

for anthophily (particularly in the Pangoniinae). The larvae of most species prey on other invertebrates and annelids.

11.21 Trichoptera and Lepidoptera: caddisflies and butterflies

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Caddisflies (Trichoptera) are inconspicuous, medium-sized, moth-like insects with aquatic larvae familiar because of their habit of constructing remarkable cases from small stones, shells or plant debris for protection. Butterflies and moths (Lepidoptera), hardly requiring introduction, are mostly medium-sized to large insects with four large wings that, in most species, are covered with microscopic, overlapping scales. The biggest difference between adult caddisflies and small butterflies of similar appearance is the presence of hairs on the wings instead of scales and the generally much longer filiform antennae. In Trichoptera the mouthparts are developed as a haustellum with reduced mandibles and maxillae, whereas in most butterflies (except the most basal taxa) the mouthparts (galeae) are developed as a long proboscis for feeding on nectar.

A further important difference, especially regarding their preservation potential as fossils, is that the larvae of butterflies and moths are nearly always terrestrial caterpillars whereas most caddisfly larvae are aquatic, and the few terrestrial forms certainly require very moist leaf litter to avoid desiccation. Both groups have a holometabolous life cycle with true larvae that are very dissimilar from the adults followed by a distinct pupal stage. Both orders have a cosmopolitan distribution and are generally phytophagous.

About 11,500 species of Recent caddisflies and about 130,000 species of Recent butterflies have been described, and current views on their internal phylogeny have recently been summarized by Grimaldi and Engel (2005).

Fossil record

The fossil history of Trichoptera and Lepidoptera was first discussed by Handlirsch (1906–08), and more recently by Carpenter (1992), Ivanov and Sukatsheva (2002), Kozlov *et al.* (2002), and Grimaldi and Engel (2005). The attributions of Permian and Triassic taxa (e.g. ‘Necrotauliidae’) that have a trichopteran habitus is problematic and most likely belong to the common stem group of Amphiesmenoptera (Trichoptera+Lepidoptera). The oldest representative of crown group trichopterans is *Liadotaulius major* from the Lower Jurassic of Germany, while the oldest known crown group lepidopteran is *Archaeolepis mane* from the Lower Jurassic of

England. True butterflies (Rhopalocera) are still unknown from the Mesozoic and occur first in the Paleocene Fur Formation of Denmark.

Crato Trichoptera: caddisflies

Adult caddisflies (Figures 11.87a–d and 11.88a–b) are rare fossils in the Crato Formation, and no larvae have yet been discovered. The presence of the flying adults and the absence of their aquatic larvae is supporting evidence that most insects from the Crato Formation are of allochthonous origin. Only a few fossil caddisflies and butterflies from Crato have been described (Martins-Neto and Vulcano, 1989b; Martins-Neto, 1999b, 2001b).

Among Trichoptera the families Calamoceratidae, Leptoceridae and Rhyacophilidae were recorded by Martill *et al.* (1993) without further information and Bechly *et al.* (2001: 45, fig. 34) figured an undetermined small trichopteran from the Crato Formation. Martins-Neto (2001b) described the following seven new taxa (note: the original description is incorrectly cited as ‘Martins-Neto, 2002b’ by Martins-Neto, 2005b: 480–481).

