

A deeper phylogeny of jumping spiders (Araneae: Salticidae)

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In a recent paper, Maddison et al. (2014) described their study of *the deep phylogeny of jumping spiders*. This study represented the use of DNA sequencing to resolve some of the most ancient divisions of evolving salticid clades, in particular those that took place prior to the Cenozoic radiation of the Salticoida. Although few spiders other than salticids were considered in this study, it did present a hypothesis of phylogeny (fig. 15) that placed the dionychan Philodromidae and the non-dionychan Oxyopidae at an equal distance from the Salticidae, more closely related to each other than to the dionychan jumping spiders. However, this relationship has not been supported by the subsequent studies of spider phylogeny that are reviewed here (e.g. Wheeler et al. 2017), which maintain the status of the Dionycha as a monophyletic clade.

The intent here (Figure 1) is to go *much deeper*, back in time more than a billion years, to follow the series of evolutionary innovations (or grades) that have led to the jumping spiders that we can observe today. Today we see the Salticidae as a large tree with many growing, or dying, branches, but not as a single lineage. If we venture into the past, however, we see the first salticid, a single species, as the final product of a single, long line of successful reproduction and evolution, from grade to grade. In this most improbable sequence of events, only one species would lead us forward at each step along the way. All other species alive at each point in time either went in a different direction, or (more likely) they became extinct. In fact, we are far more likely to find the fossils of species that became extinct along the way, than those that survived to evolve to the next grade. Here we will attempt to identify only a few of the many generations, or even species, that led to the Salticidae.

This journey is made possible by a large number of recent studies, almost entirely based on DNA-sequencing, of protist and animal phylogeny. In many cases, more recent work on this phylogeny reverses hypotheses set forth in earlier work, and it remains important to realize that even these recent proposals are hypothetical, always subject to continued testing and revision. Nonetheless, a fascinating story of innovation emerges, one that portrays a radical shift from the hypotheses of animal phylogeny set forth in the 20th century, almost entirely based on comparative morphology. Noteworthy among recent discoveries is the recognition of a long history of molecular evolution, for example the origin of light-sensitive opsins at the *Neuralia* grade (Figure 1: grade 7; Feuda et al. 2012). Even more noteworthy is the discovery of a conserved framework of regulatory genes (*homeobox* or *HOX* genes) representing a toolkit for the assembly of all animals that may date back to the origin of multicellularity (Lewis 1978; Lappin et al. 2006). This discovery has led to the emergence of a new field of *evolutionary development*, or *EVO/DEVO*. More specific discoveries relevant to our understanding of the origin of the jumping spiders include the discovery of the *Ecdysozoa* (Figure 1: grade 12) as a clade of animals that grow by molting a chitinous exoskeleton, and the related discovery that the Annelida are not ancestral to the Arthropoda (Aguinaldo et al. 1997; Giribet 2017; Giribet & Edgecombe 2020).

