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Primer

Chelicerates

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Figure 1. Examples of chelicerate diversity.
Left column, top: *Isometrus* sp. (Scorpiones). Left column: *Anoplodactylus insignis* (Pycnogonida). Middle column, top: *Mastigoproctus giganteus* (Thelyphonida). Middle column, middle: *Pseudocellus pearsei* (Ricinulei). Middle column, bottom: *Eremobates* cf. *tuberculatus*. Right column, top: *Parasteatoda tepidariorum* (Araneae). Right column, middle: Unidentified chernetid (Pseudoscorpiones). Right column, bottom: *Limulus polyphemus* (Xiphosura). Photographs courtesy of Jesús A. Ballesteros (spider), Peter Funch (horseshoe crab), and Gonzalo Giribet (all remaining images).

Compared to other arthropods, such as crustaceans or insects, the term 'chelicerate' often does not evoke a similar sense of recognition or familiarity. Yet the subphylum Chelicerata has been encountered by every living person today, frequently to the effect of fear, awe, or outright revulsion. Chelicerates include such familiar groups as spiders, scorpions, mites, and ticks, as well as an array of bizarre and unfamiliar forms, such as vinegaroons, camel spiders, and hooded tick spiders (Figure 1).

The fascination of humans for chelicerates stretches into antiquity. Greek mythology saw the anatomy of the spider as a result of Athena's punishment of the haughty Arachne, a skilled weaver who boasted of her prowess at the loom as superior to Athena's own. A scorpion, sent by a jealous Apollo to slay the hunter Orion, is among the constellations and appears in horoscopes today. In an earlier mythology, Serket, the Egyptian deification of the scorpion, was the goddess of nature, fertility, and antidotes to venomous stings.

There are about 120,000 species of chelicerate described, making them the second largest sub-phylum. Two groups of chelicerates are marine, the horseshoe crabs (Xiphosura) and the sea spiders (Pycnogonida), which together constitute less than 2% of modern chelicerate diversity. The remainder of the group is terrestrial and are collectively called arachnids (formally, Arachnida); these eight-legged arthropods represent one of the most successful animal radiations on land (Figure 2).

Like all arthropods, the body of a chelicerate is composed of segments (though these are often not apparent in the adults of some orders), as well as jointed legs. The architecture of the chelicerate body plan distinguishes them from other groups. Fundamentally, all chelicerates are divided into two body regions, the anterior prosoma (the region that bears the eyes, brain, mouthparts, and walking legs) and the posterior opisthosoma (the region that bears respiratory and reproductive organs). The seven-segmented prosoma bears six pairs of appendages: the chelicerae, which are typically used for feeding; the pedipalps, which are unique to Chelicerata and serve an array of functions; and four pairs of walking legs.

However, there are many variations of this basic plan. As an extreme example, modern sea spiders have lost the opisthosoma altogether, with most of their organ systems distributed within the legs. In addition, sea spiders bear an additional pair of appendages, the ovigers, which are used by males to carry egg masses deposited by females. In some arachnid groups, such as mites, ticks, and hooded tick spiders (the order Ricinulei), the hatchling is often hexapodous, and does not obtain the fourth pair of legs until after it molts. Finally, some groups have lost one or more sets of appendages altogether, like the gall mite family Eriophyidae, which is four-legged as an adult.

The name Chelicerata is derived from the chelicera, the anterior-most appendage. Whereas the chelicerae of such groups as daddy-long-legs, scorpions, and horseshoe crabs are chelate (appearing distally as a pair of scissors), some groups have evolved highly specialized chelicerae. In ticks, the chelicerae are part of a complex of mouthparts that are specialized for blood-feeding. In spiders, the chelicerae bear the fangs and house part of the venom gland, which can occupy much of the length of the prosoma in some groups. In general, most of the modern chelicerate species are predators or scavengers.