- *Araripleptocerus primaevus* (Figure 11.89b): earliest fossil record of the family Leptoceridae; body about 8.5 mm long; compound eyes large and prominent; antennae 1.5 times longer than wings and twice as long as body; tibial spur formula 2/2/2; forewing length 11 mm; distal fork formula 1/3/5; F₁ and F₃ with very long branches. Specimen SMNS 66281 (Figure 11.87a) is attributed to this species.
- *Raptortrichops sukatshevae* (Figure 11.89a): familia *incertae sedis*; body 11 mm long and robust; compound eyes very large; antennae slightly shorter than forewings and body; forewing length 11.5 mm; discoidal and median cell large and closed; distal fork formula 1/2/3/5. Specimen SMNS 66288 is a putative specimen of this species. Note, there are two original spellings of the genus name (*Raptortrichops* Martins-Neto, 2001b): 212 and *Raptortricops* Martins-Neto, 2001b: 224, figure 2) and of the species name (*sukatschevae* Martins-Neto, 2001b: 212 and *sukascheva* Martins-Neto, 2001b: 212).
- *Senka crassatella*: familia *incertae sedis*; body 13 mm long and robust; compound eyes large and prominent; antennae only 4.3 mm long; forewing length 14 mm; median cell closed and twice as long as the small and closed discoidal cell. Five specimens, SMNS 66284 (Figure 11.87b), SMNS 66283, SMNS 66285, SMNS 66286 and SMNS 66290, are identified as this species.
- Genus *Cratorella*: family Hydroptilidae (new attribution); small size; antennae distinctly shorter than forewing length; tibial spur formula 2–3/4/4; forewings broad in males and narrow in females; distal fork formula 1/2/3/4/5 in males and 1/3/5 in females; discoidal and median cells open; F₁ longer than F₂, F₃ and F₄ that are of similar size in males, while F₁ and F₃ are very small in females. The apparent ‘ovipositor’ described by Martins-Neto (2001b) for *C. feminina* is an extensible oviscapt, thus excluding its attribution to the Integripalpia. Indeed, it suggests instead affinities with the paraphyletic grade Spicipalpia