grade	Ma	clade name	characters for grade	outgroups	references
1		Opisthokonta	flagellate cells with single posterior flagellum, can produce extracellular chitin, ProtoHox genes	Apusomonadida, Breviata	Giribet & Edgecombe 2020; Pinsky et al. 2022
2	1300	Holozoa	multiple cell types, cellular aggregations and adhesion mechanisms, large eucaryotic prey	Holomycota: Fungi, Opisthosporidia, Nucleariida, Fonticulida	Lappin et al. 2006; Hehenberger et al. 2017; Giribet & Edgecombe 2020; Ros-Rocher et al. 2021
3				Ichthyosporea	Laumer et al. 2019; Ros-Rocher et al. 2021
4		Filozoa	unbranched non-tapering filose tentacles	Pluriformea	Shalchian-Tabrizi et al. 2008; Laumer et al. 2019; Tikhonenkov et al. 2020; Giribet & Edgecombe 2020
5		Choanozoa	colonial, collar around flagellum, cadherins, collagen	Filasterea	Shalchian-Tabrizi et al. 2008; Tikhonenkov et al. 2020; Ros-Rocher et al. 2021
6	950	Metazoa or Animalia	multicellular with axial/positional patterning, oogenesis, spermatogenesis, reduced mitochondrial genome	Choanoflagellata	Dunn et al. 2015; Ferrier 2016; Hehenberger et al. 2017; Giribet & Edgecombe 2020; Tikhonenkov et al. 2020; Ros-Rocher et al. 2021;
7		Neuralia	nerve cells and nervous system, opsins, Hox and ParaHox genes	Porifera	Nielsen 2008; Feuda et al. 2012; Wörheide et al. 2012; Pastrana et al. 2019
8		ParaHoxozoa	paired domains linked to homeodomains, triploblasty (mesoderm)	Ctenophora	Ryan et al. 2010; Dunn et al. 2015; Whelan et al. 2017
9	680	Bilateria	serotonin, cephalization, circular and longitudinal muscles, vegetal pole gastrulation	Placozoa, Cnidaria	Malakhov 2010; Dunn et al. 2015; Laumer et al. 2018, 2019; Giribet & Edgecombe 2019a, 2020
10		Eubilateria or Nephrozoa	tubular gut and long Hox cluster	Xenacoelomorpha: Xenoturbellida, Nemertodermatida, Acoela	Hausdorf 2010; Nielsen 2008; Marlétaz 2019; Giribet & Edgecombe 2019a, 2020
11	650	Protostomia	gastrulation defines mouth, ventral neurite bundles	Deuterostomia: Echinodermata, Hemichordata, Cephalochordata, Urochordata, Craniata	Malakov 2010; Dunn et al. 2015; Giribet & Edgecombe 2020
12	610	Ecdysozoa	ecdysis of hard cuticle, trilaminar cuticle, lack of locomotory cilia, lack of primary larva	Spiralia: Bryozoa, Phoronida, Brachiopoda, Annelida, Mollusca, Nemertea, Entoprocta, Cycliophora, Platyhelminthes, Gastrotricha, Syndermata, Micrognathozoa, Gnathosomulida, Chaetognatha, Rotifera, Acanthocephala, Dicyemida	Aguinaldo et al. 1997; Telford et al. 2008; Budd & Telford 2009; Rota-Stabelli et al. 2010; Dunn et al. 2015; Fröbisch & Funch 2017; Martín-Durán et al. 2016; Giribet & Edgecombe 2017; Laumer et al. 2019; Giribet & Edgecombe 2020
13				Priapulida	Martin-Durán et al. 2016; Laumer et al. 2019
14			secondary separation of ventral nerve cord into two tracts	Kinorhyncha	Martin-Durán et al. 2016; Laumer et al. 2019
15		Panarthropoda	paired segmental ventrolateral appendages, segmental leg nerves and muscles, circumoral commissures, anterior concentration of nerves	Nematoda, Nematomorpha, Loricifera	Telford et al. 2008; Rota-Stabelli et al. 2010; Dunn et al. 2015; Giribet & Edgecombe 2019b, 2020; Laumer et al. 2019; Wu et al. 2023.
16		Lobopodia	annulated lobopods	Tardigrada	Laumer et al. 2019; Wu et al. 2023
17		Arthropoda or Euarthropoda	rigid body and appendage segments with articulated exoskeleton	Onychophora	Giribet & Edgecombe 2019b, 2020; Laumer et al. 2019
18	550	Chelicerata	on 6 anterior segments: 1 pair chelicerae, 1 pair pedipalps, 4 pairs legs	Mandibulata: Myriapoda, Pancrustacea	Telford et al. 2008; Lozano-Fernandez et al. 2019; Giribet & Edgecombe 2019b, 2020
19	530	Arachnida or Euchelicerata	monolobate exopods or endites (mostly lost)	Pycnogonida	Telford et al. 2008; Dunlop et al. 2014; Lozano-Fernandez et al. 2019; Ballesteros et al. 2022
20				Acariformes	Ballesteros et al. 2022
21				Parasitiformes	Ballesteros & Sharma 2019; Ballesteros et al. 2022
22				Palpigradi, Solifugae	Ballesteros et al. 2022
23				Opiliones	Ballesteros et al. 2022
24		Arachnopolmonata	paired book lungs	Xiphosura, Ricinulei	Ballesteros et al. 2022
25	440	Tetrapulmonata	paired book lungs only on second and sometimes third opisthosomal segments, some with tergites on abdominal segments, fang grooves, prosomal/opisthosomal constriction	Scorpiones, Pseudoscorpiones	Dunlop et al. 2014; Garwood et al. 2016; Wheeler et al. 2017; Wang et al. 2018; Giribet & Edgecombe 2019b; Ballesteros & Sharma 2019; Dimitrov & Hornig 2021; Ballesteros et al. 2022; Kulkarni et al. 2023
26	425	Araneae	four pairs of spinnerets, narrow pedicel, cheliceral venom glands, male pedipalps modified for copulation	Pedipalpi: Amblypygi, Schizomida, Uropygi	Lozano-Fernandez et al. 2019; Ballesteros & Sharma 2019; Giribet & Edgecombe 2019b; Platnick et al. 2020; Ballesteros et al. 2022; Kulkarni et al. 2023
27	410	Opisthosthelae	posterior spinnerets, lack tergites	Mesothelae	Garrison et al. 2016; Wheeler et al. 2017; Ramirez et al. 2021; Kulkarni et al. 2023
28	380	Araneomorphae	one pair of book lungs, labidognath (side to side) chelicerae, cribellum (often lost)	Mygalomorphae	Wheeler et al. 2017; Ramirez et al. 2021; Kulkarni et al. 2023
29	320			Filistatidae, Hypochilidae, Synspermiata	Wheeler et al. 2017; Ledford et al. 2021; Kulkarni et al. 2023
30	270			Leptonetidae, Austrochiloidae	Wheeler et al. 2017; Ledford et al. 2021; Ramirez et al. 2021; Kulkarni et al. 2023
31	250	Entelegynae	fertilization ducts, separate from gonopore, transfer sperm to each spermatheca	Palpimanoidea	Wheeler et al. 2017; Wood et al. 2018; Ramirez et al. 2021
32	245			Araneoidea: Araneidae, Linyphiidae, Theridiidae, etc.	Kulkarni et al. 2023
33	240			Eresidae, Nicodamoidea	Kulkarni et al. 2023
34				Deinopidae, Hersiliidae, Oecobiidae	Wheeler et al. 2017; Kulkarni et al. 2023
35	230			Uloboridae	Wheeler et al. 2017; Kulkarni et al. 2023
36		TA clade	male pedipalp with tibial apophysis	Titanoeidae	Wheeler et al. 2017; Kulkarni et al. 2023
37	200	RTA clade	retrolateral tibial apophysis	Phyxelididae	Wheeler et al. 2017; Kulkarni et al. 2023
38				Zodarioidea: Penestomidae, Zodariidae	Wheeler et al. 2017; Kulkarni et al. 2023
39				Marronoidea: Agelenidae, Dictynidae, Hahnidae, etc.	Wheeler et al. 2017; Kulkarni et al. 2023
40				Sparassidae, Myrmeculitoridae	Wheeler et al. 2017; Ramirez et al. 2019; Kulkarni et al. 2023
41				Homalonychidae	Wheeler et al. 2017; Magalhaes et al. 2020; Kulkarni et al. 2023
42	100	Dionycha	ecribellate, each pretarsus with two claws and two adhesive foot pads	Oval Calamistrum clade: Lycosidae, Oxyopidae, Pisauridae, Thomisidae, etc.	Garrison et al. 2016; Wheeler et al. 2017; Azevedo et al. 2022; Kulkarni et al. 2023
43				Prodidomidae	Azevedo et al. 2022; Kulkarni et al. 2023
44		Dionycha B	not gnaphosoid-like	Dionycha A: Anyphaenidae, Gnaphosidae, etc.	Wheeler et al. 2017; Azevedo et al. 2022; Kulkarni et al. 2023
45				Corinnidae, Cheiracanthiidae, Miturgidae, Selenopidae, Viridasiidae, Xenocentidae	Azevedo et al. 2022; Kulkarni et al. 2023
46		Salticidae	large, four-layered principal eyes (AME)	Philodromidae	Azevedo et al. 2022; Kulkarni et al. 2023

