

Baltic amber fossil of *Garypinus electri* Beier provides first evidence of phoresy in the pseudoscorpion family Garypinidae (Arachnida: Chelonethi)

Находка в балтийском янтаре *Garypinus electri* Beier является первым доказательством форезии ложноскорпионов семейства Garypinidae (Arachnida: Chelonethi)

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ABSTRACT. A new fossil of *Garypinus electri* Beier, 1937, attached to the leg of a large tipuloid fly in Baltic amber, is described. This is interpreted as the first case of phoresy in the Garypinidae (here treated as a family distinct from the Olpiidae). The phylogenetic distribution of phoresy suggests that this behaviour has arisen independently at least five times in the order Chelonethi. It is argued that the pattern of clouding around fossils in Baltic amber reflects the initial zone of contact between the specimen and the resin, thus providing information about the mode of entrapment.

РЕЗЮМЕ. Из балтийского янтара описан ископаемый ложноскорпион *Garypinus electri* Beier, 1937, который прикреплен к ноге крупной типулоидной мухи. Находка интерпретируется как первый случай форезии у Garypinidae (здесь семейство трактуется отличным от Olpiidae). Филогенетическое распространение форезии предполагает, что в отряде Chelonethi данное поведение возникло независимо по крайней мере пять раз. Показано, что паттерн помутнения вокруг ископаемого в балтийском янтаре отражает исходную зону контакта между экземпляром и смолой, поставляя таким образом информацию о способе попадания в ловушку.

KEY WORDS: Pseudoscorpion, Garypinidae, phoresy, Baltic amber, fossil, taphonomy.

КЛЮЧЕВЫЕ СЛОВА: Ложноскорпион, Garypinidae, форезия, балтийский янтарь, ископаемое, тафономия.

Introduction

Phoresy is a temporary association in which one animal is transported by another of a different species without feeding on it. This behaviour is fairly widespread in pseudoscorpions, being found in at least some members of the Tridenchthoniidae, Lechtyiidae, Syarinidae, Geogarypidae, Larcidae, Sternophoridae, Cheiridiidae and

Cheliferoidea [Beier, 1948; Ressler, 1965; Muchmore, 1971; Harvey, 1985; Aguiar & Bührnheim, 1998]. Isolated records of phoresy in other families, such as Chthoniidae and Neobisiidae [Poinar *et al.*, 1998], are of questionable validity. Poinar *et al.* [1998] illustrated a “?Chthonius sp.” (Chthoniidae) on a lepidopteran in Baltic amber, but the general appearance of the pseudoscorpion suggests that it belongs in the family Lechtyiidae.

After a long controversy about the nature of the association, it is now generally accepted that phoresy in pseudoscorpions has evolved to allow species occupying patchy habitats to disperse [Legg, 1975]. Zeh & Zeh [1992a,b] have convincingly refuted previous suggestions [Vachon, 1941; Muchmore, 1971] that phoresy in this group is the incidental outcome of failed predation attempts.

Phoretic associations between pseudoscorpions and other arthropods are undoubtedly ancient. Fossil pseudoscorpions have been found attached to Coleoptera, Diptera, Hymenoptera, Lepidoptera and Opiliones in Tertiary Baltic and Dominican ambers [Poinar *et al.*, 1998]. The presence of typically phoretic families in Cretaceous ambers [Schawaller, 1991; Judson 2000; pers. obs.] suggests that this behaviour will prove to be much older.

One family that includes a significant proportion of corticolous species, but in which phoresy has not been observed, is the Garypinidae Daday¹. It is therefore of interest to report here the recent finding of a fossil garypinid, *Garypinus electri* Beier, phoretic on a tipuloid fly in Baltic amber.

Material and taphonomy

The fossil is preserved in a medium-sized piece of Baltic amber (about 29 × 19 × 6 mm) embedded in a Perspex block. The pseudoscorpion is attached by its left chela to one of two legs of a large, unidentified, tipuloid fly (rest of fly not preserved). This fossil is currently in the collection of C. & H.W. Hoffeins (Hamburg; catalogue number 1015/3), but will ultimately be deposited in the Deutsches Entomologisches Institut (Eberswalde).

