

Two novel adaptations for dispersal in the mite family Histiosomatidae (Astigmata)

Norman J. Fashing

Department of Biology, College of William and Mary, Williamsburg, VA 23185-8795, USA. E-mail: njfash@wm.edu

Two unique morphological adaptations for phoretic attachment to arthropod hosts by deutonymphs of the family Histiosomatidae are described. The deutonymphal attachment plate of *Creutzeria* from Madagascar and Seychelles has well developed suckers for attachment to smooth cuticle, as well as modifications that allow for 'grasping'. The conoidal setae are located on the posterior margin with apices modified into trifurcate, claw-like projections. Although the modified conoids are retracted and separated when the sucker plate is relaxed and flat, deutonymphs can fold the sucker plate medially and simultaneously extend the modified conoids. This action causes the medial conoids to merge and interlock their trifurcated tips above a furrow formed from the plate fold. In all probability, these deutonymphs are both entomophilous and pilicolous. The deutonymphal attachment plate of *Ceylanoetus* is enlarged, covering a significant portion of the paraproctal region. Although it has typical conoidal setae, the anterior suckers are greatly reduced and the medial suckers vestigial. The idiosoma has a truncated rear margin bearing flap-like lateral extensions that curve ventrally and surround the attachment organ. When dispersing, a deutonymph wraps the flap-like lateral extensions of its idiosoma around the anterior margin of the beetle host's tibia, thereby completely surrounding it. Although the ridged conoids probably help the deutonymph to hold its position, the ancestral attachment method by means of suckers has been lost in this genus. The term 'crurophilous' is proposed for this unique form of deutonymphal attachment.

Key words: *Creutzeria*, *Coelanoetus*, Histiosomatidae, deutonymph, hypopus, dispersal

Dispersal by species in the astigmatic mite family Histiosomatidae is typically accomplished through a heteromorphic deutonymphal instar (= hypopus). As in most free-living astigmatic species, histiosomatid deutonymphs are heavily sclerotized and resistant to desiccation, have a greatly reduced gnathosoma without a mouth or mouthparts, and most bear a ventral organ in the paraproctal region utilized for attachment to other organisms. To date, three types of deutonymphs have been recorded for this family: entomophilous, pilicolous, and inert (Evans, 1992).

Most species belong to the entomophilous group, and have a so called 'sucker plate' with setae modified into two pairs of suckers and two pairs of conoids. When dispersing, the suckers are used for attachment to the smooth surface of the arthropod host's cuticle. The pilicolous group is represented by only one genus. Instead of a typical sucker plate, *Fibulanoetus* species have a so called 'clasping organ' that has lateral flaps for clasping and thereby attaching to hairs on their scarabeid beetle hosts (Fain et al., 1980). One histiosomatid species, *Tensiosstoma veliaphilum* Wurst et Kovac, has an inert deutonymph (Wurst & Kovac, 2003). Inert deutonymphs have vestigial attachment organs and use passive dispersal. The species is unique among the Histiosomatidae in that it also produces entomophilic deutonymphs that disperse by attaching to water striders (Wurst & Kovac, 2003).

The present paper adds two mechanisms to the diversity of ways by which deutonymphs of species in the family Histiosomatidae attach to their hosts when dispersing.

