

- The North American species of the genus *Cremastocheilus* are reviewed. These belong to 5 subgenera, *Macropodina*, *Trinodea*, *Anatinodia*, *Mymcotonus*, and *Cremastocheilus*. Taxonomic changes are: The inclusion of *Cremastocheilus nitens* and *C. chapini* in the subgenus *Cremastocheilus* rather than *Mymcotonus*. Also *Anatinodia* is elevated to subgeneric status. A key to the subgenera is provided, as is a key to the species of the 5 subgenera, recognizing that the 35 species in the subgenus *Cremastocheilus* are in need of revision. A critical review of the host records, geographic distribution, and ecology of the Tribe *Cremastocheilini* (Family *Scarabaeidae*, subfamily *Cetoniinae*) is provided. This contains enormous numbers of new records for both the genera *Genuchinus* and *Cremastocheilus* both from the literature and from the extensive field work that is reported here for the first time. A Summary of the host records is presented in tabular form. This table shows the association of all species of *Cremastocheilus* with ants as adults and the larvae either associated with the vegetable material of the ant nests or with vegetable material in rodent burrows. *Genuchinus* is shown to be a general predator on soft bodied insects while the other genera of the *Cremastocheilini* are associated with plants, particularly bromeliads. A detailed study of the external morphology and sexual dimorphism of the genera *Genuchinus* and *Cremastocheilus* is presented. All species of *Cremastocheilus* can be sexed with the naked eye by the difference in the shapes of the abdominal terminal segments, wherein males have the posterior border of the last ventral abdominal segment either straight or slightly bowed, while females have this border broadly rounded. There are other microscopic sexual differences in the structure of the legs. The rest of the external morphology is also presented, particularly from the point of view of adaptations to either a predaceous or myrmecophilous existence. Particularly adapted for predation are the pointed maxillae which are used for piercing prey. Particularly adapted for myrmecophily are the mentum, the maxillae, the generally thick exoskeleton, trichomes on both the anterior and posterior angles of the pronotum, the elytra, and the legs (which are adapted to the nest substrate of the host ant nests. Exocrine glands are described for *Genuchinus ineptus* and at least 1 species of each of the 5 subgenera of *Cremastocheilus*. In general, there are no gland cells nor glandular areas in *Genuchinus* that are comparable to those of *Cremastocheilus*. The gland cells and glandular areas are quite extensive and variable among species of *Cremastocheilus*. The frontal gland of some *Cremastocheilus* (strongly developed in *C. castaneus* and the *C. canaliculatus* species group, but weakly developed in the *C. wheeleri* species group) is described for the first time. Because these glands are not found in *Genuchinus ineptus*, a species with general predatory habits, it is thought that these play a role, as yet unknown, in interactions with ants. The life cycles of the subgenera of *Cremastocheilus* are described. The general life cycle entails adult beetles eclosing in ant nests during the summer and then undertaking dispersal flights. The adults then enter ant nests and overwinter there, eating ant larvae during the winter. Another dispersal flight occurs in the spring during which the adults mate and enter ant nests again. The females then lay eggs and the adults die. The eggs hatch and the larvae spend 3 instars feeding upon vegetable material in the nests. The larvae then pupate in typical scarabaeine earthen cells made of fecal material and soil. These eclose in the summer and the cycle is repeated. Variation from species to species is largely in the timing. Leaving the nest in late summer, mating seems to be triggered by rainfall in all the species studied. Mating of *C. (Macropodina) beameri* takes place in rodent

