standards of scientific work, and often fail to satisfy the criteria of the International Rules of Zoological Nomenclature (ICZN). Numerous taxa have been established with inadequate diagnoses, creating *nomina dubia*, and many are in diploma and PhD theses, and technically are invalid, but nevertheless cited by subsequent workers. Many species names have been established in conference proceedings abstracts with the creation of *nomina nuda* and on several occasions different spellings are used from the original description by the same author. There are many incorrect citations of authorship and year of publication, as well several taxa erected on holotypes in private collections. The result is a plethora of dubiously established species and considerable taxonomic confusion.

11.2 Apterygota: primarily wingless insects

Arnold H. Staniczek and Günter Bechly

There are several small-taxa at the base of the Hexapoda lacking wings that formerly were referred to as 'Apterygota', until Hennig (1953) recognized its paraphyly with respect to the winged insects, the Pterygota. Usually five Recent higher taxa are recognized among apterygotes: Collembola (springtails), Protura, Diplura, Archaeognatha (bristletails) and Zygentoma (silverfish and firebrats), the former three often united as the Entognatha, as their mouthparts are enclosed within a gnathal pouch. Recently it has been proposed that Diplura are more closely related to the insects than to Protura and Collembola (Bitsch and Bitsch, 2000). It is generally accepted that Archaeognatha and Zygentoma have closer phylogenetic affinities to the Pterygota than to the entognathous taxa. All of these taxa, however, share a number of plesiomorphic characters such as the retention of abdominal leglets and moulting even in the adult stage.

In the Crato Formation, so far only one species each of Diplura (two specimens) and Zygentoma (two specimens) have been discovered (Figure 11.1; Plates 7a and b). The other orders are certainly to be expected in the Mesozoic of South America as well, but probably have a very low preservation potential due to a combination of their delicate anatomy, tiny size and cryptic lifestyle as soil-dwelling organisms.

Order Diplura: diplurans

Diplura is a globally distributed taxon comprising about 850 Recent species. They are generally classified into two different lineages, the Campodeomorpha (Rhabdura) and Japygomorpha (Dicellurata), which have a rather different appearance. Campodeomorph diplurans have long slender legs that enable fast movement and high agility, whereas japygomorphs are better adapted for a life within soil

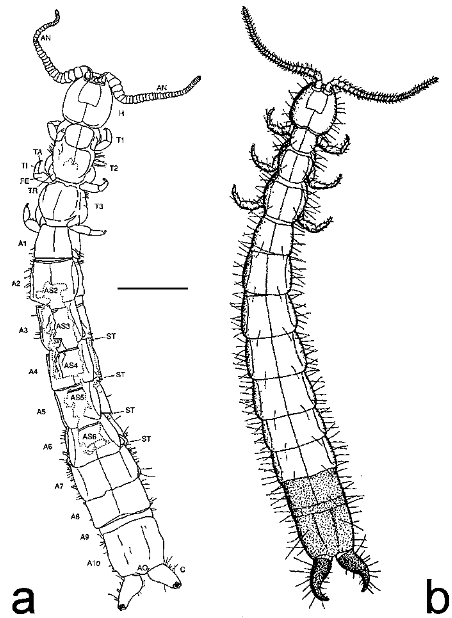

Fig. 11.1. Crato Formation dipluran: *Ferrojapyx vivax* Wilson and Martill, 2001; (a) interpretative diagram of holotype SMNS 64276; (b) restoration of the animal in life. After Wilson and Martill (2001); reproduced with kind permission of the Palaeontological Association.

interstices. While the campodeomorphs have filiform cerci consisting of many segments, the cerci of japygomorphs are transformed into unsegmented forceps. Both groups, however, are cryptozoic and confined to soil. Campodeiform diplurans are mostly omnivorous or herbivorous animals, which feed on a variety of plant matter, often rotten leaves. The japygomorphs are predominantly predators and feed on other soil-dwelling arthropods such as other entognathous insects, myriapods and mites. They generally catch their prey by grasping it with the abdominal forceps. All diplurans are small and soft-bodied hexapods of whitish colour that generally only reach a body size of a few millimetres, but some japygomorphs may achieve a larger body size, of up to 6 cm. The Campodeomorpha have long filiform antennae with up to 70 segments. As in all primarily apterous hexapods, all antennal segments are equipped with intrinsic muscles. The antennae of japygomorphs are comparably short and stout, and in some they even resemble a telescope with retractable segments.

