* species is possible when their hydrophobic secretion layer (cerotegument) on tergites extends to sternites and covers all spiracles in the coxal region. Advanced juveniles and subadults but not adults of *M. adisi* (Hoffman, 1985) from Central Amazonian floodplains possess this functional cerotegument. Yet it is absent from *M. duodecimlobatus* (Golovatch, 1996) and *M. hastatus* (Schubart, 1945) from non-flooded uplands.

РЕЗЮМЕ: Пластронное дыхание у погруженных в воду диплопод рода *Myrmecodesmus* возможно тогда, когда их гидрофобный слой секрета (церотегумент) на тергитах распространяется до стернитов и закрывает все отверстия дыхалец в районе тазиков. Поздние ювенильные и субadultные стадии, но не взрослые особи *M. adisi* (Hoffman, 1985) из пойм Центральной Амазонии обладают таким функциональным церотегументом. Однако его нет у *M. duodecimlobatus* (Golovatch, 1996) и *M. hastatus* (Schubart, 1945) из незатопляемых нагорных мест.

Introduction

Myrmecodesmus Silvestri, 1910 is a pan-Neotropical genus, ranging from Texas/U.S.A and the Caribbean in the north to Argentina in the south. Three species are known from Central Amazonia near Manaus: *M. adisi* (Hoffman, 1985), formerly *Gonographis adisi*, inhabiting a blackwater inundation forest in the Rio Negro valley, as well as both *M. minusculus* (Golovatch, 1996) and *M. duodecimlobatus* (Golovatch, 1996) from an

adjacent secondary upland forest (non-flooded terra firme) [cf. Golovatch 1996, 1999]. A fourth species, *M. hastatus* (Schubart, 1945), is widely distributed in Brazil and Argentina, probably due to association not only with human settlements, but also with ant nests and termites [see review in Golovatch 1996].

M. adisi is the only Neotropical species whose semi-aquatic immatures are capable of surviving submersion in Amazonian floodplains up to 11 months by means of plastron respiration [Adis 1986, Adis & Messner 1997, Messner & Adis 1988]. Its unique morphological structures are herewith compared with those of first specimens available of *M. duodecimlobatus* and *M. hastatus* from non-flooded habitats, to discuss the ability for plastron respiration.

Material studied

Relevant morphological structures were investigated with a Scanning Electron Microscope (Zeiss Nanolab 7), with micrographs taken from the following specimens:

Myrmecodesmus duodecimlobatus (Golovatch, 1996): 1 subad. ♀ (paratype, collection J. Adis), obtained from soil extraction in a secondary upland forest (non-flooded terra firme) at Rio Tarumã Mirim near Manaus/AM, Brazil: 25.IV.1983, leg. J.M. Rodrigues, J. Adis et al. [see Golovatch 1996].

Myrmecodesmus adisi (Hoffman, 1985): 2 immat. (V, VI), 2 subad. ♀♀, 2 ♀♀ (collection J. Adis), under submerged bark of *Aldina latifolia* in a blackwater inundation forest at Rio Tarumã Mirim near Manaus/AM, Brazil: 27.III.1984, 18.VI.1987, leg. J. Adis.

Myrmecodesmus hastatus (Schubart, 1945): 1 subad. ♀, 1 ♀; collected from the back yard of a local residence at Cuiabá/MT, Brazil: 02.VI.1999, leg. L. Wilck. Voucher specimens have been deposited in the collections of Universidade Federal do Mato Grosso, Depto. de Biologia — C.C.B.S., Cuiabá, Brazil (UFMT 3