MATERIALS AND METHODS

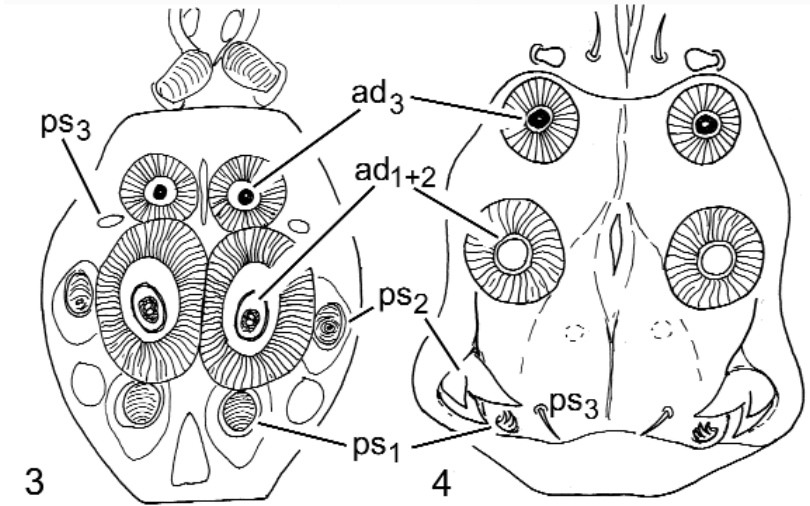
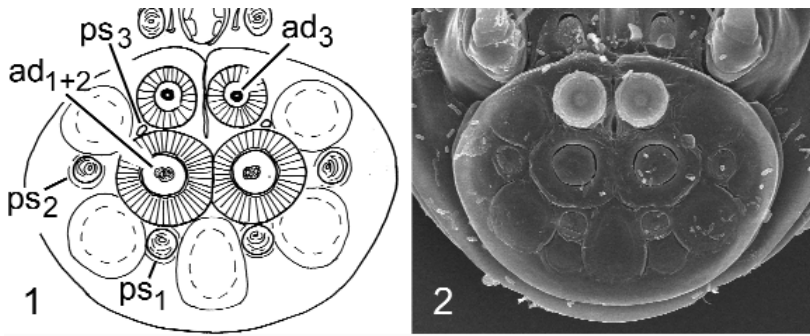
Species of *Creutzeria* used in this study came from the following localities and *Nepenthes* (= 'monkey cup', a genus of tropical pitcher plants) species: Cape York Peninsula, Australia [*N. mirabilis* (Lour.) Druce]; Brunei (*N. albomar-*

ginata T. Lobb ex Lindl., *N. ampullaria* Jack, *N. bicalcarata* Hook. f., *N. gracilis* Korth., *N. mirabilis*); Dauphin, Madagascar (*N. madagascariensis* Poirlet); Mahe, Seychelles (*N. perviellei* Bl.); Singapore (*N. gracilis*); and southern Thailand (*N. gracilis*). Specimens of *Ceylanoetus* near *excavatus* were collected from museum specimens of their phoretic beetle host (*Gondraena* spp.; Hydraenidae) that in turn were collected from southern India, and specimens of *Histiosstoma protuberans* Hughes and Jackson were collected from sap flux on an oak tree (*Quercus* sp.) near Williamsburg, VA, USA.

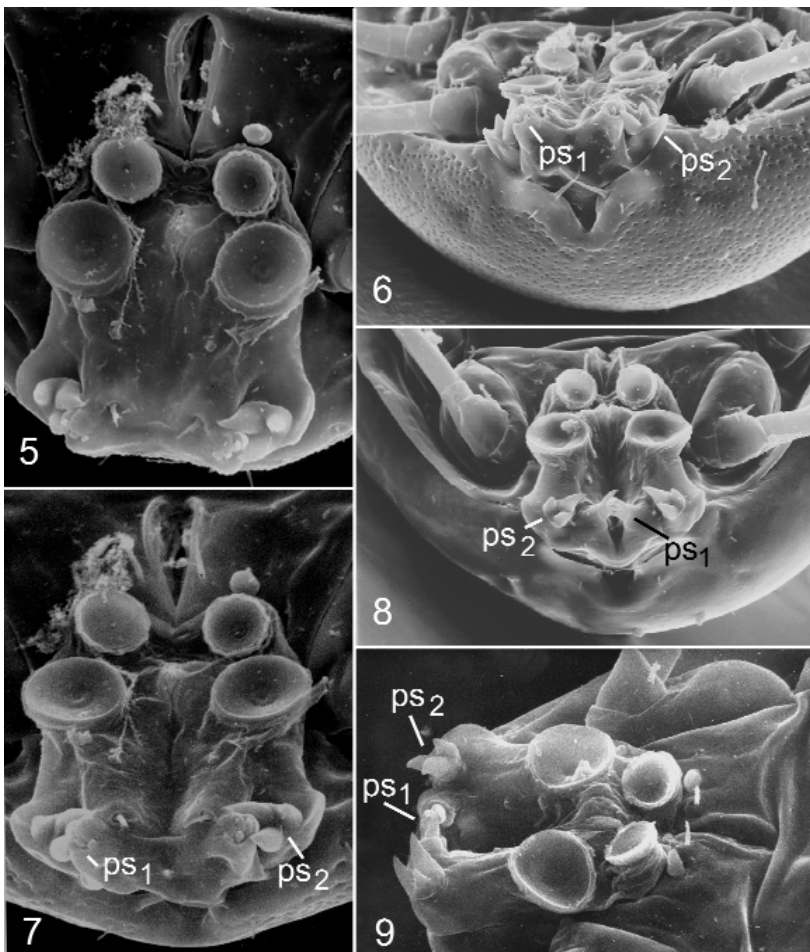
Specimens were cleared in Nesbitt's solution, mounted on microscope slides in Hoyer's medium, and examined under phase contrast and interference microscopy. Deutonymphs of *H. protuberans* (Williamsburg), *Creutzeria* n. sp. from *N. mirabilis* (Cape York Peninsula), *Creutzeria* n. sp. from *N. madagascariensis* (Dauphin), *Creutzeria* near *seychellensis* from *N. perviellei* (Mahe), and *Ceylanoetus* near *excavatus* from India were prepared for scanning electron microscopy (SEM) by dehydrating in ethyl alcohol, drying in a Samdri-PVT-3B critical point dryer (Tousimis), affixing to stubs with double-sided sticky tape, and coating with gold palladium in a Hummer Sputter System (Anatech). SEM microscopy was performed on an AMR-1810. Setal nomenclature follows Griffin et al. (1990).

