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Myrmecophagy in Mycetophiloidea (Diptera): Note on a Keroplatidae from Africa[1,2]

ABSTRACT

Information on an undescribed keroplatid fly (tribe Orfeliini) from Cameroon is presented. Its myrmecophagous larvae live in hollow stems of an understory myrmecophytic tree. Data on the biology of this fly and its interaction with one of the plant's strictly associated ant species *Cataulacus mckeyi* (Myrmicinae) showed that the number of keroplatid larvae per tree was not limited by occupation competition with the ant. Through predation on workers, keroplatid larvae may have a sizeable impact on colonies of *C. mckeyi*.

RÉSUMÉ

Nous présentons des informations sur une espèce non-décrite de Keroplatidae (tribu Orfeliini), au Cameroun. Les larves myrmécophages se développent dans les tiges creuses d'une myrmécophyte de sous-bois. Des données sur la biologie de cette espèce et son interaction avec l'une des fourmis-hôtes de cette plante, *Cataulacus mckeyi*, montrent que le nombre de larves par arbre n'est pas limité par la compétition pour l'occupation avec la fourmi. En prédatant les ouvrières, ces larves ont un impact potentiellement important sur les colonies de *C. mckeyi*.

Key words: *Africa;* Cataulacus mckeyi; *Keroplatidae;* Leonardoxa africana; *myrmecophagy; Orfeliini; tropical rain forest.*

LEONARDOXA AFRICANA (BAILL.) AUBRÉV. SUBSP. *AFRICANA* (CAESALPINIOIDEAE) is an understory tree in coastal rain forest of Cameroon (Central Africa). This myrmecophyte is strictly associated with two ant species, the formicine *Petalomyrmex phylax* Snelling and the myrmicine *Cataulacus mckeyi* Snelling (McKey 1984, 2000). Plants provide food and nesting sites to *P. phylax*, which effectively protects the young leaves against insect herbivores (Gaume *et al.* 1997). This mutualistic interaction is often parasitized by *C. mckeyi*, which uses the host plant but does not protect young leaves (Gaume & McKey 1999). To understand the factors allowing persistence of the parasitic ant in this system, I have attempted to characterize all potential mortality factors responsible for the limited life span of *C. mckeyi* colonies (Debout 2003). In addition to physical disturbances of host individuals, several biological factors such as the frequent presence of myrmecophagous dipteran larvae inside the domatia (swollen stems) of *L. a. africana* may play a role. These larvae were identified by L. Matile of the Muséum National d'Histoire

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[2] This paper is dedicated to the late L. Matile (†2001). His irreplaceable knowledge of the Keroplatidae is sorely missed.

Naturelle (MHNH; Paris, France) as belonging to the tribe Orfeliini of the subfamily Keroplatinae (family Keroplatidae, superfamily Mycetophiloidea).

Before Matile's (1990) monograph, Keroplatidae, like many dipteran families, was poorly known from all points of view (morphology, systematics, phylogeny, and biogeography). The superfamily Mycetophiloidea is comprised of relatively small gnats (4–8 mm), which are brown or black with small yellow spots and are generally known as "fungus gnats." Their two principal diagnostic characteristics are a bent thorax and long coxa. Seven families are included: Ditomyiidae, Diadocidiidae, Keroplatidae, Bolitophilidae, Mycetophilidae, Lygistorrhinidae, and Sciaridae. Generally, larvae of Mycetophiloidea are associated with fungal carpophores, in which they spin a web under the hymenium to gather spores or feed on carpophore tissues. Some exceptions to these habits are known, particularly in the Keroplatidae and the Mycetophilidae. In these families, several species have predatory larvae, which kill their prey using oxalic acid produced by salivary glands and deposited as droplets on the web. In temperate regions, adults of Mycetophilidae can be found in humid and shady places (*e.g.,* hollow trees, riverbanks, and caves). In the tropics, they principally inhabit forests and woodlands, and adults of some species can be very abundant and widespread during the rainy season; however, data on biology and ecology of Mycetophiloidea are scarce (Matile 1990).

The family Keroplatidae, comprised of three subfamilies (Arachnocampinae, Macrocerinae, and Keroplatinae), is cosmopolitan but very poorly known. About 800 species in 80 genera have been described, but numerous species await naming (and surely more await discovery). This is particularly true for the tribe Orfeliini (Keroplatinae), about which almost nothing is known. None of the known larvae of Keroplatidae develop inside mushrooms, and all spin a web that functions either to trap spores or to capture small living animal prey. All known larvae of the tribe Orfeliini are carnivorous and prey preferentially on ants (L. Matile, pers. comm.). Keroplatidae are known from all over the world (*e.g.,* Central America [Panama; Aiello & Jolivet 1996], Australasia [New Zealand; Pugsley 1983], Sri Lanka [Chandler & Matile 1998, Krombein *et al.* 1999], Japan [Uesugi 2002], and Europe [Chandler & Gatt 2000, Menzel & Ziegler 2001]). Several European surveys suggest that the North African fungus gnat fauna may share most of its species with the Mediterranean fauna but little is known beyond that. No data appear to exist about fungus gnats in tropical Africa (references in Chandler & Gatt 2000).