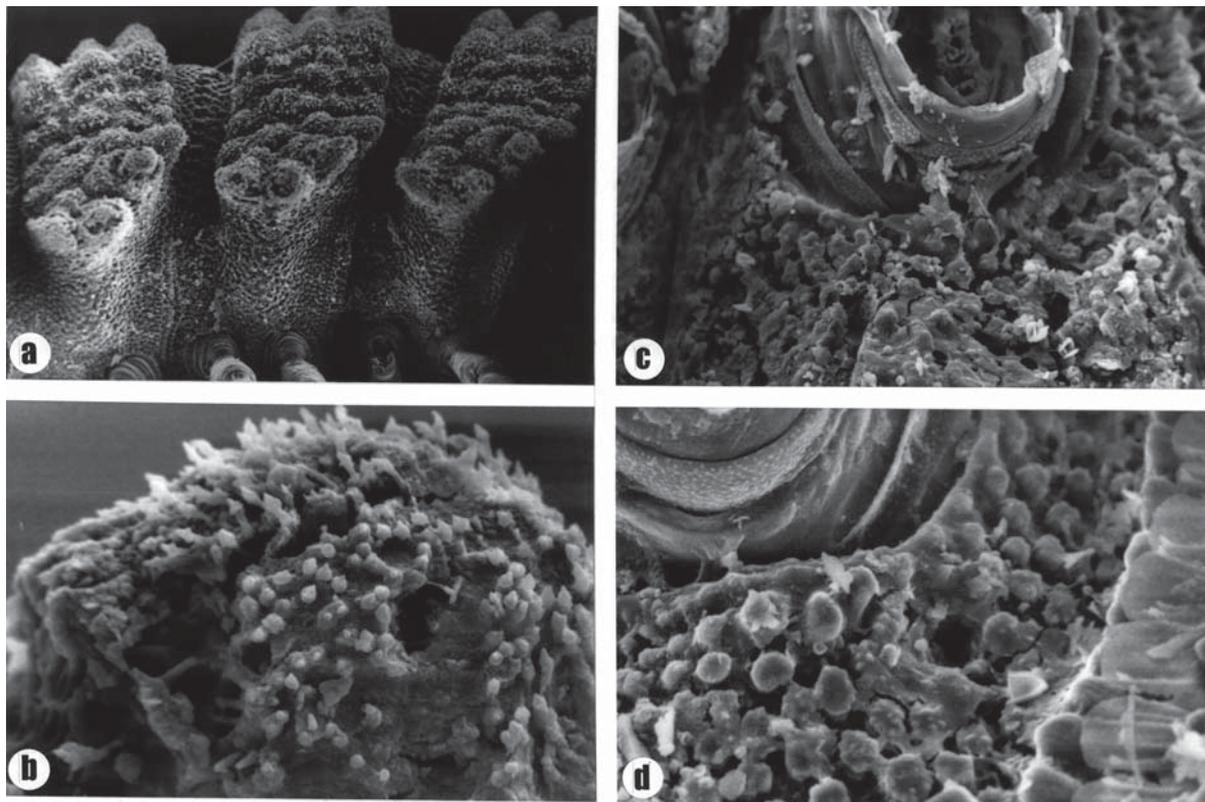


Fig. 1. *Myrmecodesmus adisi*: a — cerotegument covering the tergites and extending onto the coxal region of sternites (sbad. ♀, 250:1); b — cerotegument on tergum, with supporting secretion pillars in crevices and their knobs projecting above the surface (sbad. ♀, 2000:1); c — cerotegument covering the two spiracles in the coxal region (sbad. ♀, 1500:1); d — flat sternal cones, secretion pillars and spiracle opening in the coxal region, visible due to lack of a cerotegument (♀; 2500:1).

Рис. 1. *Myrmecodesmus adisi*: a — церотегумент, покрывающий тергиты и распространяющийся на коксальный отдел стернитов (субадульная ♀, 250:1); b — церотегумент на тергите с поддерживающими столбиками из секрета в трещинах и их вершинами, выступающими в виде бугорков на поверхности (субад. ♀, 2000:1); c — церотегумент, покрывающий оба дыхальца в районе тазиков (субад. ♀, 1500:1); d — плоские стерналильные шишечки, столбики из секрета и отверстие дыхальца в коксальном районе, видимые из-за отсутствия церотегумента (♀; 2500:1).

♂♂, 4 ♀♀, 4 immat.), Muséum d'histoire naturelle, Geneva, Switzerland (MHNG: 1 ♂, 1 ♀, 4 immat.), Zoological Museum of the State University of Moscow, Russia (ZMUM: 1 ♂, 2 ♀♀, 2 immat.) and J. Adis (CA: 1 ♂, 2 ♀♀, 4 immat.).