The head of diplurans is dorsoventrally flattened and bears prognathous mouthparts that lie within a single gnathal pouch. The internal head skeleton, the tentorium, is lacking. The maxillae are specifically interlocked with the lateral lobes of the hypopharynx and the mandible of campodeomorph diplurans bears a mobile lobe, the prostheca. All Recent diplurans lack compound eyes, but the entire body is equipped with a variety of sensory hairs. Their abdomen is composed of 10 segments, the anterior seven bearing paired leglets and often also ventral eversible vesicles that are actively used to absorb water.

Systematics and phylogeny

The phylogenetic affinities of the Diplura remain controversial, and although their monophyly has been challenged recently, the unique interlocking of the maxillae with the hypopharyngeal superlinguae, uniquely arranged leg muscles and leg pivots, the modified position of the gonopore, and the reduced eyes, mandibular molar and tentorium clearly demonstrate their monophyly (Kristensen, 1998). However, the sister group of Diplura remains debatable. Most recent authors unite Diplura and Ellipura (Collembola+Protura) in the Entognatha because the mouthparts of entognatheous hexapods lie with a gnathal pouch formed by the lateral head capsule (Hennig, 1953). On the other hand, some authors interpret filamentous cerci, an epimorphous development (the larva hatches with the final number of abdominal segments) and the 9+9+2 axonem sperm pattern as derived characters of Diplura+Insecta, the so-called Cercophora. These authors consequently assume a parallel development of entognatheous mouthparts in Diplura and Ellipura (e.g. Koch, 1997).

The extant Diplura are divided into the Rhabdura (Campodeomorpha) with two superfamilies, and the Dicellurata (Japygomorpha) with only one superfamily. The Campodeoidea comprise about 300 species and include the Procampodeidae and the Campodeidae. The Projapygoidea include only some 20 species in three families; among these the Projapygidae and Anajapygidae. The Dicellurata are represented by the superfamily Japygoidea that includes five families, among these the Japygidae, Parajapygidae and Dinjapygidae.

Evolution

Judging from their phylogenetic position as basal hexapods Diplura must have already originated by the Early Devonian, but unfortunately there are no fossils from this period that could shed light on their early evolution. The enigmatic *Testajapyx thomasi* from the Upper Carboniferous of Mazon Creek of Illinois (Kukalová-Peck, 1987) bears well-developed compound eyes, long maxillary and labial palps, and multi-articulated abdominal leglets. Its abdomen bears the typical forceps of the Rhabdura. If its description and assignment is correct, the reduction of eyes, palps and abdominal leglets in Diplura has to have been achieved independently within Rhabdura and Dicellurata.

Fossil record

The fossil record of Diplura is extremely poor. Except for the controversial *Testajapyx thomasi* there is only one Mesozoic record of Japygoidea from the Lower Cretaceous of Brazil (Wilson and Martill, 2001). A few other diplurans are recorded from Eocene Baltic amber (Weitschat and Wichard, 1998), the Pliocene of Arizona (Pierce, 1950, 1951), and from Miocene Dominican amber (Grimaldi and Engel, 2005). Unfortunately, the scarcity of fossil diplurans does not allow any substantial conclusions regarding their palaeobiology.

Crato Formation fossils

Ferrojapyx vivax (Plate 7b; Figure 11.1) is the sole japygoid described from the Crato Formation (Wilson and Martill, 2001). Due to its mode of preservation, insufficient features of *F. vivax* can be seen, preventing its attribution to any of the Recent families of Japygoidea.

Japygoidea

Family *incertae sedis*

Ferrojapyx vivax Wilson & Martill, 2001

Material: holotype SMNS 64276 (Plate 7b; Figure 11.1); specimen MB.1999.9 MB. J.2017 at MNB.

Diagnosis: body length 17 mm; antennae with 40 segments; abdominal tergites 1–8 with median suture, abdominal tergite 9 significantly shorter, and abdominal tergite 10 significantly longer with pair of paramedian grooves; abdominal styli conical; forcipate cerci with similar arms, each with a curved inner margin and lacking obvious denticles.

Order Zygentoma: silverfishes and firebrats

The Zygentoma comprise only about 470 Recent species, all of which are small, ranging between 1.5 and 2 mm in body length. Their general appearance is rather uniform, with a dorsovenrally flattened wingless body, long antennae and three long terminal appendages. Some species, such as the well-known silverfish *Lepisma saccharina* and the firebrat *Thermobia domestica*, are cosmopolitan. Others, such as the relic *Tricholepidion gertschi* from California, have a very restricted distribution. It is generally accepted that the Zygentoma form the sister group of pterygote insects. They are herbivorous, feeding mainly on algae and fungi. Their body is mostly covered with scales and the head bears orthognathous mouthparts with dicondylous mandibles. Compound eyes and ocelli are largely reduced or entirely lacking and the abdomen bears styli and coxal vesicles on different abdominal segments.

