Arthropods: Evolution and Ecology

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Economic and Ecological Significance of Arthropods in Diversified Ecosystems

Sustaining Regulatory Mechanisms

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Arthropods: Evolution and Ecology

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A.K. Chakravarthy, Vasudev Kammar, and P.R. Shashank

Abstract

Arthropods constitute the dominant group in the animal kingdom and are a major part of global biodiversity. There are 1,302,809 species of arthropods described that include 45,769 fossil species. Arthropods are the most successful group found in almost all biogeographical regions and ecological zones and have a dominating influence on other elements of biodiversity. The Insecta have 1, 070,781 species and it alone accounts for over 80 % of all arthropods. Another major group is Arachnida having 114, 275 described species of which 55, 214 species are mites and ticks. Arthropods contribute to human food supply, pollinate crops, help maintain ecosystem sustainability by biologically suppressing destructive arthropods, but cause and transmit diseases to humans and livestock and incur crop losses. Invasive arthropods can negatively impact natural resources.

Keywords

Arthropods • Ecology • Evolution • Importance

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1.1 Introduction

Today one single phylum of the animal kingdom is dominating on the planet Earth. On land, in the sea, even in the air itself, they are the true masters of the Earth. They are the arthropods. The name Arthropodsis is derived from the Greek *arthros* which means jointed and *poda* which means foot (Harper 2014) including the familiar arachnids, crustaceans, and insects. All arthropods have jointed appendages. This evolutionary innovation is probably the key to the stunning success of this diverse group. There are about ten billion arthropods alive at any one time.

Arthropods range in size from microscopic plankton to a few meters long. Their versatility and adaptability has rendered them to become the most species-rich members of all ecological guilds in most environments. There are over a million described species of arthropods, making up more than 80 % of all described living animal species. Out of these, insects alone form about three-fourths of the total organisms present on the Earth (Chapman 2009).

The evolutionary ancestry of arthropods dates back to the Cambrian period. The group is generally regarded as monophyletic, and many analyses support the placement of arthropods with cycloneuralians (or their constituent clades) in a superphylum. Overall, however, the basal relationships of Metazoa are not yet well resolved. Likewise, the relationships between and among phyla in Arthropoda still remain obscure.

The versatility of arthropods is such that they are dominant on land in both species richness and rank numerically the most prominent benthic, freshwater and marine ecosystems. Arthropods are immensely successful in every possible habitat on the land, be it equator or the poles or from high mountains to deep ocean trenches. Many arthropods cause economic loss to humans as most of them carry and spread diseased vectors and plant pests but also a boon as a veritable food resource (honey, edible food such as crabs, lobsters, and shrimps). They are also vital to the functioning of all ecosystems and a beneficial to humans in many ways. In addition to deriving nutrition from arthropods (e.g., directly or indirectly from bees, crabs, lobsters, and shrimps), humans probably could not survive ecologically without them (James 2003).

Arthropod is segmented which differs from annelids, but with an evolutionary tendency toward the fusion of several metameres into the body region (tagmata) with specialized crustaceans having two; however, myriapods (mostly millipedes and centipedes) lack tagmata. Arthropods have chitinous and proteinaceous exoskeletons which are frequently strengthened with calcium salts. Non-chitinized appendages of the exoskeleton project inward to aid muscular attachment. The continued somatic growth is rendered possibly by periodic ecdysis, a relatively strenuous and often dangerous process. In some arthropods, modified exoskeleton has aided in flying. The organ complexity of arthropods is very high among all invertebrates with the exception of molluscan cephalopods. The internal cavity is called hemocoel and accommodates all the vital organs. Blood called hemolymph circulates through an open circulatory system. However the coelom does not function as a hydrostatic organ as in annelids. Respiration is by diverse processes, viz., through the skin in small species, using gills in aquatic forms and through tracheae or book lungs in terrestrial arthropods. Reproduction is mostly dioecious although some forms exhibit parthenogenesis. Courtship and parental care, although less evident, are found in some members. With the exception of few aquatic forms which fertilize externally, internal fertilization is the norm. Most of the internal fertilization is by indirect transfer of the sperm via an appendage or by "suction" from the ground, rather than by direct injection. With the exception of scorpions which are viviparous, all arthropods lay eggs. The young ones are fully mature when born is some but in most arthropods eggs molt into immature forms without appendages, grow in cocoons, molt several times, and metamorphosize into adults. Similarly parental care ranges from non-existent to vivipary which further extends to the first molt of the young as in scorpions. The neural system in most arthropods is highly developed. In fact, the arthropod brain is one of the most complex of all living organisms.

