

There are several specimens of Fulgoroidea from the Crato Formation in various collections (e.g. at SMNS), and among them a number of new species of Lalaclidae (Figures 11.52a and b). There are also some specimens that could be attributed to other fulgoroid families, i.e. Fulgoridae (Figures 11.52c and d, Plate 12c) and very probably Derbidae and Achilidae (Figure 11.52e). These rich collections need further study as they could provide answers to a number of important phylogenetic and taxonomic questions.

11.14 Coleorrhyncha: moss bugs

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Coleorrhyncha (also called Peloridiomorpha) are small, rarely medium sized (2–5.5 mm), insects with a mixture of cicadomorphan and bug-like characters, representing a separate suborder within the Hemiptera. The body is dorsoventrally flattened, with tegmina folding flat, their commissural margins and apices overlapping in repose. In macropterous forms the left tegmen is always over, so the postapical-area overlap in the underlying right tegmen is delimited better, with thinner veins, usually arranged in a somewhat different way than the left one. The head is opisthognathous, with a long rostrum directed caudad. The antennae are short and few-segmented, supra-antennal continuous from eye to eye. Macropters have three ocelli; the lateral ones are placed at anterior head margin, close to the compound eyes, and are untraceable in known fossils, and the median ocellus is placed above the ledge. The pronotum bears paranotal expansions and overlaps the mesonotum up to the apices of the parapsides. The scutellum is margined by grooves fixing the clavi in repose. Thoracal pro- and mesepisterna have anapleural clefts. The coxae are pagiopodous with exposed trochantines. Tarsi are two-segmented, with the first segment small; in jumping forms (extinct) hind tarsi are three-segmented, with the basitarsomere being the largest, armed as well as hind tibiae. The tegmina has a precostal carina, simple veins Rs and CuA_1 , and vein M is three-branched, with crossvein-like CuA_2 and three crossveins (arculus, $r-m$ and $m-cu$) and an ambient vein separating the appendix; sometimes venation is partly reticulate. The clavus with claval veins is in form of a letter Y, its stalk bearing a short interalar coupling lobe. The hind wing has simple venation and a straight anterior margin, the jugal lobe folding beneath in repose. The abdomen is flattened with laterotergites facing ventrad and bearing spiracles. The female seventh sternite is elongate, concealing the base of the cutting ovipositor. The pygofer (i.e. male ninth segment) is barrel-shaped, sometimes with lateral projections, parameres protruding and elbowed. The development is hemimetabolous with adult-like nymphal stages. Nymphs are flat, non-jumping, with antennae and legs short, broad paranota

and long rostrum (Popov and Shcherbakov, 1991, 1996). Modern Coleorrhyncha – members of family Peloridiidae – are phytophagous and have a cryptic lifestyle on mosses in the wet and cool *Nothofagus* forests of southern South America, Australia, Tasmania, New Caledonia, Lord Howe Island and New Zealand. Such a circum-Antarctic relict distribution suggests an Early Cretaceous Gondwana origin of the crown group. Eskov (1984) and Eskov and Golovatch (1986) argued that Recent transoceanic disjunctive distributions of various taxa (including far-southern taxa) are merely remnants of a transpolar distribution in the geological past. However, this ‘ousted relicts’ hypothesis cannot be applied to the Peloridiidae, as it probably never existed in the Northern Hemisphere, even if it is applicable to Coleorrhyncha as a whole (Popov and Shcherbakov, 1996). Peloridiidae seems to be connected with *Nothofagus* forests. The history of *Nothofagus* is rather well documented by fossil pollen, leaves and wood (Romero, 1986; Tanai, 1986). Its biogeography was recently analysed by Linder and Crisp (1996) and the results discussed by Ladi-ges *et al.*, (1999). Extant Peloridiidae are usually found in damp moss, often on decaying mossy trunks and twigs of *Nothofagus* (in Southern Hemisphere), or still occasionally feed on moss rhizoids, or even on wood-destroying fungi or on lichens (Popov and Shcherbakov, 1996).

