

Notes on mating and oviposition of a primitive representative of the higher Forficulina, *Apachyus chartaceus* (de Haan) (Insecta: Dermaptera: Apachyidae)

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> Abstract

Mating, oviposition, and selected details of the egg surface in the basalmost clade of the higher Forficulina, Apachyidae, were described, using *Apachyus chartaceus* (de Haan, 1842) as a representative. The mating of *A. chartaceus* is of the end-to-end type with the partners being dorsoventrally reversed. Throughout copulation, the male tightly holds the female's postabdomen using his forceps. This manner of mating is unique in Dermaptera, likely autapomorphic to Apachyidae, and perhaps correlated with life under bark. The eggs of *A. chartaceus* have an adhesive substance, by which they attach to the substratum; this is also found in basal Forficulina but is uniquely plesiomorphic for higher Forficulina. *A. chartaceus* does not show intensive maternal care; this is overall a secondary condition or may be accidentally caused under rearing, while the absence of some aspects of brood care (especially transport of eggs) is more likely plesiomorphic. *Apachyus* thus shows a mixture of unique apomorphic features and features that are uniquely plesiomorphic for higher Forficulina.

> Key words

Apachyus chartaceus, Apachyidae, Dermaptera, higher Forficulina, mating, oviposition, rearing, egg structures.

1. Introduction

Dermaptera comprise the 11 families Karschiellidae, Diplatyidae, Pygidicranidae, Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, Chelisochidae, Arixeniidae, and Hemimeridae (HAAS & KLASS 2003), and about 2,000 species have been described (SAKAI 1996). Hemimeridae and Arixeniidae have curious features due to specialisation to their epizoid ways of life, and have often been dealt with as independent suborders, i.e., Arixeniina and Hemimerina, respectively (NAKATA & MAA 1974). The greater part of Dermaptera is composed of the nine remaining families, to which the typical earwigs belong, being named the Forficulina (JARVIS et al. 2005). Among the Forficulina, the Karschiellidae, Diplatyidae and Pygidicranidae, all of which retain many ancestral char-

acteristics, are called the “basal Dermaptera”, which are surely paraphyletic, and the six remaining, more derived families are grouped into the “higher Forficulina”. The latter group is most likely a monophylum (HAAS & KLASS 2003; KLASS 2003), though possibly only with inclusion of Hemimeridae and Arixeniidae, which might be in different subordinate positions within the “higher Forficulina”. Apachyidae has been regarded as the basalmost clade of the higher Forficulina, possessing primitive features concerning the wing structure and reproductive system (HAAS 1995). This agrees with the results of JARVIS et al. (2005), who suggested Apachyidae to be the sister group of the non-pygidicranid Forficulina including Hemimerina from their molecular-based phylogenetic analysis.

Based on characteristics of the female postabdomen, KLASS (2001: pp. 278, 304) very tentatively proposed Apachyidae to be the sister group of the epizoic Hemimeridae. In contrast, the preliminary results of COLGAN et al.'s (2003) molecular-based phylogenetic study of Dermaptera, which included *Apachyus petersoni* Borelli, 1925, suggest that Apachyidae is close to Pygidicranidae, although the support for this relationship is weak. Therefore, Apachyidae is a very significant group for reconstructing the origin and ground-plan of the higher Forficulina or Dermaptera and perhaps also the origin of the epizoic lifestyle.

Apachyidae includes only two genera, *Apachyus* and *Dendroiketes*, with altogether 15 species limited to the Oriental, Australian, and Ethiopian zoogeographical regions (STEINMANN 1989). The knowledge on the biology of the group has remained sketchy and fragmentary. On this background, we tried to clarify the behavior in mating and oviposition of Apachyidae, using *Apachyus chartaceus* (de Haan, 1842) as an exemplar. Knowledge of reproductive biology will also be helpful in establishing a rearing technique for apachyid species, which in turn would ease further studies on the life history of these earwigs.