The young of the Arthropods usually develop by cleaving of the cytoplasmic layer above a yolky sphere. Although larvae or discrete juveniles characterize terrestrial and aquatic forms, the aquatic larvae do not resemble the trochopore larvae of related phyla.

1.2 Evolutionary Relationships

Arthropods were earlier associated with the phylum Annelida because of their segmented body. But recent molecular data does not provide evidence for such a relationship, but places them closer to other phyla which shed their cuticle during ecdysis during growth such as the phyla Tardigrada, Onychophora, Nematoda, and Nematomorpha along with more distantly related Priapulida and Kinorhyncha (Resh and Carde 2009). The evolutionary lineages with other phyla with respect to similar characters are detailed below.

1.2.1 Segmentation

The embryos of all arthropods consist of a segmented body, built from a series of repeated modules. It is summarized that the last common ancestor of all living arthropods consisted of a series of undifferentiated segments, each segment with a pair of appendages that functioned as limbs. However, in both living and fossil arthropods, the segments are focused into tagmata in which segments and their appendages discharge specific functions (Ruppert et al. 2004), which is clearly evident in the three-part body of insect and the two-part bodies of spiders. In fact, the segmentation of body in mites is invisible. In addition arthropods have an acron in the front of the mouth and a telson at the rear end. Acron has eyes mounted on it (Ruppert et al. 2004) (Table 1.1).

Arthropod appendages originally bifunctional, those in the upper region functioning as gills while those on the lower side served as legs. In living arthropods, the appendages have been modified to discharge varied functions as gills, mouthparts, antennae (Gould 1990), or claws (Shubin et al. 2000). In many arthropods

Table 1.1 Diversity of arthropoda and two related phyla

Taxon	No. of estimated (~) or described species	Some biological features
Phylum Arthropoda	~2–6 million	Insects, arachnids, crustaceans, millipedes, and other invertebrates with segmented bodies and appendages on one or more segments; mostly with hard, chitinous exoskeleton that is periodically molted
Subphylum Trilobita	~15,000+	Extinct marine trilobites
Subphylum Chelicerata	~99,000–1 million	Originally marine but subsequent evolution has primarily been in terrestrial habitats
Order Xiphosura	5	
Class Arachnida	~98,000+	Marine horseshoe crabs
Class Eurypterida	300	Spiders, scorpions, and mites
Class Pycnogonida	1300	Extinct sea scorpions
		Sea spiders
Subphylum Myriapoda	~13,500	Terrestrial millipedes, centipedes, and others
Class Chilopoda	2800	
Subclass Epimorpha	1600	Predaceous centipedes mostly in tropical forest floor, 0.5–30 cm long
Subclass Anamorpha	1200	
Class Symphyla	160	Small (2–10 mm), mostly herbivorous, live in forest litter, sometimes called garden centipedes (pseudocentipedes), or just symphylans
Class Diplopoda	~10,000	
Subclass Penicillata	160	Millipedes
		Millipedes with a soft, noncalcified exoskeleton covered with tufts of setae or bristles (used as defense against ant and other predators)
Subclass Chilognatha	10,000	Millipedes with hard exoskeleton and chemical defenses against predators
Class Pauropoda	500	Minute (<1.5 mm) dwellers in soil and leaf litter
Subphylum Hexapoda	~5+ million	Insects, springtails, bristletails, etc.
Class Entognatha	11,000	Wingless springtails, two-pronged bristletails, and other wingless insects with internal mouthparts
class Elliplura	9600	Wingless entognathous (order Protura and Collembola or springtails)
Order Diplura	1000	
Class Insecta	~5+ million species	Blind, wingless inhabitants of forest litter, entognathous
Order Archaeognatha		
Subclass Dicondylia	500	Winged and wingless insects, all adults with six pairs of legs
	915,300+	Primitive, wingless insects, jumping bristletails
		Mostly winged insects (grasshoppers, true bugs, beetles, flies, butterflies, ants, etc.) and a few wingless species (silverfish)
Subphylum Crustacea	~52,000+	Shrimp, crabs, water fleas, barnacles, copepods, etc.