The pseudoscorpion (Fig. 1) is surrounded by a white layer of cloudy amber. Such clouding, which is common in Baltic amber fossils, is sometimes referred to as '*Schimmel*' (German for 'mildew') and has long been interpreted as the result of decomposition [Mierzejewski, 1978; Schlüter & Kühne, 1975]. However, the

¹ The Garypininae were previously treated as a subfamily of the Olpiidae [Chamberlin, 1930], but as argued elsewhere [Judson, 1992; in prep.] they deserve to be recognized as a separate family.

true cause is almost certainly the *post mortem* dispersion of body fluids into the surrounding resin, leading to the formation of an emulsion where the specimen was in contact with the resin [Weitschat & Wichard, 1998, 2002]. The effect is similar to that seen in seen in Canada balsam preparations made with insufficiently dehydrated material. Schlüter & Kühne [1975] suggested that the uneven distribution of clouding around fossils was due to heating by direct sunlight, with the side facing the sun becoming clear, while the opposite face remained cloudy. However, even if the temperatures reached were high enough to result in a clearing effect (which is far from certain), this explanation is implausible because the difference in temperature between the exposed and shaded side of the specimen would not have been sufficient to produce such well marked patterns. It is much simpler to assume that the distribution of clouding corresponds to the area of contact between the animal and the resin during the initial stage of its entrapment. As long as the animal remained on the surface of the resin, it would become progressively dehydrated through both the loss of fluid into the resin and evaporation from the parts that remained exposed in the air. The amount of clouding produced in a subsequent flow that covered the specimen would accordingly be reduced or eliminated. This explanation requires the trapped animal to have remained at the surface of the resin, rather than sinking—an assumption supported by the fact that most fossils are preserved at the interface between flow lines within amber. Variations in the degree of clouding between different fossils would be due not to differing conditions of sunlight, as Schlüter & Kühne [1975] imagined, but to a combination of factors, including the degree of dehydration of the specimen, its size, the permeability of its cuticle and the composition of the resin (which would also change according to the length of exposure, due to the loss of volatile components).

It follows from this interpretation that the pattern of clouding around a specimen provides an indication of how it became trapped in the resin. Pseudoscorpions in amber usually show ventral clouding, indicating that they became trapped by walking onto the surface of the resin.

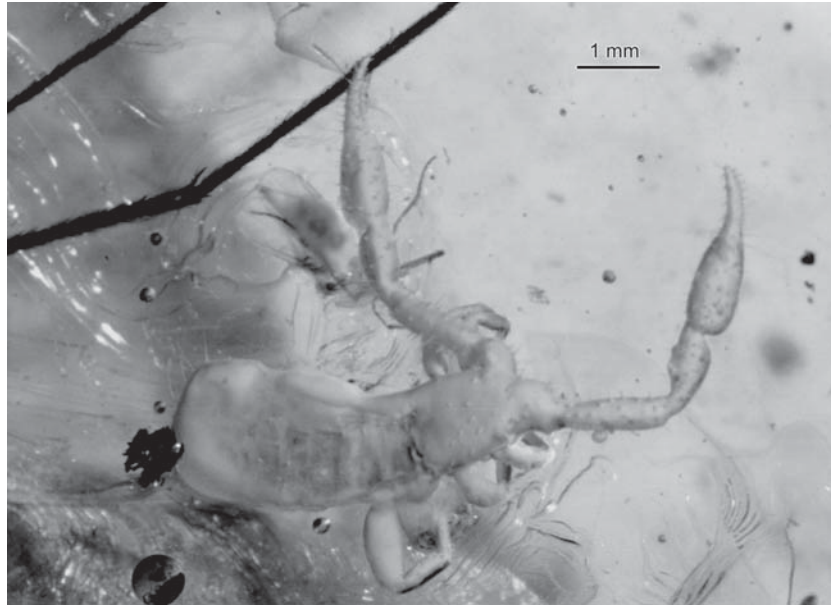


Fig. 1. Adult of *Garypinus electri* Beier, attached by its left chela to the leg of a tipuloid fly in Baltic amber. The apparent whiteness of the pseudoscorpion is due to a layer of cloudy amber. Part of a second leg of the fly can be seen in the upper-left corner of the photograph.

Рис. 1. Взрослая особь *Garypinus electri* Beier, прикрепленная своей левой клешней к ноге типулоидной мухи в балтийском янтаре. Вероятно, что беловатость ложноскольпона обусловлена слоем помутненного янтара. Часть второй ноги мухи видна в верхнем левом углу фотографии.

Specimens with dorsal clouding are rarer, since this would require that either they fell onto the resin or that the resin flowed over them. In this case the pseudoscorpion would usually remain exposed at the outer surface, reducing its chances of being preserved. The complete clouding of a specimen would be the result of rapid engulfment in the resin, before significant dehydration had occurred. In the case of the pseudoscorpion considered here, this is consistent with the idea that the pseudoscorpion was attached to the fly, which dragged it under the surface of the resin. Furthermore, the ventral surface of the pseudoscorpion faces the outer (convex) surface of the flow, meaning that it entered the resin 'upside-down', which would be an unlikely orientation for a non-phoretic individual.