Figure 1. Hypothetical grades of evolution leading to the Salticidae. The estimated time of origin for some of these grades is shown in millions of years (Ma, millions of years ago). Not all sources agree on this arrangement.

We start with the *Opisthokonta* (Figures 1-2: grade 1). This grade is more than one billion years old, but already represents much of the progress that we see in our modern jumping spider. These eucaryotes were essentially unicellular but may have already developed aggregate or clonal multicellularity (Tikhonenkov et al. 2020). We think that eucaryotic cells originated with a *single* event (1.5-2.0 Ba), a kind of *endosymbiosis* between procaryotes in which some bacteria evolved into mitochondria, but the true nature of these complex cells remains a subject for active investigation (Baluška et al. 2004; Lane 2017). This sets the stage for our journey to the Salticidae, as each step along the way included a series of single events like this, comprising an unbroken line of descent that *might* have ended at any stage.



GRADE 1: Opisthokonta: Holomycota: Fungi: Mycenaceae: *Favolaschia calocera* R. Heim, California, 11 JAN 2024, © Alan Rockefeller, CC BY 4.0, iNaturalist obs. 196416305.



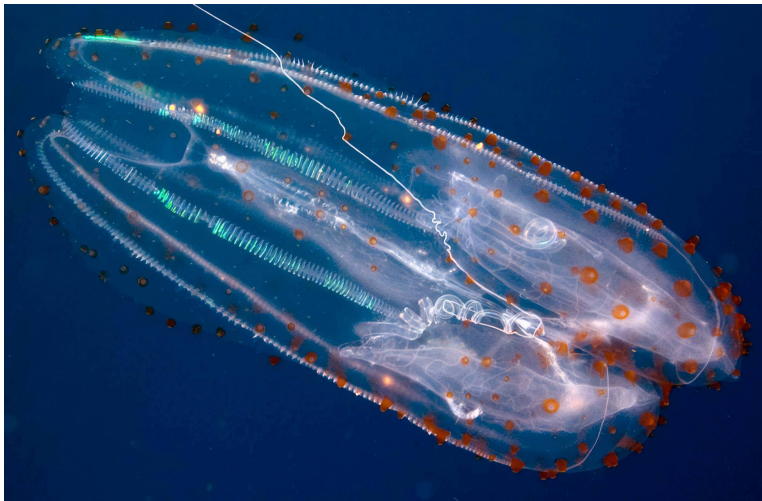
GRADE 6: Metazoa: Porifera: Demospongiae: Haplosclerida: Phloeodictyidae: *Siphonodictyon coralliphagum* Rützler 1971, Cuba, 29 MAY 2023, © Robin White, CC BY-NC 4.0, iNaturalist obs. 152795763. Variable boring sponge, boring into a coral head.

Figure 2. Early grades in the evolution of the Salticidae. Although quite divergent, each of these organisms shares important synapomorphies related to multicellularity and cell differentiation with the jumping spiders.

The Opisthokonta already had *chitin synthetases*, and these would be subject to many different lines of evolution in their descendants (Morozov & Likhoshway 2016). They also had a form of regulatory HOX genes (Lappin et al. 2006), genes that have been most studied in bilaterian animals far down the line (grade 9). Opisthokonts had a *single* posterior flagellum (Pinskey et al. 2022), something that would be lost by most fungi (Holomycota) but retained, in the next stage, by the *Holozoa* (grade 2). These motile structures would be retained in the animals, where they perform an important function in both spermatozoa and epithelial cells.