Results and discussion

In *M. adisi*, the cerotegument is a rapidly drying white hydrophobic secretion layer being deposited shortly after or during moulting over the entire cuticula. It extends from the tergites onto the coxal region of the sternites, where it covers the spiracles in immature stages (advanced juveniles V, VI and subadults; Fig. 1a, c). The entire layer is supported by small secretion pillars located between cuticular tuberculi on the tergites and cuticular cones on the sternites (Fig. 2). A thin air casing is held in this cavity, 6.4–9.6 µm in depth on the tergites and about 5.0 µm on the sternites. This cerotegument is hydrophilous on the outside but hydrophobic on its inner surface, and has a rough surface with irregular cracks and crevices (Fig. 1b). Invisible from the outside it enables plastron respiration where the concentration of dissolved oxygen is high enough, i.e., in the upper water layers of blackwater inundation forests [cf. Adis & Messner 1991]. In

adults, the cerotegument hardly surpasses the sternal region, i.e., it has no connection with the spiracles (Fig. 1d). For this reason adults cannot withstand flooding and die during the beginning of the flood period. In addition, submersion is made difficult due to the uncovered part of the hydrophobic cuticula.

Subadult and adult *M. hastatus* carry the same type of cerotegument on their sternum when compared to *M. adisi*. It is firmly supported by secretion pillars (Fig. 3a, b). In the tergal region, however, the secretion layer does not cover the spiracles (Fig. 3c, d). As in adult *M. adisi*, the secretion pillars between the cuticular cones are clearly visible. The spiracle itself carries no plastron-retaining microtrichia at its entrance which would enable respiration underwater, as found in several polydesmidan species inhabiting wetland habitats of different climatic zones [Adis & Messner 1997]. For these reasons subadult and adult *M. hastatus* are solely covered by an air casing in their sternal region when being submerged, secured by the dorsal cerotegument, and die within few hours [Adis, unpubl.]. This was also observed in immatures of *Poratia obliterated* (Kraus 1960), a common pyrgodesmid in Amazonian floodplain and

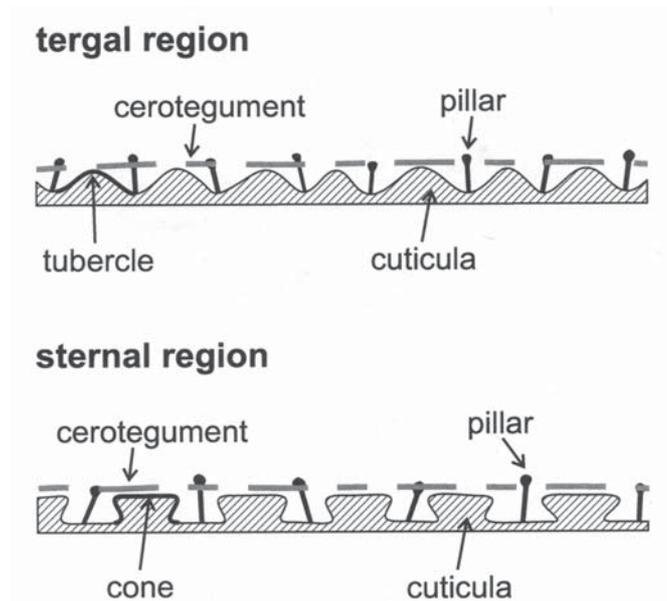


Fig. 2. Schematic presentation of secretion pillars that support the cerotegument in *Myrmecodesmus adisi* immatures: in the tergal region, pillars are located between cuticular tubercles (top) and in the sternal region between cuticular cones (bottom).

Рис. 2. Схема, показывающая столбики из секрета, которые поддерживают церотегумент у незрелых *Myrmecodesmus adisi*: в районе тергита эти столбики расположены между кутикулярными бугорками (сверху), а в районе стернита между кутикулярными шишечками (внизу).