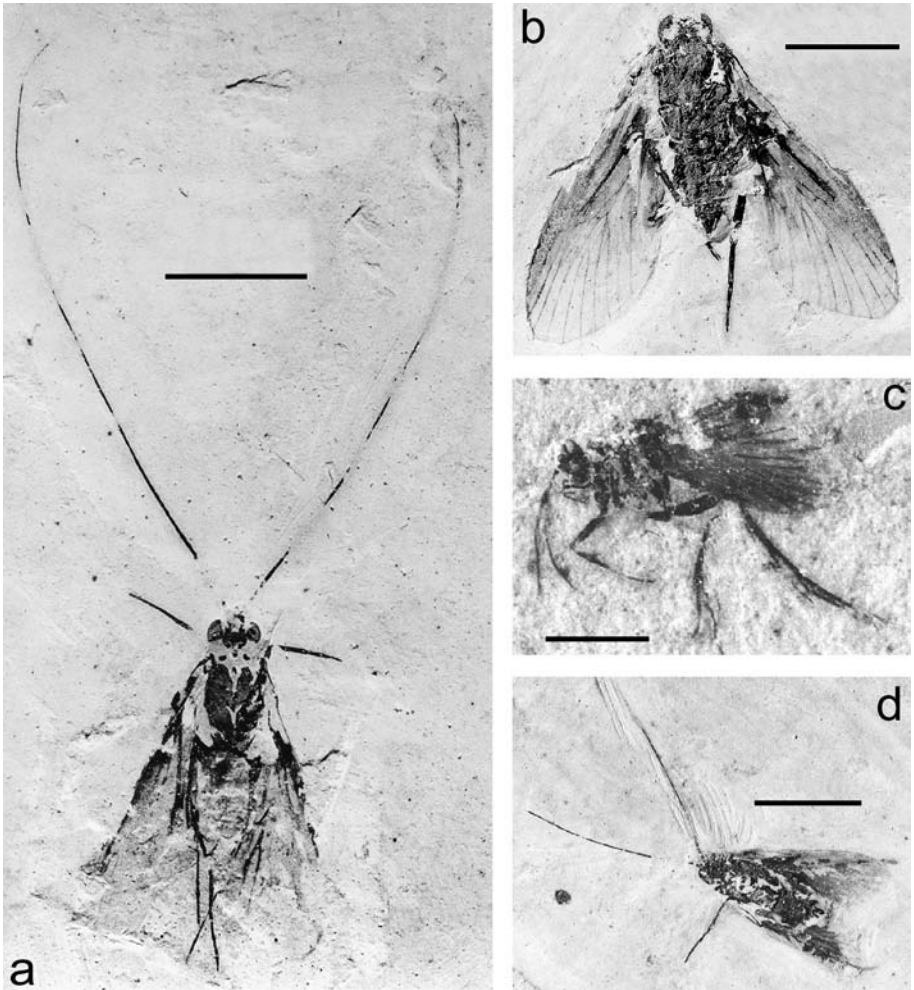


Fig. 11.87. Crato Formation Trichoptera: (a) Leptoceridae, *Araripeleptocerus primaevus*, SMNS 66281; (b) Familia incertae sedis, *Senka crassatella*, SMNS 66284; (c) Hydroptilidae, *Cratorella* cf. *media*, SMNS 66278; (d) undescribed gen. et sp. nov., SMNS 66282. Scale bars, 5 mm; except c, 1 mm.

(Rhyacophiloidea=Glossomatidae+Hydroptilidae+Rhyacophilidae+Hydrobiosidae), and is further supported by the five-segmented maxillary palps and the short antennae. Due to the small size of this species and its short antennae, it is probably allied with the micro-caddisflies Hydroptilidae rather than the Rhyacophilidae (contra Martins-Neto, 2001b), even though the longer basal segment of the maxillary palps and the tibial spur formula would exclude a position in crown group Hydroptilidae.

- *Cratorella magna*: body and forewing length approximately 7 mm; hind tibia 2.5 times length of hind femur. In the original description Martins-Neto (2001b) used the spelling '*C. maga*' (*sic*), but this is obviously an incorrect original spelling due to a *lapsus calami*,