(continued)

Table 1.1 (continued)

Taxon	No. of estimated (~) or described species	Some biological features
Class Branchiopoda	500	Small crustaceans mostly confined to inland waters (freshwater through hypersaline), small, and common in lakes and ephemeral habitats without fish
Subclass Sarsostraca	200	
Subclass Phyllopoda	300	Brine and fairy shrimp
Class Remipedia	12	Water fleas (cladocerans), clam shrimp, shield shrimp
Class Cephalocarida	9	Remipedes; ancient, vermiform crustaceans found in marine caves; estimated diversity may be an order of magnitude higher
Class Maxillopoda	13,400	
Subclass Thecostraca	1320	Horseshoe shrimp; primitive, live in soft marine sediments
Subclass Tantulocarida	10	Crustaceans characterized by a reduced abdomen mostly lacking appendages
Subclass Branchiura	200	True barnacles and small groups of parasitic taxa
Subclass Pentastomida	100	Highly modified parasites of deep-sea crustaceans, estimated diversity over 1000 species
Subclass Mystacocarida	12	
Subclass Copepoda	11,690	Fish lice and carp lice; ectoparasites on fish and a few amphibians
Class Ostracoda	~8000+	Tongue worms, highly modified parasites of tetrapod vertebrates
Subclass Myodocopa	900	
Subclass Podocopa	7000	Interstitial species living in shallow or intertidal waters; reported diversity artificially low from similar external anatomy and habitat
Class Malacostraca	~29,000	Dominant crustaceans in zooplankton; a few parasites of marine fish and invertebrates
Subclass Phyllocarida	39	
Subclass Hoplocarida	400	Seed or mussel shrimps; enclosed in a bivalve chitinous carapace; total diversity is probably at least 20,000
Subclass Eumalacotraca	~29,000	Ostracodes with poorly calcified carapace; brood care within parent carapace
		Ostracodes with a hard carapace
		Crabs, water scuds, isopods, mantis shrimp, etc.
		Leptostracans; small filter feeders
		Mantis shrimp; they kill by smashing or spearing the prey
		Lobsters, king crabs, isopods (e.g., pill bugs), shrimp, amphipods; thoracic limbs jointed for walking or swimming
Phylum Onychopora	90	Velvet worms; mostly confined to tropical habitats
Phylum Tardigrada	1047	Water bears in aquatic and moist terrestrial habitats

Source: James (2003)

they have disappeared from some regions of the body, especially abdominal (Ruppert et al. 2004).

Tropical and subtropical systems have provided fascinating opportunities for studying evolutionary processes. For instance, the Indian subcontinent is an interesting entity given that it has been an island during much of its history following separation from Madagascar and currently is isolated from Eurasia by the Himalayas in the north and the Indian Ocean in the south. Recent molecular studies on a number of endemic taxa from India have reposted endemic radiations. These studies suggest that the uniqueness of Indian biota is not just due to diverse origin but due to evolution in isolation. The isolation of India has generated peculiarities typically seen on oceanic islands (Karanth 2015).

Among arthropods, insects have been extensively studied for evolutionary lineages. Fossil records have also facilitated understanding evolutionary relationships among arthropods and their relatives. There are two schools of thought for evolution of arthropods and insects separately. Arthropods identified as fossils are abundant in deposits dating back to the Cambrian period. The phylum Arthropoda is closely linked with two other phyla, the velvet worms (Onychophora) and water bears (Tardigrada). Both phyla have common characters of nonliving cuticle and they have appendages. However, the cuticle is not hard, and the appendages are not jointed.

The oldest insect fossil *Rhyniognatha hirsti* is estimated at 407–396 million years ago (Devonian period), which coincides with the age of fishes and growth of forests on dry land. The evolution and diversification of insects continued with new insect orders appearing through the Paleozoic, Mesozoic, and Cenozoic eras (Engel and Grimaldi 2004).

The change in global climate during the history of the Earth was invariably accompanied by changes in diversity of insects. The pterygotes were radiated in the Carboniferous, while the Endopterygota species underwent another major radiation in the Permian. The modern day insects are descendants of those that evolved from the survivors of the mass extinction at the Permian–Triassic boundary. Most modern insect families made their appearance during the Jurassic; they further evolved in the cretaceous. By the Tertiary, many more modern insect genera are believed to have been existed. It took about 100 million years for insects to evolve to forms similar to modern day forms (Resh and Carde 2009).

Appearance of all insect species, extant or extinct, are presented in Table 1.2 with the insect orders being presented at the fleas (Siphonaptera) appearing during Mesozoic is at the upper portion of the table, while the springtail fossils (order Collembola) are the oldest known fossils occurring at the Devonian period.