Systematics, phylogeny, evolution and fossil record

There are only 13 genera and 25 Recent species known, which are all classified in the single Recent family Peloridiidae (Evans, 1981; Burckhardt and Agosti, 1991; Burckhardt and Cekalovic, 2002). Coleorrhyncha have often been grouped together with Sternorrhyncha and ‘Auchenorrhyncha’ (i.e. suborders Fulgoromorpha and Cicadomorpha) in a paraphyletic taxon ‘Homoptera’, but since Schlee (1969) Peloridiidae are regarded as the sister group of Heteroptera, which was also confirmed by DNA studies (Ouvrard *et al.*, 2000) and comparative studies on male genital structures (Yang, 2002). Recent critics of this phylogenetic hypothesis are believed unfounded (see Grimaldi and Engel, 2005: 313) and are mainly based on typological reasoning. Schlee’s (1969) proposal was criticized by Popov and Shcherbakov (1991, 1996; see Figure 11.53), who stated that synapomorphies of Coleorrhyncha and Heteroptera are at least dubious, and these two groups disagree in fundamental apomorphies. According to the latter authors, Coleorrhyncha and Heteroptera evolved from generalized ‘Cicadomorpha’ (a paraphyletic group) as independent stocks, acquired wing coupling of the same type and dorsoventrally flattened habitus with forewing overlap in parallel, and therefore are separated at subordinal level. Nevertheless, it must be emphasized that some autapomorphic differences and a putative parallelism in some of the potential synapomorphies does not invalidate the numerous other morphological and molecular synapomorphies of Coleorrhyncha and Heteroptera. The close relationship of Coleorrhyncha,

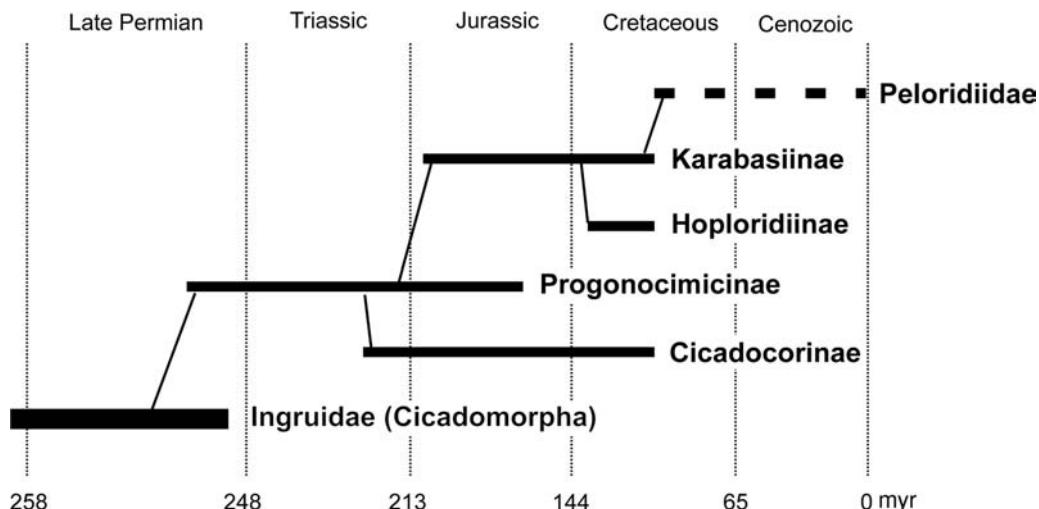


Fig. 11.53. Range chart for clades within the Coleorrhyncha.

Cicadomorpha and Heteroptera is supported by the presence of vibrational communication in these groups. Sweet (1996) hypothesized that large apodemes present at the posterior margin of the first and second abdominal dorsal sclerites in Peloridiidae are tymbal-like organs without a resonator. This assumption is supported by the recorded signals, hypothesized as disturbance calls or spontaneous calls in the context of initiating courtship, as has been observed in other hemipterans (Hoch *et al.*, 2006).