Systematic position

The fossil can be readily assigned to the Garypinidae by virtue of the divided arolia, the paraxially offset pedicel of the chela and the basal concentration of the trichobothria of the

internal series. The large size and general form of the specimen indicate that it is conspecific with *Garypinus electri* Beier, 1937. The only notable discrepancy is that Beier [1937] described the anterior legs as having a "short, freely mobile patella" whereas in the new fossil the patella is distinctly longer than the femur and the joint between them is only submobile. It is no longer possible to check the unique type of *G. electri*, which was presumably destroyed along with the greater part of the amber collection of the Danzig Museum [Penney, 2003]. Because the fossil studied here is otherwise similar to the original description, it is assumed that Beier was in error concerning the patella. Beier himself does not seem to have placed much weight on his interpretation, since he did not regard it as an obstacle to placing this species in *Garypinus* Daday, extant members of which have a long, submobile patella.

Even if the incongruity of the patellar form is removed, it is clear that *electri* does not belong in the genus *Garypinus*. Important differences include the presence of fields of secre-

tory setae on male sternites VI–VIII [Beier, 1937], the angular form of the chelal hand and the arrangement of the trichobothria of the movable finger (*st* and *sb* level). In these respects, *electri* resembles three extant species currently placed in the genus *Serianus* Chamberlin: *S. sahariensis* Mahnert, 1988, from northern Africa, *S. biimpressus* (Simon, 1890), from northern Africa and the Middle East, and *S. validus* (Beier, 1971), from the Middle East and Central Asia [Mahnert, 1988, 1991; Dashdamirov & Schawaller, 1993]. However, because there is reason to doubt whether the assignment of these species to *Serianus* is correct, *electri* is left in *Garypinus* for the moment.

Discussion

Given that the Garypinidae include a number of corticolous species, the existence of phoresy in this family is hardly unexpected: without this means of dispersal it would be difficult for such species to colonize new trees. What is surprising is that no case of phoresy has yet been observed in extant species of this group. This might simply be because corticolous species are infrequent in the northern hemisphere, where historically most observations have been carried out. It may also be that phoresy is a relatively infrequent event in species (including Garypinidae) that occur under the bark of living trees, which is a more stable habitat than, for example, decaying wood or mammal nests. Because it is unlikely that the phoretic habit has since been lost, cases involving extant Garypinidae should be found in future.

The only other cases of phoresy observed for Garypoidea are those of *Larca* species (Larcidae) on mosquitoes [Ressler, 1965; Benedict & Malcolm, 1977], and *Geogarypus amazonicus* Mahnert (Geogarypidae) on beetles [Aguiar & Bührnheim, 1998]. Vachon's [1941] listing of *Garypus saxicola* Waterhouse (Garypidae) as a phoretic species is erroneous, being based on a misinterpretation of Waterhouse's [1878] description of predation on flies.

The distribution of phoretic behaviour within Chelonethi does not concord with their phylogeny, which suggests that this behaviour has

evolved more than once in the order. Exactly how often is difficult to determine, because new cases may be discovered in the future and our understanding of the phylogeny of the group is not entirely satisfactory. For example, according to Harvey's [1992] classification it would be parsimonious to assume that phoresy arose independently in the Cheiridioidea and Cheliferioidea, whereas if these are accepted as sister groups [Judson, 2000], it is simpler to assume that their common ancestor was phoretic. Nevertheless, it seems likely that phoresy has evolved independently on at least five different occasions in pseudoscorpions. This number might seem rather high, but it should be borne in mind that phoresy is probably a prerequisite for a specialized adaptation to temporally unstable niches (e.g., tree bark and the nests of animals), which means that there would be a strong selective pressure for species colonizing such habitats to evolve phoresy. The prehensile palps of pseudoscorpions can be viewed as a morphological pre-adaptation for phoresy and it appears to have been a relatively simple matter to modify their predaceous behaviour in order to find carriers. Some species are able to colonize temporary niches without phoresy, but to do so they must presumably remain generalists, capable of living in a variety of habitats (e.g., certain Pseudogarypidae and Olpiidae).

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References

- Aguiar N.O. & Bührnheim P.F. 1998. Phoretic pseudoscorpions associated with flying insects in Brazil // *J. Arachnol.* Vol.26. P.452–459.
- Beier M. 1937. Pseudoscorpione aus dem baltischen Bernstein // *Festschr. Strand.* Bd.2. S.302–316.
- Beier M. 1948. Phoresie und Phagophilie bei Pseudoscorpionen // *Österreich. Zool. Zeits.* Bd.1. S.441–497.