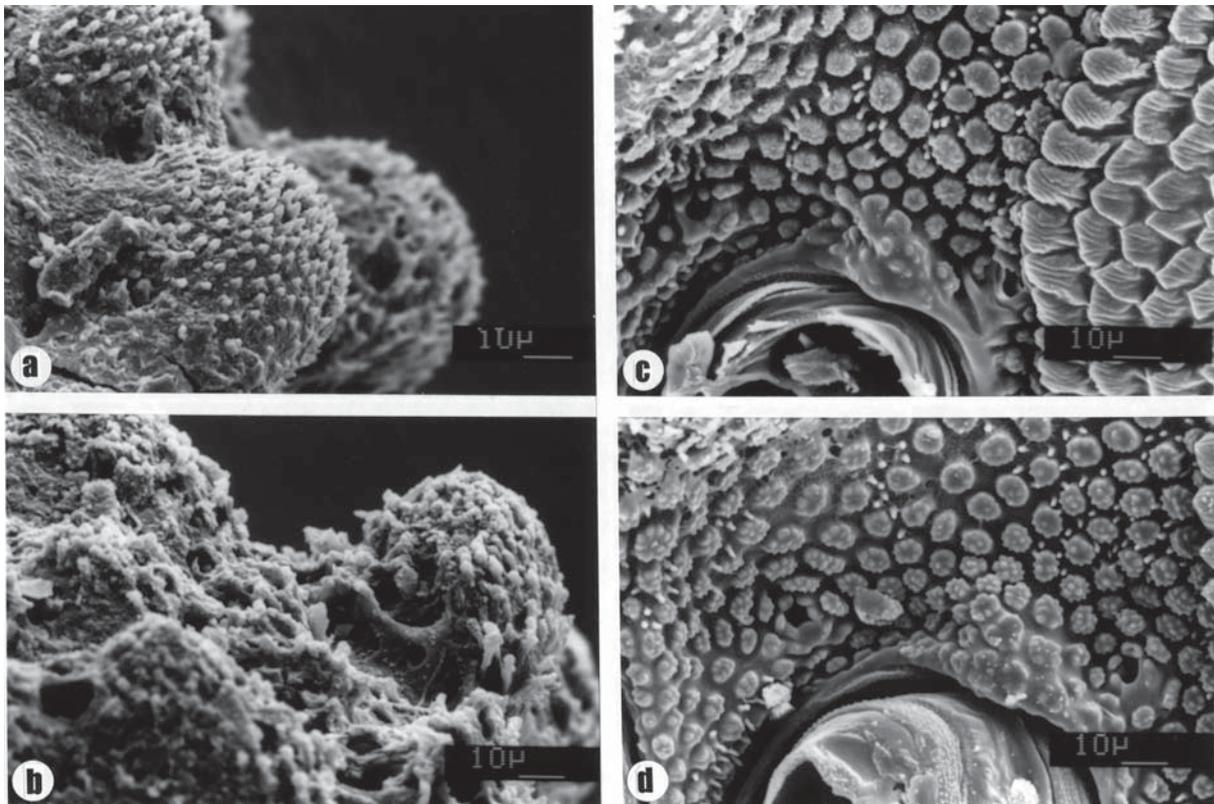


Fig. 3. *Myrmecodesmus hastatus*: a, b — cerotegument covering the tergite, and knobs of secretion pillars projecting above the surface (a: sbad. ♀, b: ♀; both segment V); c, d — flat sternal cones, secretion pillars and spiracle openings in the coxal region, visible due to lack of a cerotegument (c: sbad. ♀, segment VI; d: ♀, segment V). Scale bar in µm.

Рис. 3. *Myrmecodesmus hastatus*: a, b — церотегумент, покрывающий тергит, и бугорки столбиков из секрета, выступающие на поверхности (a: субад. ♀, b: ♀; у обоих сегмент V); c, d — плоские стернальные шишечки, столбики из секрета и отверстия дыхалец в районе тазиков, видимые из-за отсутствия церотегумента (c: субад. ♀, сегмент VI; d: ♀, сегмент V). Масштаб в мкм.

