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Insect Diversity

1. Introduction

In this chapter, we shall examine the evolutionary development of the tremendous variety of insects that we see today. From the limited fossil record it would appear that the earliest insects were wingless, thysanuranlike forms that abounded in the Silurian and Devonian periods. The major advance made by their descendants was the evolution of wings, facilitating dispersal and, therefore, colonization of new habitats. During the Carboniferous and Permian periods there was a massive adaptive radiation of winged forms, and it was at this time that most of the modern orders had their beginnings. Although members of many of these orders retained a life history similar to that of their wingless ancestors, in which the change from juvenile to adult form was gradual (the hemimetabolous or exopterygote orders), in other orders a life history evolved in which the juvenile and adult phases are separated by a pupal stage (the holometabolous or endopterygote orders). The great advantage of having a pupal stage (although this is neither its original nor its only significance) is that the juvenile and adult stages can become very different from each other in their habits, thereby avoiding competition for the same resources. The evolution of wings and development of a pupal stage have had such a profound effect on the success of insects that they will be discussed as separate topics in some detail below.

2. Primitive Wingless Insects

The earliest wingless insects to appear in the fossil record are Microcoryphia (Archeognatha) (bristletails) from the Lower Devonian of Quebec (Labandeira *et al.*, 1988) and Middle Devonian of New York (Shear *et al.*, 1984). These, together with fossil Monura (Figure 2.1A) and Zygentoma (silverfish) (Figure 2.1B) from the Upper Carboniferous and Permian periods, constitute a few remnants of an originally extensive apterygote fauna that existed in the Silurian and Devonian periods. Primitive features of the microcoryphians include the monocondylous mandibles which exhibit segmental sutures, fully segmented (i.e., leglike) maxillary palps with two terminal claws, a distinct ringlike subcoxal segment on the meso- and metathorax (in all remaining Insecta this becomes flattened and forms part of the pleural wall), undivided cercal bases, and an ovipositor that has no gonangulum.

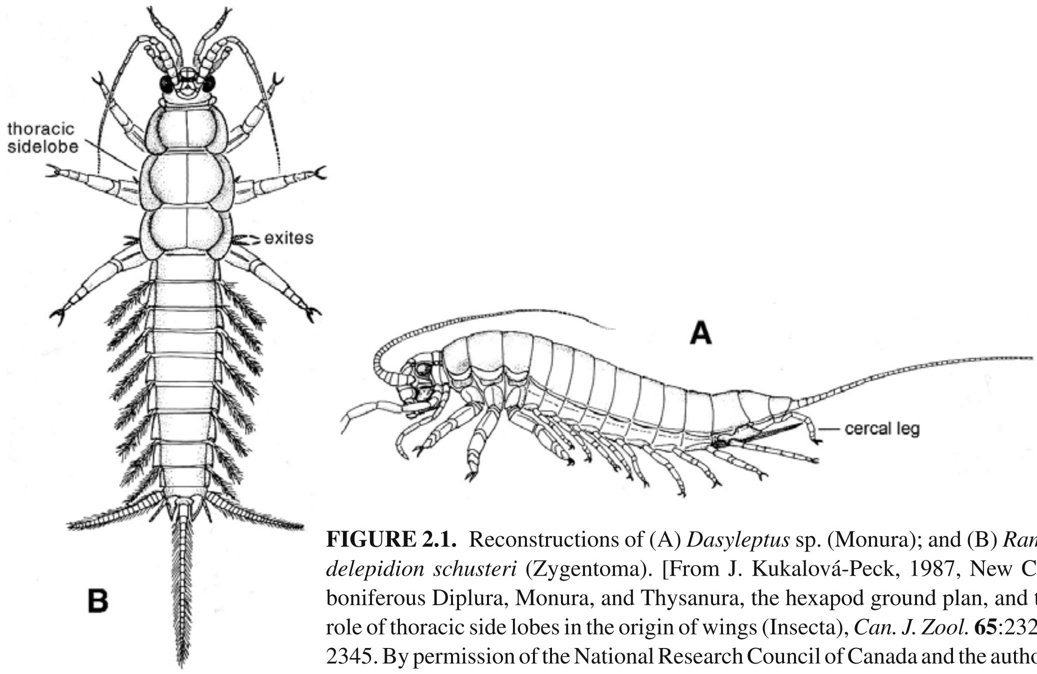

FIGURE 2.1. Reconstructions of (A) *Dasyleptus* sp. (Monura); and (B) *Ramsdelepidion schusteri* (Zygentoma). [From J. Kukalová-Peck, 1987, New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta), *Can. J. Zool.* **65**:2327–2345. By permission of the National Research Council of Canada and the author.]

The early bristletails, like their modern relatives, perhaps fed on algae, lichens, and debris. They escaped from predators by running and jumping, the latter achieved by abrupt flexing of the abdomen.

Monura are unique among Insecta in that they retain cercal legs (Kukalová-Peck, 1985). Other primitive features of this group are the segmented head, fully segmented maxillary and labial palps, lack of differentiation of the thoracic segments, segmented abdominal leglets, the long caudal filament, and the coating of sensory bristles over the body (Kukalová-Peck, 1991). Features they share with the Zygentoma and Pterygota are dicondylous mandibles, well-sclerotized thoracic pleura, and the gonangulum, leading Kukalová-Peck (1987) to suggest that the Monura are the sister group of the Zygentoma + Pterygota. Carpenter (1992), however, included the Monura as a suborder of the Microcoryphia. Shear and Kukalová-Peck (1990) suggested, on the basis of their morphology, that monurans probably lived in swamps, climbing on emergent vegetation, and feeding on soft matter. Escape from predators may have occurred, as in the Microcoryphia, by running and jumping.

In contrast to their rapidly running, modern relatives, the early silverfish, for example, the 6-cm-long. *Ramsdelepidion schusteri* (Figure 2.1B), with their weak legs, probably avoided predators by generally remaining concealed. When exposed, however, the numerous long bristles that covered the abdominal leglets, cerci, and median filament may have provided a highly sensitive, early warning system. Of particular interest in any discussion of apterygote relationships is the extant silverfish *Tricholepidion gertschi*, discovered in California in 1961. The species is sufficiently different from other recent Zygentoma that it is placed in a separate family Lepidotrichidae, to which some Oligocene fossils also belong. Indeed, *Tricholepidion* possesses a number of features common to both Microcoryphia and Monura (see Chapter 5, Section 6), leading Sharov (1966) to suggest that the family to which it belongs is closer than any other to the thysanuranlike ancestor of the Pterygota.