Systematics and phylogeny

The Zygentoma are often considered to be monophyletic, although *T. gertschi* retains many plesiomorphic features not otherwise found in the remaining taxa. Putative shared derived characters such as a special mode of cleavage (but not confirmed in *Tricholepidion*), a special mode of sperm deposit, and a unique specialized articulation between the cercal base and tergum X however support its monophyly (Koch, 2003). Other characters, including the loose dicondylous mandible, the loss of hypopharyngeal superlinguae, and the fused tentorium are either groundplan characters of insects, reductions or are absent in the basal taxon *Tricholepidion* (Staniczek, 2000).

Zygentoma are classified into five families; Lepidothrichidae, Nicoletiidae, Protrinemuridae, Maindroniidae and Lepismatidae. The Zygentoma generally retain an arrangement of mandibular musculature similar to that seen in primitive Pterygota. Additionally, *T. gertschi* retains a zygomatic mandibular muscle. Anterior and posterior tentorial arms are generally separated from each other, but in the Maindroniidae there is a fused tentorium, as in Pterygota. If the Zygentoma prove to be monophyletic, the Lepidothrichidae would be the sister group of the remaining Zygentoma. In this case, the changes in mandibular musculature and tentorium would have occurred twice within the Zygentoma and in the Pterygota, respectively.

Evolution

The Recent relic silverfish *T. gertschi* (Wygodzinsky, 1961) shows that many of the characters generally attributed to the Zygentoma evolved within the order, but their scarce fossil record unfortunately provides few clues to the early events in their evolution. As in Diplura, the meagre fossil record allows few conclusions regarding the palaeobiology of Zygentoma.

Fossil record

Except for a single Mesozoic record (Sturm, 1998), the Zygentoma are known mostly from Tertiary amber (Mendes, 1997a, 1998a; Sturm and Mendes, 1998; Weitschat and Wichard, 1998; Sturm and Machida, 2001). Even fossil Lepidothrichidae are known only from Baltic amber (Silvestri, 1912), but clearly the splitting of the different higher taxa within Zygentoma had already occurred by the Caenozoic. There are some other early records of insects that have been tentatively assigned to Zygentoma, but their state of preservation does not allow a definite assignment (Shear *et al*., 1984; Kukalová-Peck, 1987; Kluge, 1996).

Crato fossils

The first records of Zygentoma from the Crato Formation are those of Bechly (1998a). Two specimens of Lepismatidae were described by Sturm (1998). Since then, a further undescribed specimen (Plate 7a) was found in the Stuttgart (SMNS) collection. Due to their relatively poor state of preservation, neither a determination of the sex, nor a formal taxonomic description as a new species, has been possible. Consequently, these specimens have only been determined as "Lepismatidae gen. spec. 'Araripe'" by Sturm (1998).

Lepismatidae

Lepismatidae gen. spec. 'Araripe' Sturm, 1998

Material: no. B 99 at SMF; no 1998 III/4 at BSPGM; and no. SMNS 66535 (Plate a). A fourth specimen without number from AMNH was figured by Grimaldi and Engel (2005: 152, figure 5.6).

Diagnosis: body 10.5–14 mm long and 3–4 mm wide; head orthognathous; filiform antennae 10.5–13.5 mm long; filiform cerci (12–18 mm long, the only 8.8-mm-long cerci in specimen B 99 are obviously broken off) and terminal filum (13–21 mm long), all provided with setae; wingless; body robust; legs stout with flattened, broad and oval-shaped coxae.

11.3 Persisting-type stem group Ephemeroptera

Rainer Willmann

Organisms do not evolve at equal rates. While many Recent taxa are of entirely modern appearance, others are plesiomorphic in many respects, and in some insects plesiomorphic structures determine their body plan. This is not necessarily related to the age of the respective taxa, but of course some taxa, be it species or large species groups, have become separated from their sister group only recently, while others are very old and have changed little, even over several tens of millions of years. In both cases the latter types of organism have been called living fossils, a term introduced by Charles Darwin. However, such types have lived at any time in the history of life. As the term living fossil cannot well be applied to relatively plesiomorphic fossil species or species groups, the term persisting type, first introduced by Huxley, may be applied. Such types belonging to ephemeropteroid insects in its widest sense were in existence in the Lower Cretaceous of Brazil (Figures 11.2 and 11.3; Plates 7c–h).

