

Arthropod Evolution

1. Introduction

Despite their remarkable diversity of form and habits, insects possess several common features by which the group as a whole can be distinguished. They are generally small arthropods whose bodies are divisible into cephalic, thoracic, and abdominal regions. The head carries one pair of antennae, one pair of mandibles, and two pairs of maxillae (the hind pair fused to form the labium). Each of three thoracic segments bears a pair of legs and, in the adult, the meso- and/or metathoracic segments usually have a pair of wings. Abdominal appendages, when present, generally do not have a locomotory function. The genital aperture is located posteriorly on the abdomen. With few exceptions eggs are laid, and the young form may be quite different from the adult; most insects undergo some degree of metamorphosis.

Although these may seem initially to be an inauspicious set of characters, when they are examined in relation to the environment it can be seen quite readily why the Insecta have become the most successful group of living organisms. This aspect will be discussed in Chapter 2.

In the present chapter we shall examine the possible origins of the Insecta, that is, the evolutionary relationships of this group with other arthropods. In order to do this meaningfully it is useful first to review the features of the other groups of arthropods. As will become apparent below, the question of arthropod phylogeny is controversial, and various theories have been proposed.

2. Arthropod Diversity

Arthropods share certain features with which they can be defined. These features are: segmented body covered with a chitinous exoskeleton that may be locally hardened and is periodically shed, tagmosis (the grouping of segments into functional units, for example, head, thorax, and abdomen in insects), presence of preoral segments, paired jointed appendages on a varied number of segments, hemocoelic body cavity containing ostiate heart enclosed within a pericardium, nervous system comprising dorsal brain and ventral ganglionated nerve cord, muscles almost always striated, and epithelial tissue almost always non-ciliated.

Though the “true” arthropods fit readily within this definition, three small groups, the Onychophora, Tardigrada, and Pentastoma, whose members are soft-bodied, wormlike animals with unjointed appendages, are less obviously arthropodan and each is usually given separate phylum status.

2.1. Onychophora, Tardigrada, and Pentastoma

The approximately 200 extant species of Onychophora (Figure 1.1A) are terrestrial animals living on land masses derived from the Gondwanan supercontinent: Africa, Central and South America, and Australasia (Tait, 2001). They are generally confined to moist habitats and are found beneath stones in rotting logs and leaf mold, etc. They possess a combination of annelidan and arthropodan characters and, as a result, are always prominent in discussions of arthropod evolution. Although covered by a thin arthropodlike cuticle (comprising procuticle and epicuticle, but no outer wax layer—see Chapter 11), the body wall is annelidan, as are the method of locomotion, unjointed legs, the excretory system, and the nervous system. Their arthropodan features include a hemocoelic body cavity, the development and structure of the jaws, the possession of salivary glands, an open circulatory system, a tracheal respiratory system, and claws at the tips of the legs. Among living arthropods, myriapods resemble the Onychophora most closely: their body form is similar, tagmosis is restricted to the three-segmented head, exsertile vesicles are present in Diplopoda and Symphyla as well as in some onychophorans, a digestive gland is absent, the midgut is similar, the genital tracts of Onychophora resemble those of myriapods, the gonopore is subterminal, and certain features of embryonic development are common to both groups (Tiegs and Manton, 1958). However, this resemblance is superficial. Recent onychophorans are but the remnants of a more widespread fauna (fossils from the Carboniferous are very similar to modern forms) that may have evolved from marine lobopods in the Cambrian period.

Tardigrades are mostly very small (<0.5 mm long) animals, commonly known as water bears (Figure 1.1B). The majority of the 800 extant species are found in the temporary water films that coat mosses and lichens. A few live in permanent aquatic habitats, either marine or freshwater, or in water films in soil and forest litter (Kinchin, 1994; Nelson, 2001). Their body is covered with a chitinized cuticle and bears four pairs of unjointed legs, each

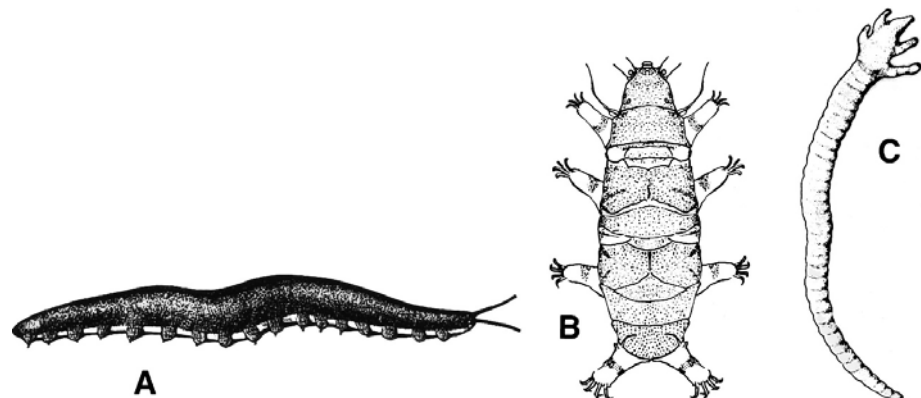


FIGURE 1.1. (A) *Peripatopsis* sp. (Onychophora); (B) *Pseudechiniscus suillus* (Tardigrada); and (C) *Cephalobaena tetrapoda* (Pentastomida). [A, from A. Sedgewick, 1909, *A Student's Textbook of Zoology*, Vol. III, Swan, Sonnenhein and Co., Ltd. B, C, from P.-P. Grassé, 1968, *Traité de Zoologie*, Vol. 6. By permission of Masson et Cie.]