RESULTS AND DISCUSSION

Deutonymphs of histiosomatid species typically disperse by means of phoresy, utilizing an arthropod that has a similar habitat preference. Like other entomophilous astigmatic species, the attachment organs are located on a rigid, plate-like structure often referred to as a 'sucker plate'. The well developed sucker plate of *H. protuberans* (Figs. 1, 2) is typical of most species in the family Histiosomatidae. Two pairs of suckers more or less surround the anus, and under phase



Figures 1-4 Attachment plates of histiostomatid species. (1) Drawing, *Histiostoma protuberans*; (2) SEM photograph, *H. protuberans*; (3) Drawing, *Creutzeria* n. sp. from Australia; (4) Drawing, *Creutzeria* n. sp. from Madagascar. Setal codes are explained in the text.



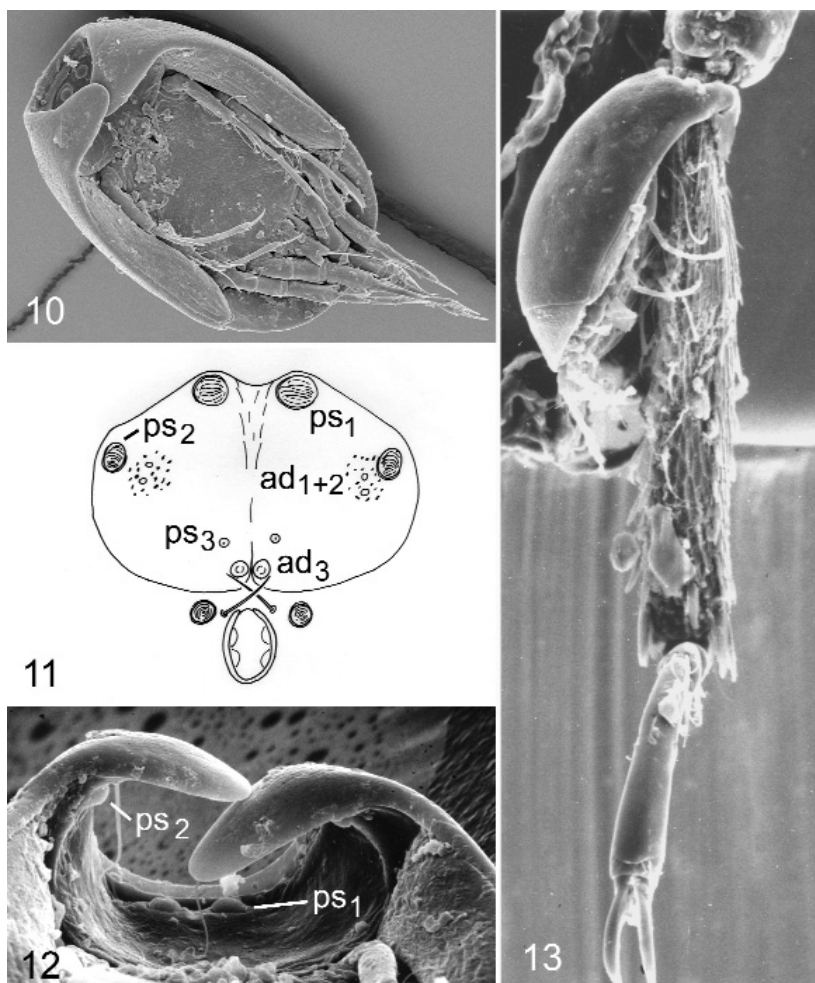
Figures 5-9 SEM photographs of attachment plates. (5) Ventral view of relaxed plate, *Creutzeria* n. sp., Madagascar; (6) Posterior view of relaxed plate, *Creutzeria* n. sp., Madagascar; (7) Tangential view of relaxed plate, *Creutzeria* n. sp., Madagascar; (8) Posterior view of contracted (folded) sucker plate, *Creutzeria* near *seychellensis*; (9) Lateral view contracted (folded) sucker plate, *Creutzeria* near *seychellensis*. Setal codes are explained in the text.