Numerous mayflies of the crown group Ephemeroptera (about 3,100 described Recent species) have been described from Triassic, Jurassic, Cretaceous and Cenozoic strata including the Crato Formation (see review by McCafferty, 1990). No

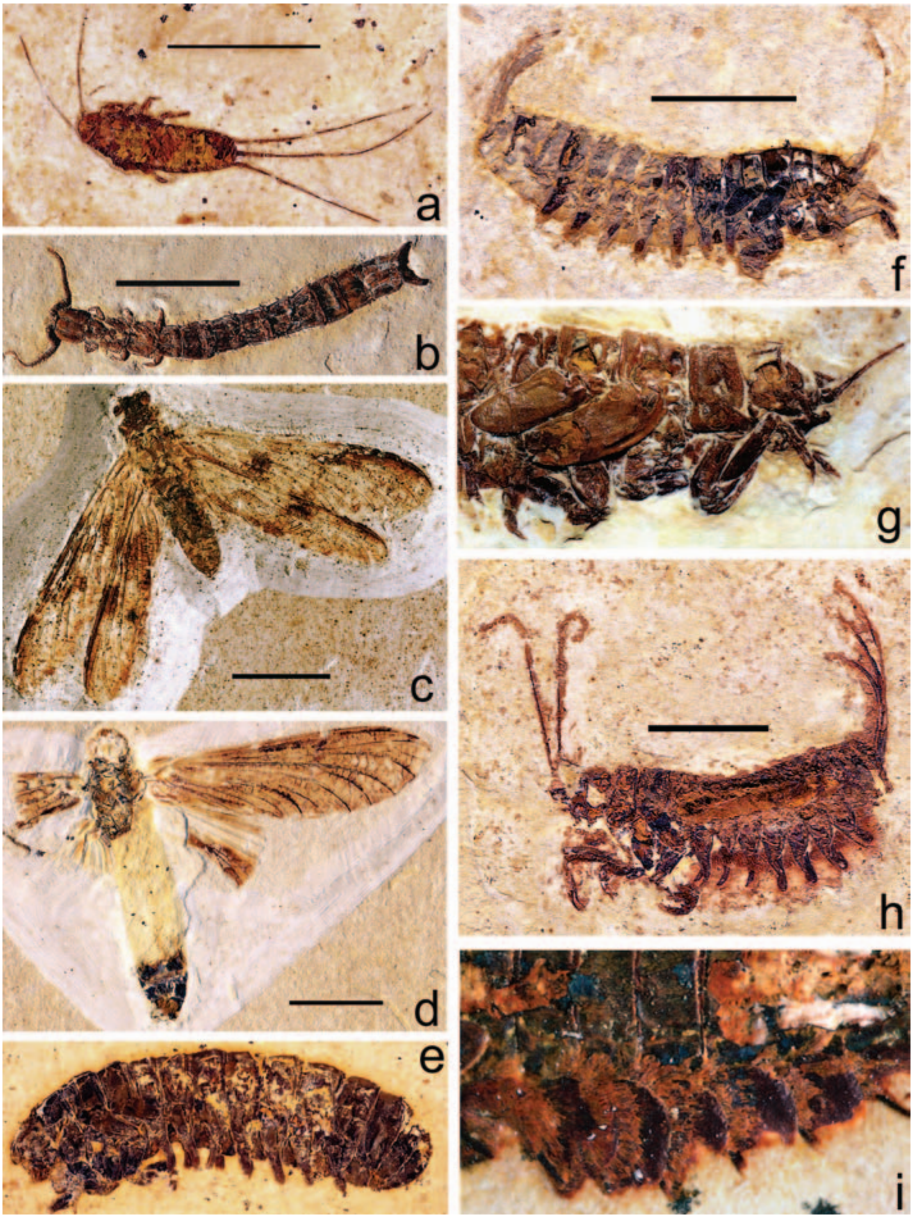

Plate 7. Crato insects: (a) Zygentoma, Lepismatidae gen. et sp. nov., SMNS 66535; (b) Diplura, Japygoidea, *Ferrojapyx vivax* Wilson and Martill, holotype, SMNS 64276; (c) *Cretereisma antiqua* sp. nov., holotype SMNS 66546 (Photo B. Schuster); (d) *Cretereisma schwickertorum* sp. nov., holotype SMNS 66598, ventral aspect; (e) *Cretereisma* sp., nymph, SMNS 66673; (f) *Cretereisma* sp., nymph, SMNS 66547; (g) *Cretereisma* sp., nymph no. 512 MURJ; (h) *Cretereisma* sp., nymph, SMNS 66599; (i) Ephemeroptera, Hexagenitidae, *Protoligoneuria limai*, larval gills with tufts, MSF Q4. Scale bars, 10 mm.