In the Holozoa, *fibronectins*, important components of the extracellular matrix of multicellular organisms, appeared; these were retained in the subsequent grade (3, unnamed) which saw the addition of a C-type lectin that plays a role in cell-cell adhesion (Hehenberger et al. 2017). In the *Filozoa* (grade 4) laminins and fibrinogen_C were added to the extracellular matrix, as were transmembrane proteins (Cadherins) associated with cell-cell connections. In the *Choanozoa* (grade 5), more laminins were added to the repertoire, as was fibrillar collagen, a key component of elastic connectivity tissue; in the *Metazoa* (*Animalia*, grade 6, Figure 2) new groups of laminins also appeared (Hehenberger et al. 2017). Thus it is clear that evolution of multicellularity from grade 2 (Holozoa) to grade 6 (Metazoa), innovations arose that gave rise to the variety of epithelial (characterized by cell-cell attachment to form layers) and connective tissues (characterized by the extracellular matrix) that we find in modern animals.

The next grade (*Neuralia*, grade 7, Figure 3) is somewhat controversial, as the relationship between sponges (Porifera), comb-jellies (Ctenophora), and the rest of the animals is not fully resolved. Figure 1 depicts the hypothesis that, with the addition of both nerve and muscle cells, the *Neuralia* emerged as *derived sponge larvae* with the ability to use bioelectric communication cells (neurons, with Na^+/K^+ ion channels) to coordinate the movement of specialized contractile cells (Nielsen 2008). At this grade, organisms had all four kinds of tissue that we recognize today, at least at some rudimentary level: epithelial, connective, nervous, and muscle. Grade 8 (*ParaHoxozoa*; Ryan et al. 2010, Figure 3) is also controversial, but most studies agree that this is a monophyletic group. Parahoxozoan ancestors are thought to resemble the planula larvae found in some Cnidaria, and parahoxozoans (Placozoa, Cnidaria, Bilateria) have novel classes of Hox/Paradox genes, allowing selection to work on new directions of development (Ryan et al. 2010).



GRADE 7: Neuralia: Ctenophora: Tentaculata: Lobata: Leucotheidae: *Leucothea pulchra* Matsumoto 1988, Santa Catalina, 11 NOV 2014, © Neil McDaniel, CC BY-NC 4.0, iNaturalist obs. 97160773.

GRADE 8: ParaHoxozoa: Cnidaria: Scyphozoa: Rhizostomeae: Versurigidae: *Versuriga anadyomene* (Maas 1903), East Timor, 14 MAY 2017, © Icolmer, CC BY-NC 4.0, iNaturalist obs. 109823165. With symbiotic fish.

Figure 3. Divergent representatives of two subsequent grades, able to coordinate movement with contractile muscle cells and bioelectric signalling. These are motile, predatory marine organisms.

This brings us to the *Bilateria* (grade 9), animals characterized by their bilateral symmetry (Malakhov 2010). Leaving behind some *rhabditophoran platyhelminthes*, the *Nephrozoa* (grade 10, Figure 4) have a one-way digestive tube, from mouth to anus (Hausdorf 2000). The xenacoelomorphs, shown as an outgroup at this level in Figure 1, may actually be deuterostomes (Marlétaz 2019).

Next we have the classical split between the *Protostomia* (grade 11, Figure 4) and the Deuterostomia. For a long time the two clades were separated by the site of gastrulation during development, thought to correspond to the mouth in protostomes, and the anus in deuterostomes. However it now appears that some ancient protostomes gastrulated just like deuterostomes, and the mouths of all Metazoa may actually be homologous (Martindale 2013). However, the separation of protostome and deuterostome clades has been well supported in studies of molecular phylogeny (e.g., Cardoso et al. 2006). Deuterostomia, including the tunicates, echinoderms, and chordates like ourselves, is a particularly diverse and successful group in its own right. The best known of all animals are the *bony fish* (Deuterostomia: Chordata: Vertebrata: *Osteichthyes*) a clade that includes not only the symbiotic fish shown in Figure 3, but also all of the amphibians, reptiles, birds and mammals (Evans 2009). Thus the protostome/deuterostome split represents the event that led jumping spiders and humans to evolve in separate directions.



GRADE 10: Nephrozoa: Deuterostomia: Chordata: Tunicata: Ascidacea: Aplousobranchia: Diazonidae: *Rhopalaea fusca* (Herdman 1880), Philippines, 6 NOV 2018, © John-Paul Cassez, CC BY-NC 4.0, iNaturalist obs. 80111270. Blue tunicate.



GRADE 11: Protostomia: Spiralia: Platyhelminthes: Tricladida: Geoplanidae: *Diversibipalium engeli* (Hartog 1968), Singapore, 4 MAY 2018, © budak, CC BY-NC 4.0, iNaturalist obs. 12157364.

Figure 4. Grades 10 and 11. Adult tunicates are usually sessile (some are detached and roll on the sea bottom), but they begin their lives as mobile, planktonic larvae. The Spiralia are diverse, including annelids and molluscs. Many Platyhelminthes (flatworms) are parasitic or aquatic in freshwater and marine environments, but some, like the one shown here, are terrestrial.

At grade 12 (Figure 5) a quite different organism emerged, one quite unknown and unexpected until its recent discovery, the ancestor of the *Ecdysozoa* (Aguinaldo et al. 1997). With DNA sequencing, overwhelming support emerged for a link between roundworms (Nematoda), long thought to represent a more primitive group, and arthropods. This replaced the long-held view, based on morphology, that arthropods had evolved from segmented worms (Annelida). Features (*synapomorphies*) of the *Ecdysozoa* include first and foremost, *ecdysis*, the molting of an external skeleton or *trilaminar cuticle*, accompanied by the lack of motile cilia, as well as a terminal (at the anterior end) mouth (Budd & Telford 2009). Up to this point we might think of the ancestral salticid as something like a worm, perhaps like a transparent marine larva. But with the cuticle, we have a creature that was ready to move out into freshwater or onto the land, with protection against water loss in a dessicating environment. The cost of this innovation, of course, was that this creature would have to molt in order to grow.