burrows. Males seem attracted to females from a distance but the mechanism of this remains obscure. In the subgenus *Trinodia*, mating takes place on sandy washes or roadsides where females land. In the subgenus *Myrmecotonus*, mating also takes place in sandy areas. In *C. (Cremastocheilus)* mating takes place on sand bars along rivers in the southeastern U.S. and in sand dunes in northeastern U.S. The females dig down into the sand. Males locate these places by some unknown mechanism and then dig down to copulate with the females. Field experiments showed unequivocally that males dig only into areas occupied by females. No sex-specific Sex attractant glands have been located in females so far. Dispersal to ant nests occurs after mating except for *C. (Macropodina) beameri* which lays its eggs in the rodent burrows and then probably disperses to ant nests. Beetle activity going in and out of nests was studied using wire hardware cloth screens over entrances to *Mynnecocystus* nests. The mesh size was such that the ants could move freely in or out but the beetles got stuck by their thoraces. The direction then could be interpreted by the direction in which they got stuck. By this method, *C. stathamae* was shown to leave nests from 23 June to 1 September with a peak on 6 July, just after the beginning of the summer rains. Beetles entered nests from June 23 to August 3, however 39% entered on July 16, probably pulsed by the leaving time which was correlated with the rains. Life cycle timing: *C. (Macropodina)* develop in the nests of Wood rats (*Neotoma* sp.). Females lay about 40 eggs each. The 3 larval instars to pupation take about 1 month. Pupae are found from late August to well into September. In other subgenera as well, larvae are found in parts of the nest devoid of ants, The timing is similar in all the subgenera found with ants. Mortality factors: While ants attack *Cremastocheilus* adults, there is no evidence that they are ever killed by ants nor is there evidence that ants kill larvae nor hard earthen pupae cases which protect the pupae. During dispersal flights and mating, the adults are exposed to predation and evidence is presented that shows predation by horned toads, spiders, magpies, and tiger beetles. Probably most mortality occurs in the larval and pupal stages where the beetles are attacked by internal parasites and fungus. Further mortality is caused by limitation of the food supply during the larval stage. Reentering nests: Females of *C. (Macropodina) beameri* select specific rodent and other burrows, attract males for mating, and then enter the burrow for oviposition. *C. stathamae* are carried into the ants nests from as far away as 25ft. The beetles appear to land spontaneously after flying randomly over *M. depilis* nesting areas. Then they wander about waiting for the ants to carry them into the nests. *Cremastocheilus hirsutus* fly low over the ground searching for *Pogonomyrmex barbatus* nests, land, and move straight for the nest entrances which they enter unhindered. Among all species, the ants frequently eject beetles but the net movement is in. Ants frequently attacked *Cremastocheilus* in laboratory observation nests when they were introduced. These attacks seldom resulted in the death of the beetles and the beetles were eventually ignored. When the beetles entered brood chambers, where they fed upon larvae, they were mostly ignored and even licked assiduously by the ants. A principle defensive behavior by the beetles is feigning death (letisimulation). The beetles give off an unpleasant "dead fish odor" when collected in the field. Experiments show that this substance functions to fend off some predators but further experiments indicated that these substances were ineffective against both ants and kangaroo rats. Experiments with various species of *Cremastocheilus* adults indicate that the adults eat only ant larvae. The beetles will eat larvae of non-host ants but show

preferences for the larvae of their normal hosts. Under the same experimental conditions, *Genuchinus ineptus* adults will feed on a variety of insect adults and larvae. Field experiments on the function of trichome secretions did not indicate that they function to attract ants at a distance nor are they involved in worker acceptance. Laboratory experiments in which areas with a high concentration of gland cells were presented to ants showed that no ants were attracted. Laboratory introduction of *Cremastocheilus hamisii* adults into *Fornica schauinslandi* nests yielded many interactions including ants licking the anterior pronotal angles, the mentum area where the frontal glands empty and a carina over the eye with a dense pad of short setae. These are areas of concentration of gland cells and these are the first observations of licking by ants in specific sites containing exocrine glands. Radioisotope experiments showed food exchange among ants but never from ants to beetles. Other experiments showed that ants can pick up radioactivity from the beetles without feeding on trichome secretions. Evolutionary pathways: Adult *Cremastocheilini* probably followed the evolutionary route from adult predation on soft bodied insects to specialized feeding upon ant brood and the subsequent development of the beetle larvae in vegetable material in the ant colonies. Thus *Genuchinus ineptus* makes a logical outgroup in that they are general predators probably feeding mostly on Diptera larvae associated with Sotol plants in the field. The major evolutionary step taken by *Cremastocheilus* was to specialize on ant brood. Then the species radiated into ant colonies inhabiting southwestern North America. Most of the ant hosts invaded have quantities of vegetable material in their nests sufficient to support several developing scarab larvae. Host colonies are large, contain accessible brood, and are usually dominant foragers. Evidence supports the idea that the species of *Cremastocheilus* have differences in behavior and morphology that reflect adaptation to the behavioral ecology of different species of ants rather than different evolutionary levels of integration into ant colonies.