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Ways of formation of anthophily among beetles

Many mature beetles as many other insects of recent abundant orders feed on flowers of high plants often acting herewith as their pollinators. This mutual relation is usually called as either anthophily (or more precisely anthophagy) or entomophily depending on whether dealing with insects or plants. As it is argued by many authors this relation was extremely productive at some stages of historic development of both plants (ROBERTSON, 1904; DIELS, 1916; TAKHTADJAN, 1934; 1970 and others) and insects, including beetles (i.e. GRINFELD, 1978; RODENDORF, 1980). The transmission of pollen or microspores as well as spores is noted not only for Angiospermae but also for Gymnospermae, Pterophyta, Bryophyta and Fungi (see reviews: FEGRI a.van der PIJL, 1962, CARTER, 1963).

Anthophagy is rather common among many coleopterous groups so much so that it seems quite obvious that anthophilous forms had to arise independently. It is also evident that ways of formation of anthophilous mode of life could be readily distinguished in different beetle lineages. So far as it follows from fossil records recently interpreted by PONOMARENKO & ZHERICHIN (1980), the pollino- or spermatophagy developed even before phyllophagy proper, the problem of development of eating the generative organs of high plants is likely to be immediately connected with the problem of development of eating living high plants as a whole.

It is possible to divide all the cases of anthophagy into two forms: 1) imaginal and 2) complete (if all active instars feed on generative plant organs, such cases are observed in Nitidulidae, Phalacridae, Nemonychidae, Curculionidae and others). Ecological and trophic divergence of several coleopterous groups as well as probably numerous secondary transitions to anthophagy make difficult to clear up how anthophilous forms initially arose and also their relationship with their possible ancestors.

The Nitidulidae studied by the author in detail present a generalized Cucujoid family and consist of 6 subfamilies, 4 of which are either entirely floricolous or comprise some forms associated with flowers. Primary food for archaic Nitidulids included appearantly spores and hyphae of the fungi and slime moulds (Myxophyta). These ancient forms fed also on fermenting sap exuding from trees just as do modern Nitidulinae, Carpophilinae, Cryptarchinae and Calonecrinae. Sap feeding is common and yet facultative for adults of many recent species while for the Calonecrinae it is the only known source for both adults and larvae. The Nitidulinae are most diverse and at the same time they have the largest numbers of symplesiomorphies (KIREJTSHUK, 1982) among Nitidulids. This subfamily are mainly fungivorous but some of their representatives are scavengers on decayed organic matter, inquilines in ant nest, furthermore flower- and even leaf-consumers. Within the subfamily there are at least 3 independent lineages attaining obligate anthophagy. One of them is represented in a primitive and hardly modified Epuraea genera-complex. Adults of some Epuraea species are common visitors of flowers, probably feeding on pollen (imaginal anthophagy), but their derivative allies, the genera Haptoncus, Haptoncognathus, Mystrops and others anthophagous in imaginal instar or many are completely anthophagous of both adults and larvae. The second lineage leading to anthophagy gave the Aethina genera-complex, where there are a number of adult pollen-feeders but no completely anthophagous species. The highly specialized Anister species with obscure kinship, though may be related to Aethina-complex are known to be leaf-mining of both larvae and imagoes (i.e. JELINEK, 1981). Third lineage is presented by the Cychramus genera-complex among which imaginal anthophily seems to be rather common and at least Xenostrongylus species of this complex became completely phytophagous with larvae leaf-mining and adults skeletonizing the lower epidermis of leaves or feeding on plant surface, frequently on flowers. The subfamily Carpophilinae are also generally mycetophagous, most common under bark, rotten wood and fruits infested by fungi, fermenting tree sap etc., but adults of some species (e.g. the Palearctic Carpophilus chalybaeus Murr., some of its Nearctic and many of its tropical congeners as well) collected on flowers only, probably feed on pollen. The subfamily Cryptarchinae are almost entirely mycetophilous and some of them are observed as predators in subcortical habitats. The archaic and yet specialised subfamily Kateretinae contain anthophagous forms, but some larvae feed in gynaeceum and later in immature fruits or seeds. At last the Meligethinae are widespread, except South America, and fairly common pollen-feeders on flowers, but adults of some primitive representatives from tropical Africa (f.i. Metapria and Microporus species) are known as usual visitors of soft fruits, and occasionally of those beginning to decay (such as Treculia spp.). It is worth to notice that all known anthophagous larvae have many features rather similar to those of Coccinellidae and even Chrysomelidae (see f.e. BÖVING & CRAIGHEAD, 1931; CROWSON, 1955; GILLOGLY, 1962).

Following from the above data we may suggest a fashion of trophic transformation within the Nitidulidae. Complete mycetophagy, in a broad sense, gave rise first to imaginal anthophagy, which led, in turn, to complete anthophagy with larval feeding on gynaeceum as well as immature fruits and seeds and then there appeared a possible basis for a transition to leaf-mining, i.e. phyllophagy proper. This way it bears some resemblance to that in Symphyta (Hymenoptera). The imaginal and next complete anthophagy are the more possible that spores of the archaic groups of the high plants as well as, appearently, pollen of the advanced ones seem to preserve in general a considerable chemical similarity to the fungal spores. Perhaps, both anthophagy and entomophily (or cantharophily) of plants should be simultaneously forming at the primary stage of imaginal anthophily.

