one pointed and one round breast, both arms up, hair up. Dame 4 has a protective element, a concern for the living, very differently displayed than the unborn child of the *Venus of Laussel.* But it is Dame 5 that mainly catches our attention. Here in 1907 Picasso has painted "liberated" woman equal to man—she is a thinker, her left arm rests on her knee and chin, a classic thinker position and its thickness reads that she is formidably powerful in this field. While she has her back to us, she has twisted her head around not unlike the owl—the symbol of wisdom. She will not be taken for granted, yet her features with the large breasts, broad hips are the most childbearing and conventionally attractive.

Both works have a mystery and beauty. Both are acts of artistic creation separated by 23,000 years and deriving from vastly different cultures—one pre-agricultural, the other technological. And yet in spite of this, they explore similar themes with a similar "language." Just as we can appreciate the *Venus of Laussel*, one can imagine prehistoric people grasping the meanings of Picasso's work—concepts of womanhood. Picasso's work at the very least, then, may suggest ways in which art exists independently of the linguistic milieu of the artist.

The many common elements in these two works of art show an ability to communicate universally and a wealth of information. The type of information also gives us a sociological insight as to what was seen as important at the time. In both cases a tribe or person who has access to these artworks was able to see the key elements were not the size of the hands or facial characteristics but concepts.

Did art precede language and evolve as an advantageous form of communication? Art is old, every culture has it, and it communicates universals as well as packages of information reliably and efficiently. It does not require the anatomical specializations of language, and was reasonably well developed in Neanderthals. A hunter in the pre-linguistic and pre-writing age may depict information graphically and to someone who has never been on a hunt this would be valuable and informative. Fertility images may have served to reinforce group norms and beliefs. One might argue that memes communicated artistically shift survival from being based not simply on the biologically fittest but on the fittest who work within the language of art (create, interpret, read, re-create), and those who best make use of the information it transmits.

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— ORDE LEVINSON

ARTHROPODS

Arthropods (hexapods, myriapods, crustaceans, and chelicerates) are triploblastic Metazoa characterized by a segmented, hardened, chitinous cuticular exoskeleton and paired, jointed appendages. This exoskeleton is composed of a series of dorsal, ventral, and lateral plates that periodically undergo molting (ecdysis). Primitively, arthropods share a compound eye with a subunit structure that is unique within the animal kingdom. Arthropods are the most diverse creatures on Earth, with the number of known species approaching one million, and perhaps ten times as many left to discover. Arthropods are found on all continents, in the deepest oceans, and on the highest mountains. They can be extremely small ($<$ 1 mm, mites and parasitic wasps) to rather large ($>$ 4 m Japanese spider crabs). They are herbivores, predators, and parasites, solitary and intensely social. Not only are they hugely diverse, but they also occur in amazing numbers, constituting the great majority of animal biomass.

The geological history of arthropods extends over 525 million years (to the Lower Cambrian) with now extinct lineages of great diversity (e.g., trilobites). This history has undergone several dramatic rounds of extinction and diversification, most prominently in the Paleozoic era near the end of the Ordovician period and at the Permian-Triassic boundary. The Cambrian and Ordovician fossil record of arthropods is exclusively marine, but terrestrial forms (including arachnids, millipedes, and centipedes) appear from the Upper Silurian, more than 400 million years ago.

Today, there are four main lineages of arthropods: Hexapoda (insects), Myriapoda (centipedes, millipedes, and relatives), Crustacea (shrimps, crabs, lobsters, crayfish, barnacles, etc.), and Chelicerata (sea spiders, horseshoe crabs, and arachnids). There are several extinct groups including trilobites, marrellomorphs, anomalocaridids, and euthycarcinoids, which may well be equal in stature to those we know today.