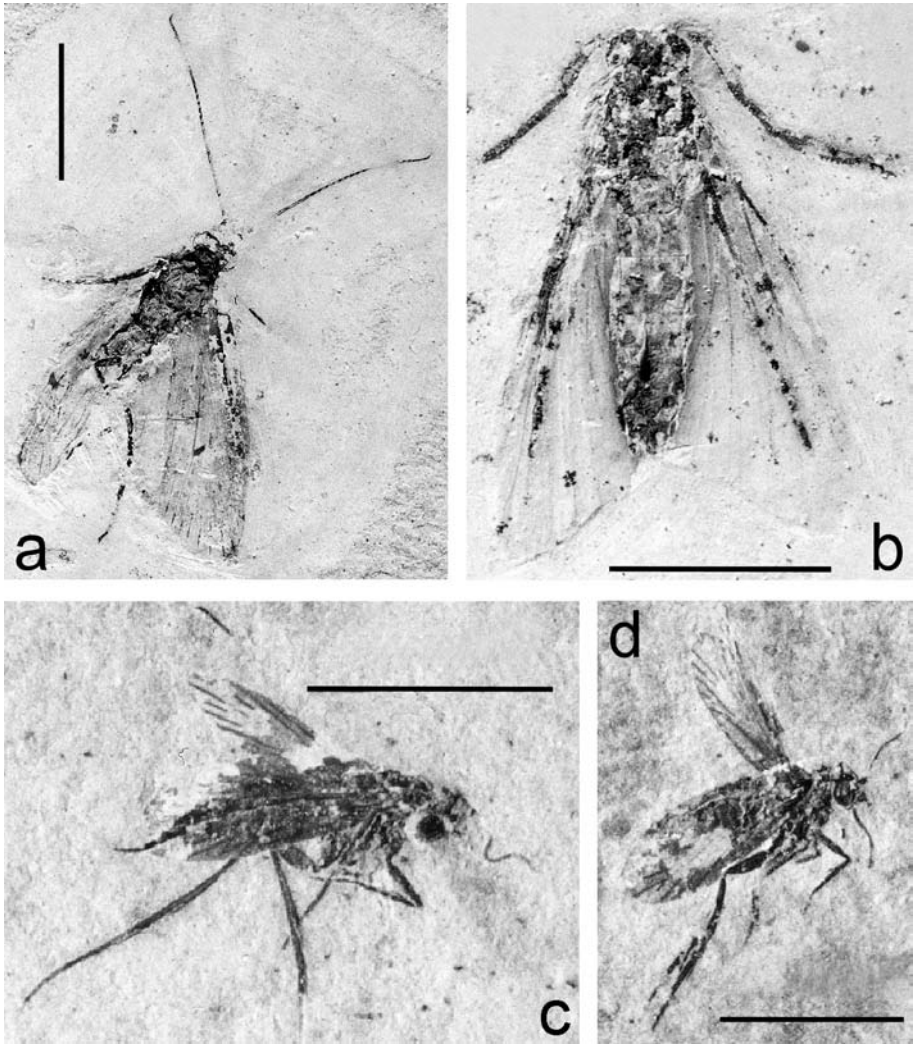


Fig. 11.88. Crato Formation Trichoptera and Lepidoptera: (a) Trichoptera, gen. et sp. nov. SMNS 66287; (b) Trichoptera, gen. et sp. nov., SMNS 66568; (c) Lepidoptera, Micropterygidae, *Parasabatanica caldasae*, SMNS 66279; (d) Lepidoptera, familia *incertae sedis*, *Gracilepterix pulchra*, SMNS 66277. Scale bars: a,b, 5 mm; c,d, 3 mm.

as is clearly documented by the derivation *nominis* and the further uses of this species name in the same publication. Consequently, the correct name of this species is *Cratorella magna*. Three specimens (SMNS 66280, 66561 and 66570) are identified as this species.

- *Cratorella media*: body and forewing length 3.4 mm; hind tibia two times length of hind femur. A single specimen (SMNS 66278) is similar to this species (Figure 11.87c) but it has a somewhat larger body length of 4.3 mm and could represent a new species.

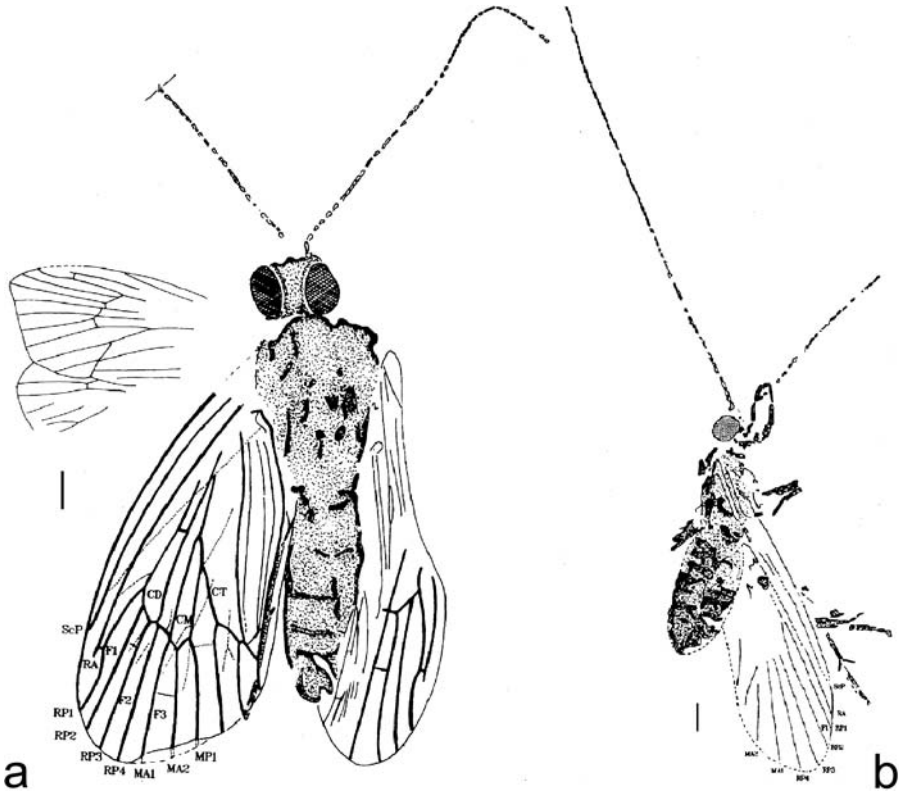


Fig. 11.89. Crato Formation Trichoptera: (a) *Raptortrichops sukatschevae* Martins-Neto, 2001, holotype, RGMN-T013; (b) *Araripeleptocercus primaevus* Martins-Neto, 2001, holotype, RGMN-T012. Scale bars, 2 mm. After Martins-Neto (2001).

