

ON THE DRYOPOID AFFINITIES OF BUPRESTIDAE

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ABSTRACT

The family Buprestidae seems to share common ancestry with, or be derived from, the Dryopoidea (excluding Ptilodactylidae). Its origin appears to be independent from those of the Armatopoidea and Elateroidea. Within the Dryopoidea, the Buprestidae may have their closest affinities with the Elmidae and Lutrochidae.

Buprestid beetles were for a long time associated by systematists with Elateridae, Throscidae, and Eucnemidae in a grouping commonly known as Sternoxia, and this view has been maintained as recently as 1971 by Hatch, and 1972 by Leseigneur. Serious doubts about a particular affinity of Buprestidae to these families had been voiced as early as 1900 by Lameere on general grounds, and were expressed also by Sharp & Muir (1912) on the structure of the male genitalia, by Forbes (1926) on wing-venation and folding, by Poll (1932) on the Malpighian tubules, and by Crowson (1944) on the met-endosternite. Böving & Craighead (1931) in their larval system, though retaining Buprestidae in their rather ill-defined Elateroidea, implied the unnaturalness of this grouping by suggesting a polyphyletic derivation of Elateroidea from Dryopoid ancestors. Crowson (1955) seems to have been the first formally to distinguish a superfamily Buprestoidea, and in 1973, the same author redefined it in a key to superfamilies of Elateriformia.

A particular affinity of Buprestidae to Dryopoidea was suggested by Obenberger (1948 pers. comm. to R. A. Crowson). Further evidence in support of it was adduced by Crowson (1955) and strengthened by Kasap & Crowson (1975) on internal abdominal structures and the ventral nerve cord.

There are a number of structural features, unusual in the Elateriformia, which primitive Buprestidae (e.g., Schizopinae) share with certain Dryopoid groups. These include only two, rather than three, connate basal ventrites in the abdomen; the metasternum with complete transverse and longitudinal sutures; a strongly deflexed head with short rather dorsally inserted antennae; male with paraprocts not fused dorsally in front of the proctiger; meso- and metathoracic ganglia more or less fused; fusion of abdominal ganglia 6, 7, and 8; testes with long spermtubes more or less spirally twisted together and enclosed in a common membrane; and some details of the abdominal musculature (Kasap & Crowson 1975). Within the Dryopoidea, it is notable that the closest approach to Buprestidae in these features is to be found, not in the supposedly primitive Elichadidae and Ptilodactylidae (Crowson 1978), but in Elmidae-Larinae and Lutrochidae.

Of the basic features of Buprestidae, plesiomorphic ones that would preclude derivation from the higher Elateriform groups Elateroidea and Cantharoidea include the presence of a well marked complete transverse suture in the metasternum, the three ocelli of the first instar *Schizopus* larva (Rees 1941), the six

Malpighian tubules, and the presence of a free larval labrum. The first two of these would also argue against a possible derivation from Armatopodea, whose adults never have a transverse suture in the metasternum and whose known larvae never have more than one ocellus. It would thus appear that if any Elateriform superfamily is to show particular affinities to Buprestidae, it should be either Byrrhoidea or Dryopoidea. Modern Byrrhidae would seem to be ruled out as Buprestid ancestors by their complete lack of metasternal transverse suture, and perhaps also by the firm dorsal fusion of the paraprocts in the males. This last feature is admittedly somewhat controversial, in that many authors have interpreted the proctiger as the tergite of abdominal segment 10 rather than 9, and the paraprocts as representing tergite 9—in which case it would be natural to take the dorsal fusion of the paraprocts as a primitive condition. The major arguments against this theory are (1) that there is no distinct tenth abdominal segment in normal beetle pupae; (2) the proctiger is at least in some species connected by direct longitudinal muscles with tergite 8 (Hieke 1966); (3) dorsal fusion, or even contact, of the paraprocts is very rare in females; and (4) in some Coleoptera the paraprocts may fuse ventrally in front of sternite 9.

As previously noted, within Dryopoidea the forms most closely approaching Buprestoidea in the characters we have considered are certain Larinae and Lutrochidae. *Lutrochus*, together with Dryopidae, Limnichidae, and Heteroceridae, is probably ruled out as a potential ancestor of Buprestidae by the reduced and modified ovipositor, without distinct coxites and styli (in Buprestid females there is a pair of articulated apical appendages probably representing coxites or styli), and *Lutrochus* also by the reduced wing-venation with only four anal veins in the main group.