Hexapoda. The insects are by far the most diverse known arthropod group (but mites might come close), with hundreds of thousands of species known to science. Hexapods are characterized by possession of three body tagma (head, thorax, abdomen), the second of which possesses three limb-bearing segments. Insecta comprise most of the diversity within the Hexapoda, insects being those hexapods with an antenna developed as a flagellum without muscles between segments. The hexapod head (like that of crustaceans and myriapods) has a large, generally robust mandible used for food maceration, a single pair of sensory antennae, and both compound and simple eyes. There are thirty commonly recognized hexapod "orders" further organized into several higher groups: Entognatha (those with internal mouthparts)—Protura, Diplura, and Collembola (springtails); Archaeognatha (bristletails); Zygentoma (silverfish); Ephemerida (mayflies), Odonata (damselflies and dragonflies); orthopteroids—Plecoptera (stoneflies), Embiidina (web spinners), Dermaptera (earwigs), Grylloblattaria (ice insects), Phasmida (walking sticks), Orthoptera (crickets, grasshoppers), Zoraptera, Isoptera (termites), Mantodea (praying mantises), Blattaria (roaches); hemipteroids—Hemiptera (true bugs and hoppers), Thysanoptera (thrips), Pscoptera, Pthiraptera (lice); and the Holometabola—Coleoptera (beetles), Neuroptera (lacewings, dobsonflies, snakeflies), Hymenoptera (bees, ants, and wasps), Trichoptera, Lepidoptera (moths and butterflies), Siphonaptera (fleas), Mecoptera (snow fleas), Strepsiptera and Diptera (flies). Basal hexapods (Protura, Collembola, Diplura, Archaeognatha, and Zygentoma) are wingless, whereas the more derived insect orders generally possess two pairs of wings. The Neoptera (Pterygota—winged insects except for the "paleopteran" ephemerids and odonates) possess wing hinge structures that allow their wings to be folded back over their abdomen. Those insects with complex development, Holometabola, are the most diverse, with beetles leading the way with over 300,000 recognized species. Insects are found all over the world in terrestrial and freshwater habitats, and many have economic importance as pests, or medical interest for causing or carrying disease. There is an extensive fossil record of insects from the Devonian *Rhyniella*, through other Paleozoic and Mesozoic deposits, to the dramatic and beautiful amber-preserved insects from Lebanon, the Baltic, and the Dominican Republic.

Myriapoda. The centipedes, millipedes, symphylans, and pauropods are multilegged soil-adapted creatures. Generally without compound eyes (except for scutigeromorph centipedes), but possessing a single pair of sensory antennae, the myriapods are most easily recognized by their large numbers of legs and the trunk not being differentiated into distinct regions (tagmata). Almost all postcephalic segments bear a single (centipedes, pauropods, symphylans) or double pair of legs (millipedes) numbering into the hundreds in some taxa. These arthropods are generally small (< 5–10 cm), but there are several dramatically larger examples (*Scolopendra gigantea*) at 30 centimeters or more. There are four main lineages of myriapods: Diplopoda (millipedes), Chilopoda (centipedes), Pauropoda, and Symphyla. The basic division among myriapods lies between the Chilopoda, which have the genital opening at the posterior end of the body, and the other three lineages, grouped as Progoneata on the basis of the genital opening being located anteriorly on the trunk, behind the second pair of legs. The millipedes are the most diverse group, with approximately 10,000 species. The chilopods are the other diverse group (approximately 2,800 known species). Pauropods and symphylans are less speciose, with a few hundred described taxa. In general, myriapods are soil creatures feeding on detritus, with the centipedes exclusively predatory and possessing a modified fang and the ability to deliver toxins to their prey. It is probable but not universally agreed that the myriapods share a single common ancestor. The movement of the head endoskeleton, structure and musculature of the mandible, and most DNA sequence evidence support the single origin of Myriapoda, but several hypotheses place myriapod lineages with hexapods. There are few well-preserved myriapod fossils, but the extant chilopod order Scutigeromorpha and the diplopod group Chilognatha both have fossil representatives from the Late Silurian. The extinct group Arthropleurida, thought to be members of the Diplopoda, may have reached 2 meters in length.

Crustacea. Crustaceans are perhaps the most morphologically diverse group of arthropods (over 30,000 species known), with huge variation in numbers and morphology of appendages, body organization (tagmosis), mode of development, and size (< 1 mm to > 4 m). These creatures are generally characterized by having two pair of antennae (first and second), biramous (branched) appendages, and a specialized swimming larval stage (nauplius). They usually possess both simple ("naupliar") and compound eyes (the latter frequently stalked). Like myriapods and hexapods, crustaceans possess strongly sclerotized mandibles that are distinguished by frequently having a segmented palp. The Crustacea are generally marine, with several freshwater and terrestrial groups (e.g., some isopods, the wood lice). Crustacean phylogeny is an area of active debate, with the status of some long-recognized groups under discussion. Currently, several higher groups are recognized, with their interrelationships (and even interdigitiation) unclear: Remipedia (twelve species; *Speleonectes*, *Lasionectes*, and three other genera), Cephalocarida (few species; *Hutchinsoniella* and three other genera), Branchiopoda (1,000 species; fairy shrimp, water fleas, tadpole shrimp, clam shrimp), Maxillopoda (10,000 species; copepods, barnacles, ostracods, fish lice), and Malacostraca (20,000 species; mantis shrimp, crayfish, lobsters, crabs, isopods, amphipods). Many of the debates on crustacean relationships center on the position of the recently discovered remipedes as either the most basal lineage resembling, in some respects, the first Crustacea or a more derived position having little to do with crustacean origins. The fossil group Phosphatocopina are probably the earliest Crustacea or the closest relatives of the extant Crustacea, first occurring in the Lower Cambrian in England, and being known from fine preservational quality (notably in the three-dimensional Orsten Cambrian fauna).