Recent Peloridiidae and †Karabasiidae are placed in the superfamily Peloridioidae, while the †Progonocimicidae are placed in their own superfamily, Progonocimicoidea (Popov and Shcherbakov, 1991). The Peloridiidae are not known from the fossil record, so that all fossil Coleorrhyncha belong to Progonocimicidae (comprising Progonocimicinae and Cicadocorinae) from the upper Permian and Triassic of Australia and from the Triassic, Jurassic and Lower Cretaceous of Eurasia, and to Karabasiidae (comprising Karabasiinae and Hoploridiinae) from the Late Jurassic and Early Cretaceous of Eurasia (Popov and Shcherbakov, 1991, 1996; Carpenter, 1992: 259–260).

Both fossil families are of doubtful monophyly (see Figure 11.53), and both are only stem group representatives of the Recent crown group Coleorrhyncha, because they still have a rather cicadoid wing venation (Grimaldi and Engel, 2005) and other plesiomorphies (see below). Furthermore, even the attribution to the stem group of Coleorrhyncha is not yet very strongly founded and they could also turn out to be stem group representatives of the clade formed by the sister groups Coleorrhyncha+Heteroptera.

Ingruidae, believed to constitute the earliest side branch of ‘Cicadomorpha’, evidently gave rise to both Coleorrhyncha and ‘Cicadomorpha’: Scytinopteroidea,

the latter being ancestral to Heteroptera. The oldest Progonocimicinae (uppermost Permian) are very similar and easily derived from certain Ingruidae, and they retain numerous characters inherited from ancestral 'Cicadomorpha' or even from Archescytinoidea (Paleorrhyncha, ancestral to other Hemiptera). Earliest members of Coleorrhyncha, Progonocimicinae, would have been good jumpers, but already somewhat flattened. Their hind tibiae (at least in Cicadocorinae) have two lateral and sometimes apical movable spurs. Hind tarsi are three-segmented, with basitarsomere the largest, and basitarsomere and midtarsomere have apical pectens of macrosetae bearing teeth. They probably would have had non-jumping nymphs and have been phloem-feeders. Their descendants, the earliest Karabasiidae, became less vagile and acquired wing polymorphism, present also in Recent, relic Peloridiidae. Karabasiidae: Karabasiinae had the hind tarsi with basitarsomere and midtarsomere bearing lateroapical teeth. The nymphs were slow-moving, non-jumping, resembling corticolous nymphs of Cicadellidae: Ledrinae and especially Phloeidae (Heteroptera: Pentatomoidea), probably living on relatively thick plant stems and were cryptic due to a cone-like shadowless habitus. Karabasiidae: Hoploridiinae were probably also corticolous and convergently similar to Aradidae (nymphs and adults), jumping or non-jumping, with cryptic habitus and long rostrum, being bark-dwellers and associated with thick plant stems. They probably evolved due to retention of certain nymphal features at the adult stage resulting in the loss of jumping ability, flatness, wide paranota and somewhat reduced tegmina. Peloridiidae arose from Karabasiinae, constituting a blind offshoot of the peloridioid lineage. They acquired the uniform areolation of both the wide paranota and the precostal carinae, and a distinct terminal Sc. Peloridiidae lost the R stem in the hind wing, their nymphs became differently shaped, the dorsum being more flat and the anal tube invisible from above (Popov and Shcherbakov, 1991, 1996; Shcherbakov and Popov, 2002). Peloridiidae are found in damp moss, often on decaying mossy trunks and twigs of *Nothofagus*, and have retained a cryptic habitus as a non-functional heritage from corticolous ancestors. It seems that Recent Peloridiidae, probably similar to their ancestors, are phloem-feeders, or occasionally feed on moss rhizoids, or even on wood-destroying fungi. Of course, the lifestyle of the modern Coleorrhyncha cannot be generalized easily to the fossil stem group representatives, so that the occurrence of such fossil coleorrhynchans does not provide any useful information about the palaeohabitat or the palaeoclimate.