Many lineages of chelicerates have captured scientific and public interest. Spiders are renowned for the biomechanical properties of their silks, with different types of silk conferring different degrees of strength, elasticity, and adhesion. Some groups of daddy-long-legs (the order Opiliones) are markedly poor transoceanic dispersers, and thus serve as the mainstay of biogeographic inquires focused on how continental drift has shaped the diversification of ancient animal groups. Two of the venomous orders, spiders and scorpions, include many species notorious for their toxicity to humans, with envenomation constituting a serious health hazard in some parts of the world. Similarly, another pair of orders, the mites and ticks, include numerous disease vectors that affect human health.

An elusive evolutionary history

Despite the advent of genome scale datasets and improvements in phylogenetic methods, the phylogeny of chelicerates remains largely unresolved. Paleontologists and molecular phylogeneticists hold markedly differing views of chelicerate phylogeny, with some even contesting the monophyly of Arachnida. This ground of contention stems from several peculiarities of chelicerates, and involves ancient origins, rapid radiation, extinction and unequal rates of evolution in the group.

The first *bona fide* chelicerates to appear in the fossil record date to the Middle Cambrian (ca. 500–510 million years ago) and consist of marine groups, including the putative larvae of sea spiders. Body fossils recognizable as modern chelicerate orders appear later, in the Ordovician (the oldest horseshoe crab fossil is ca. 445 million years old) and the Silurian (the oldest sea spider and scorpion body fossils). In the early arachnid fossil record, all the major lineages appear in a short window of time during the Devonian, a phenomenon suggestive of an ancient, rapid radiation at the base of arachnids.

Separately, various lineages of chelicerates have experienced extinction to differing degrees. Entire orders of Chelicerata have gone extinct, like the sea scorpions (Eurypterida, which includes some of the largest arthropod fossils, over two meters long). Extinctions on this scale are problematic for inferring phylogeny because extinct orders are difficult to integrate into modern phylogenetic datasets as tips on a tree. Some modern lineages exhibit the signature of high rate of lineage turnover as well. Horseshoe crabs have persisted for nearly 450 million years, but the order is represented today by just four species, whose most recent common ancestor (MRCA) is estimated to have lived in the Cretaceous. Modern scorpions represent a small branch of a once diverse Paleozoic assemblage that may have included some aquatic forms. The result of such episodes of extinction is that the datasets of paleontologists and molecular phylogeneticists differ markedly in composition. Datasets of chelicerate paleontologists are taxonomically richer, but have orders of magnitude fewer phylogenetic characters than molecular datasets.

A further challenge to consensus in chelicerate phylogeny results from unequal rates of evolution across arachnid orders. Specifically, four orders of miniature arachnids — mites, ticks, pseudoscorpions, and palpigrades — exhibit much faster sequence evolution than their larger-bodied counterparts. The placement of these rapidly evolving lineages in molecular phylogenies is unstable and prone to a systematic error called long branch attraction; these four orders are drawn together and typically fall outside of horseshoe crabs in molecular phylogenies, resulting in a paraphyletic Arachnida (i.e., with horseshoe crabs nested deeply inside the arachnid tree). Theoretically, this artifact can be overcome in part by improved taxonomic sampling to ‘break’ the long branches. In the case of chelicerates, this strategy is limited in effectiveness; owing to the extinction experienced by various chelicerate orders, there is a finite limit to the benefits of taxonomic sampling. As a case in point, the ancient order of horseshoe crabs is survived today by only four species spanning three genera.

The chelicerate tree of life, therefore, is one of the most challenging puzzles in phylogeny, featuring a combination of ancient, rapid radiation, limits to taxonomic sampling imposed by extinction and lineage turnover and multiple long-branch orders. The most difficult aspect of evaluating arachnid monophyly is that there are very few morphological characters or other external arbiters (e.g., genome duplication, rare genomic changes) to support the existence of arachnids as a natural group.