A reconstructed modular organism of the last known common ancestor of arthropods is a module covered with its own armored plate (sclerite) with a pair of biramous limbs. However there is some debate as to whether this organism was uniramous or biramous. It had a ventral mouth, preoral antennae, and dorsal positioned eyes. This arthropod was a generalist feeder of sediment (Bergström and Hou 2003).

Table 1.2 Select fossil records of class Insecta

Era	Period	Dates (MYA)*	Fossil record of insect order with comments
Cenozoic	Quaternary	3–0	No records
	Neogene	23–3	No records
	Paleogene	66–23	Mantophasmatodea (apterous carnivores, closest phylogenetic relationship with Grylloblattidae and Phasmatodea)
Mesozoic	Cretaceous	146–66	Siphonaptera (fleas, phylogenetically closer to Diptera and Mecoptera), Zoraptera (angel insects, Hemimetabola, these are link between orthopteroids and hemipteroids), Strepsiptera (endoparasites, they have twisted hind wings), Mantodea (praying mantis), and Isoptera (termites)
	Jurassic	200–145	Dermaptera (earwigs), Lepidoptera (moths and butterflies), Blattodea (cockroaches)
	Triassic	251–200	Hymenoptera (wasps), Trichoptera (caddish flies)
			Phasmatodea (leaf and stick insects), Odonata (dragonfly and damselfly)
Paleozoic	Permian	299–251	Raphidioptera (snake flies) Megaloptera (alderflies and dobsonflies), Thysanoptera (thrips), Diptera (flies), Neuroptera, Embiidina (web spinners), Mecoptera (scorpion flies), fossil hemipteroids
			Plecoptera (stone flies), Coleoptera (beetles)
			Grylloblattodea (rock crawlers, Hemimetabola, closely related to Orthoptera and Dermaptera)
	Carboniferous	359–299	Zygentoma (silverfish), Psocoptera (book lice)
			Hemiptera (bugs), Diplura, Miomoptera (extinct fossil order), Orthoptera (grasshoppers and crickets)
			Ephemeroptera (mayflies), Palaeodictyopteroidea (an extinct superorder of Paleozoic beaked insects and represents the important terrestrial herbivores)
			Protodonata
	Devonian	416–359	Archaeognatha (bristletails), Collembola (springtails)
	Silurian	444–416	No records
	Ordovician	488–444	No records
	Cambrian	542–488	No records

Sources: Gullan and Cranston
Engel and Grimaldi (2004)
**MYA* million years ago

Drosophila remains the best study model organism with widest availability of genetic tool. The bulk of genetic studies for behavioral isolation have been conducted on *Drosophila*. Species like *D. mauritiana*, *D. sechellia*, *and D. santomea* found in islands of Mauritius are known as "island endemic" species. *Drosophila simulans*, *D. mauritiana*, and *D. sechellia* diverged around quarter of a million years ago. Although relatively young, the species in this clade have diverged enough to show post-zygotic isolation. Hybridization between these species produces sterile males (according to Haldane's rule) but, conveniently for genetic analysis, produce fertile females.

1.2.2 Fossil Records

The earliest arthropods, the Ediacaran animals, namely, *Parvancorina* and *Spriggina*, lived 555 million years ago, while small arthropods with bivalve-like shells were found in fossil beds in China dating 541–539 million years ago (early Cambrian) (Lin et al. 2006; Mc Menamin 2003). The class was however quite diverse suggesting that they had been around for quite some time (Lieberman 1995). However, reexamination of the Burgess Shale, fossils belonging to 505 million years ago revealed many arthropods in the 1970s but they could not be placed in any of the existing arthropod group (Whittington 1979).

Earliest crustacean fossils are recorded at around 513 million years ago in the Cambrian (Budd et al. 2001) fossil shrimp date back to a little later period but occurred abundantly on the seabed (Callaway 2008) during Ordovician period (Zhang et al. 2007). Up till now Crustaceans have lived only in aquatic medium; probably they failed to develop excretory systems to conserve water.

With a jointed exoskeletons that could prevent desiccation, could support against gravity, and could aid locomotion outside the water, arthropods were predisposed to terrestrial life which they did about 450 million years ago as evidenced by terrestrial tracks left by them. The earliest identifiable terrestrial arthropods are from the Silurian period about 419 million years ago (Cowen 2000; Pisani et al. 2004) (Fig. 1.1).

