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, *Latiscutella 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: Progonocimicidae, 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

Yuri A. Popov and Günter Bechly

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 Mesotrephidae (Early Cretaceous) of Kazakhstan, the water boatmen of Velocorixinae (Late Jurassic–Early Cretaceous of Mongolia and China),

the belostomatid subfamily Stygeonepinae (Late Jurassic of Germany and Early Cretaceous of Spain), and the saldoid family Archegocimicidae, the lygaeoid family Pachymeridiidae and the aradoid family Kobdocoridae from the Early Cretaceous of Mongolia (Popov, 1986). The cimicomorphan plant bug family Miridae, which was rather abundant in the Late Jurassic of south-western Kazakhstan (Popov, 1968; Herczek and Popov, 2001), has not yet been recorded from any Lower Cretaceous localities at all, even though a cimicomorphan bug from the Crato Formation was recently figured by Grimaldi and Engel (2005: figure 8.79) and could belong to Miridae.

Some groups of terrestrial bugs became more abundant and more widespread during the Early Cretaceous, for example, the littoral saldoid Archegocimicidae and the terrestrial Pachymeridiidae as well as some Cydnidae (subfamily Amnestinae). Among cimicomorphan bugs three specimens of Reduviidae have been recognized. Aquatic bugs are also abundant in the Late Jurassic and the Early Cretaceous, mainly represented by the Recent families Corixidae (mostly subfamily Diaprepocorinae and Velocorixinae), Naucoridae, Notonectidae and Belostomatidae, and also two extinct families †Scaphocoridae and †Mesotrephidae (Popov, 1971).

In a short review of 73 bugs from the Crato Formation (Grimaldi and Maisey, 1990) Belostomatidae among water bugs and most terrestrial Pentatomomorpha (11 specimens) dominated. Some 30 specimens of undetermined Heteroptera mostly belonged to the lygaeoid Pachymeridiidae, including five species of Lygaeoidea. Judging from their figures (Grimaldi and Maisey, 1990: figures 1D, H, J, N and O) they are most probably the saldoid Archegocimicidae, and close to the extinct subfamily †Enicocorinae (Shcherbakov and Popov, 2002), one of the dominant saldid groups in the Early Cretaceous of the eastern part of East Siberia, Mongolia and China.

In the last 15 years new heteropteran material (≈130 specimens) from the Crato Formation, collected under a collaborative programme with the Universidade Federal do Ceará, Departamento Nacional da Produção Mineral, Divisão de Crato, Centro de Pesquisas da Chapada do Araripe and, more recently, the Universidade Regional do Cariri, has added considerably to our knowledge of the heteropterofauna.

All of this new material can be referred to modern families, and although much of the material is awaiting formal description, the following aquatic bugs have been identified at familial level: Naucoridae (15 specimens), Notonectidae (three specimens), Corixidae (three specimens) and Belostomatidae (25 specimens), represented mostly by nymphs (belostomatids dominate the fossil bugs in many of the Crato collections).

There are also three specimens of semi-aquatic water striders *Cretaceometra brasiliensis* Popov and Nel (Hydrometridae), one specimen of amphibious

Veliidae and six specimens of saldoid leptopodomorphan bugs (Archegocimicidae). The remainder are terrestrial bugs belonging the lygaeoid family Pachymeridiidae (≈80 specimens), which are also the most common and widespread bugs in the Lower Cretaceous of Asia and America, and the Pentatomorpha (Cydnidae, three specimens; Aradidae, one specimen).

Crato bugs

Although several bug species have been described from the Crato Formation, Martins-Neto (2005b) lists only two species of Belostomatidae (*Araripebelostomum martinsnetoi* Nel and Paichler, 1994 and *Neponymphes godoii* Zamboni, 2001) in his compilation of fossil insects from the Crato Formation. Three further heteropteran taxa (*Latiscutella santosi* Pinto and Ornellas, Martins-Neto and C., 1994, *Cratocoris schechenkoae* Martins-Neto, Popov and Zamb., 1999 and *Cratogocimex popovi* Martins-Neto, 2002) are also listed in this publication, but are erroneously attributed by Martins-Neto (2005b) to Coleorrhyncha: Progonocimicidae.