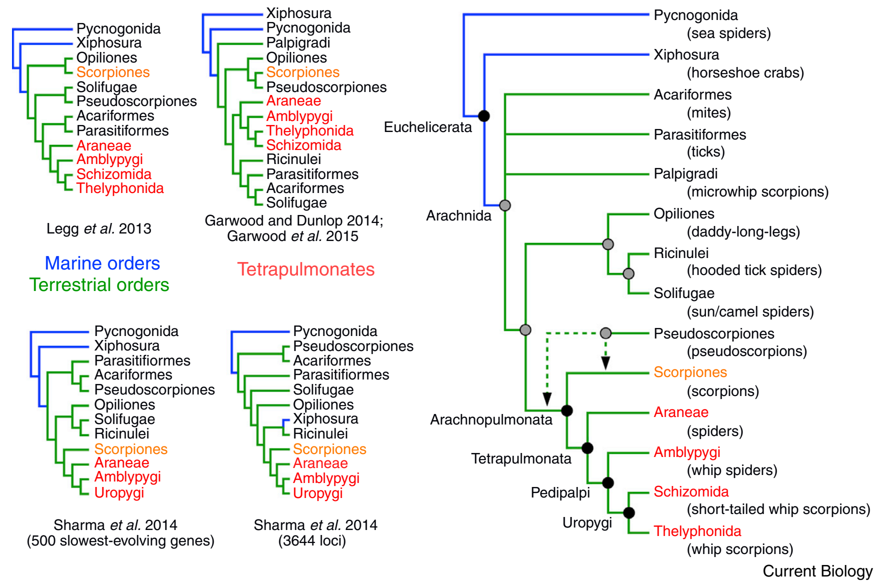

Figure 2. Left: Historical hypotheses of chelicerate ordinal relationships based on morphological analyses (top) and phylogenomic datasets (bottom).
Right: Consensus tree topology of chelicerate relationships, largely based on slowly-evolving genes. Black circles on nodes indicate robustly resolved nodes. Gray circles on nodes indicate nodes that can be recovered with high support, but are sensitive to the addition of fast-evolving datasets.

Nevertheless, some parts of the chelicerate tree have been successfully resolved by molecular data (Figure 2). After some decades of dispute, phylogenomic datasets have solidified the placement of sea spiders as the sister group of the remaining chelicerates. Phylogenomic data have also strongly supported the sister group relationship of scorpions and tetrapulmonates (spiders and three related orders of arachnids), a group called 'Arachnopulmonata', which is united by the presence of an ancient genome duplication at its base and possession of a unique arachnid respiratory organ called a 'book lung'. The book lung comprises dense stacks of lamellae organized like the pages of a book, with pairs of these organs occurring on the ventral surface of the opisthosoma of arachnopulmonates.

This derived position of scorpions in the tree is interesting because paleontologists have interpreted a large assemblage of Paleozoic scorpions to be aquatic. If this is correct, the position of scorpions implies (even if Arachnida is monophyletic) that at least two terrestrialization events have occurred in chelicerate history — one transition at the base of Arachnida and one other at the base of the modern scorpions. The relationships of the remaining arachnid orders, and particularly of mites and ticks, remain shrouded in mystery.

Chelicerate behavior

The anatomy of many chelicerates, as well as the potency of some of their venomous constituents, may be partly responsible for their broad perception as raptorial, predatory animals. Indeed, most of the modern chelicerate species are predators or scavengers, and some species are even dangerous to humans, such as the notoriously venomous black widow and brown recluse spiders, and several species in the scorpion family Buthidae, whose sting is lethal to humans. But the ferocity of their reputation belies the intricacies of their behavior, particularly when offspring care is concerned. Various groups of chelicerates have independently evolved forms of parental care. Horseshoe crabs, for instance, will migrate seasonally to beaches to spawn *en masse* during full moon night, with females laying thousands of eggs in pebbly sand. The concealed eggs that survive predation will hatch and the hatchlings — called trilobite larvae — will complete development in the adjacent tidal flats. Sea spiders take brood care one step further, with males adhering fertilized egg masses to their ovigers (egg-carrying appendages) with the aid of secretions from their cement glands. The fathers thus tend to the offspring.