Fossils of many spiders including many from the modern families date back to Jurassic and Cretaceous periods (Vollrath and Selden 2007). Aquatic forms with gills were found to live in Silurian and Devonian periods, while the earliest terrestrial forms with book lungs date back to early Carboniferous period (Jeram 1990). Around 420 million years ago, the oldest known arachnid (*Palaeotarbus jerami*) (Dunlop 1996) appeared. True spiders appeared in the late Carboniferous period about 299 million years ago. However, around 386 million years ago in the Devonian period, *Attercopus fimbriunguis*, bearing the earliest known silk-producing spigots appeared, but lacked spinnerets which characterize true spiders (Selden and Shear 1996).

The earliest insects seemed to have appeared in the Silurian period although the oldest insect fossil, that of *Rhyniognatha hirsti*, dated the Devonian era but it had mandibles similar to those of winged insects (Engel and Grimaldi 2004). By the late

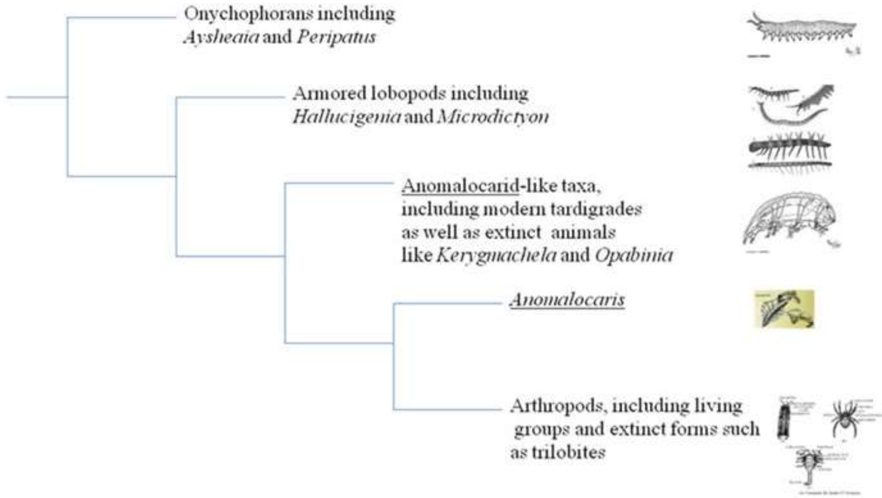

Fig. 1.1 Evolutionary family tree 1. Simplified and modified summary of Budd's "broad-scale" cladogram (Dunlop 1996)

Carboniferous, around 300 million years ago, there were already about 200 species of insects; some were enormously big and already exhibited different food habitat such as herbivory, detritivory, and insectivory. Among the social insects, ants and termites appeared in the early Cretaceous, and among the advanced social insects, bees evolved in late Cretaceous rocks, but they became abundant only in the Middle Cenozoic (Labandeira and Eble 2000).

The origin of arthropods presents an interesting evolutionary development of theories beginning 1952–1977 with the concept that they are polyphyletic and lack a common arthropod ancestor but evolved from three separate groups of "arthropods" originating from (a) wormlike ancestors, (b) chelicerates (spiders and scorpions), and (c) Uniramia (onychophorans, myriapods, and hexapods). This theory failed to include trilobites whose evolutionary relationships remained unexplained. The lack of common ancestry of the three groups was attributed to differential chemical means of hardening of the exoskeleton, differences in the anatomy of their compound eyes, and differential anatomy of the segments and appendages in the head; the supported argument emphasized the biramous limbs of crustaceans serving as gills and legs and the uniramous limbs of the other two groups serving as legs. Similarities between the three groups were attributed to convergent evolution (Gillott 1995).