The first Early Cretaceous bugs from Brazil were described by Pinto and Ornellas (1974) from the Codo Formation (Maranhao State): *Latiscutella santosi* and *Pricecoris beckerae*. They were originally placed in two monobasic families †Latiscutellidae and †Pricecoridae but were later transferred to the true burrower bugs of the Recent family Cydnidae (Popov and Pinto, 2000). Mesozoic representatives of this family (the subfamily Amnestinae) are most common and widespread in the Early Cretaceous of Asia (mainly in Siberia, Mongolia and China) and parts of South America. Later, *Latiscutella santosi* was also recorded from the Crato Formation (Martínez, 1982).

The amnestin cydnid *Clavicoris cretaceous* Popov and *Cretacoris gurvanicus* Popov from the lowest Lower Cretaceous of western Mongolia (Gurvan-Eren Formation) were described as the borrower bugs and assigned to the extinct subfamily †Clavicorinae (Popov, 1986). On account of the scutellum not being enlarged, the long and well-developed clavus forming a distinct claval commissure and the similar hind wing venation, these Early Cretaceous cydnids were considered to be related to the living Neotropical Amnestinae and were later included within this subfamily (Popov and Pinto, 2000).

After re-examining of the types of Early Cretaceous cydnids from Brazil and some of the abundant Cretaceous cydnids from Siberia and Mongolia we concluded that there are no cardinal external differences between all the Cretaceous Cydnidae. Mesozoic cydnids compared to some modern Amnestinae show the same ‘ground plan’ at the subfamily level, retaining the ancestral condition with a non-enlarged scutellum and opposite clavi touching to form a distinct claval commissure. The

main external differences separating Mesozoic amnestines from the Recent ones are their longer claval commissure and larger average size.

These similarities are deemed sufficient to unite the Cretaceous and possibly even perhaps all Mesozoic Cydnidae, along with the Recent amnestines, into a single subfamily Amnestinae *sensu lato* (Popov and Pinto, 2000), including the Brazilian Early Cretaceous †Pricecoridae, †Latiscutellidae (Martins-Neto, 1987b) and Asiatic †Clavicorinae (Popov, 1986). Thus Amnestinae, now restricted to the Neotropical and Nearctic Regions, were widespread in the Mesozoic, especially the Early Cretaceous, in modern South America, Western Europe and Asia (East Siberia, Mongolia and China).

Suborder Nepomorpha (Hydrocorisae): water bugs

Belostomatidae: giant water bugs

The giant water bugs of the family Belostomatidae (Figures 11.54a–c) are one of the oldest, common and widespread aquatic heteropterans among all water bugs of the Late Jurassic and Early Cretaceous of Western Europe, Asia (Siberia, Kazakhstan, Mongolia and China), the USA and Brazil. The oldest belostomatids are from the Late Triassic of Virginia, USA (Grimaldi and Engel, 2005: figure 8.69). The stygeonepinous belostomatid *Iberonepa romerali* Martínez-Delclós, Nel and Popov, 1995 occurs frequently (mainly as nymphs) in the Lower Cretaceous of Las Hoyas, Spain, while *Mesobelostomum deperditum* (Germar) is frequent (mainly as adults) in the Upper Jurassic Solnhofen Formation in southern Germany (Popov, 1971). So far some 14 species in 13 genera belonging to two recent subfamilies Lethocerinae and Belostomatinae, and one extinct subfamily †Stygeonepinae, have been recorded from the Mesozoic.

Martins-Neto (1978b) first mentioned the belostomatids from the Lower Cretaceous of Brazil, where they appear to be abundant, mostly immature individuals, and most probably belong to the recent subfamily Belostomatinae. It is possible that they are related to the peculiar Recent monotypic Neotropical subfamily Horvathiniinae that is known mainly from Brazil. Two other Crato belostomatids were illustrated but not named or described by Grimaldi and Maisey (1990: figures 2F and H).

The first true belostomatid from the Crato Formation was described by Nel and Paicheler (1992). Named *Araripebelostomum martinsnetoi* it is considered to belong to the subfamily Belostomatinae. Zamboni (2001) described a late nymphal stage of a belostomatid from the Crato as *Neponymphes*, but it is probably congeneric with *Araripebelostomum* Nel and Paicheler, 1992 and is similar to the belostomatid figured by Grimaldi and Maisey (1990). Zamboni (2001) described a second belostomatid from the Crato Formation, *Paranoika placida* Zamboni,