- *Cratorella minuta*: body and forewing length 3 mm; hind tibia 1.5 times length of hind femur.
- *Cratorella feminina*: body length 2.6 mm; forewing length 3 mm; forewing narrow with very small F_1 and F_3 (female).

Many of the attributions and descriptions of Crato Formation Trichoptera require re-evaluation: the diagnosis of the monotypic genus *Raptortrichops* contradicts the description and figure of its type species concerning the length of the antennae; the figure and diagnosis of the monotypic genus *Araripeleptocercus* contradicts the statement of the antennal length in the description of the type species; the alleged sexual dimorphism (see above) within the genus *Cratorella* is insufficiently documented and it is unclear whether the features of *C. feminina* are dimorphic or taxonomic; the diagnosis of *Cratorella* provided by Martins-Neto (2001b) is a composite of the character patterns of four different species that might not even

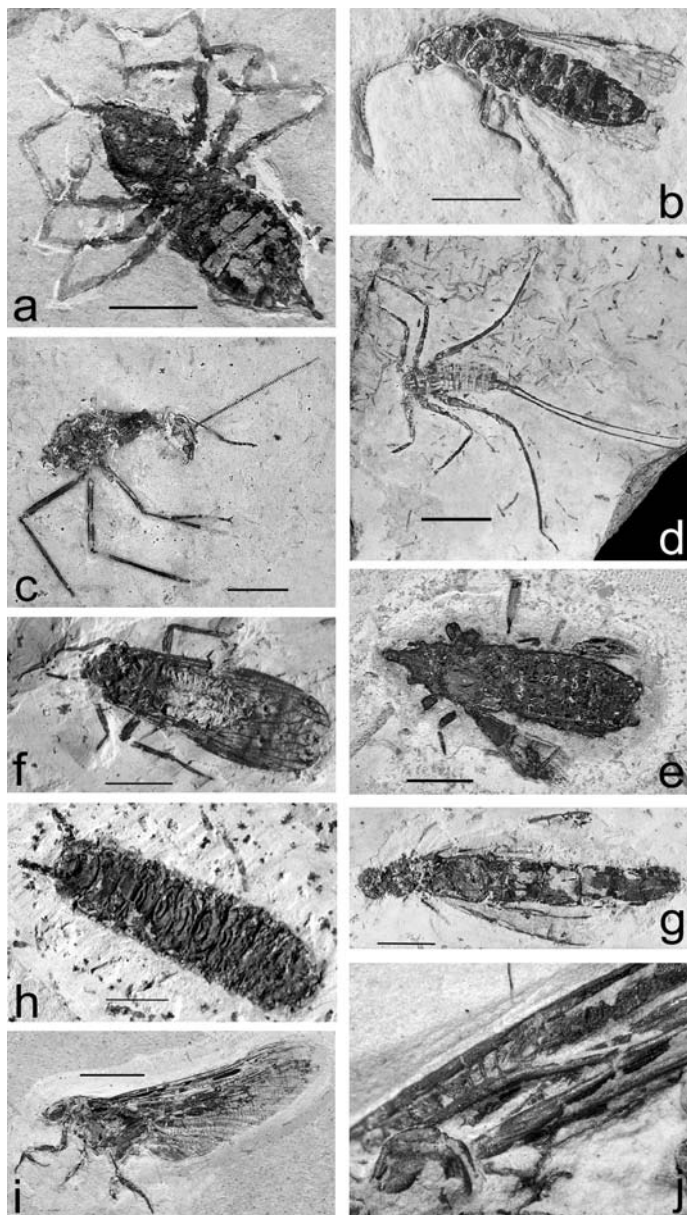


Fig. 11.90. Problematic arthropods: (a) unidentified arachnid, possibly Solifugae, Z21 coll. MSF; (b) Umenocoleidae, *Ponopterix* sp. preserved in lateral aspect, SMNS 66563; (c) Dictyoptera, possibly Raphidiomimidae, Z100 coll. MSF; (d) a large and weird-looking insect, probably Orthoptera, R29 coll. MSF; (e) a strange new Heteroptera, MURJ without number; (f) Holometabola, possibly Megaloptera, H80 coll. MSF; (g) Holometabola, putative ship-timber beetle, Coleoptera, Lymexylidae, SMNS 66534; (h) larva of unidentified holometabolous insect, H99 coll. MSF; (i) Ephemeroidea, undescribed stem group mayfly (not identical with *Cretereisma* gen. nov.), SMNS 66550, body size and structures of head and legs of this new taxon might even better correspond to the stem group mayfly larvae of the 'Ananas' type than the adults of *Cretereisma* described by Willmann in this volume (Section 11.3); (j) detail of same specimen SMNS 66550, costal brace like Permian Protereismatidae. Scale bars: 5 mm; except d, 20 mm; i, 10 mm.

belong to the same genus. A careful revision by a specialist on fossil Trichoptera would be very useful. Furthermore, there are several putative new genera and species to be described, such as specimens nos SMNS 66282 (Figure 11.87d), SMNS 66287 (Figure 11.88a) and SMNS 66568 (Figure 11.88b), which are clearly distinct from any described species.

