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Insects of the Crato Formation

11.1 Introduction

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Insects are by far the most diverse group of multicellular organisms on our planet. Of about 1,625,000 described species of prokaryotes, protoctists, fungi, plants and animals, more than 1 million is represented by arthropods, of which insects constitute the largest group with about 854,000 described species. The estimations of the number of still undescribed species, especially in the vanishing tropical rainforests, are ranging from 2 million to 80 million species! The most species-rich groups within insects are the holometabolous orders Coleoptera (beetles), Hymenoptera (ants, wasps and bees), Diptera (mosquitoes and flies) and Lepidoptera (moths and butterflies). Among the hemimetabolous orders, which lack a pupal stage in their ontogenetic development, the Hemiptera (aphids, scale insects, cicadas and bugs) are the largest group, while all other insect orders have much fewer species.

Even though relatively small animals, the extremely large number of individuals makes insects a very significant part of the total terrestrial biomass in many biotopes. For example, in tropical rainforests, the ants and termites have a higher total biomass than all the vertebrates combined.

Insects are not only diverse in terms of species number and number of individuals, but also in their astonishing anatomical and ecological variability. Insects populate nearly every available habitat on the planet, except for the open seas and the frozen polar regions. They live under water, on the water surface, in soil, in wood, in deserts and in forests, in arid and humid regions, in mountains and in caves, and they were the first organisms to conquer the skies.

Insects have developed appendages for all kinds of locomotion, from wings for flight, to burrowing legs for digging, strong hind legs for jumping, predatorial legs for catching prey, cursorial legs for running on the ground and climbing in vegetation, and specialized legs for walking on the water surface or for diving and swimming. Even subaqueous jet propulsion is found in some dragonfly larvae.

They have developed an equal diversity of mouthparts that allows nearly any kind of feeding, from chewing mouthparts for herbivory and carnivory or omnivory, licking mouth parts for feeding on nectar and pollen, to piercing mouth parts for sucking plant juices or the blood of other animals.

Insects are also masters of camouflage and no other group of organisms has developed so many and striking cases of mimesis and mimicry. Even communication with sounds and voices is not the exclusive domain of vertebrates, with stridulation independently developed in unrelated insect groups from cicadas (Hemiptera) and orthopterans (Ensifera and Caelifera) to longhorn beetles (Cerambycidae). There is even an aquatic larva, the Japanese relict dragonfly *Epiophlebia superstes*, that can utter a sound.

Finally, some insect groups, especially among the termites, ants and bees, alongside humans, have developed eusocial states with distinct castes and tremendous ‘cultural achievements’. These include war campaigns, mass defensive attacks, enslavement of other species, the cultivation of fungi, animal husbandry, and construction of buildings that are a million times bigger than themselves and made comfortable with sophisticated climatization systems. All of this was achieved in animals with tiny brains and their skeletons on the outside. Insects are truly remarkable animals.

Insect evolution

The enormous diversity and evolutionary success of the insects can perhaps be attributed to three major evolutionary innovations: moving from water to dry land, development of wings and flight and an adaptive radiation in co-evolution with flowering plants.

Contrary to earlier theories that insects are most closely related to terrestrial myriapods, new molecular and ontogenetic evidence suggests that insects are *just* terrestrial crustaceans of remipedian and malacostracan affinity (Richter, 2002; Fanenbruck *et al.*, 2004). Insects are thus derived from marine crustacean-like arthropods that already had an exoskeleton, walking limbs, compound eyes and sensory antennae. These features were excellent pre-adaptations for the first evolutionary leap, the conquest of the land in the late Silurian and Lower Devonian (about 430 mya). The oldest known insects were small primarily wingless forms and stem from this era, like the famous fossil springtail *Rhyniella praecursor* from the Devonian Rhynie cherts of Scotland.

While adapting to a terrestrial lifestyle, the number of legs was reduced to just three pairs, the number of antennae reduced to a single pair, and the mode of reproduction changed from external insemination with liquid sperm under water, to an external insemination with terrestrial deposition of spermatophores. The first terrestrial insect ancestors were probably very small animals capable of breathing through their skin in moist habitats. This method of gaseous exchange paved the way for the later evolutionary development of sophisticated cuticular invaginations (tracheae) as respiratory organs.