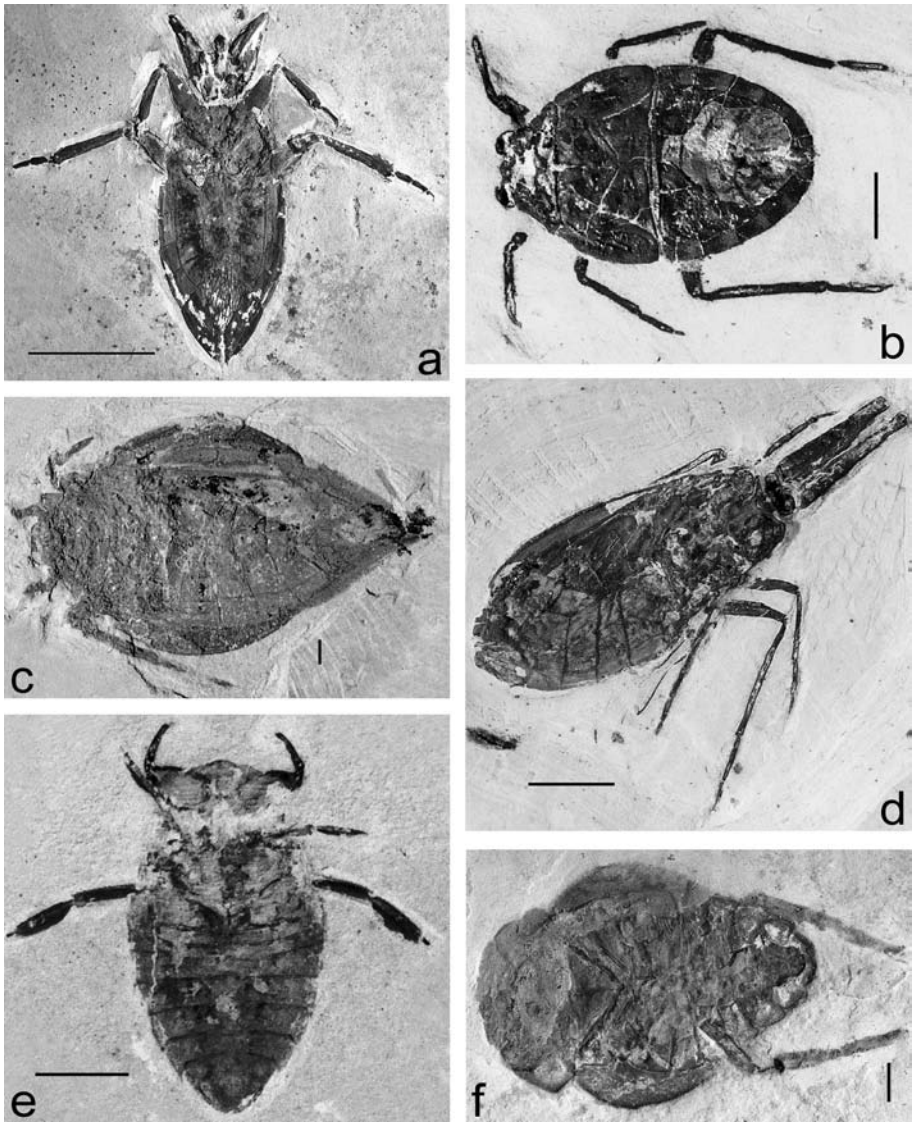

Fig. 11.54. Crato Formation Heteroptera: (a) Belostomatidae, B122 SMF; scale bar, 15 mm; (b) Belostomatidae larva, SMNS 66563; scale bar, 2 mm; (c) Belostomatidae, new species, F104/G81 coll. MSF; scale bar, 2 mm; (d) Nepidae, SMNS 66380; scale bar, 5 mm; (e) Naucoridae, G58 coll. MSF; scale bar, 5 mm; (f) Naucoridae, new species, SMNS 66377; scale bar, 5 mm.

Martins-Neto and Popov, and placed it in a new family †Paranoikidae. However, *Paranoika placida* clearly belongs with the Belostomatidae and should be placed in the subfamily Belostomatinae. Moreover, one cannot exclude that this belostomatid also belongs in *Araripebelostomum*. Consequently, the family Paranoikidae must be considered as a junior synonym of Belostomatidae. Just recently Nel and Waller

(2006) described *Lethocerus vetus* as one of the oldest representatives of the Recent subfamily Lethocerinae from the Crato Formation, which is also found in the Codo formation and seems to have been rather common.

Nepidae: waterscorpions

Several specimens of the family Nepidae have been found in the Crato Formation, for example in the collections of MNB and SMNS in Germany (Figure 11.54d), but none have been described yet.