Many arachnids are no less dedicated as parents. Within the tetrapulmonates, females of vinegaroons and whip spiders carry their eggs in a brood sac underneath the opisthosoma. Upon hatching, the juveniles will migrate to the dorsum of the female's opisthosoma, where she will bear them until they are old enough to disperse and begin feeding. In scorpions, females are exclusively live-bearing, but the form of brood care is the same, with the clutch of scorplings carried on the female's back after birth. Spiders exhibit an array of parental care behaviors, but will typically encase eggs in a cocoon that is maintained in a web or a burrow. Exceptions include species of wolf spiders, where females will carry the cocoon with them, and again, carry spiderlings on their back when the eggs hatch.

In some tropical daddy-long-legs species, males will sometimes form territories and defend harems of females from rivals. The territorial male will fertilize several females, which lay eggs and guard their broods. As in many animals, a subset of these species includes an alternative mating strategy: smaller 'effeminate' males that superficially resemble females will travel between harems and attempt copulations. In other daddy-long-leg species, the role of the sexes is reversed, with the males tending to the care of eggs deposited by multiple females, a condition comparable to sea spiders.

An extreme form of brood care, matriphagy, has been reported in some arachnids, such as pseudoscorpions. All pseudoscorpions exhibit some degree of parental care, with females carrying the eggs underneath their opisthosoma until hatching; in some groups, females will construct brood chambers or nests for nymphal care. In the case of one Neotropical species, *Paratemnoides nidificator*, conditions of food deprivation cause the mother to leave her nest and submit to predation by her offspring. This behavior is hypothesized to reflect a last-ditch solution by the female to provision the nymphs.

Most chelicerate species are solitary, though a form of sociality has evolved repeatedly in some groups of spiders, which will form colonies of thousands of individuals sharing a web and cooperating in prey capture. But even in solitary species, courtship behavior is diverse and sometimes visually spectacular. Some arachnid orders (e.g., scorpions, pseudoscorpions, vinegaroons, whip spiders) perform a *promenade á deux*, a courtship dance where the male and female partner face each other and move back and forth, while the male searches for a suitable surface to deposit a spermatophore (sperm packet). In some species of the scorpion family Diplocentridae, venom is involved, with the male anesthetizing the female with his sting during the dance. In groups such as peacock spiders, the courtship dance is composed of both complex movements by the male, as well as a stunning display of color.

Developmental disparities

Embryonic development in chelicerates (Figure 3) follows some broadly conserved patterns. Embryos develop the prosoma first and add segments posteriorly. The appendages develop as small buds of tissue, which then elongate and later form segment boundaries. In later embryonic stages, the mouth migrates to a subterminal position below the chelicerae and the eyes are formed. In some species of daddy-long-legs, the longest leg pair develops wrapped around the body in order to accommodate its length.

The embryonic development of spiders is unusual in several aspects. The early embryo of a spider bears a particular region called a cumulus, a group of cells that acts as the organizer of the major body axes.

When a cumulus is grafted from one embryo into another, the result is the generation of a second anterior-posterior axis — a two-headed embryo — and a recapitulation of a classic experiment in embryology on the Speemann-Mangold organizer of amphibian embryos. Recent work has begun to reveal the molecular mechanisms that underlie the formation, migration, and regulative activity of the cumulus. It is not known whether a cumulus is common to all chelicerates; data from ticks and horseshoe crabs suggest that a cumulus may not be restricted to spiders, but the embryos of these groups are not as well understood as their spider counterpart. The instability of arachnid relationships does not aid the reconstruction of cumulus evolution either.

Separately, spider embryos undergo an unusual process called inversion, wherein the embryo will split along the ventral midline partway through its development. The two halves of the embryo will migrate dorsally; the opisthosomal segments meet in the dorsal midline, followed by the prosomal segments. The embryo thereafter retracts to fuse once more along the ventral midline. Ventral closure of the prosoma occurs first, then the opisthosoma. The outcome of this process is the internalization of the yolk, which sustains the spider embryo in its first postembryonic stage (a non-feeding 'larval' stage where they barely move). The significance of this event is not understood, because these embryonic movements are clearly not required for internalization of yolk. In scorpions and harvestmen, the yolk is internalized by simple upward growth on the sides of the body, and a similar hatchling is produced. Only in orders of arachnids closely related to spiders (e.g., Thelyphonida and Amblypygi) has inversion been reported and may represent a derived feature uniting the tetrapulmonates (spider and their allies; Figure 1).