The second major evolutionary innovation occurred during the Lower Carboniferous (or perhaps in the Late Devonian), when insects developed wings and conquered the air. This achievement led to the first radiation and increase in diversity and population density of insects, although the biggest evolutionary leap was yet to come. Among the numerous advantages of flight is the ability to escape easily from predators, a greater chance to locate food, suitable habitats or sexual mates and an improved panmixia of the gene pool. Correlated with the evolution of insect flight, some spiders developed the ability to construct complex webs to exploit this new resource of airborne protein. The oldest fossil records of pterygote insects stem from the lower Namurian (about 324 mya) of Germany (*Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996) and the Czech Republic (unnamed Archaeoptera; Prokop *et al.*, 2005). Wings developed either from mobile lateral thoracic gills of aquatic insect larvae, similar to the abdominal gills of modern mayfly larvae, or from originally immobile lateral expansions of the thoracic tergae, known as paranota. Both of these conflicting hypotheses are supported by substantial neontological and palaeontological evidence, so that a final decision is not possible with the current state of knowledge. During the Carboniferous and Permian some winged insects reached tremendous sizes with wing spans of up to 60–75 cm. This era of flying giants ended in the Triassic, perhaps correlating with the appearance of pterosaurs as the first active flying vertebrates to feed on airborne insects. Due to the successive evolution of different flying vertebrates (pterosaurs, birds and bats) it appears that no giant flying insects ever evolved again. Of course, the great Permian mass extinction might also have contributed to the decline of the giant pterygotes.

The third and final great leap in evolution is the remarkable co-evolution of flowering between the flowering plants and some insect groups as their pollinators. This co-evolution started at least as early as the Early Cretaceous, thus exactly at the time that the Crato Formation limestones were deposited. Early modes of this symbiosis were probably rather crude, perhaps similar to the way modern tropical water lilies, *Nymphaea* spp., are pollinated by certain beetles that became enclosed within the flowers at night and literally ransack their floral "prison" in a futile attempt to escape. Later, more sophisticated mechanisms evolved involving highly complex flower organs and specialized mouth parts of their pollinators. In many cases these plants became dependent on a single insect species for pollination, which themselves solely depend on one plant species as a source of food. The most highly evolved mechanisms are found in orchids, which 'betray' their pollinators with flowers that mimic female insects in shape, colour, setation and even the scent of their sexual pheromones. The co-evolution of plants and insects led to the biggest radiation in the evolution of life, which is not only documented by the enormous number of species of flowering plants compared to that of gymnosperms, but also by the fact that precisely those insect orders that are associated with angiosperms belong to the groups with the highest number of species (see above).

This co-evolution seems to have reached a maximum in the beginning of the Caenozoic era, as nearly all fossil insects from Eocene amber more or less equal their Recent relatives, and can often be classified in modern genera. The only significant changes in insect evolution during the Tertiary have been major shifts of biogeographical ranges due to dramatic changes of the climate and vegetation. For example, there are numerous insects found in Baltic amber that are today restricted to tropical forests in Latin America, Africa or Oceania.

The destruction of these tropical forests at an alarming rate of nearly 10,000 m^2/s is the cause a dramatic human-made mass extinction event the likes of which this planet has not seen before. This could even represent the final major event in the evolution of insect diversity, since it is calculated that around 140 species are disappear every single day from our planet.

Insect phylogeny and palaeoentomology

A revolution in insect systematics and phylogenetic research was instigated by German entomologist Willi Hennig (1969), the founder of modern phylogenetic systematics. Numerous subsequent cladistic analyses have greatly expanded our knowledge of the evolutionary relationships of the various insect higher taxa. Especially important has been the rise of molecular research which has led to new insights (some highly surprising) into our understanding of insect interrelationships, for example concerning the sister group of Hexapoda or the relationships of the recently discovered new living insect order Mantophasmatodea. Excellent summaries of the current knowledge of insect phylogeny have been provided by Kristensen (1995) and Grimaldi (2001), and particularly important is the seminal work by Grimaldi and Engel (2005). The first comprehensive treatment of fossil insects was provided by Handlirsch (1906–1908), followed by Rohdendorf (1969; translated into English in 1991), Hennig (1969), Carpenter (1992) and Rasnitsyn and Quicke (2002), and again important analyses of fossil insects are included in Grimaldi and Engel (2005).