Naucoridae: creeping water bugs

The Naucoridae (Figures 11.54e and f), like Belostomatidae, are also one of the oldest and widespread groups of water bugs. They appear first in the Upper Triassic deposits of Australia (Tillyard, 1922), North America (Olsen *et al.*, 1978), Central Asia (Kazakhstan and Kirghizia) and Eastern Europe (Ukraine), and can be among the most common water bugs in several Cretaceous sites (e.g. the Gurvan-eren Formation in West Mongolia contains abundant nymphs and adults of the naucoroid *Mongolonecta indistincta* Popov; 1986). Naucoroids account for about 80% of heteropteran specimens in the Lower Cretaceous Purbeck Limestone Group (southern England), although dominated by one or two common species (Popov *et al*., 1994).

Santos (1971) described 11 specimens of naucoroid bugs from the Lower Cretaceous (Aptian) Areado Formation of Minas Gerais, Brazil, as *Saucrolus silvai* Santos, 1971, establishing for them a new monotypic family †Saucrolidae which was tentatively placed in Crustacea *incertae sedis*. The taxon was later transferred to the Coleoptera (Martins-Neto, 1999a) and then to the Heteroptera as superfamily Naucoroidea, family *incertae sedis* (Martins-Neto, 2001a). As a result of these systematic changes the †Saucrolidae can be considered as a synonym of Naucoridae. Later, two more naucorid bugs were described from the Crato Formation as *Cratocora crassa* (Figure 11.57c) and *Cratopelocoris carpinteroi* (Figure 11.57e) by Ruf *et al*. (2005).

Notonectidae: backswimmers

Notonectidae (Figure 11.55a), or backswimmers, from the Crato and Codo Formations can be assigned to the recent subfamily Notonectinae and are very similar to the notonectids *Canteronecta irajai* Mazoni, 1985, from the Lower Cretaceous of Argentina (La Cantero Formation; San Luis Province) and to species of the genus *Clypostemma*, which is widespread in the Lower Cretaceous of East Asia (East Siberia, Mongolia and China). This similarity of the notonectid from the Crato Formation and that from *C. irajai* Mazoni had previously been suggested by Grimaldi and Maisey (1990). Examining the photographs of type material of *C. irajai* (Mazzoni and Hünicken, 1984), one can notice that part of the type specimens seems to belong to Notonectidae and the other part to Naucoridae.