Apachyus chartaceus is distributed on the Peninsula of Malaysia, Borneo and Sumatra (KIRBY 1904; BURR 1911). It has an extremely dorsoventrally flattened habitus, and the adults are about 3 cm in body length (Figs. 1–3). Both the forewings (sclerotized tegmina) and the hindwings are well developed, and they can fly (our pers. observ.). The forceps are large, crescent-shaped without medial teeth, and similar in shape between males and females (Figs. 1–3). Between the bases of the paired forceps is a large, semi-circular process, the “anal process” (BURR 1910), which according to KLASS (2001: p. 278) consists of the posterior part of tergite X, tergite XI, and perhaps a dorsal telson sclerite. The combination of large crescent-shaped forceps and anal process reminds us of a cap-opener (Figs. 1–3, 6).

2. Material and methods

The *Apachyus chartaceus* specimens were collected in tropical rain forests in Ulu Gombak, the State of Selangor, Malaysia. We collected 10 juveniles, three males and seven females in February 2009 and four juveniles, one male and two females in April 2010. All individuals were hiding between the trunk and bark of living or dead trees.

The *Apachyus chartaceus* specimens were reared in the laboratory at 25°C. They were kept separately in a plastic vessel (10 cm in height and 8 cm in dia-

meter) with wet soil (Fig. 4), in which a cylinder made of non-woven pulp-polyethylene fabric was put. Different from the adults, the juveniles could not walk on the vertical plastic surface, and settled on the fabric cylinder. *A. chartaceus* was fed on several killed *Drosophila* flies every several days. For mating, a pair collected from the field or a pair raised to adulthood in the laboratory was kept in a single rearing vessel for several days. The *A. chartaceus* individuals reared stayed in the space between the vessel wall and fabric cylinder, and their behavior could be easily observed through the transparent vessel wall.

After being cleaned in physiological saline, Ephrussi-Beadle's solution (0.75% NaCl + 0.035% KCl + 0.021% CaCl₂), the eggs were pricked with a fine needle and fixed in FAA (ethyl alcohol : formaline : acetic acid = 15 : 5 : 1) for 12 h.

For scanning electron microscopic observation, the eggs fixed with FAA were dehydrated in a graded ethyl alcohol series, transferred to and dipped in acetone for a time, in order to remove oil from the inside, which often emerges onto the egg surface and makes it dirty. The eggs processed in acetone were hydrated in a graded ethyl alcohol series and then postfixed with 1% OsO₄ for 1 h. The fixed eggs were again dehydrated in a graded ethyl alcohol series, dried with a critical point dryer TOSIMIS Samdri®-PVT-3D, coated with gold, and observed under a scanning electron microscope TOPCON SM-300.

3. Results

The *Apachyus chartaceus* specimens stayed in the narrow space between the fabric cylinder and vessel wall (Fig. 4). Without the cylinder in the vessel, they did not mate or lay eggs. A pair mated while placed on the vertical surface of the fabric cylinder (Fig. 5). Mating was of the end-to-end type with the male and the female being dorsoventrally reversed (Fig. 5A,B). Throughout the copulation, the male tightly held his partner's postabdomen with his forceps in a symmetrical manner (Fig. 5C,C'). The duration of mating was relatively long, and in one case lasted at least five hours. The pair repeatedly mated during several days. Even when disturbed, the pair ran around but maintained the copulation.