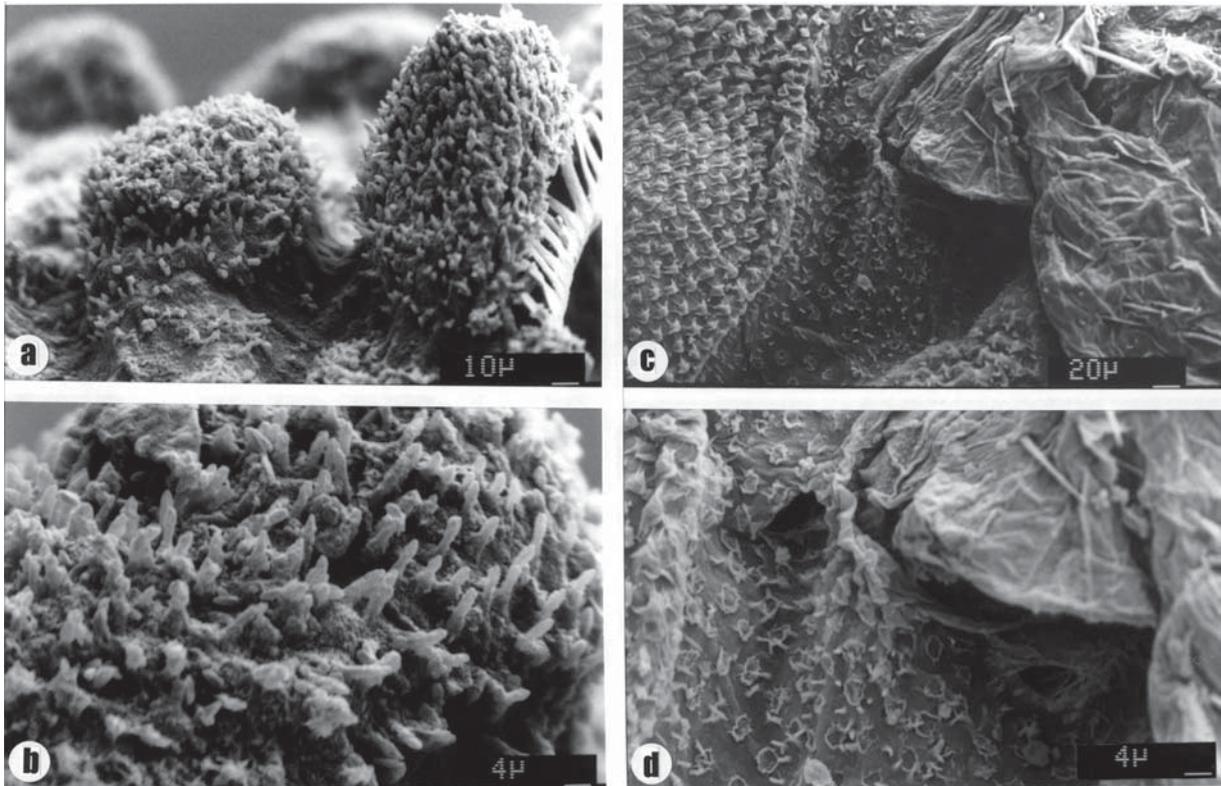


Fig. 4. *Myrmecodesmus duodecimlobatus* (sbad. ♀): a, b — cerotegument covering the tergite, and knobs of secretion pillars projecting above the surface (a: segment XIV; b: segment XIII); c, d — tile-shaped sternal cones, small setiform secretion pillars and spiracle openings in the coxal region, visible due to lack of a cerotegument (c: segment X, d: segment XII). Scale bar in μm .

Рис. 4. *Myrmecodesmus duodecimlobatus* (субад. ♀): a, b — церотегумент, покрывающий тергит, и бугорки столбиков из секрета, выступающие на поверхности (a: сегмент XIV; b: сегмент XIII); c, d — черепицеобразные стерналиные шишечки, маленькие, похожие на щетинки столбики из секрета и отверстия дыхалец в районе тазиков, видимые из-за отсутствия церотегумента (c: сегмент X, d: сегмент XII). Масштаб в мкм.

upland forests [Adis et al. 2001; Golovatch & Sierwald, 2001], which has the same morphological structures and dies about 24 hours following submersion (water temperature 24°C , $6.5 \text{ mg O}_2/\text{l}$) [cf. Messner & Adis 1988].

Material of the terricolous *M. duodecimlobatus* contained only one subadult female. Structures are similar to those of *M. hastatus* (Fig. 4a–d) and plastron respiration is therefore considered impossible. Of the 41 specimens of *M. duodecimlobatus* collected, 80% were found to inhabit the upper soil layers (0–3.5 vs. 3.5–7 cm depth) [Adis & Golovatch, unpubl.]

Only two other examples are presently known for Polydesmida in which an amphibious mode of life is facilitated by means of a functional cerotegument: the circumtropical *Aporodesminus wallacei* Silvestri, 1904 (Pyrgodesmidae), recorded as semiaquatic from Australian creeks, and *Serradium semiaquaticum* Enghoff et al., 1998 (Polydesmidae), endemic to several Italian caves [Adis et al. 1997, 1998].

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