GRADE 12: Ecdysozoa: Nematomorpha: Gordioida: Gordioidea: Gordiidae: *Gordius* Linnaeus 1758, California, 14 APR 2017, © Kat Halsey, CC BY-NC 4.0, iNaturalist obs. 5750531. Horsehair worm.



GRADE 15: Panarthropoda: Tardigrada: Eutardigrada, Pennsylvania, 18 JUL 2021, © John J. Lisowski, CC BY-NC 4.0, iNaturalist obs. 87667554. Water bear.

Figure 5. Grades 12 and 15. The *Ecdysozoa* links nematodes, nematomorphs and arthropods to a common ancestor with the ability to shed a protective trilaminar cuticle as it grew. With panarthropods like this minute, aquatic tardigrade, we see the appearance of paired, segmental appendages.

Jumping ahead to grade 15 (*Panarthropoda*, Figure 5) we have a clade that now finds substantial support, linking the arthropods with both tardigrades and onychophorans (Rota-Stabeli et al. 2010; Giribet & Edgecombe 2019b). All have a paired segmental legs, and functionally distinct groups of segments (*tagmata*) such as the head, thorax and abdomen of insects, the head and trunk of myriapods, or the prosoma and opisthosoma of spiders. After the *Lobopodia* grade (grade 16, Figure 6) we arrive at the *Arthropoda* (or *Euarthropoda*, grade 17, Figure 6), now generally accepted as a monophyletic group (Giribet & Edgecombe 2019b) containing the *Mandibulata* (*Eucrustacea* and *Myriapoda*) and the *Chelicerata* (grade 16). One important (outgroup) finding at this level is that the Insecta are nested within the Pancrustacea between groups formerly placed in the Crustacea, now recognized as paraphyletic. The relationship of the three large arthropod clades has been contentious (Miyazawa et al. 2014), but recently the concept of the Mandibulata as a sister clade to the Chelicerata has been better supported (Giribet & Edgecombe 2019b).



GRADE 16: Lobopodia: Onychophora: Peripatopsidae: *Diemenipatus taiti* Oliveira, Ruhberg, Rowell & Mayer 2018, Tasmania, 8 JAN 2023, © Gonzalo Giribet, CC BY-NC 4.0, iNaturalist obs. 147071532. Viviparous velvet worm.



GRADE 17: Arthropoda: Mandibulata: Pancrustacea: Malacostraca: Decapoda: Stenopodidae: *Stenopus tenuirostris* De Man 1880, Bali, 9 NOV 2012, © uwkwaj, CC BY-NC 4.0, iNaturalist obs. 159913109. Blue banded coral shrimp.

Figure 6. Grades 16 and 17. The Onychophora, or velvet worms, are successful predators with many species in terrestrial, mostly tropical habitats. With flexible legs, they resemble giant tardigrades. The Mandibulata is by far the most successful group of animals, including the myrapods and the pancrustaceans; the latter group includes the insects and a diverse array of crustaceans, mostly marine.

The *Chelicerata* (grade 18, with two chelicerae, two pedipalps and four pairs of legs in that order) has been recognized for a long time, although the relationship of sea spiders (Pycnogonida) and horseshoe crabs (Xiphosura) to the various arachnid orders has been contentious. Here the distance of the pycnogonids is maintained, but the marine xiphosurans are placed in the *Arachnida* (grade 19, Figures 7-8) along with a variety of terrestrial forms that include those with paired book lungs (*Arachnopulmonata*, grade 24, Figure 7), following more recent studies cited in Figure 1. Xiphosura transitioned from a marine to a freshwater environment in the Palaeozoic (Bicknell & Pates 2020). These studies support the view that the *Arachnopulmonata* represent a shift from an aquatic to a terrestrial life, with *book lungs* in place of book gills (Dunlop 1998; Ballesteros & Sharma 2019; Ballesteros et al. 2022). In other arthropod groups (e.g. Hexapoda, some Isopoda) we can find similar instances of *terrestrialization*. The book lung itself is a remarkable innovation that supports gaseous exchange by allowing hemolymph to flow freely between a series of thin-walled, parallel air sacs (Hill 2020, 2023b).



GRADE 19: Arachnida: Xiphosura: Limulidae *Limulus polyphemus* (Linnaeus 1758), Massachusetts, 21 MAY 2015, © D. Bray, CC BY-NC 4.0, iNaturalist obs. 177332203. Atlantic horseshoe crab.

GRADE 24: Arachnopulmonata: Scorpiones: Buthidae: *Centruroides exilicauda* Oliveira, Ruhberg, Rowell & Mayer 2018, Baja California, 12 JAN 2023, photo by Philipp Hoenle, CC(0), iNaturalist obs. 147109930. Bark scorpion.

Figure 7. Grades 19 and 24. The Xiphosura have paired book gills under the opisthosoma (*thoracetron*). Although the group has a long fossil record, there are only 4 living species (Lamsdell 2020). Scorpions, with paired book lungs, chelicerate pedipalps, and an unusual appendage at the rear of the opisthosoma, are now diverse and successful.