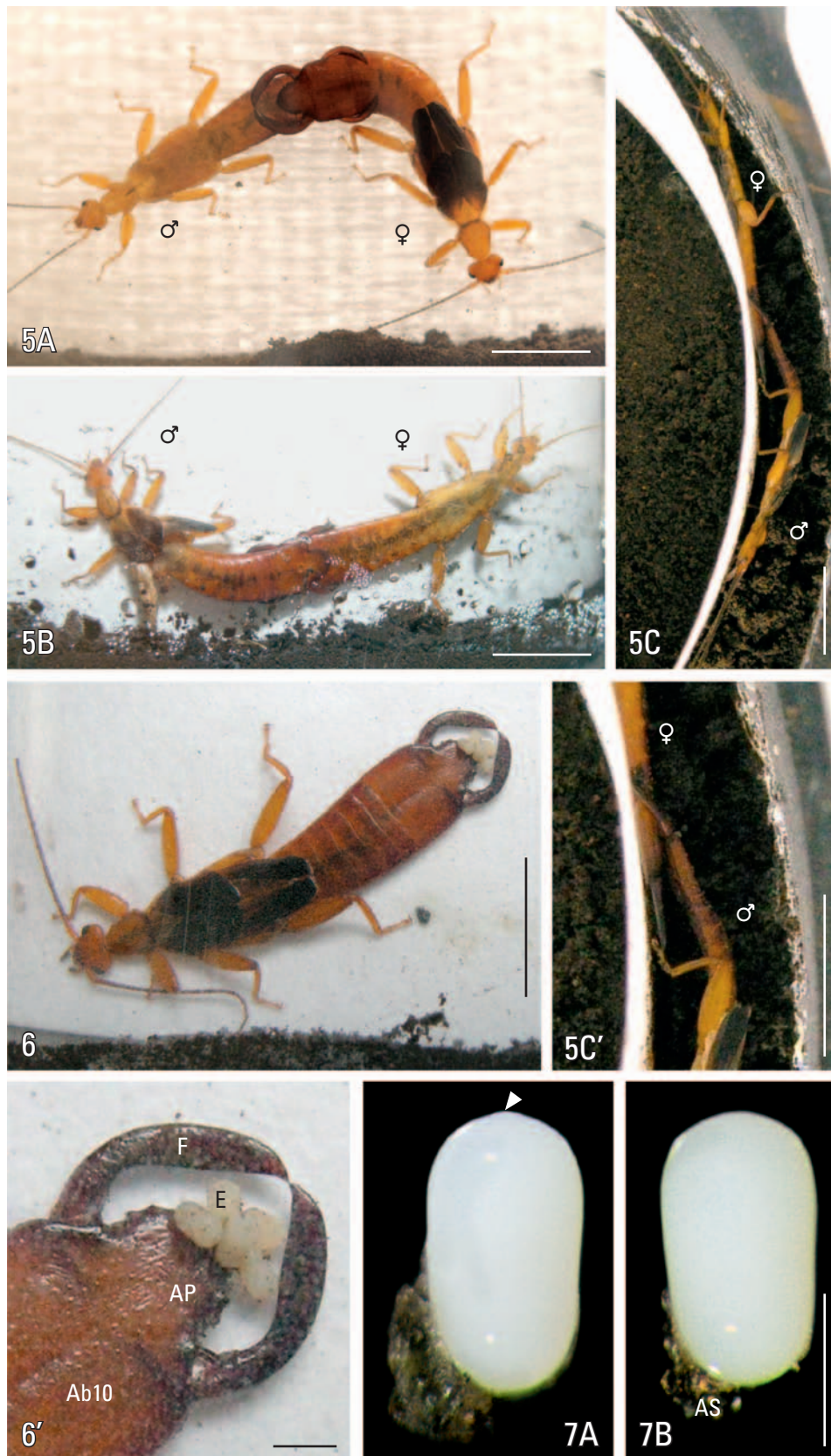
Among 14 females – including five that emerged from among the 14 juveniles – three deposited eggs: the numbers of eggs deposited were 7, 10 and 25. The eggs were laid one by one and with some interspace onto the wall of the rearing vessel and fabric cylinder, and they were tightly adhered to the substratum. Once we observed a female to bring a mass of sev-



Figs. 1–4. *Apachyus chartaceus* (de Haan, 1842) and a vessel for rearing it. **1:** Male. Scale bar = 1 cm. **2:** Female. Scale bar = 1 cm. **3:** Ultimate instar juvenile. Scale bar = 1 cm. **4:** Rearing vessel. Scale bar = 5 cm. FC = fabric cylinder.

eral eggs on her anal process (Fig. 6); the next day the egg mass was found to fall on the ground, where the eggs remained as a cluster. It is known that females of the higher Forficulina take great care of their eggs and hatched juveniles (overview in MATZKE & KLASS 2005). However, we did not once observe any evidence of active egg-caring behavior of *Apachyus chartaceus* females.