Spiders are also distinguished from other chelicerates by the presence of spinnerets, the posterior appendages that bear the spigots (silk-spinning organs) and develop on two segments of the opisthosoma. Intriguingly, the spinnerets, as well as respiratory organs like book lungs, resemble the limb bud primordia of earlier stages' walking legs and occur in the same region within each segment (as paired ventral organs, along the posterior boundary of the segment). In such groups as tarantulas, the spinnerets are fully segmented and articulated; they can be moved at the joints in the same way as walking legs. Which appendages spinnerets are homologous to remains in dispute; they are thought to be the descendants of ancestral gills, modified walking legs, or independent derivations that have coopted some leg-patterning genes.

After hatching from the egg, arthropods grow by a series of molts, wherein its exoskeleton is shed and a new one is deposited at each molt. There is a general distinction in the patterns of growth of marine and terrestrial arthropods. Comparably to the distantly related marine crustaceans, the marine orders of Chelicerata exhibit indirect development via an incompletely segmented hatchling. In sea spiders, the typical protonymphon larva has four segments and bears three sets of appendages; at each molt, it will add segments at the posterior end of the body, until the final arrangement (usually, an eight-segmented body plan) is achieved, and subsequent molts will contribute only to growth of the body. Horseshoe crabs have a rather unusual mode of development; the embryo will undergo four molts in the egg prior to its hatching and is visibly mobile in later molts inside the embryo. Paralleling the sea spiders, the embryonic stages are incompletely segmented and will add segments to the posterior end of the body at each molt. The hatchling itself is called the 'trilobite larva' after its superficial resemblance to the renowned extinct arthropods; it too will add posterior segments to the body with further molts.

By contrast, arachnids are typically fully segmented upon hatching and thus resemble miniature adults when they leave the egg. The completion of segmentation during embryogenesis in the terrestrial chelicerates is paralleled by a similar mode of development in terrestrial hexapods

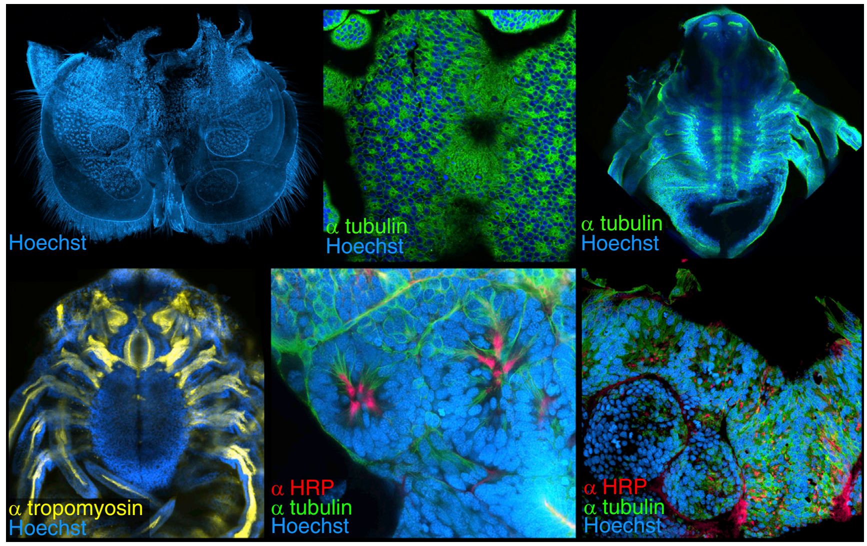

Figure 3. Confocal fluorescence microscopy highlights facets of chelicerate development.
Top row, left: The first book gill of a trilobite larva. Top row, middle: Early neurogenesis in the daddy-long-legs *Phalangium opilio* begins with inward migration of cells from the ectoderm (the regularly spaced concentrations of tubulin, in green). Top row, right: In a later stage, the ventral nerve cords of this daddy-long-legs are visible. Bottow row, left: Embryonic muscles in prosoma of *Phalangium opilio*. Bottow row, middle: Embryonic development of lateral eyes in the spider *Parasteatoda tepidariorum*; the antibody HRP marks elements of the central nervous system. Bottow row, right: Posterior view of the same embryo. The black "V"-shaped space in the top right of this panel shows the splitting of the spider embryo (inversion). The two lobe-shaped structures to the lower left of this panel are the developing anterior (larger lobe) and posterior (smaller lobe) spinnerets—the silk-spinning organs of the spider.