contrast microscopy reveal spoke-like supports radiating from a central ring. The anterior suckers are thought to be derived from setae ad_3 , and the median suckers from combined setae ad_1 and ad_2 . The attachment plate also has two pairs of conoidal setae, ps_2 located lateral to the median suckers, and ps_1 situated medially and posterior to the median suckers. Setae ps_3 , discernible under phase and interference microscopy, is represented only by small alveoli lateral to the junction of the anterior and median suckers. Five oval, ring-like structures can often be seen, and represent apodemes that function for plate rigidity. Retractor muscles inserting on the center of each sucker create a vacuum when contracted, thus providing the suction necessary for deutonymphs to attach to the smooth cuticle of an arthropod host. In their detailed study of the morphology of deutonymphs of *Caloglyphus boharti* Cross, Woodring & Carter (1974) could not determine the function of the conoidal setae. The conoidal setae have a series of concentric ridges that probably grip the host's cuticle, thereby holding the deutonymph in place and preventing shifting.

Species in the genus *Creutzeria* inhabit the fluid-filled pitchers of the insectivorous plant genus *Nepenthes*. Deutonymphs of species from Southeast Asia and northern Australia possess attachment organs that are typical sucker plates, bearing two pairs of well developed suckers and two pairs of ridged conoidal setae (Fig. 3). Like the sucker plates of typical histiostomatids, those on species from the Seychelles and Madagascar contain two pairs of suckers,

however they strongly differ in other respects making setal homologies difficult to interpret (Figs. 4-9). The small alveoli representing setae ps_3 are no longer visible on the anterior portion of the plate, but a pair of stout setae, not present on the typical histiostomatid sucker plate and interpreted to be setae ps_3 , are found on the posterior margin. Setae ps_1 and ps_2 are no longer conoids, and setae ps_2 are no longer located lateral to the medial suckers. Located on the posterior margin of the plate are two pairs of retractable structures which I interpret as modified conoidal setae ps_1 and ps_2 . Both have apices modified into trifurcate, claw-like projections, however setae ps_2 are much larger than ps_1 (Figs. 4-9). Setae ps_2 appear to be only partially retractable, whereas setae ps_1 are almost fully retractable (Figs. 5-7). The attachment plate is elongate and thick and overhangs the posterior margin of the idiosoma. It can be folded medially (Figs. 8, 9), and the rear margin of the idiosoma is indented to facilitate the folded plate (Figs. 6, 8). When the attachment plate is relaxed and flat, trifurcate setae ps_1 and ps_2 are retracted and separated (Figs. 5-7). However, when the sucker plate is folded, the medial trifurcate setae ps_1 merge and interlock their tips above a trough formed in the plate fold (Figs. 8, 9).