Scientific importance of the Crato insects

The limestone quarries of the Crato Formation represent a particularly interesting fossil locality, because not only were they deposited at a time when plant/insect co-evolution was in its early stages, but also these limestones yield both plant and insect fossils in the same strata. This importance is further increased by the fortunate circumstance that many tens of thousands of fossils have been discovered already, representing most orders of insects, and generally with excellent preservation of delicate details, sometimes even of soft tissues or colour pattern (see Chapter 7).

Important collections of Crato Formation insects can be studied in the following institutions:

- Brazil: Sociedad Brasileira de Paleoartropodologia (RGMN) in Ribeirão Preto/São Paulo, Museu de Zoologia in São Paulo; Museu do Paleontologia Santana do Cariri; Centro de Pesquisas Paleontologicas da Chapada do Araripe in Crato.
- USA: American Museum of Natural History (AMNH) in New York.
- Japan: Kitakyushu Museum of Natural History & Human History (KMINH) in Kitakyushu, Tokyo University/National Science Museum (NSMT) in Tokyo, and collection Masayuki Murata (MURJ) in Kyoto (deposited partly at KMNH).
- France: Museum National d'Histoire Naturelle (MNHN) in Paris.
- United Kingdom: Geology Department of the University of Leicester (LEIUG), and Natural History Museum (NHM) in London.
- Germany: Museum für Naturkunde in Berlin (MNB), Bayerische Staatssammlung für Paläontologie und Historische Geologie *BSPGM* in Munich, Naturmuseum Senckenberg (SMF) in Frankfurt, Staatliches Museum für Naturkunde Karlsruhe (SMNK), Staatliches Museum für Naturkunde Stuttgart (SMNS), Jura-Museum Eichstätt (JME), and ms-fossil (MSF) in Sulzbachtal.
- Italy: Museo Civico di Storia Naturale (MCSNM) in Milan.

Until recently there were hardly any fossil insects known from this crucial period of Earth's history, such that Willi Hennig (1969) even commented "Einer der beklagenswertesten Mängel in unseren Kenntnissen der Stammesgeschichte der Insekten ist das fast völlige Fehlen von Fossilfunden aus der Kreide" ["One of the most unfortunate gaps in our knowledge of insect phylogeny is the nearly complete lack of fossils from the Cretaceous"]. Since then numerous localities yielding Cretaceous insects have been discovered, for example in Southern England (Weald), Spain (Sierra de Montsech and Las Hoyas), Commonwealth of Independent States (Magadan, South Kasakhstan and Transbaikals), Western Mongolia, China (Gansu, Hebei, Shandong, Liaoning and Inner Mongolia), Botswana (Orapa), South-west Egypt (Abu Ras), the USA (Fox Hill, Colorado), Australia (Koonwarra, Victoria) and various Cretaceous amber sites from Lebanon, Siberia (Taymyr), Myanmar (Burma), Spain (Alava), France (Besonnais), Canada (Cedar Lake and Medicine

Hat) and the USA (Alaska and New Jersey). These localities provide an exciting opportunity for interesting comparisons of the Cretaceous insect faunas in both the New and Old Worlds, and the southern (Gondwana) and northern (Laurasia) hemispheres. However, none of these localities can match the Crato Formation in the sheer number of fossils, their diversity and their quality of preservation. Consequently, the Crato Formation is considered by palaeoentomologists as one of the most important Mesozoic localities of all for fossil insects.

The first record of insects from the Crato Formation was a mayfly nymph discussed by Costa-Lima (1950) and described by Demoulin (1955). Since then, numerous contributions by various specialists followed and have been summarized by Brito (1984), Schlüter (1990), Grimaldi (1990, 1991), Martill (1993), Bechly (1998a–c), Bechly *et al.* (2001a), Martins-Neto (1991a–d, 1992d, 1996b, 2005a, 2005b), and Grimaldi and Engel (2005).