Crato Lepidoptera: moths and butterflies

Lepidoptera are extremely rare in the Crato Formation and only members of the microlepidopteran grade occur. Martins-Neto and Vulcano (1989b) and Martins-Neto (1999, 2001b) described the following five taxa.

- *Parasabatınca caldasae*: Micropterygidae; body length 3.5–5 mm; forewing length 3–3.5 mm; R₂ and R₃ ending near apex. Besides the holotype, a single specimen (SMNS 66279) has been identified as this species (Figure 11.87c).
- *Undopterix caririensis*: Undopterigidae; hind wing length 3.1 mm; M₁+M₂ fork slightly posterior to R₄+R₅ fork; CuA ending at anal margin near apex.
- *Gracilepteryx pulchra*: in familia *incertae sedis*; similar to *Undopterix*; body length and forewing length about 3 mm; hind wing length 2.3 mm; R₁ forking anteriorly of R₂+R₃ and R₄+R₅ forks in forewings; Sc and R₁ unbranched in hind wings. One specimen of this species (SMNS 66277) has been identified (Figure 11.87d). This fossil butterfly was incorrectly listed as *Gracilepteryx (sic)* by Martins-Neto (2005b).
- *Xena nana* Martins-Neto, 1999b: Eolepidopterigidae. This taxon seems to be similar to *Eolepidopterix* and is said to be described by ‘Martins-Neto, 2000’ according to Martins-Neto (2005b), which seems to be a *lapsus* and should be ‘Martins-Neto, 1999b’.
- *Psamateia calipsa* Martins Neto, 2002: the present author could not locate the publication with this description, which is mentioned by Martins-Neto (2005b).

All the above species belong to the most primitive and most basal grade of Lepidoptera, and thus not within the Glossata, although Martins-Neto (2005b: 480) attributed all five species to the Eolepidopterigidae, but without explication. However, Grimaldi and Engel (2005: 562, figure 13.16) figured an unnamed primitive moth (AMNH SF 46441) with a piercing oviscapt similar to the Recent families Eriocraniidae and Acanthopteroctetidae that are indeed basal Glossata. This fossil could be the most derived Lower Cretaceous lepidopteran yet discovered, if it should not turn out to be just a small trichopteran like *Cratorella media*.

References

- Achtelig, M. 1967. Ueber die Anatomie des Kopfes von *Raphidia flavipes* Stein und die Verwandtschaftsbeziehungen der Raphidiidae zu den Megaloptera. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* **84**: 249–312.