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(insects and allies) and may reflect an ancient and convergent solution to life on land.

Chelicerates and humans

Several aspects of human life are directly affected by the biology of chelicerates. The blood of the Atlantic horseshoe crab, *Limulus polyphemus*, is harvested in large quantities annually for the preparation of *Limulus* amoebocyte lysate, which is used for the detection of Gram-negative bacteria. Overharvesting of *L. polyphemus* has led to conservation concerns for North Atlantic populations.

Certain arachnid groups have direct impacts on human health, namely, as disease vectors, agricultural pests, and parasites. As examples, dust mites (multiple species and genera, but frequently associated with the genus *Dermatophagoides*) can cause or exacerbate allergies and asthma. The Varroa mite (*Varroa destructor*) adversely affects apiculture and severe infestations can eliminate honey bee colonies. Spider mites (Tetranychidae) are pests of some agricultural products and require management. Many species of ticks are vectors of disease. Examples of tick-borne illness include Lyme disease tularemia, anaplasmosis, spotted fever, and Rickettsiosis.

In tropical and subtropical parts of the world, encounters with hazardous arachnids (principally spiders and scorpions) constitute a public health concern. Annually, it is estimated that 3250 people are fatally stung by scorpions, with 1000 of these in Mexico alone. Modern research efforts are aiming to harness the potency of arachnid venoms for biomedical advancement. Components of both spider and scorpion venoms are believed to hold potential for pain suppression. Scorpion venom has been used for years as an alternative treatment for cancers in parts of the Caribbean, and its potential applications for targeting tumors have gained significant attention in the past few years.

Biomedical applications of spider silk are similarly of great interest. Natural spider silk bears many desirable properties and has thus been proposed as a key target for ongoing research efforts. Silk genes have been sequenced, isolated, and inserted into cell cultures and transgenic mammals to increase silk yield. Other approaches have targeted the production of synthetic silk, which holds the potential to surpass the properties of natural silk, exceed the strength of metals, and serve such needs as the production of protective fabrics and fulfilling uses in engineering and medicine. To date, a major challenge for both natural and synthetic spider silk remains its production in sufficient quantities for biomedical use.

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African bush elephants respond to a honeybee alarm pheromone blend

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We here report the responses of African bush elephants (*Loxodonta africana*) to a crude approximation of the honeybee alarm pheromone blend. We show that the elephants had an avoidance response to the semiochemical blend. The use of honeybee alarm pheromones to manage elephant movements in a non-invasive manner, using natural cues to which elephants may have an evolved response, holds potential for development of new options for an integrated system for elephant movement management and protection.

African elephants may inflict damage on farming areas, infrastructure, and desirable habitats in conservation areas, exacerbating wildlife-human conflict [1,2]. Conventional management action often involves killing the ‘problem animals’, often accompanied by intensified calls to reinstate elephant culling programs within conservation areas. Developing passive means of managing elephant behavior, movement and environmental impacts is thus a priority in many African countries, and other parts of the world. African elephants are strongly deterred by African honeybee (*Apis mellifera scutellata*) colonies, and methods have been developed to protect small farms and trees from elephants using bee hives [3,4]. While the use of hives is an effective natural option, there are logistic issues with maintaining large numbers of bee hives necessary for the protection of extensive fence-lines (e.g. large national parks) [1]. Elephants avoid the sight of beehives [1] and honeybee sounds [5]. However, in addition to sound and visual stimuli, African elephants have an acutely developed sense of smell, and much of their behavior is mediated by smell, rather than sound or visual stimuli [6,7].