Adult Larinae are less Buprestid-like than *Lutrochus* in having three rather than two connate ventrites and in having a distinct fronto-clypeal suture, but they usually have five anal veins in the main group and may have wing-venation almost identical with that of Schizopinae.

Furthermore, female Larinae have ovipositors of types which could be ancestral to those of Buprestidae. It is interesting that a recent study of gut-contents has shown that larvae at least of *Lara* feed extensively on waterlogged wood of submerged logs (Anderson *et al.* 1978, 1979), a habit which might well be widespread in Larinae and perhaps in other Dryopoidea and which might represent an initial step in the direction of typical Buprestid habits.

One way of estimating the likelihood of such a development is to look for possible parallels in other groups of insects. In larval and pupal adaptations, as pointed out particularly by Hinton, there are numerous parallels between Dryopoidea and various Nematoceran Diptera. One family which may be particularly interesting from this point of view is Psychodidae. Many larvae of this group, e.g., of *Pericoma*, *Sycorax*, and *Maruina* are rheophilous or hygropetricolous, and some such habits are likely to be ancestral in the family, being found also in related groups like Blephariceridae and Deuterophlebiidae. Such Psychodid larvae show notable parallels with those of Elmidae and *Lutrochus* in mouthparts, antennae, general body form, etc., with the important difference that, with the Dipteran lack of legs, they tend to develop suckers for holding on to the substratum in turbulent conditions. One group of the family, however, has developed wood-boring larval habits, the subfamily Trichomyiinae, and its larvae differ from those of *Pericoma*, etc., in many of the same respects as Buprestid larvae differ from those of Larinae, etc. However, the

analogy does not extend as far as the development of a spiracular closing apparatus or cryptonephrism in the *Trichomyia* larvae, which are consequently restricted to damp decaying wood (Krivosheina & Mamaiev 1967).

The secondary development of an effective spiracular closing apparatus in Buprestidae, in apparent breach of Dollo's Law, has no known parallel in Diptera, but has at least one apparent parallel in Coleoptera, in the Throscid-Eucnemid line of the Elateroidea. It may be that the possibility of redeveloping a spiracular closing apparatus exists in the Elateriformia, but not in the Diptera, on account of the presence in many of the former group of special muscle functioning in the moulting of typically biforous spiracles (Hinton 1955), which could be converted to serve a closing apparatus. On this hypothesis, those Elateriformia in which a closing apparatus is present, i.e., the Buprestidae, Throscidae-Eucnemidae, and Brachypsectridae, should have a different spiracular moulting process from typical Elateriformia, dispensing with the need for a special muscle.

If, as these considerations suggest, the Buprestidae developed from true Dryopoid ancestors, perhaps from a common stock of primitive Elmidae and Lutrochidae, then either we should reduce Buprestidae to the status of a family in Dryopoidea, or the Dryopoidea themselves should be split into several superfamilies, if we are to conform to the principles of phylogenetic classification. There are, in fact, reasons for suspecting that Armatopoeidea, Elateroidea, and Cantharoidea may all be derived directly or indirectly from ancestors whose characters would have caused us to include them in Dryopoidea as now defined. The Dryopoid affinities of Armatopoeidea and Elateroidea, however, would seem to lie with the Ptilodactylidae rather than with the Dryopid-Elmid line, so that Buprestidae might remain in Dryopoidea even after the separation from the superfamily of the Ptilodactylid group.

A classificatory expression of these ideas would be to redefine Dryopoidea so as to include Buprestidae but exclude Ptilodactylidae, with the latter family possibly transferred to a redefined Armatopoeidea. Difficulties for such a system would be posed by Eulichadidae and Chelonariidae—the former group showing almost equal affinities to Ptilodactylida and to Psephenidae, while the latter tends to resemble Ptilodactylidae in adult characters but approaches Dryopidae and Lutrochidae in larval structure.

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CORRECTION

In *Hylobothynus* article by Ratcliffe (1981, Coleopt. Bull. 35:303-306), couplet 2' on p. 306 should read "Base of pygidium . . ." not "Base of pronotum . . ."