However, research in the 1990s led to the acceptance of arthropods as monophyletic originating from a common arthropod-like ancestor. Budd after analyzing *Kerygmachela* (1993) and *Opabinia* (1996) argued that these two were similar to onychophorans and to "lobopods" of the early Cambrian. And in the "evolutionary tree," he presented these two as "aunts" and "cousins" of all the arthropods (Fig. 1.2). This interpretation made the meaning of arthropod "irrelevant." Claus Nielsen

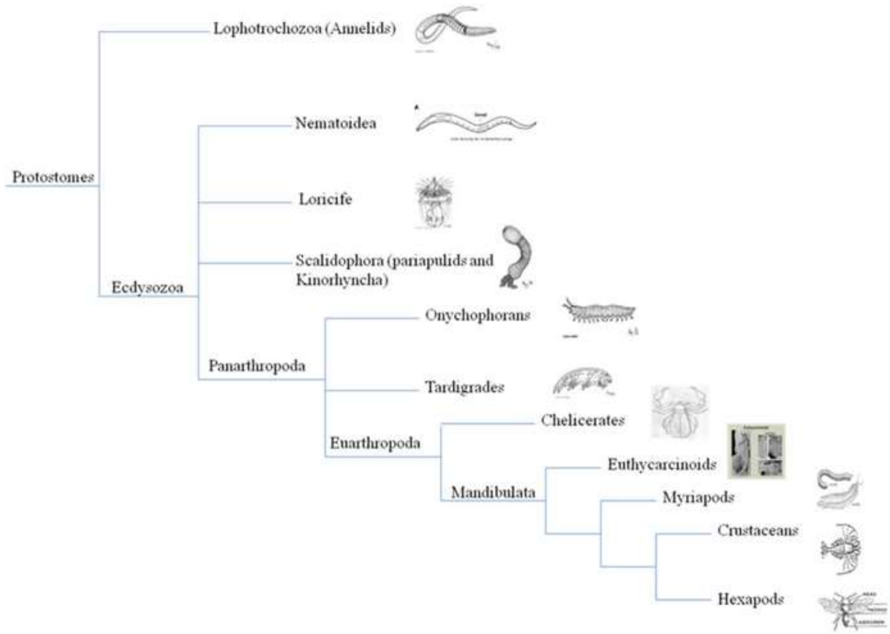

Fig. 1.2 Evolutionary family tree 2. Relationships of Ecdysozoa to each other and to annelids, including euthycarcinoids (Modified from Dunlop 1996)

proposed two nomenclatures: "Panarthropoda" (all arthropods) and "Euarthropoda" ("true arthropods"). The latter group was characterized by jointed limbs and hardened cuticle.

Even the argument that arthropods were a "sister group" to anomalocarids was unacceptable to Bergstrom and Hou (2003). The premitive arthropods were mud eaters, filtering food particles from mud using unspecialized number of appendages which acted as both gills and legs. In contrast Anomalocarids were big in size and had specialized mouth and grasping appendages; they had fixed number of body segments, some of which were modified into gills and tail fins. In contrast *Parapeytoia* was similar to earlier arthropods in having legs and a backward-pointing mouth and was considered a closer relative to arthropods than *Anomalocaris* (Bergstram et al. 2003). In a later publication, Hou et al. (2006) place arthropods closer to lobopods and tardigrades than anomalocarids.

For a long time, annelids were considered as the closest relatives of arthropods based solely on the common character of their segmented body. Together they were termed as Articulata. There were also views that arthropods are closely related to nematodes, priapulids, and tardigrades, but they lacked convincing relationships among them (Fig. 1.2) till the 1990s. But evidence from molecular phylogenetic analyses of DNA sequence revealed similarities between arthropods, nematodes, priapulids, and tardigrades except Annelids, all of which were placed under superphylum labeled Ecdysozoa ("animals that molt"); further evidence for this grouping

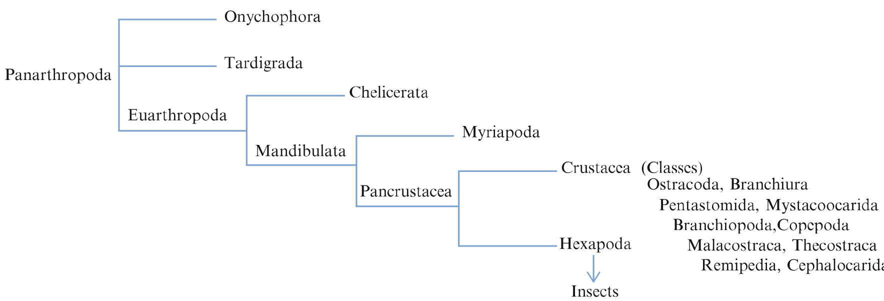

Fig. 1.3 Evolutionary family tree 3. Phylogenetic relationships of the major extant arthropod groups, traditional sub phyla Regier et al. (2010)

came from anatomy and development of member species. The annelids along with mollusks and brachiopods were placed in another superphylum, Lophotrochozoa (Schmidt-Rhaesa et al. 1999). If the Ecdysozoa theory is correct, then the common feature of arthropods and annelids, that is, having a segmented body, has evolved independently or inherited from an older ancestor. It is likely that it was lost during evolution in the non-arthropod members Ecdysozoa.