Myrmecophagous keroplatids are known from Central America (Aiello & Jolivet 1996) and Sri Lanka (Chandler & Matile 1998, Krombein *et al.* 1999). Larvae are found in domatia of the myrmecophytes (*e.g., Humboldtia laurifolia* Vahl [Leguminosae: Caesalpinioideae] and *Besleria formicaria* Nowicke [Gesneriaceae]) hosting colonies of ants. Larvae spin a strand of silk that runs the length of the domatium. Larvae are primarily myrmecophagous, but may also feed on dead animal matter or on insects other than ants present in the domatia. Larvae capture live prey using their silk strand (Aiello & Jolivet 1996). The impact of these predators on growth and survival of incipient ant colonies may be especially high, since as many as 50 ant heads can be found in one keroplatid-occupied domatium of *H. laurifolia* (Chandler & Matile 1998). Two oviposition strategies are known in myrmecophagous keroplatids: female flies sometimes oviposit on the inner wall of the chosen domatium close to the entrance hole and in other cases, female flies "shoot" eggs through the entrance holes (Kovac & Matile cited in Chandler & Matile 1998).

This paper is the first report of a myrmecophagous Keroplatidae in Africa. They thus occur in three tropical continents, and although reports are few and scattered, may be widespread. The fly I studied is a frequent occupant of *L. a. africana* domatia. Despite repeated efforts, I was unable to rear this fragile fly. As species determination requires examining male genitalia, identification of this fly, or its description as a new species, is not yet possible. Samples of larvae of the species investigated in this study have been deposited in the insect voucher collections at the MNHN (Paris, France) and the American Museum of Natural History (New York, New York).

To estimate the frequency and distribution of this keroplatid fly, I examined occupants of domatia in *L. a. africana* trees. The distribution of *L. a. africana* is patchy and a patch ("population") is often comprised of between 100 and 500 trees. Each tree is occupied by a single nest of a single ant species. The two ants associated with *L. a. africana* occur at different frequencies and differ essentially in colony size, longevity, and proportion of domatia they occupy. On average, 75 percent of available trees are occupied by *P. phylax*, while frequency of occupancy by *C. mckeyi* varies from 0 to 30 percent of trees

(A. Daleck, pers. comm.). Colony size of *P. phylax* can reach up to 10,000 workers, whereas a colony of *C. mckeyi* is comprised of up to only hundreds of individuals (Gaume 1998).

This study was carried out principally in a population of *L. a. africana* (named BOU) located in rain forest near the village of N'kolobondé (3°13′N, 10°15′E; 150 m elev.), Littoral Province, Cameroon. In the study area, a 2500 m^2 quadrat (a 50 × 50 m area divided into 5 × 5 m grids) was laid out in the population and all trees were censused and mapped. A total of 277 *L. a. africana* trees were located in the study area. The mean local density was 0.15 trees per m^2. Of all the trees, 68 percent were occupied by *P. phylax*, 16 percent were unoccupied, and 14 percent were occupied by *C. mckeyi*. Occupants of the remaining 2 percent could not be assessed because their crowns were too high to examine.

I also studied the frequency and abundance of keroplatids in *Leonardoxa* trees for six other different plant populations taken from an 85 km long transect. I focused on the presence of keroplatids in trees occupied by *C. mckeyi*. I collected 76 nests of *C. mckeyi* by complete dissection of the host tree. Occupants of domatia in a tree constitute a "nest," and a single colony occupies one to several "nests" (*i.e.,* individual trees; Debout *et al.* 2003). All domatia occupants were counted and preserved in 95 percent ethanol.

In the system we studied, keroplatid larvae were found in domatia of trees occupied by *C. mckeyi* and those occupied by *P. phylax*. Larvae are elongate with translucent brownish heads (Fig. 1A), and their length may attain that of the occupied domatium (3–4 cm). Each larva is solitary, resting alone on a strand of silk that is connected by perpendicular silk threads to the walls of the domatium. Larval development requires more than three weeks, and larvae are often parasitized by undetermined hymenopteran parasitoids, as was also noted by Aiello and Jolivet (1996). Preliminary tests on their myrmecophagy showed no preferences of larvae for one or the other of the two ant species that inhabit domatia of *L. a. africana* (G. Debout, pers. obs.). When an ant is caught in the silk web, the larva spins a silk cocoon around it and then eats the ant from the inside, leaving the cuticle intact (Fig. 1B). In the study site BOU, 75 percent of all trees occupied by *C. mckeyi* contained at least one keroplatid larva.