Such a trophic transformation, as far as I know, has not yet attracted the attention of investigators of beetles, although somewhat similar view on close links of saprophagy and anthophily (f.e. GRINFELD, 1978) or on transition from mycetophagy in rotten wood to imaginal anthophagy is as ancient as recent beetles (PONOMARENKO, 1969; CROWSON, 1981 and so on) were yet proposed. Nevertheless, CROWSON in his last generalizing work (1981) pointed out ways of formation of herbaceous beetles conflicted with the fashion established in the Nitidulidae. He concludes that phytophagous beetles were originated from mycetophagous subcortical forms through boring first inside dead and later in living wood, or from the same mycetophilous forms through an intermediate stage of feeding on fungi attacking herbaceous plants of associated with honey-dew exuded by Homoptera.

We may, however, assume that the way of trophic transformation established for Nitidulidae could frequently have occurred also in other beetle families. This way does not exclude that one drawn up by CROWSON, but both appear to be equally possible and had likely taken place in historic development of different groups.

Imaginal anthophily with larval mycetophily arose in ancient Archostemata primarily completely mycetophagous. At least recent Cupedidae rather similar to fossil ones display the same mode of life. Except Nitidulidae and Cupedidae this is shown also in Dascillidae, Lycidae, Phalacridae, perhaps Alleculidae, Mordellidae, Oedemeridae, Anthribidae. It may be possible that this habit also characterized ancient Scarabaeoidea so far as the Mesozoic ones were likely to be the main mycetophilous (PONOMARENKO & ZHERICHIN, 1980).

Apart from the Nitidulidae the second stage, i.e. complete anthophagy initially appeared occurs also in Boganiidae, Languriidae, Erotylidae (including Pharaxonothidae appearently dwelling in male cones of Cycadaceae), Mycetophagidae, Anthribidae, Nemonychidae, Oxycorinidae, Attelabidae and perhaps Phalacridae. It is important to note that among the anthophilous forms retaining this stage until today there is a number of stroble-dwellers on various Gymnospermae, including the Cycadales very prominent in the Jurassic fossils and the Coniferales as well. Moreover, many of the forms from these families or their probable ancestors are known just from the Jurassic (ARNOLDI and other, 1977; CROWSON, 1981). It is seen that the mentioned groups are regarded as phyletic branches united into one of chief stocks of Polyphaga (Cucujiformia).

The third stage of trophic transformation led to phytophagy through anthophagy comprises phytophagous larvae and still anthophagous adults. It concerns Nitidulidae, Byturidae, Attelabidae as well as perhaps Phalacridae, Mordellidae and Bruchidae. If so, the Nitidulid trophic transformation could have indeed taken place in the past (likely yet in the Triassic) of many families of Cucujoidea and Curculionoidea. It regards also, perhaps, anthophilous groups of the Chrysomeloidea which at that time were present by Chrysomelidae and Cerambycidae and possibly Bruchidae, appearently also associated with the Jurassic Gymnospermae. Such an assumption is possible by taking into consideration the ideas of BÖVING & CRAIGHEAD (1931), as well as LAWRENCE & NEWTON (1982), on the phylogeny of this superfamily and also that the Bruchid-like feeding could be a primary type of trophic of the archaic Chrysomeloid forms but not of Cerambycid-like one which follows from CROWSON's viewpoint. At least one known fact: the abstantion of Bruchid females from ovipositing before pollen-eating supports an ancient development of their anthophagy.

The next way of the formation of imaginal anthophagy is from phytophagy as it appeared in CROWSON's conclusion. It might occur in Buprestoidea and Elateroidea (both Elateriformia). A similar way seemed to be in some advanced Chrysomelidae, probably Apionidae and other derivative Curculionidea as secondary transition from phyllophagy, formerly arose through an initial anthophagy passed by their ancient ancestors.

The third possible way of the formation of imaginal anthophagy consists in a transition to it from initial predation. GRINFELD (1978) confirmed it with numerous data. This is probably characteristic for Staphylinoidea, some Cantharoidea, many Cleridae and Melyridae of Cleroidea as well as, perhaps, some Coccinellidae of Clavicornia and Anthicidae of Heteromera. This is common among unspecialized predaceous groups which did not go through "pre-adaptation" for pollen-eating is due to their macetovorous origin.

Some scavengers on organic matter of various nature pass also to imaginal anthophagy. This way was likely possible for the floricolous adults of Silphidae, Dermestidae and, perhaps, Alleculidae.

Finally, the appearence of imaginal anthophagy in the Meloidae with parasitic larvae is still unclear, but it is possibly correlated with the evolution for searching of hosts from among anthophilous Hymenoptera.

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