Chelicerata. The sea spiders, horseshoe crabs, and arachnids are characterized by division of body segments into two tagmata: prosoma and opisthosoma (generally), and the first leg-bearing head segment being modified into chelifores or chelicerae. With the exception of horseshoe crabs (the American *Limulus* and the Asian *Carcinoscorpius* and *Tachypleus*), chelicerates do not possess compound eyes, and none have antennae. Horseshoe crabs and arachnids have one pair of median eyes, whereas sea spiders have a second pair. Of the three main divisions of chelicerates (Pycnogonida—sea spiders [1,000 species], Xiphosura—horseshoe crabs [four species], and Arachnida—spiders, scorpions, etc. [60,000 species]), the sea spiders and horseshoe crabs are marine and the remainder terrestrial, with the exception of some groups of mites. Many groups of Acari (mites and ticks) are parasites of plants and animals, both vertebrates and invertebrates, and being ecto- and endoparasitic, mostly of respiratory organs. The arachnids are the most diverse component of the Chelicerata, with the Acari and Araneae (spiders) constituting the vast majority of taxa. Other arachnid groups include Opiliones (harvestmen, daddy longlegs), Scorpiones (scorpions), Solifugae (sun, camel, or wind spiders), Pseudoscorpiones ("false" scorpions), Ricinulei, Palpigradi (micro-whip scorpions), Amblypygi (tailless whip scorpions or whip spiders), and Uropygi (vinegaroons). The Paleozoic eurypterids are an aquatic (mostly brackish water) group, generally considered to be the closest relatives of Arachnida, though some workers consider them especially related to scorpions. The largest eurypterids are 1.8 meters long, among the largest arthropods ever. The sea spiders graze on corals, anemones, or seaweeds, and vary in size from quite small (< 1 cm) to almost a meter in leg span. Horseshoe crabs and arachnids are almost entirely predatory, with spiders the dominant arthropod predators in many environments. Horseshoe crabs scavenge and prey on small animals in seaweeds, and like the Opiliones, they digest their food internally. Most arachnids, however, digest food extraorally, ingesting their prey in the form of digested fluids.

Close Relatives. The closest relatives of the arthropods are the enigmatic water bears (Tardigrada) and velvet worms (Onychophora). All of these animals share paired appendages and a chitinous cuticle. There are approximately 800 species of tardigrades that live in marine, freshwater, and terrestrial habitats. Terrestrial tardigrades are mostly found on mosses and bryophytes and may occur in huge densities (hundreds of thousands to millions per square meter). Tardigrades are small (between 150 and 1,000 microns), have a round mouth, four pairs of legs, the last one being terminal, and, like arthropods and a few other taxa, grow by molting. Terrestrial tardigrades live in extreme environments supporting desiccation or freezing by entering into cryptobiosis. Tardigrades have been experimentally subjected to temperatures between −272°C and +340°C, or between 160,000 psi to pure vacuum, excessive concentrations of gases, and radiation, and returned to active life. The cryptobiotic stage has been recorded to last over 100 years, and in this stage they can be dispersed by wind. The Onychophora are a group of exclusively terrestrial, predatory creatures that live in humid temperate (mostly Southern Hemisphere) and tropical forests. The velvet worms are characterized by a soft body with pairs of "lobopod" walking limbs, a pair of annulated antennae, jaws, and oral ("slime") papillae. About 150 extant species have been named, but there were many more types including marine "armored" or plated lobopods in the Early Paleozoic. Onychophorans and arthropods share a dorsal heart with segmental openings called ostiae, and a unique structure of the nephridia, the excretory organs. Lack of these organs in tardigrades may be due to miniaturization. It is thought that the Tardigrada are the sister taxon (closest relative) of the Arthropoda and the Onychophora the next closest relative.

More Distant Relatives. It has been long thought that there was an evolutionary progression from wormlike creatures, to lobopodous forms like Onychophora, to modern arthropods. This was expressed in the "Articulata" hypothesis that linked annelid worms (polychaetes and oligochaetes, including leeches) to the Onychophora and Arthropoda. Recent work, especially from DNA sequences, has largely replaced this view, allying arthropods, tardigrades, and onychophorans with other molting creatures such as the nematodes, kinorhynchs, and priapulids in the Ecdysozoa (after ecdysis or molting); and uniting the annelids with molluscs, nemerteans, sipunculans, and entoprocts in the Trochozoa (or Lophotrochozoa of some authors).