The missing groups of insects

The number of arthropod taxa from the Crato Formation is impressive: Scorpiones, Uropygi, Amplypygi, Araneae (Orthognatha and Labidognatha), Solifugae, Acari, Ostracoda, Conchostraca, Decapoda and Chilopoda have all been reported from among the non-hexapods. Even a brief glance at this list demonstrates an unusual mix of aquatic and terrestrial forms. In the Hexapoda, the insects, the list is even longer: Diplura, Zygentoma, Ephemeroptera, Odonata, Dermaptera, Mantodea, Blattaria (including Umenocoleoidea), Isoptera, Chresmododea, Phasmatodea, Orthoptera (Ensifera and Caelifera), 'Auchenorrhyncha' (Cicadomorpha and Fulgoromorpha), Coleorrhyncha, Heteroptera, Megaloptera, Raphidioptera, Neuroptera (Planipennia), Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera and Lepidoptera. The most frequent groups are Orthoptera, Blattaria, Hemiptera and Ephemeroptera (larvae of the type *Protoligoneuria*), which together represent more than 80% of the fossil arthropod material based on a study of 3,651 fossil arthropods from the Crato Formation that had not been selected in preference of certain taxa (Bechly, 1998c).

But while the taxa present in the formation suggest an unusual taphocoenosis, the absence of certain groups is also perplexing. Completely missing (so far) are most of the tiny, ground-dwelling or ectoparasitic (often wingless) insect orders (Collembola, Protura, Archaeognatha, Zoraptera, Embioptera, Psocoptera, 'Mallophaga', Thysanoptera, Sternorrhyncha, Anoplura, Siphonaptera and Strepsiptera), but their absence can be relatively easily explained by their cryptic lifestyle and their small size, which makes their fossilization unlikely (however, Martill and Davis (1998) reported putative eggs of lice or mites in a fossil feather from this locality). The same is also true for the absence of the smaller arachnid groups Ricinulei, Palpigradi and Acari (only a single specimen is known), and the myriapod groups Pauropoda, Symphyla and Diplopoda. The rarity of centipedes (four specimens), and of Diplura (two specimens) and Zygentoma (three specimens) is propably due to the same reasons. The complete absence of terrestrial Isopoda and of Opiliones is harder to explain. The absence of Mantophasmatodea may be due to the biogeographical absence of this order from South America, but on the other hand this appears unlikely considering the Recent occurrence in southern Africa and Baltic amber. Maybe they have just been overlooked or misidentified. The absence of Grylloblattodea is easily explained by their ecology, which confines them to mountainous cool and humid areas of the Northern Hemisphere. The extreme rarity of Mecoptera, of which only two specimens have been discovered, can similarly be attributed to their preference for moist habitats. The absence of Macrolepidoptera and especially of diurnal butterflies (Papilionoidea) is presumably due to the late occurrence of these groups in the evolution of insects (the oldest known fossils are from the Paleocene Fur Formation of Denmark). However, the complete absence of any Plecoptera (adults and larvae) is odd and cannot easily be explained, especially considering the striking abundance of both adults and larvae of nearly all other groups of aquatic insects, including clearly rheophilic ephemeropteran and odonatan families that usually co-exist with several species of plecopterans in Recent Neotropical habitats.

A further ‘missing taxon’ is Gerridae. These water striders are present in Recent South America so their absence may be due to a major biogeographical shift in their distribution since the Cretaceous. Considering the relatively frequent occurrence of adult Trichoptera, the complete absence of larval specimens and the extreme rarity of aquatic larvae of Diptera and Coleoptera is also unusual, because the aquatic larvae of Heteroptera, Odonata and Ephemeroptera are found in abundance. Until recently the absence of the odonate suborder ‘Anisozygoptera’, that represents a paraphyletic grade in the stem group of Anisoptera and is abundant in nearly all other Mesozoic sites with fossil dragonflies, was perplexing. However, recently two specimens of Stenophlebiidae have been discovered from the Crato Formation and are described below. Such ‘late’ discoveries clearly demonstrate a continued need for collecting. Finally, a surprising phenomenon is the presence of several species of Raphidioptera in the Crato Formation. It is surprising because Recent snake-flies are confined to the Northern Hemisphere. Thus a plausible explanation is required to explain their extinction in South America and determine when it happened.