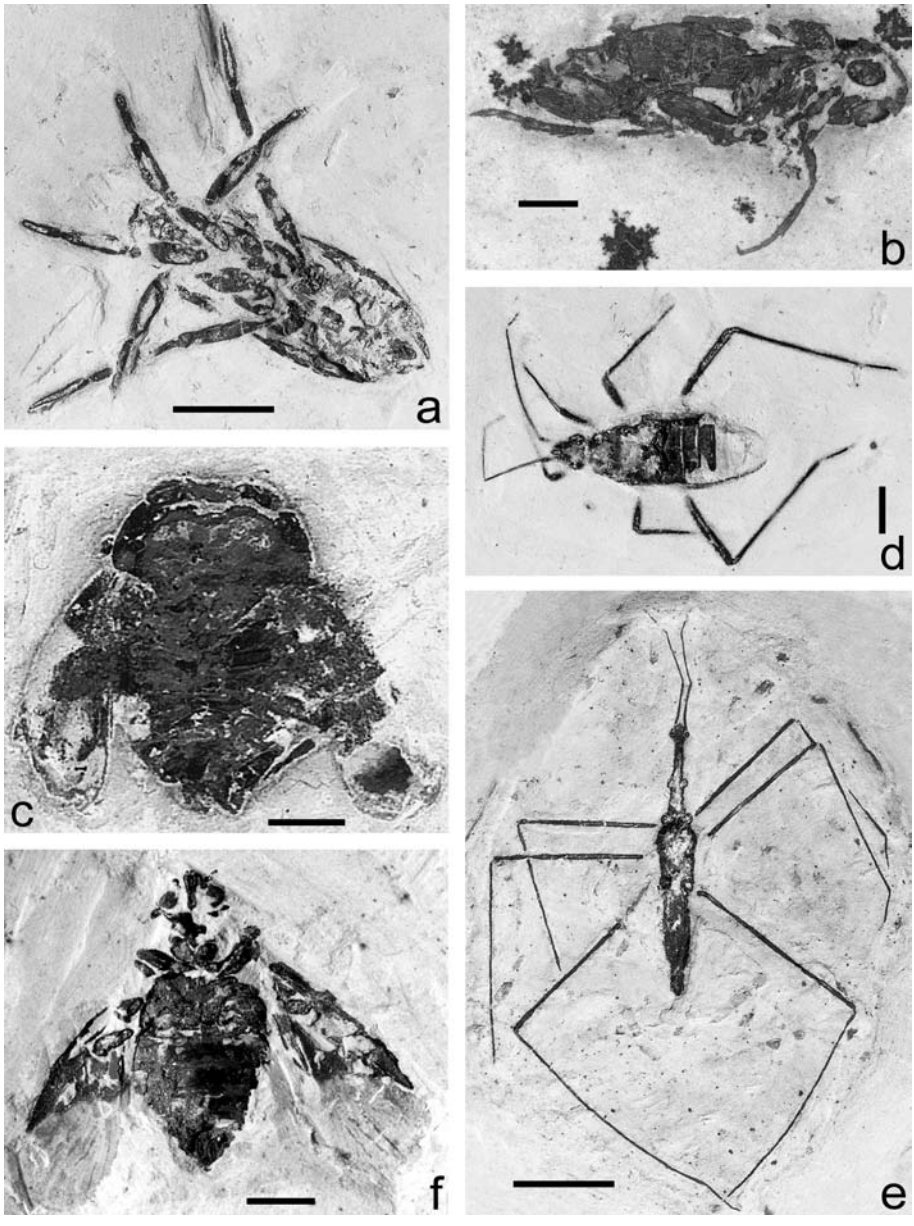

Fig. 11.55. Crato Formation Heteroptera: (a) Notonectidae, SMNS 66382; scale bar, 5mm; (b) Corixidae? (or Notonectidae or Cicadomorpha), SMNS 66436; scale bar, 1 mm; (c) Gelastocoridae, *Cratonerthra estevezae*, holotype SMNS 65416; scale bar, 2 mm; (d) Mesovellidae or Archegocimidae, SMNS 66371 scale bar, 2 mm; (e) Hydrometridae, SMNS 64654; scale bar, 5 mm; (f) Pachymerididae, SMNS 66359; scale bar, 2 mm.

Corixidae: water boatmen

Corixidae (Figure 11.55b), or water boatmen, are cicada-like water bugs that mostly feed on algae. They are quite rare in the Lower Cretaceous of Brazil with only a few (three or four) undescribed specimens known. Initial examination suggests that the Crato corixiids are similar to *Rhomboidella popovi* Mazzoni and Hünicken, 1987 from the Lower Cretaceous La Cantera Formation of Argentina. Elsewhere Corixidae are quite common among late Mesozoic entomofaunas, especially in Western Europe (mainly in Spain), Siberia, Mongolia and China, where they reach their greatest taxonomic diversity in the Late Jurassic to Lower Cretaceous.

Most late Mesozoic fossil corixids belong in the subfamily †Velocorixinae and the Recent plesiomorphic subfamily Diaprepocorinae, of which Recent representatives are only known from South Australia and New Zealand (Andersen and Weir, 2004). It is possible that some members of the Diaprepocorinae belong to the Recent subfamily Micronectinae, as the Recent Neotropical genus *Tenagobia* is widespread in the Western Hemisphere. Fossil micronectins are also known from the Oligocene Tremembé Formation, São Paulo State, Brazil (Martins-Neto, 1998e), and are similar to *Tenagobia*.

Gelastocoridae: toad bugs

Littoral nepomorphan bugs are represented in the Crato Formation by the Gelastocoridae, or toad bugs, which are quite typical, although never numerous, for the Lower Cretaceous of South America (Brazil and Argentina). Two species, *Cratonerthra corinthiana* (Figure 11.57d) and *Cratonerthra estevezae* (Figures 11.55c and 11.57f) were described by Ruf *et al*. (2005) and placed in the gelastocorid subfamily Nerthrinae. They also described the new genus and species *Pseudonerthra gigantea* for which they erected the new family †Pseudonerthridae that seems to be the sister group of Gelastocoridae.

Rumbucher (1995: 54–55, figure 6) copied from Maisey (1991) a figure of a fossil gelastocorid bug from the Crato Formation that he erroneously identified as myrmelionid 'antlion' larva.