As a general rule, keroplatid larvae were frequent in trees occupied by the ant species *C. mckeyi*. Among the 76 collected nests, 71 percent (*i.e.,* 54 nests) harbored from 1 to 13 keroplatid larvae. This occupation rate is not trivial because for the 54 trees with keroplatids, the proportion of domatia occupied by these larvae averaged 11 percent of all domatia (*i.e.,* 3.9 ± 0.5 domatia). There was no correlation between size of the ant colony and the number of keroplatid larvae occupying its tree ($R^2 = 0.045$; $P = 0.07$), or between colony size and the ratio of domatia occupied by larvae to domatia occupied by ants ($R^2 = 0.064$; $P = 0.03$). This occupation frequency ratio was relatively constant (0.29 ± 0.07). I postulate that this high occupation rate may have a great impact on ant colonies if the daily predation rate by larvae is high.

On trees occupied by *C. mckeyi*, the number of larvae was correlated with the number of available empty domatia ($R^2 = 0.33$; $P < 0.001$). Nevertheless, when several keroplatid larvae were present on the same tree, they were dispersed over the entire tree (no aggregation of larvae), and many domatia remained unoccupied either by ants or by larvae. This paradox between the high frequency of keroplatids—the larvae were encountered in all *Leonardoxa* populations and were present in up to 75 percent of *Cataulacus*-occupied trees—and the low density of occupation per tree may be due to an avoidance behavior reflecting high intraspecific competition. If larvae reach densities at which significant intraspecific competition occurs, this would be a further clue that keroplatids may have a sizeable impact through predation on workers of *C. mckeyi* colonies. The low density of occupation per tree, however, could also be a strategy to avoid hymenopteran parasitoids (or could simply be the result of parasitoid attack).

Preliminary dissection data on 10 *P. phylax*-occupied trees suggested that keroplatids showed no preference for either ant species, as indicated by frequency of occupation. In the site BOU, 6 of the 10 *P. phylax*-occupied trees studied had 2–7 keroplatid larvae (*i.e.,* a 4 % occupation frequency of all domatia per tree) and the occupation ratio (keroplatid-occupied domatia to *P. phylax*-occupied domatia) was around one-third (0.30 ± 0.19), as in *C. mckeyi*-occupied trees. Indeed, when compared to the 12 *Cataulacus*-occupied trees dissected during the same field session at the same site, neither the mean proportion of all domatia occupied by keroplatid larvae (*t*-test; $P = 0.40$) nor the mean ratio of domatia occupied by larvae to domatia occupied by ants (*t*-test; $P = 0.97$) was significantly different in trees occupied by the two ants.

Further work to evaluate the impact of keroplatids on this system will require rearing enough larvae to obtain at least one male for species determination or description. Fungal infection appeared to be an

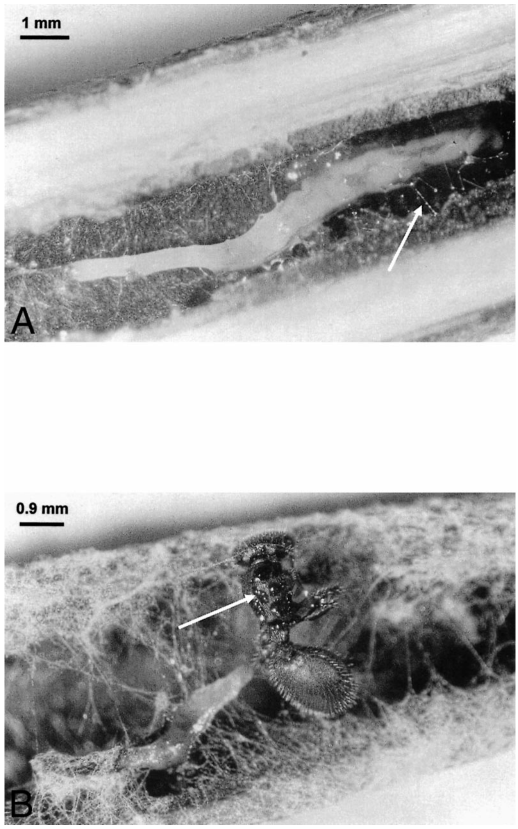

FIGURE 1A. An elongate larva of the undetermined keroplatid (subfamily Keroplatinae, tribe Orfeliini), on its strand of silk, inside a domatium of *Leonardoxa africana* subsp. *africana*. The perpendicular silk threads that connect the central web to the domatium walls can be seen (white arrow). B. A worker of *Cataulacus mckeyi* caught in the silk web product by the larva. The larva is spinning a silk cocoon around the ant. The white arrow shows droplets (probably of oxalic acid) on the dorsal surface of the alitrunk of the worker.