The eggs of *Apachyus chartaceus* were ellipsoid in shape, with the anterior half slightly swollen, and a little less than 1 mm in length (Fig. 7). They were white since the whitish yolk was visible through the transparent chorion (Fig. 7). The eggs were covered with a secretion, which was abundant in the posterior half. This secretion or “adhesive substance” acted as a “glue” adhering the egg to the substratum. When



Figs. 5–7. Mating and eggs of *Apachyus chartaceus* (de Haan, 1842). **5:** Mating. 5A: Male (left, ventral view) and female (right, dorsal view). 5B: Male (left, dorsal view) and female (right, ventral view). 5C: Lateral view. 5C': Enlargement of the connection. Scale bars = 1 cm. **6:** Female with an egg mass on her anal process. Scale bar = 1 mm. **6':** Enlargement of the postabdomen. Scale bar = 1 mm. AP = anal process; Ab10 = 10th abdominal segment; E = eggs; F = forceps. **7:** Egg. 7A: Moistened egg with swollen adhesive substance (AS). An arrowhead shows the approximate position of the circular spot seen light microscopically (Fig. 8A) or the chorionic elevation seen scanning electron microscopically (Fig. 8B) revealed on the anterior pole of the egg. 7B: Dried egg with desiccated adhesive substance. Scale bar = 500 μ m.

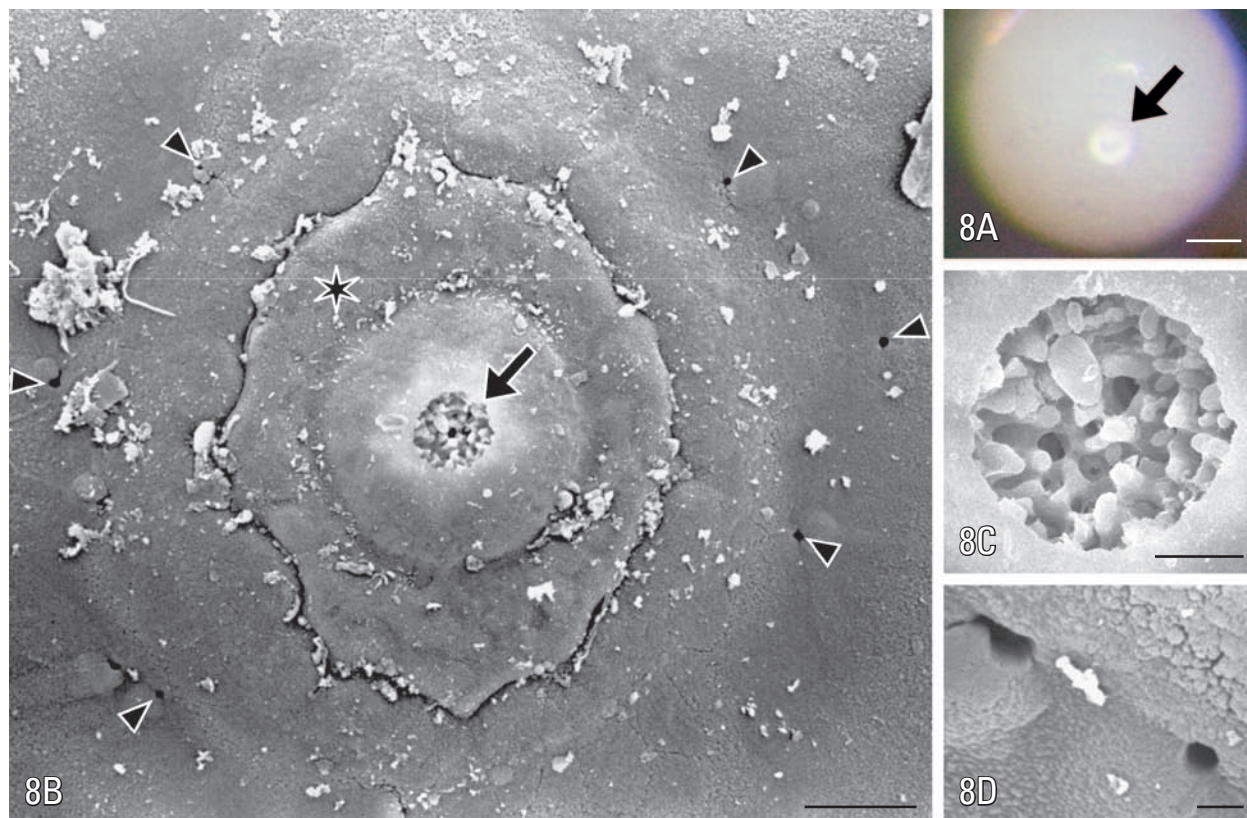


Fig. 8. Structures around the anterior pole of the egg of *Apachyus chartaceus* (de Haan, 1842). **A:** Light micrograph showing a circular spot (arrow). Scale bar = 100 μm . **B:** Scanning electron micrograph showing a low chorionic elevation, which is light microscopically detected as a whitish circular spot as shown in A. Scale bar = 20 μm . Arrow = central depression with porous structure; arrowheads = small pores circularly arranged; star = low chorionic elevation. **C:** Enlargement showing the central depression of porous structure. Scale bar = 5 μm . **D:** Enlargement showing two of the small circularly arranged pores. Scale bar = 2 μm .