Some taxonomic problems

During work on this chapter, the contributors discovered that several scientific publications on Crato Formation insects do not comply with the common international 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

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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

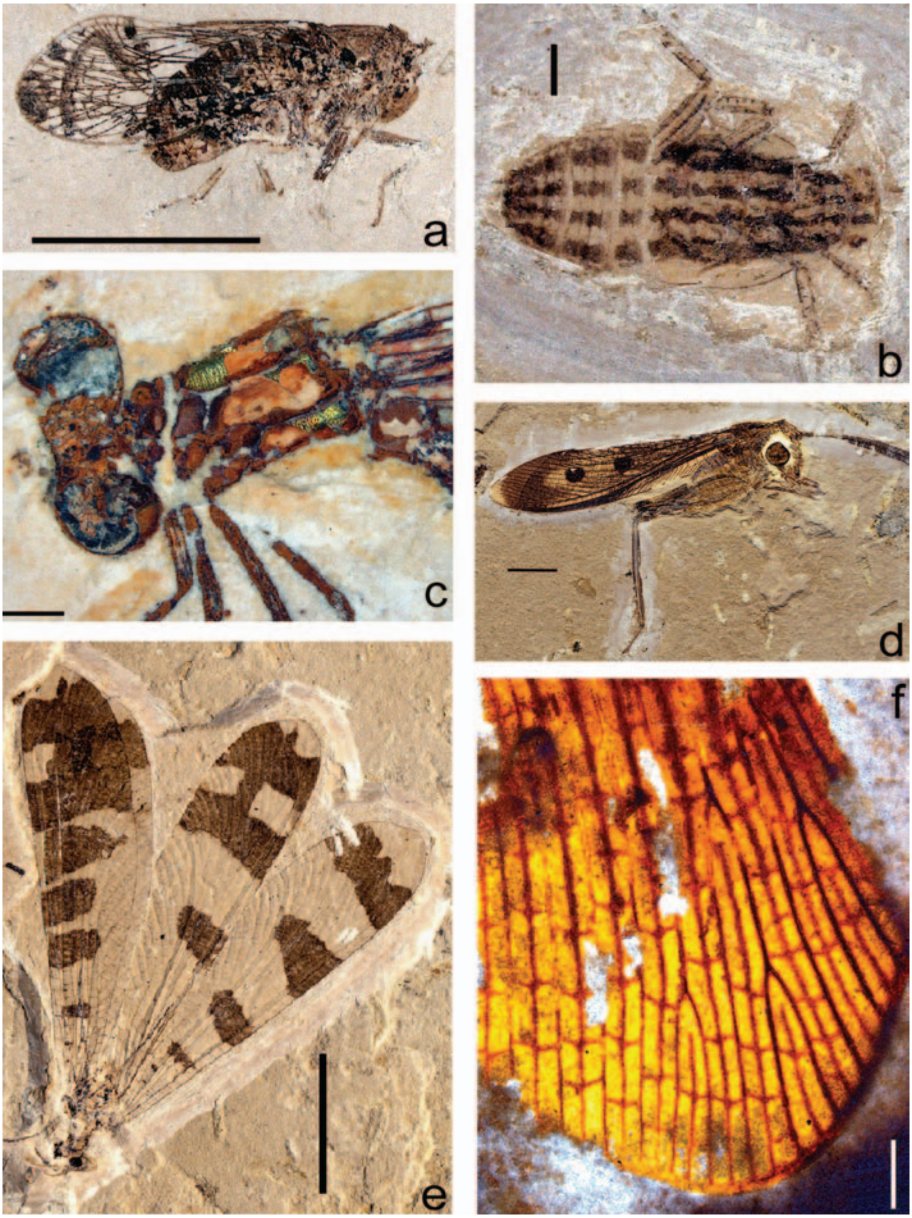

Plate 2. Colour preservation in Crato Formation insects. (a) Spots on the wings of a cicadomorph; scale bar, 10 mm. (b) Stripes on the body of a probable cockroach larva, scale bar, 2 mm. (c) Metallic green colour preserved on thorax of the odonatan *Cretarchistigma* (?) *essweini*, SMNS 66393; scale bar, 1 mm (this is the oldest fossil record of preserved interference colours!). (d) Spots and anterior wing stripe on an orthopteran; scale bar, 5 mm. (e) Spots on the wings of the neuropteran *Baisopardus cryptohymen*, holotype SMNS 65470. (f) A roach wing, acid-prepared from both sides and embedded in synthetic resin; scale bar, 0.5 mm.