1.3 Classification (Fig. 1.3)

Arthropods are typically classified into five sub phyla ("Arthropoda" ITIS Report, 2006) which are shown below:

1. **Trilobites** are a group of formerly numerous marine animals that disappeared in the Permian–Triassic extinction event, though they were in decline prior to this killing blow, having been reduced to one order in the late Devonian extinction.
2. **Chelicerates** include spiders, mites, scorpions, and related organisms. They are characterized by the presence of chelicerae, appendages just above or in front of the mouth. Chelicerae appear in scorpions as tiny claws that they use in feeding, but those of spiders have developed as fangs that inject venom.
3. **Myriapods** comprise millipedes, centipedes, and their relatives and have many body segments, each bearing one or two pairs of legs. They are sometimes grouped with the hexapods.
4. **Crustaceans** are primarily aquatic (a notable exception being woodlice) and are characterized by having biramous appendages. They include lobsters, crabs, barnacles, crayfish, prawns, shrimp, and many others.
5. **Hexapods** comprise insects and three small orders of insect-like animals with six thoracic legs. They are sometimes grouped with the myriapods, in a group called Uniramia, though genetic evidence tends to support a closer relationship between hexapods and crustaceans.

There are a number of fossil forms from the early Cambrian which either lack affinity to any of the above sub phyla or show characters common to many of them and hence difficult to place, e.g., *Marrella* (Whittington 1971).

1.4 Ecology

Arthropods are biologically distinct group of invertebrates, found in a wide range of habitats. Having evolved long back they comprise about three-fourths of the animals living on Earth and include insects, spiders, crustaceans, centipedes, and millipedes. These diverse animals perform multiple functions and hence are ecologically important. Evolutionary biology and chemical-mediated ecology are today gaining ground mostly in developing countries, and most of the developing countries are situated in the tropics and subtropics. A deep understanding of the evolutionary processes is required to tackle the most pressing problems the human race faces on the planet Earth. Plants produce and emit a wide range of chemicals that provide information by a range of plant-associated arthropods. Plant body odors provide information on the ecology of plant–arthropod interactions that can be exploited for increasing crop productivity and sustaining biodiversity.

1.4.1 Urbanization and Arthropod Ecology

Traditional agricultural practices were in synchrony with nature and sustained natural balance; hence, their populations seemed to be a balance of existence between human beings, plants, and animals. But as the human race increased, the need for land also increased. Technological developments and advancements provided increased food production. Commercial farming was carried out over larger areas and land grew increasingly important as a source of food. This adversely affected the ecological balance of organisms resulting in the destruction of habitat of insects, arachnids, centipedes, and millipedes. Hedgerow vegetation at fringes and scrub patches were eliminated to expand the crop fields to extensive areas. This change in landscape forced terrestrial arthropods to migrate and seek food elsewhere, where it could be found abundantly. Before long they came back and discovered their old habitats but in a new form. The area had become a vast region of field crops, orchards, and vegetations providing rich natural functions. Arthropods started finding concentrate food supply in a single location and invaded these places in swarms. But their arrival was considered as plagues and infestations by humans. Moths, beetles, and locusts became problematic to farmers, since they were aggressive and attacked human beings who tried to drive them away. Several species of insects and other arthropods became pests and caused crop losses. This led to introduction of pesticides concocted from chemicals which could eradicate the pest's existence. Pesticides were successful as they slowly eliminated pest infestation and afforded protection to crops.

1.4.1.1 Ecological Importance of Terrestrial Arthropods

Very soon, pesticides were discovered to be harmful as they contaminated the soil, water, and air. Additionally, continuous agricultural studies revealed that crop yields were not as much as expected despite the absence of pest infestation. Scientists found winds to be insufficient to disperse the seeds. Since different crops had different systems of releasing their pollens and have different mechanisms of pollination and fertilization.