the egg was artificially moistened, the largely swollen adhesive substance was soft and sticky (Fig. 7A), but once dry, it shrunk and became hard (Fig. 7B), yielding adhesive power. Light microscopic observation revealed a circular spot about 85 μm in diameter at the anterior pole of the egg (Fig. 8A). Under a scanning microscope, this structure proved to be a low elevation of the chorion (Fig. 8B). In the center of this chorionic elevation, there was a depression about 10 μm in diameter, in whose center a porous structure was visible (Fig. 8B,C). Around the chorionic elevation, small pores about 1–2 μm in diameter were circularly arranged (Fig. 8B,D).

4. Discussion

The copulation of Apachyidae was observed for the first time: it is 1) of the end-to-end type, 2) with the male tightly and symmetrically grasping the female's postabdomen using his forceps throughout mating, and 3) with the pair keeping a posture in which they are dorsoventrally reversed.

The posture in *Apachyus chartaceus* is peculiar among Dermaptera and may be regarded as an autapomorphy of Apachyidae. In other Dermaptera, the pairs do not dorsoventrally reverse their postures, but usually the males twist their postabdomen during mating (GÜNTHER & HERTER 1974; BRICEÑO & EBERHARD 1995; KAMIMURA 2006). The functional advantage might be correlated with the life of *A. chartaceus* under bark, where abdominal twisting would be difficult, as it needs additional vertical space. And thanks to the abnormal mating posture the animals do not need to leave their sheltered micro-habitat for mating and thus avoid exposure to predators.

It is also unusual that the males hold their partners with their forceps. Apart from *Apachyus chartaceus* we only know the example of *Pseudomarava prominens* Steinmann, 1990 (Spongiphoridae) in BRICEÑO & EBERHARD (1995): the male of *P. prominens*, which possesses crescent-shaped forceps suitable for holding like *A. chartaceus*, grasps the female prior to copulating and inserts his penis without twisting his abdomen. However, once the end-to-end copulation without dorsoventral reverse has succeeded, the male releases the female, different from *A. chartaceus*, where the grasping continues throughout mating.

The pairs of *Apachyus chartaceus* did not cease mating if disturbed, and only ran around to escape, maintaining the connection. This may be unusual in Dermaptera, in which disturbed pairs usually stop copulating, and we have few examples for keeping the copulation under disturbance: *Tagalina papua* (de Bormans, 1903) (Pygidicranidae) in MATZKE & KLASS (2005) and *Euborellia cincticollis* (Gerstaecker, 1883) (Anisolabididae) in KNABKE & GRIGARICK (1971).

The eggs of *Apachyus chartaceus* have an adhesive substance in their posterior half, and are deposited and stuck to the substratum. Among Dermaptera, an adhesive substance which attaches the egg to the substratum has been reported only in two families of the basal Dermaptera, i.e., the Diplatyidae and Pygidicranidae: for Diplatyidae, *Diplatys greeni* Burr, 1904 (GREEN 1898), a Papua New Guinean gen. sp. (MATZKE & KLASS 2005), and *Diplatys flavicollis* (Shiraki, 1907) (SHIMIZU & MACHIDA 2009, 2011); for Pygidicranidae, *Tagalina papua* (de Bormans, 1903), *Tagalina burri* Hincks, 1955, and *Paracranopygia siamensis* (Dohrn, 1863) (MATZKE & KLASS 2005: figs. 2–10). In both families, being more posteriorly restricted than in *A. chartaceus*, the adhesive substance is located at the posterior pole of the egg. In the Papua New Guinean diplatyid (MATZKE & KLASS 2005) and *D. flavicollis* (SHIMIZU & MACHIDA 2009, 2011), the adhesive substance forms a stalk, and SHIMIZU & MACHIDA (2009) named it the adhesive stalk. The present finding of the adhesive substance in *A. chartaceus* is the first report for the higher Forficulina. We encountered a case where the eggs were carried as a cluster on the female's anal process. This might have been an accident, but it could alternatively be a step preceding deposition on the substratum.