Crato fossils

Several specimens of Progonocimicinae have been discovered among the Crato insect fossils but not yet described. They represent the first New World fossil records of the stem group of Coleorrhyncha. The presence of Peloridiomorpha

was first mentioned by Maisey (1991: 434), and a very well-preserved specimen (AMNH SA45253) was figured by Grimaldi and Engel (2005: figure 8.55). Three specimens, SMNS 66408 and SMNS 66423 (Plate 15b), and SMNS 66431 (Plate 15c), are present in the SMNS collection. According to Ruf *et al.* (2005: 73) there are two monotypic families of Coleorrhyncha from the Crato Formation currently in the process of description by Martins-Neto. Martins-Neto (2005b: 479) lists three Crato Formation taxa, *Laticutella santosi* Pinto and Ornellas, Martins-Neto and C., 1994, *Cratocoris schechenkoae* Martins-Neto, Popov and Zamb., 1999 and *Cratogocimex popovi* Martins-Neto, 2002, as belonging in Coleorrhyncha: Progonocimidae, but there is no justification for these referrals of taxa, which had been previously described and unequivocally considered as Heteroptera (see below).

11.15 Heteroptera: bugs

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Heteroptera, or true bugs, are one of the most diverse and important groups among both Recent and fossil insects. Their phylogeny was summarized by Schuh and Slater (1995) and Grimaldi and Engel (2005), and they are generally treated as a suborder of Hemiptera. The majority of over 75 accepted families occur everywhere except Antarctica. According to Schaefer (1996) there are approximately 37,000 described Recent species and perhaps approximately 25,000 species still awaiting description. So far nearly 1000 fossil heteropteran species belonging to various families have been described from Cenozoic of Western Europe (mainly in Germany, Spain, France, Czech Republic, Denmark and Baltic countries), China, and North (Oligocene of Florissant) and South America (Oligocene of São Paulo State, Brazil).

In contrast to the Mesozoic heteropteran fauna of Eurasia, that of South America is almost unknown and our knowledge is practically restricted to the Lower Cretaceous of Brazil (Crato Formation, Codo Formation and Areado Formation) and Argentina (La Cantera Formation). The majority of Cretaceous specimens are still undescribed.

The Early Cretaceous Heteroptera are quite similar to Late Jurassic assemblages which are mainly known from Eurasia. The transition from Jurassic to Cretaceous assemblages was marked by the appearance of such families as the semi-aquatic Hydrometridae or Veliidae, the phytophagous Tingidae and Aradidae, and the predatory Reduviidae: the latter still very rare in the Early Cretaceous. Some high-ranking taxa disappeared at this time, too, including the pleoid families Scaphocoridae (Late Jurassic) and Mesotrehidae (Early Cretaceous) of Kazakhstan, the water boatmen of Velocorixinae (Late Jurassic–Early Cretaceous of Mongolia and China),