Gerromorpha and Leptopodomorpha (Amphibicorisae): amphibic shore bugs

This is a relatively diverse group of bugs ($\approx$ 1,860 species in eight Recent families) that includes the well-known pond skaters. All inhabit aquatic environments, where they can often be found walking on the surface film. All are predatory, and some are found in marine environments (Grimaldi and Engel, 2005). Contrary to established opinion gerromorphan bugs are not so rare in the Mesozoic. *Engynabis tenuis*

Bode from the Lower Jurassic, Toarcian, Posidonia Shales of northern Germany is possibly the oldest representative, and is undoubtedly a member of Mesoveliidae.

Three of the Recent families occur in the Late Jurassic and Early Cretaceous; Hydrometridae (water measurers), Mesoveliidae (water treaders) and Veliidae (riffle bugs; Andersen, 1998). Mesoveliids are quite numerous in the Upper Jurassic of Kazakhstan, *Karanabis kititshenkoi* B.-M. (Becker-Migdisova and Popov, 1963) in the Lower Cretaceous of East Siberia and Mongolia, and in the Lower Cretaceous of Victoria (Australia), *Duncanovelia extensa* Jell and Dunc. (Jell and Duncan, 1986; Grimaldi and Engel, 2005: figure 8.65). Gerridae (water striders) are known from Tertiary amber, but are still completely unknown from the Mesozoic.

The first Gerromorpha to be formally described was the hydrometrid (three specimens), *Cretaceometra brasiliensis* Nel and Popov, 2000. A second Crato hydrometrid, *Incertametra santanensis* (four specimens; Figure 11.58), was described by Goodwyn (2002), who also figured three specimens as Hydrometridae *indet*. (gen. et sp. nor.; Figure 11.55e) and also one as *Cretaceometra* cf. *brasiliensis*. Most probably *Cretaceometra* and *Incertametra* are congeneric, the few small differences simply reflecting natural variation.

A specimen figured by Grimaldi and Maisey (1990: figure 1D), denoted as 'Gerromorpha?', appears to belong to the family Veliidae (riffle bugs), whose representatives are widespread elsewhere, including the Cretaceous of the Kazakhstan, Mongolia and China.

Fossil bugs very similar to the gerromorphan family Mesoveliidae and/or the leptopodomorphan family †Archegocimicidae (Figure 11.55d) occur frequently in the Crato Formation, but are still undescribed.

Suborders Pentatomomorpha and Cimicomorpha (Geocorisae): terrestrial bugs

The terrestrial Heteroptera are very diverse and numerous among true bugs. The lygaeoid family Pachymeridiidae (Figure 11.55f), presumably basal for the Pentatomomorpha, is one of the most abundant and widespread groups in Mesozoic faunas, especially in the Late Jurassic and Early Cretaceous. Most have been described from the Lower Cretaceous of Mongolia (Popov, 1986) and Siberia (Popov, 1990) but several have been reported from the Lower Jurassic of Germany (Handlirsch, 1925, 1939; Bode, 1953). However, the pentatomomorph bugs are one of the least-studied heteropterans of the Early Cretaceous of Brazil. A pachymeridiid was described from the Crato Formation, *Cratocoris shevchenkoae* Martins-Neto, Popov and Zamboni, 1999 (Figures 11.57a and b), and placed in the Coreoidea as family uncertain. Several specimens of the coreoid families Alydidae and Coreidae (*sensu lato*) have also been discovered in the Crato Formation (Figures 11.56a and b), but are as yet undescribed.