Diplatyidae, Pygidicranidae and Karschiellidae have complicated external female genitalia, which includes the presence of an ovipositor (2 pairs of gonapophyses and 1 pair of gonoplacs, with much variation) and usually IXth-segmental accessory glands – all corresponding with the ground plan of Insecta-Dicondylia (KLASS 2003). The accessory glands of abdominal segment IX are in many other Insecta the source for substances added to the egg surface either for adhesion or other purposes. MATZKE & KLASS (2005) proposed that in the basal Dermaptera the accessory glands likewise yield the secretions for egg attachment and the gonapophyses provide the ability for targeted deposition of the eggs (which due to their attachment cannot be translocated later, as it is done in higher Forficulina). Female genitalia are strongly simplified, the ovipositor is reduced, and the accessory glands are absent in all higher Forficulina studied so far (GILES 1961; BHATNAGAR 1964; for Eudermaptera K.-D. Klass & K. Schneider pers. comm.). Unfortu-

nately, female genitalia have not yet been studied in an apachyid, and it is thus unknown for the group whether accessory glands are present and what is the degree of differentiation of the ovipositor (which, if present, must be short, since no valves are seen to surpass the subgenital plate). Both the presence and the absence of accessory glands in *Apachyus* would be of special interest – the former in a phylogenetic context (perhaps a unique plesiomorphy of Apachyidae among higher Forficulina), the latter in a functional context (where do then the secretions for egg attachment come from?).

At the anterior pole of the eggs of *Apachyus chartaceus*, small pores are circularly arranged, and at the center of the pore group a single pore with porous inner structures is present. Our knowledge on egg structures of Dermaptera is very scanty, and we have only a study on those of *Forficula auricularia* L., 1758 by CHAUVIN et al. (1991). The pore structures in *A. chartaceus* eggs closely resemble those found in *F. auricularia*. CHAUVIN et al. (1991) identified the circularly arranged pores and the single central pore with inner porous structures as aeropyles and a micropyle, respectively, although they did not show any evidence.

For very few species of Diplatyidae and Pygidicranidae a few elements of maternal brood care have been reported (MATZKE & KLASS 2005: table 3): (1) Mothers remain associated with eggs and (2) with young first instar nymphs, and both (3) eggs and (4) nymphs are defended. These are likely groundplan elements of brood care in Dermaptera (but there are no data on Karschiellidae). In higher Forficulina (5) transport of eggs, (6) cleaning of eggs with mouthparts, (7) assistance to nymphs in hatching from the eggs, and (8) grasping of nymphs with mouthparts (to collocate them) have additionally been reported. These elements have most likely evolved at the base of or within the higher Forficulina. In contrast, in this study, we did not observe any behavior suggestive of maternal care in *Apachyus chartaceus*. The absence of the behavioural elements (1)–(4) may be interpreted as secondary. The elements (6), (7), and (8) of brood care could be either primarily absent (not yet evolved in this basal lineage of higher Forficulina) or secondarily absent (included in a general reduction of brood care as evidenced by absence of features (1)–(4)). However, it is possible that the lack of caring elements is an effect of rearing in unusual and stressful conditions. The absence of (5), egg transport, may plausibly be considered primary, since egg transport may be unlikely to co-occur with eggs fixed to the substrate. On the other hand, diplatyids have been observed to translocate freshly laid eggs prior to the hardening of the adhesive substance (SHIMIZU & MACHIDA 2011).

5. Conclusions

The present study revealed that *Apachyus chartaceus* has an apomorphic copulation posture including dorsoventrally reversed partners and a continued grasp by male cerci, both unique among Dermaptera; its eggs are attached to the substratum by an adhesive substance, which is uniquely plesiomorphic among higher Forficulina but usual in basal Dermaptera; maternal brood care has not been observed at all, which is unique among forficuline earwigs and at least partly apomorphic. The mixture of unique apomorphic features and features that are uniquely plesiomorphic for higher Forficulina makes Apachyidae a highly interesting study taxon.

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