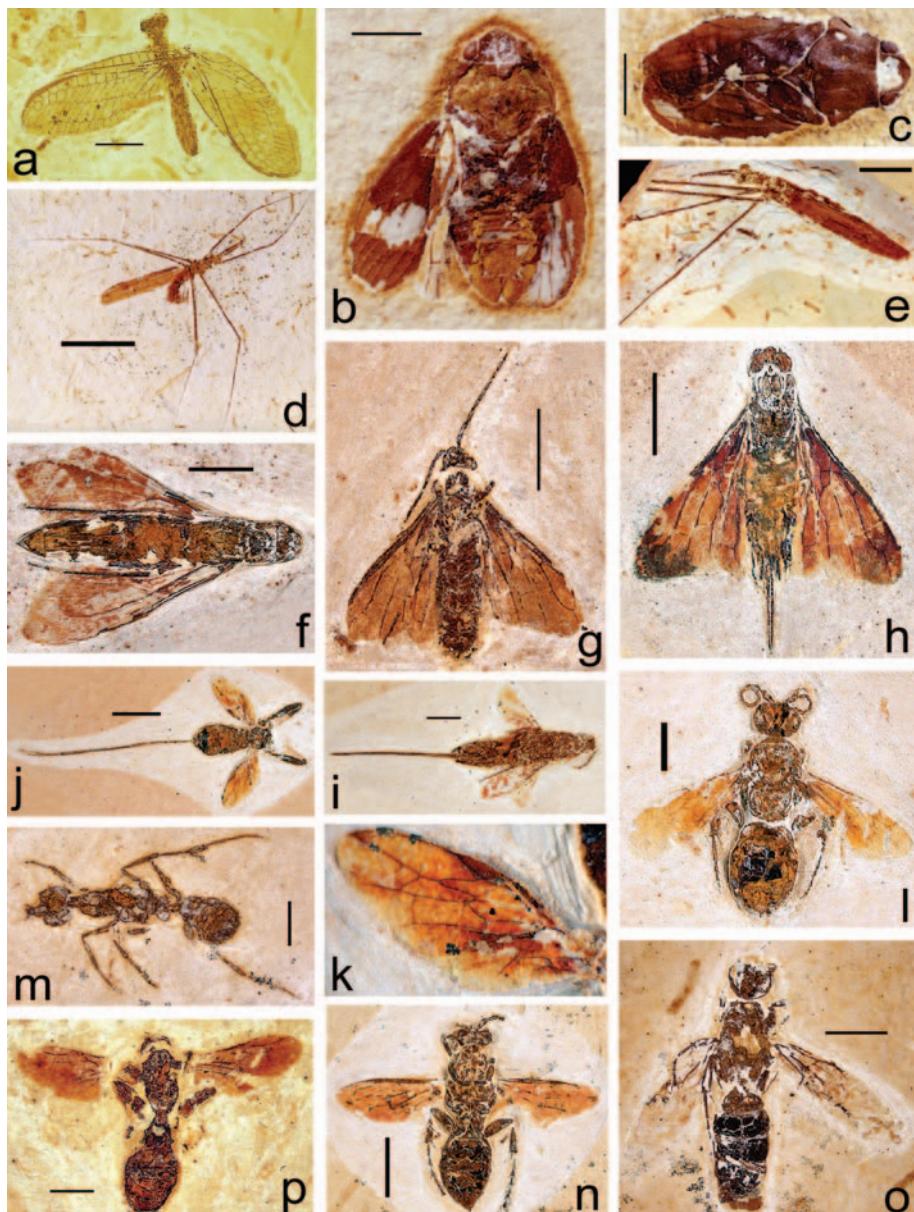


Plate 15. Crato insects: (a) Neuroptera, Hemerobiiformia, Mesochrysopidae gen. et sp. nov., priv. coll.; scale bar, 5 mm; (b) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66423; scale bar, 2 mm; (c) Coleorrhyncha, Progonocimidae gen. et sp. nov. SMNS 66431; scale bar, 2 mm; (d) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., SMNS prelim. no. 0134 (old no. H56), scale bar = 20 mm; (e) Chresmododea, Chresmodidae, *Chresmoda* sp. nov., ex MSF coll G88; scale bar, 10 mm; (f) Hymenoptera, Anaxyelidae, MURJ without number; scale bar, 5 mm; (g) Anaxyelidae, *Protsyntexis* sp., SMNS 66304; scale bar, 5 mm; (h) Siricidae, MURJ without number; scale bar, 5 mm; (i) Ichneumonoidea, MURJ without number; scale bar, 5 mm; (j) Ephialtitidae, *Cretephialtites kourios*, MURJ without number; scale bar, 5 mm; (k) Ephialtitidae, *Cretephialtites kourios*, right wings, MURJ without number, without scale; (l) Pompilidae, MURJ without number; scale bar, 2 mm; (m) Formicidae, Mymecinae, *Cariridris bipetiolata*, SMNS 66565; scale bar, 2 mm; (n) Tiphidae, *Architiphia rasnitsyni*, MURJ without number; scale bar, 5 mm; (o) Tiphidae, ?Myziniinae, SMNS 66303; scale bar, 5 mm; (p) Vespidae, ?Eumeninae, SMNS 66295; scale bar, 2 mm.