Extinct Lineages. No doubt there are more extinct than extant lineages of arthropods. More likely than not, most will remain unknown to science, but several major groups we do know about have a great effect on our notions of higher level relationships among the arthropods (living and extinct). Trilobites are the best known group of extinct arthropods. First known from the Lower Cambrian, trilobites had huge radiations in the

Paleozoic. Trilobites were an exclusively marine group (4,000 species described) characterized by two longitudinal furrows dividing the body into three lobes (hence the name). The body segments are organized into three tagma (cephalon, thorax, pygidium). Trilobites possessed compound eyes, a single pair of antennae, and had biramous appendages. All postantennal appendages in trilobites are basically similar in structure. Trilobites are closely related to the Chelicerata, together with numerous other extinct lineages constituting the group Arachnata. Anomalocaridids are a group of large (up to 2 m), predatory Cambrian arthropod relatives. With unmineralized, but sclerotized cuticle, they were known initially only by their raptorial feeding/grasping appendages, which were anterior to a circular mouth that was surrounded by a ring of plates. Their phylogenetic affinities are uncertain, but most recent work places them in the stem group of the Arthropoda, probably more closely related to extant arthropods than are tardigrades. Marrellomorphs are a clade known from the Burgess Shale (Middle Cambrian, Canada) and Hunsrück Slate (Lower Devonian, Germany) that possess two pairs of antenniform limbs and two pairs of long spines that curve back over the body. *Marrella* is the most abundant arthropod in the Burgess Shale fauna. Euthycarcinoids are a somewhat enigmatic group from the Lower Silurian to the Middle Triassic with potential affinities with myriapods or crustaceans. They possessed a single pair of antennae and numerous pairs of uniramous legs. Lopodian taxa were largely unknown until recent soft-part preserved specimens (mainly from China and from the Burgess Shale) were found. The marine lobopodians are thought to be related to living terrestrial Onychophora or Tardigrada, and possessed elaborate spines and armored plates. The "Orsten" fauna of Sweden contains amazingly well-preserved three-dimensional Upper Cambrian fossils, most importantly of basal crustacean taxa. Several of these forms (e.g., *Martinssonia*) are important to understanding the origins and relationships of the Crustacea. Among the most productive Paleozoic fossil deposits are the Burgess Shale, Chengjiang, Orsten, Rhynie Chert, Gilboa, and Mazon Creek deposits.

Arthropod Interrelationships. The question of arthropod relationships has been and is still unsettled. Of the living taxa (Chelicerata, Crustacea, Myriapoda, Hexapoda), it seems clear that those groups that possess mandibles (robust, sclerotized, chewing mouthparts), Crustacea, Myriapoda, and Hexapoda, share a unique common ancestor. The biting edge of mandibles is formed by the same segment, the coxa, of the same limb (third limb-bearing segment in Crustacea). Within this group things become less clear. There are two main competing hypotheses: Tracheata (myriapods and insects) and Tetraconata or Pancrustacea (crustaceans and insects). The Tracheata hypothesis is supported by anatomical evidence, notably the similar tentorial head endoskeleton, an absence of limbs on the head segment (intercalary segment) innervated by the third brain ganglia, and similar respiratory and excretory organs. Molecular sequence data and an alternative set of anatomical features, notably eye structure and neurogenesis, support the Tetraconata.

One of the major ecological questions surrounding arthropod evolution is the question of the number of invasions of land, or at least the number of transitions between marine and terrestrial environments. The origin of the Arthropoda is undoubtedly marine, but the Onychophora, Arachnida, and several Malacostraca have independently invaded land. If the group Tracheata is upheld, there was one more invasion by the common ancestor of myriapods and insects. If, however, crustaceans and insects are the closest relatives, two additional transitions are implied. Several other issues remain unresolved as well, especially regarding the placement of the Pycnogonida, which could well constitute the sister group to all the remaining extant arthropods, and the relationships of extinct lineages both to living taxa and the overall scheme of arthropod history.

[*See also* Animals; Insects.]

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ARTIFICIAL LIFE

Evolution in nature is characterized by many levels of hierarchy, including the gene, the individual, the population, and the ecosystem. Intensive study can be made within any of these levels of organization, or others, but the interactions across these levels of hierarchy are also important in determining the patterns of evolution. For