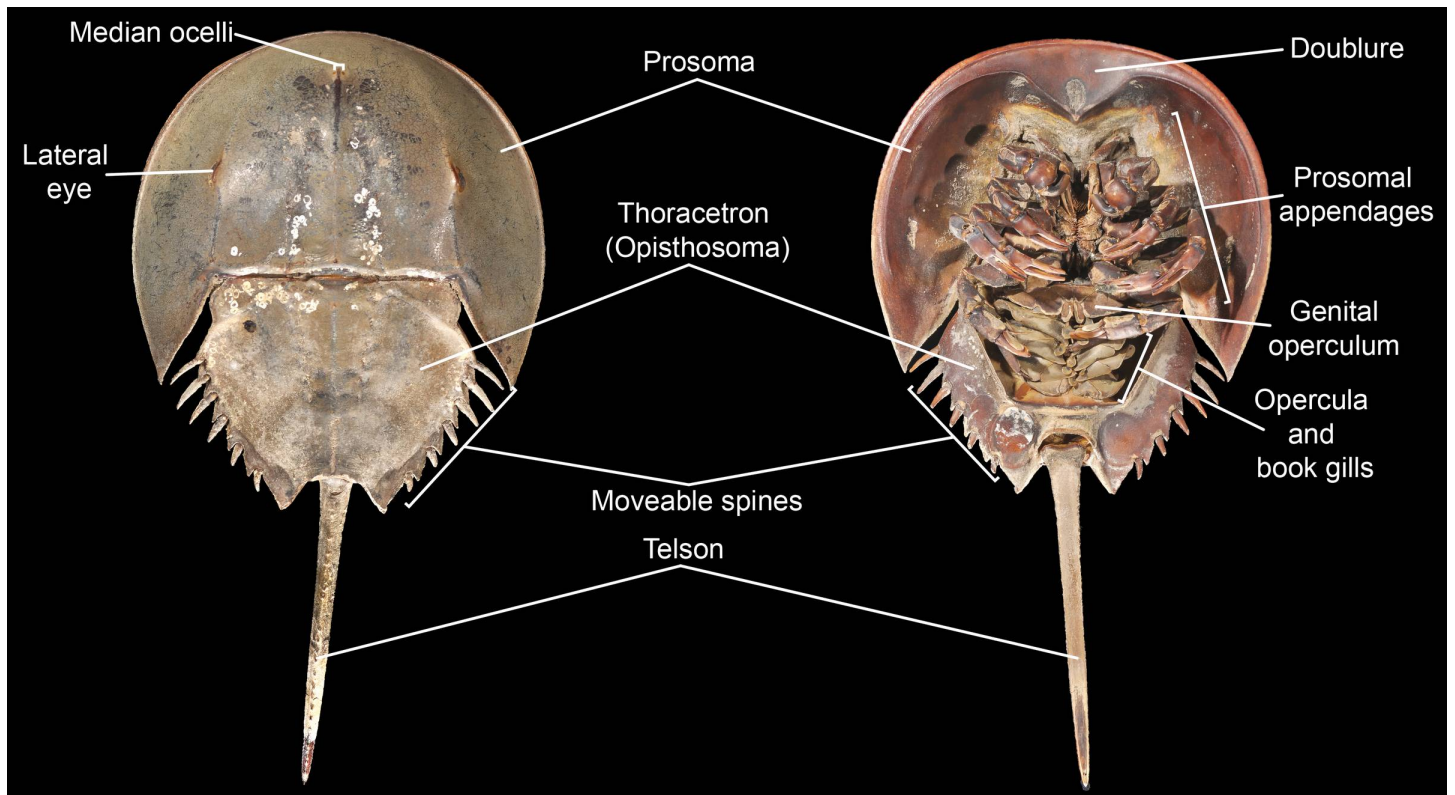


Figure 8. External features of a living xiphosuran, *Limulus polyphemus* (original photo by James Lamsdell, after Lamsdell 2020, used under a CC BY 4.0 license). The lateral eye is a compound eye. Note the chelicerate appendages.

In the next grade (*Tetrapulmonata*, grade 25, Figure 9) we find the spiders grouped with the Pedipalpi (Amblypygi, Schizomida, and Uropygi), in a clade where many representatives have two pairs of book lungs, one pair on each opisthosomal segment 2 and 3 (Dunlop 1998; Scholtz & Kamenz 2006). From early terrestrial tetrapulmonates came the earliest spiders (*Araneae*, grade 26, Figure 9), characterized by their ability to release silk (!) through paired spinnerets, further constriction of the first opisthosomal segment (the pedicel) that converted the opisthosoma into a versatile appendage for the application of silk, cheliceral venom glands, and their remarkable male pedipalps. While male scorpions and Pedipalpi deposit their sperm packets on the ground (Alexander 1957; Seiter et al. 2020), male spiders use their pedipalps as syringes to collect sperm from a sperm web, and then deposit this sperm directly into the epigynum of the female. These innovations are extraordinary, and their origin is difficult to explain. Although living Mesothelae (Figure 9) are now found only in East Asia, fossil Mesothelae are known from the Carboniferous of both North America and Europe (Selden 2021). Based on fossil evidence, some authors have also recognized two intervening grades (25.1, Devonian, *Serosdiastida* and 25.2, late Carboniferous, *unnamed* leading to both †*Chimerarachnida* and the *Araneae*) (Garwood et al. 2016; Wang et al. 2018).