Several species of insects pollinate, and each species foraged for nectar and incidentally carried pollen. These species included bees, wasps, ants, butterflies, moths, flies, beetles, etc. Pollen grains became accidentally attached to their body, legs, and other body parts and were transferred to other agricultural crops. Soon it was discovered that most plants actually produced scents to send signals to insects that food in the form of nectar was available. Thus, plant volatiles and other semio-chemicals played a pivotal role in tritrophic interactions. Studies have found that only an estimated 10 % of pollen are used to produce flowers and in turn fruits. The rest are meant for the insects as enticements, to forage and open up their pollen sacs, chew on their seeds, or serve as agents for dispersal of pollens.

1.4.2 Pollination

Initially, the farmers went for large-scale production of maize because it did not require pollination, but this did not provide the ultimate solution to what was ailing the commercial agricultural industries. This happened in mostly temperate regions. In the tropics and subtropics, usually the new crop is cultivated in patches and later it occupies a large area.

Cattle, of the best livestock breed, are ideally fed with alfalfa, forage legumes, and silage and are the best sources of calcium and protein. Almost one-third of all cattle feeds are derived from agricultural products that relied on pollination in order to have good harvest. In developing countries in the tropics, cattle have alternate, diverse feeds, although they form poor substitutes.

As there were not enough insects foraging for food as inorganic fertilizers and pesticides affected their populations, most farms resorted to hand pollination. Even natural habitats of arthropods were no longer available because of rapid disturbance to natural settings. Forests became denuded as trees were being cut down, while most of the available land was put to alternate uses.

Soon farmers realized that manual pollination costed them as much as 25 % more in labor costs. An estimated annual cost of $11 million was being spent for hand pollination alone. The role of arthropods in pollination of crops, especially in arid and semiarid regions, is crucial. To remedy the situation, insects, mostly beetles, were imported and propagated in nest sites, which resulted in 20 % increase in crop yields and savings of about $115 million in dispensing with hand pollination. In tropics and subtropics, shrub and mild patches and roadside vegetation could help in sustaining pollinators and other beneficial arthropods.

Studies on management of plant pathogenic fungi and bacteria revealed the crucial role played by centipedes and millipedes in the process. The imbalance in the prey–predator relationship caused by inadequate number of centipedes and millipedes led to not only escalated plant diseases but also increased insect pests. The carnivorous arthropods which include cockroaches, spiders, mites, ticks, and all other insects which prey on smaller species maintain ecological balance. A good balance of these arthropods keeps the insect prey numbers under check.

In fact, ecological significance becomes economic importance as human beings find more use in the substances secreted or produced by different species of arthropods. Some of these are:

- Bees produce honey and their honeycombs contain beeswax.
- The pollen stored in honeycombs are rich mixture of vitamins, enzymes, and amino acids which have therapeutic benefits.
- Bee propolis, which is a dark resinous substance produced by bees as they feed on buds and barks of trees, was/is widely used for its antibiotic properties.
- Silk-producing arthropods, like those produced by caterpillars to protect their cocoons, were found to be strong enough to use and be woven into fabrics. Obviously, this discovery is the basis of ancient China's silk industry.
- In recent years, the spiders' web was discovered to have tensile strength; they became essential raw materials for Kevlar vests, fishing nets, surgical sutures, and adhesives as they contained natural antiseptics.
- The arthropod insect *Laccifer lacca* provides an organic resin known as shellac.

1.4.2.1 Ecological Role of Aquatic Arthropods

Aquatic arthropods comprise of members of sub phylum Crustacea such as shrimps, crabs, lobsters, prawns, water fleas, barnacles, and krill. The latter are small shrimp like aquatic creatures, and they represent the bottom of the aquatic arthropod's food chain. Arthropods in aquatic ecosystems play a vital role in the turnover of mineral elements and in regulating gaseous cycles. Aquatic arthropods that move about can easily migrate to places of food sources where they can find food to sustain their communities. Their appendages allow them to swim easily in the oceans' currents and movements. Krill, a basic food of larger aquatic arthropods, can be found abundantly almost anywhere, particularly where phytoplankton communities exist.

The main importance of these aquatic arthropod species to human beings is their function in the food chain and the indirect economic benefits mankind derives. For example, the blue crab provides livelihood to the coastal communities in the Gulf of Mexico, as major commercial capture fisheries provide jobs and other economic support. This has become the case in other tropical countries like India, Bangladesh, Sri Lanka, etc. Their annual catch is estimated at $40 million. However, due to the continuous spate of environmental problems, including the recent BP oil spill disaster in the Gulf, the presence of the blue crab in the communities' marsh edges and in sea grasses is said to be in critical conditions. Many aquatic arthropods are in peril due to pollution in major river systems.

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