- Benedict E.M. & Malcolm D.R. 1977. Some garypoid false scorpions from western North America (Pseudoscorpionida: Garypidae and Olpiidae) // *J. Arachnol.* Vol.5. P.113–132.
- Chamberlin J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part II. The Diplosphyronida (Arachnida-Chelonethida) // *Ann. Mag. Nat. Hist. Ser.10.* Vol.5. P.1–48, 585–620.
- Dashdamirov S. & Schawaller W. 1993. Pseudoscorpions from Middle Asia, part 2 (Arachnida: Pseudoscorpiones) // *Stuttg. Beitr. Naturkd. Ser.A. Hft.496.* S.1–14.
- Harvey M.S. 1985. The systematics of the family Sternophoridae (Pseudoscorpionida) // *J. Arachnol.* Vol.13. P.141–209.
- Harvey M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida) // *Invertebr. Taxon.* Vol.6. P.1373–1435.
- Judson M.L.I. 1992. African Chelonethi: studies on the systematics, biogeography and natural history of African pseudoscorpions (Arachnida). Ph.D. thesis, Leeds Univ. 248 p.
- Judson M.L.I. 2000. *Electrobisium acutum* Cockerell, a cheiridiid pseudoscorpion from Burmese amber, with remarks on the validity of the Cheiridioidea (Arachnida, Chelonethi) // *Bull. Nat. Hist. Mus. London (Geol.)*. Vol.56. P.79–83.
- Legg G. 1975. The possible significance of spermathecae in pseudoscorpions (Arachnida) // *Bull. Br. Arachnol. Soc.* Vol.3. P.91–95.
- Mahnert V. 1988. Zwei neue Garypininae-Arten (Pseudoscorpiones: Olpiidae) aus Afrika mit Bemerkungen zu den Gattungen *Serianus* Chamberlin und *Paraserianus* Beier // *Stuttg. Beitr. Naturkd. Ser.A. Hft.420.* S.1–11.
- Mahnert V. 1991. Pseudoscorpions (Arachnida) from the Arabian Peninsula // *Fauna Saudi Arabia.* Vol.12. P.171–199.
- Mierzejewski P. 1978. Electron microscopy study on the milky impurities covering arthropod inclusions in the Baltic amber // *Pr. Muz. Ziemi.* No.28. P.79–84.
- Muchmore W.B. 1971. Phoresy by North and Central American pseudoscorpions // *Proc. Rochester Acad. Sci.* Vol.12. P.79–97.
- Penney D. 2003. *Afrarchaea grimaldii*, a new species of Archaeidae (Araneae) in Cretaceous Burmese amber // *J. Arachnol.* Vol.31. P. 122–130.
- Poinar G.O., Čurčić B.P.M. & Cokendolpher J.C. 1998. Arthropod phoresy involving pseudoscorpions in the past and present // *Acta Arachnol.* Vol.47. P.79–96.
- Ressl F. 1965. Über Verbreitung, Variabilität und Lebensweise einiger österreichischer Afterskorpione // *Dt. Ent. Z. Bd.12.* S.289–295.
- Schawaller W. 1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber // *Palaeontology.* Vol.34. P.971–976.
- Schlüter T. & Kühne W.G. 1975. Die einseitige Trübung von Harzinklüssen — ein Indiz gleicher Bildungsstände // *Entomol. Ger.* Bd.1. S.308–315.
- Vachon M. 1941. Remarques sur la phorésie des Pseudoscorpions // *Ann. Soc. Ent. Fr.* T.109 [1940]. P.1–18.
- Waterhouse C.O. 1878. Description of a new species of Chernetidae (Pseudoscorpionidae) from Spain // *Tr. Entom. Soc. London.* Vol.26. P.181–182.
- Weitschat W. & Wichard W. 1998. Atlas der Pflanzen und Tiere im Baltischen Bernstein. Munich: Verlag Dr F. Pfeil. 256 S.
- Weitschat W. & Wichard W. 2002. Atlas of plants and animals in Baltic amber. Munich: Verlag Dr F. Pfeil. 256 p.
- Zeh D.W. & Zeh J.A. 1992a. On the function of harlequin beetle-riding in the pseudoscorpion *Cordylocheres scorpoides* (Pseudoscorpionida: Chernetidae) // *J. Arachnol.* Vol.20. P.47–51.
- Zeh D.W. & Zeh J.A. 1992b. Failed predation or transportation? Causes and consequences of phoretic behavior in the pseudoscorpion *Dinocheirus arizonensis* (Pseudoscorpionida: Chernetidae) // *J. Insect. Behav.* Vol.5. P.37–49.