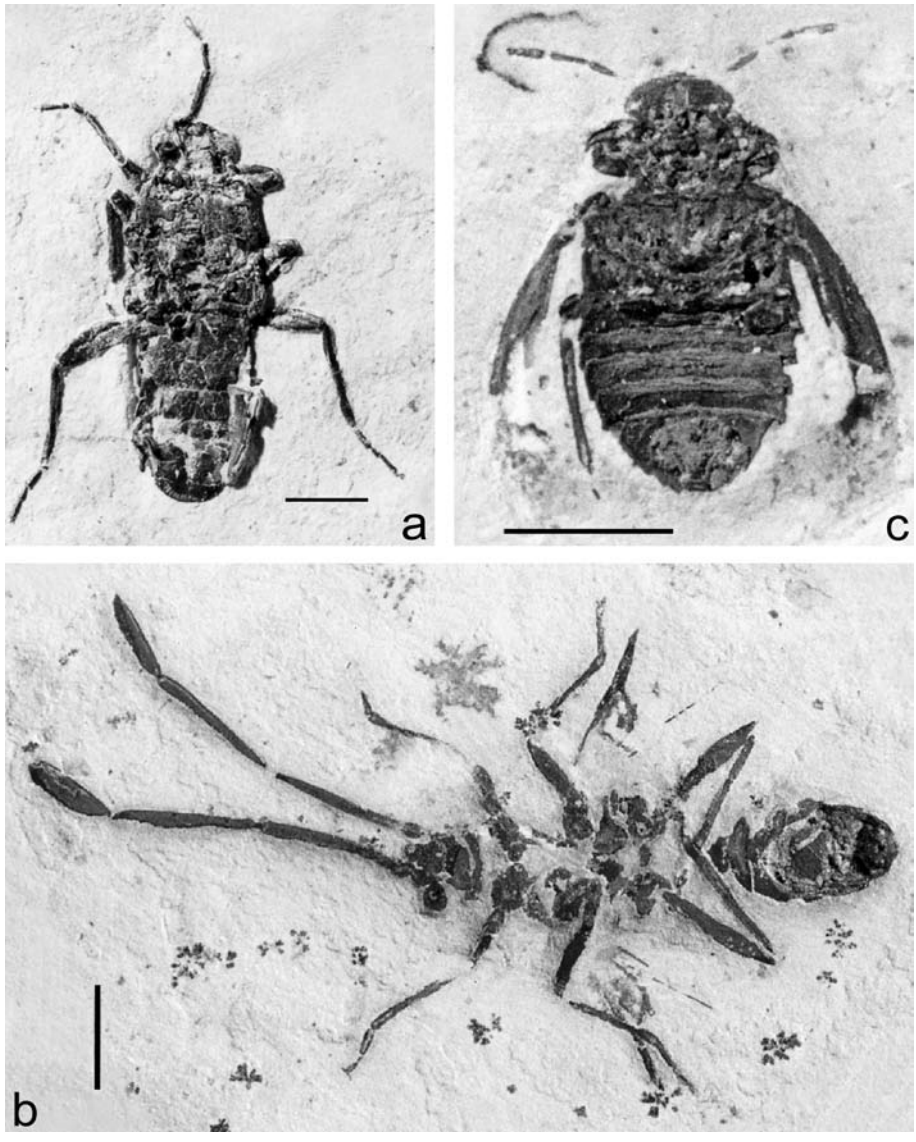

Fig. 11.56. Crato Formation Heteroptera: (a) Coreidae, SMNS 66360; (b) Coreidae, SMNS 66365; (c) Cydnoidea, SMNS 66357. Scale bars, 2 mm.

Another pentatomomorphan bug from the Crato Formation belongs to the peculiar Recent family Aradidae whose recent representatives are distributed all over the World and are mostly connected with tree bark. The Crato specimen appears to belong in the modern subfamily Mezirinae.

Most fossil aradids can be assigned to the recent genus *Aradu*s (Kormilev and Popov, 1989) and are known from the Late Jurassic of Kazakhstan, the later Early