GRADE 25: Tetrapulmonata: Pedipalpi: Uropygi: Thelyphonidae: *Mastigoproctus tohono* Barrales-Alcalá, Francke & Prendini 2018, Arizona, 13 AUG 2016, © brian-maltais, CC BY-NC 4.0, iNaturalist obs. 9453407. Vinegaroon or tailed whipscorpion.

GRADE 26: Araneae: Mesothelae: Liphistiidae: *Liphistius desultor* Schiøtte 1849, Penang, 2 MAR 2022, © Albert Kang, CC BY-NC 4.0, iNaturalist obs. 107813223.

Figure 9. Grades 25 and 26. There are presently 126 living species of whipscorpions (Uropygi) and they have a long fossil history dating back to the Pennsylvanian (Santana et al. 2024). The East Asian Mesothelae represent the most basal group of spiders, with two pairs of book lungs and four pairs of spinnerets at a central position on the underside of the opisthosoma. Note also the prominent tergites on the dorsal opisthosoma of this *Liphistius*, similar to those seen on *Mastigoproctus*.

In recent years, there has been much work on the phylogeny of spiders (e.g. Garrison et al. 2016; Wheeler et al. 2017; Wood et al. 2018; Ledford et al. 2021; Ramírez et al. 2019, 2021; Azevedo et al. 2022; Kulkarni et al. 2023), and there is general agreement on the major grades (or corresponding clades) that we will review here, although the placement of some families and genera varies. The fossil record for these groups (Selden et al. 2009; Dunlop et al. 2023) suggests a more recent origin than does the DNA sequencing (Fernández et al. 2018; Dimitrov & Hormiga 2021).

Separate from the Mesothelae, the remaining spiders are placed in the *Opisthothelae* (grade 27, Figure 10). The name of this clade is a reference to the fact that the spinnerets in this group are now situated at the *rear* of the ventral opisthosoma. In the *Opisthothelae*, opisthosomal ganglia have generally migrated

into the prosoma to fuse with prosomal ganglia into a single mass, and, although the opisthosoma is still segmented, tergites are lacking. There are only 2-3 pairs of spinnerets in this group. Our next grade, the *Araneomorphae* (grade 28, Figure 10), includes all of our "modern" spiders, generally with labidognath (operate in a transverse plane, or side-to-side) chelicerae. The araneomorph ancestor is now thought to have been *cribellate* (with fused plate or cribellum, bearing many small silk spigots, instead of a pair of anterior medial spinnerets); this feature has been retained in many spider families, and lost in others (Coddington & Levi 1991).



GRADE 27: Opisthothelae: Mygalomorphae: Theraphosidae: *Cyriopagopus* Simon 1887, Pahang, Malaysia, 17 JUL 2011, © Vojtěch Vít, CC BY-NC 4.0, iNaturalist obs. 149389853.



GRADE 28: Araneomorphae: Filistatidae: *Filistata maguirei* Marusik & Zamani 2015, Iran, 16 FEB 2018, © Alireza Zamani, CC BY-NC 4.0, iNaturalist obs. 37931245. Cribellate crevice weaver.

Figure 10. Grades 27 and 28. There are many different mygalomorphs today, characterized by the parallel, parasagittal (*orthognath*) alignment of their chelicerae. The Theraphosidae is the largest family in the group, including the largest of all spiders. In some countries, these are popularly known as *tarantulas*, and kept as low-maintenance pets. Filistatids like this *Filistata* are near the base of araneomorph evolution. Their anterior medial spinnerets have fused to form a cribellum with many small ducts. This produces a kind of kinky silk that entangles prey in the webs of these spiders.

We still have much to learn about the evolution of specific traits in spiders, but two important and well-known grades below the Araneomorphae are the *Entelegynae* (grade 31, Figure 11) and the *RTA clade* (grade 37, Figure 11). Whereas other araneomorphs (haplogynes) use the median gonopore of the female for both the deposition of sperm and oviposition, entelegyne females have a pair of separate copulation ducts for the injection/collection of sperm (Figure 12). Since the Eocene (~45Ma) the great majority of araneomorph spiders have been entelegynes, mostly araneoid web spiders or members of the RTA clade; however the most common araneomorph fossils from the Cretaceous (120-99Ma) are haplogyne members of the Synspermiata and the Palpimanoidea (Magalhaes et al. 2020). This represents a virtually complete conversion of the spider fauna to the entelegyne model since the late Cretaceous, a process that may have resulted, in part, from the great extinction of terrestrial and shallow water fauna at the end of the Cretaceous. Just as the mammals emerged in the Cenozoic to replace the great dinosaurs, so the entelegynes came into their own.

The RTA clade includes about half of all living spiders, mostly wandering rather than web spiders. The RTA (retrolateral tibial apophysis) of the male pedipalp supports positioning and attachment to the female epigynum during copulation, and is thought to play a role in sexual selection (Huber 1995), much

like a lock and key. The success of the wandering spiders with an RTA may relate to their need to position each pedipalp and mate more quickly and efficiently than their web-dwelling counterparts.



GRADE 31: Entelegynae: Eresidae: *Eresus moravicus* Řezáč, 2008, Czechia, 13 OCT 2021, © Standa Pavouk, CC BY-NC 4.0, iNaturalist obs. 145273658. Cribellate velvet spider.



GRADE 37: RTA clade: Sparassidae: *Tyrostola barbata* L. Koch 1875, Queensland, 3 MAR 2021, © Christian Perrin, CC BY-NC 4.0, iNaturalist obs. 70598953. Huntsman spider.