Although Beaver (1985) included *Creutzeria* sp. in his food web of the *N. madagascariensis* arthropod community, he did not investigate the biology of the pitcher inhabitants. Ratsirarson & Silander (1996), in a more complete study, found that *Creutzeria* deutonymphs disperse by clinging to



Figures 10-13 *Ceylanoetus* near *excavatus*. (10) Ventral view of idiosoma; (11) Drawing of attachment plate; (12) Attachment plate below wing-like flaps of idiosoma; (13) Deutonymph attached to tibia of the aquatic beetle *Gondraena* sp. (Hydraenidae). Setal codes are explained in the text.

the thorax of adult frit flies (Diptera: Chloropidae). They based this conclusion on only two actual observations of flies harboring phoretic deutonymphs and a positive association between the number of mites and the number of chloropids. Unfortunately the method of attachment used by the deutonymph was not reported and therefore remains unknown. Based on attachment plate morphology, it is possible that deutonymphs have two different methods for attachment to the host insect. While the well developed suckers would allow for attachment to the smooth cuticle of the host thorax, the retractable trifurcate setae ps_1 and ps_2 appear to be modified for grasping and it is possible they are used to grasp or surround a small hair on the host.

The attachment plate and idiosomal shape of *Ceylanoetus* deutonymphs are unique, in fact so unique that they prompted Mahunka (1973) to not only establish a new genus but also a new subfamily for the single, poorly preserved specimen he studied. The ovoid idiosoma tapers posteriorly and has a truncate rear margin (Fig. 10). The venter is concave anteriorly and becomes more so posteriorly. Flap-like lateral extensions on the rear margin of the idiosoma curve ventrally and contact in the center (Figs. 10, 12). The attachment organ deviates considerably from the typical entomophilous type of most histiostomatids. It is large, relatively featureless, and extends laterally along the concave walls of the rear idiosomal margin (Figs. 11-12). The anterior suckers (ad_3) are greatly reduced and the medial suckers vestigial, their presence consisting of laterally displaced pigmented areas containing the paired vestigial alveoli of setae ad_1 and ad_2 (Fig. 11). Setae ps_2 are widely separated conoids located on the lateral margins of the enlarged attachment plate, and setae ps_1 are conoids located medially on the posterior margin (Figs. 11, 12). The oval, ring-like structures are not visible, indicating that the apodemes that provide the rigidity necessary for sucker function in entomophilous deutonymphs are not present. The loss of the apodemes is associated with the loss of suckers on the attachment plate.

The genus *Ceylanoetus* is known only from deutonymphs. Specimens of the species used in this study (*C. near excavatus*) were collected from museum specimens of their dispersal agent, small aquatic beetles in the genus *Gondraena* (Hydraenidae) that inhabit the pools in splash zones near waterfalls. When dispersing, a deutonymph wraps the flap-like lateral extensions of its idiosoma around the anterior margin of the beetle host's tibia, thereby completely surrounding it (Fig. 13). Rather than using suckers, the deutonymph is secured to the host by the idiosomal extensions. The two pairs of ridged conoidal setae probably help hold the deutonymph in position on the host leg. Much of the ancestral function of the entomophilous attachment organ appears to have been lost in this genus.

Deutonymphs of *Creutzeria* species from Madagascar and Seychelles are unique in that they have attachment plates with two pairs of well developed suckers for attachment to smooth cuticle, as well as conoidal setae modified

for grasping or surrounding a hair. In all probability these species are both entomophilous and pilicolous. Although *Fibulanoetus* species also have attachment plates with suckers and structures for grasping, the anterior suckers are quite reduced and the median suckers vestigial (Fain et al., 1980). The reduced size/absence of suckers indicates that deutonymphs are most likely not entomophilous, and they have only been observed attached to hairs. Deutonymphs of *Ceylanoetus* have an attachment organ that places them in an entirely new functional category. Although modified for grasping, deutonymphs do not clasp a hair but rather surround an entire leg segment of the host insect. In addition, they use wing-like extensions of the idiosoma rather than modifications of the attachment plate for this purpose. I propose a new category, crurophilous (= lover of legs), to accommodate deutonymphs that attach to their host in this manner.

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