important mortality factor in my rearing attempts. Use of antifungal solutions appears to enhance the probability of larval survival to adulthood (P. Jolivet, pers. comm.) and this should be incorporated in future attempts. Observations must be conducted on more *P. phylax*-occupied trees to determine if prevalence of keroplatids is equivalent to that on trees occupied by *C. mckeyi*. It will be of particular interest to more precisely define the impact of this predator on growth and survival of incipient ant colonies (regular predation may have an especially high impact on small colonies) or on foundresses attempting to establish a new colony. Dietary habits and preferences of this keroplatid must be studied by choice experiments. Finally, it must be determined whether ant workers can avoid domatia harboring a keroplatid larva or are attracted to investigate these domatia. With the addition of this first record from Africa, such flies appear to be widespread in tropical regions. They are likely to occur in many myrmecophytes. Abundant in the system I studied, they may have an important impact on numerous ant–plant symbioses. Unfortunately, they have been virtually ignored. This paper is offered in hope that it will encourage those studying other ant–plant systems to look a little more closely for these potentially important ant predators.

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Aiello, A., and P. Jolivet. 1996. Myrmecophily in Keroplatidae (Diptera: Sciaroidea). J. N.Y. Entomol. Soc. 104: 226–230.

Chandler, P., and P. Gatt. 2000. Fungus gnats (Diptera: Bolitophilidae, Keroplatidae and Mycetophilidae) from the Maltese islands. Stud. Dipterol. 7: 69–81.

Chandler, P. and L. Matile. 1998. A new species of *Platyceridion* Tollet (Diptera, Keroplatidae) with a larva predatory in ant infested internodes of *Humboldtia laurifolia* Vahl. Stud. Dipterol. 5: 163–173.

Debout G. 2003. Parasite et mutualisme de protection—Le cas de *Cataulacus mckeyi*, fourmi symbiotique de *Leonardoxa africana africana*. Ph.D. dissertation. Université Montpellier II, Montpellier, France.

———, E. Provost, M. Renucci, A. Tirard, B. Schatz, and D. McKey. 2003. Colony structure in a plant-ant: Behavioural, chemical and genetical study of polydomy in *Cataulacus mckeyi* (Myrmicinae). Oecologia 137: 195–204.

Gaume L. 1998. Mutualisme, parasitisme, et évolution des symbioses plantes-fourmis: le cas de Leonardoxa (Légumineuse) et de ses fourmis associées. PhD thesis, 200 pp., ENSAM-University of Montpellier 2, Montpellier.

———, and D. McKey. 1999. An ant–plant mutualism and its host-specific parasite: Activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. Oikos 84: 130–144.

———, ———, and M. C. Anstett. 1997. Benefits conferred by "timid" ants: Active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. Oecologia 112: 209–216.

Krombein, K. V., B. B. Norden, M. M. Rickson, and F. R. Rickson. 1999. Biodiversity of the domatia occupants (ants, wasps, bees and others) of the Sri Lankan myrmecophyte *Humboldtia laurifolia* Vahl (Fabaceae). Smithsonian Contributions to Zoology 603. Smithsonian Institution Press, Washington, DC.

Matile L. 1990. Recherche sur la systématique et l'évolution des Keroplatidae (Diptera: Mycetophiloidea). Mémoires du Muséum National d'Histoire Naturelle, série A (Zoologie), tome 148. Editions du Muséum National d'Histoire Naturelle, Paris, France.

McKey D. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rain forest in Cameroon. Biotropica 16: 81–99.

———. 2000. *Leonardoxa africana* (Leguminosae: Caesalpinioideae): A complex of mostly allopatric subspecies. Adansonia 22: 71–109.

Menzel, F., and J. Ziegler. 2001. New records of Diptera from the Hohe Tauern National Park (Austria), including information on flower visiting and the description of two new black fungus gnat species (Sciaridae). Stud. Dipterol. 8: 355–409.

Pugsley, C. W. 1983. Literature review of the New Zealand glowworm *Arachnocampa luminosa* (Diptera: Keroplatidae), in the Glowworm Cave, Waitomo. J. R. Soc. N.Z. 14: 387–407.

Uesugi, K. 2002. Notes on the genus *Neoplatyura* of Japan including the description of three new species (Diptera: Keroplatidae). Stud. Dipterol. 9: 191–202.

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