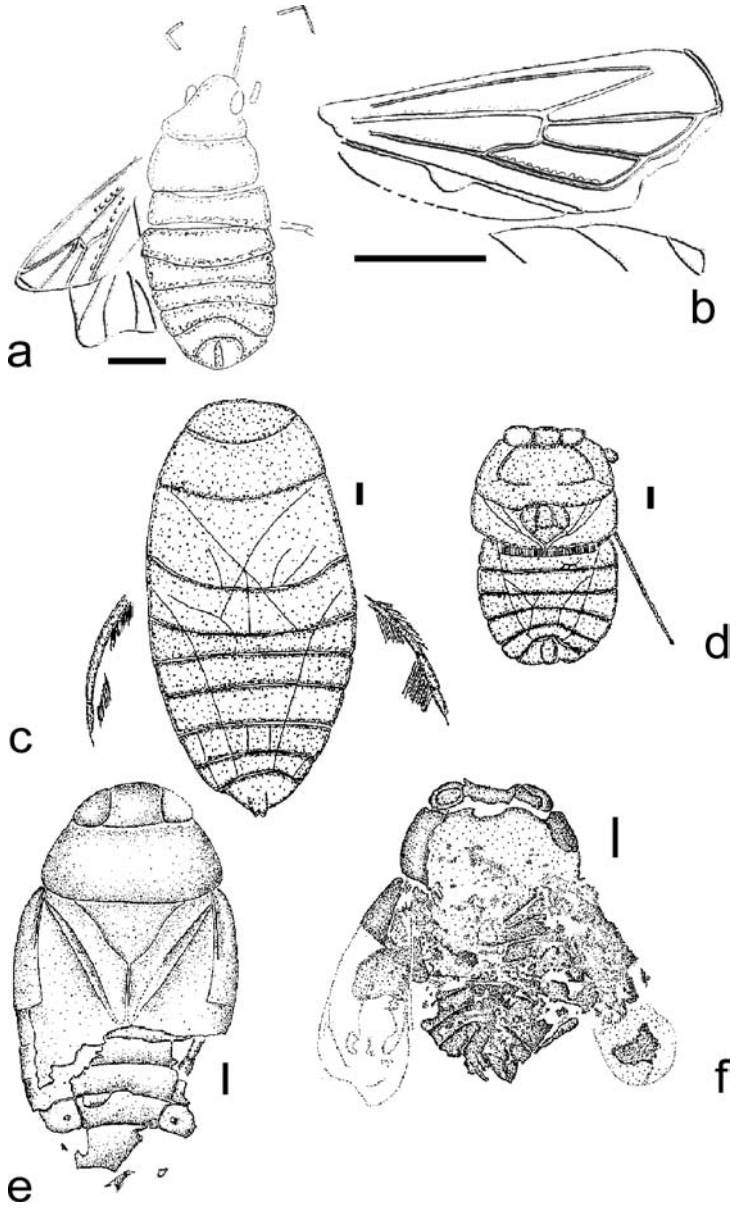

Fig. 11.57. Crato Formation Heteroptera: (a) *Cratocoris shevchenkoae* Martin-Neto, Popov and Zamboni, 1999, holotype, RGMN-T032; (b) hemi elytron of specimen in a; (c) *Cratocora crassa* Martins-Neto, 2005, holotype, MPFT-1–026; (d) *Cratonerthra corinthiana* Martins-Neto, 2005, holotype, MPFT-1–027; (e) *Cratopelocoris carpinteroi* Lopez Ruf and Perez Goodwyn, 2005, holotype, RGMN 499; (f) *Cratonerthra estevezae* Lopez Ruf and Perez Goodwyn, 2005, holotype, SMNS 65416. Scale bars, 1 mm. Illustrations (a, b) after Martin-Neto *et al.* (1999); (c–f) after Ruf *et al.* (2005).

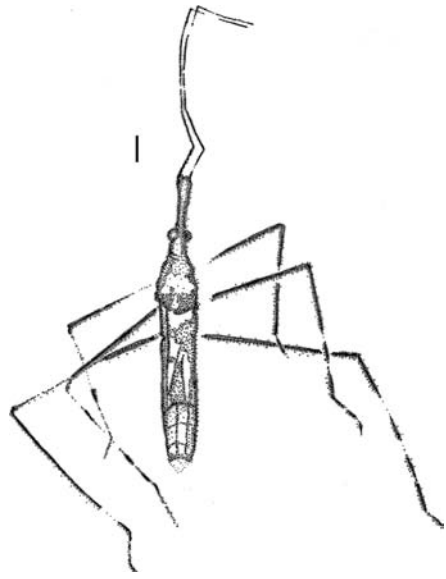

Fig. 11.58. Crato Formation Hydrometridae: *Incertametra santanensis* Goodwyn, 2002, holotype SMNS 64652; scale bar, 1 mm. After Goodwyn (2002).

Cretaceous of Central Mongolia (Aptian, Bon-Tsagan) Popov, 1986, and from the Late Cretaceous of north-east Siberia (Santonian, Magadan district). The Cydnoidea (Figure 11.56c) have already been discussed above. Unfortunately, a great number of terrestrial bugs from the Crato Formation have yet to be evaluated.

11.16 Neuropterida: snakeflies, dobsonflies and lacewings

Rafael G. Martins-Neto, Sam W. Heads and Günter Bechly

The Neuropterida, instantly recognizable by their proportionally large, hyaline wings and net-like venation, are one of the most basal groups of Holometabola and comprise the Raphidioptera (snakeflies), Megaloptera (dobsonflies and alderflies) and Neuroptera (lacewings and antlions). Aside from their typically busy venation, the Neuropterida are characterized by the fusion of the gonoplacs in the ovipositor, a medially divided metapostnotum, a proventriculus with an unpaired diverticulum and the first abdominal tergum having a caudally bifid longitudinal sulcus (Kristensen, 1991; Grimaldi and Engel, 2005). Although neuropterid monophyly is well established, the internal relationships of the group have proved difficult to resolve and remain controversial (Grimaldi and Engel, 2005). All three orders are represented in the Crato Formation, although many of the taxa (particularly the