Figure 11. Grades 31 and 37. The great majority of modern spiders are entelegynes, with separation of copulatory ducts from oviposition ducts (*gonopores*) of the female epigynum. Entelegynes in turn can be divided into two large groups, one (the RTA clade) distinguished by the presence of a *retrolateral tibial apophysis* on the male pedipalp.

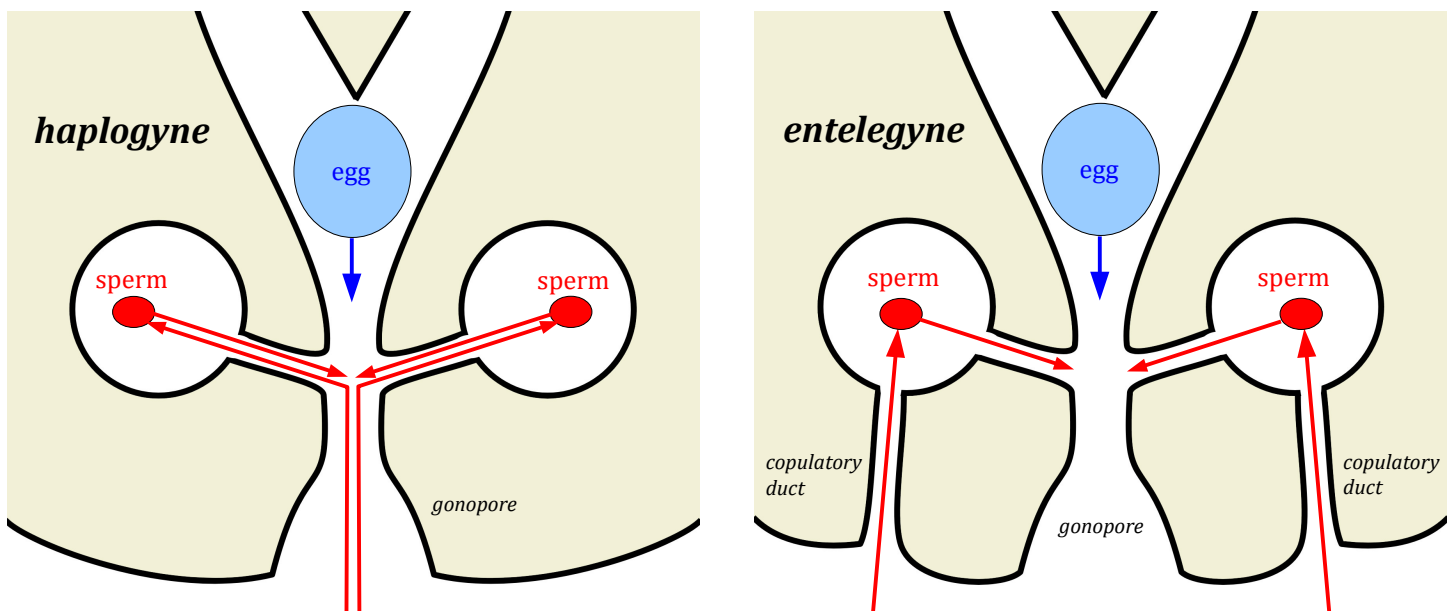


Figure 12. Structure of the epigynum in spiders (after Uhl et al. 2009). The *haplogyne* arrangement, with a single median gonopore serving as both the copulatory duct and ovipositor, is considered to be primitive in spiders. In the Entelegynae (grade 31), sperm is deposited by the male through a pair of copulatory ducts leading to the spermathecae, and only later passes through a pair of fertilization ducts to fertilize each egg as it passes through the medial *uterus externa*. A recent study (Zhan et al. 2019) has refined our understanding of the entelegyne condition, which appears to include a *secondary uterus externa* connected to the two fertilization ducts leading from the sperm reservoirs (*spermathecae*).

The next important grade in this journey is the ecribellate *Dionycha* (grade 42, not the genus of flowering plants by the same name!). Usually each pretarsus of a dionychan spider is equipped with one pair of claws (anterior and posterior) attached to a claw lever, whereas many other spiders have a third (median) claw firmly attached to that claw lever. Their pretarsus also (usually) has two plates (again anterior and posterior) of tenent setae, one on either side of the claw lever. Through the use of two tendons that work in opposition to internal fluid pressure, the pretarsal claws and tenent plates can be independently extended and retracted, allowing the spider to either walk on silk with the claws, or cling to a surface with the tenent setae (Hill 2010c). The phylogeny for the *Dionycha* shown here (Figure 1) differs somewhat from that of Wheeler et al. (2017), and includes the Prodidomidae (Ramírez et al. 2019; Azevedo et al. 2022). Another recent study of five families, based on mitogenomic data, found that Selenopidae was more closely related to the Salticidae than to the Miturgidae (Li et al. 2022).

Apart from the Prodidomidae, the *Dionycha* are divided into two well-supported clades, one (*Dionycha A*) characterized by their "gnaphosoid" appearance, and including species previously placed in the Gnaphosidae (*sensu lato*). The *Dionycha B* (grade 44, Figure 13) includes the rest of them. Not long ago, the crab spiders (Thomisidae) were thought to be dionynchans, but we now see them as close relatives of the Lycosidae, within an *Oval Calamistrum* clade. Ramírez (2014) published a useful and very extensive treatise on the morphology and phylogeny of the *Dionycha*, although some of his proposals, including a sister relationship of the Thomisidae to the (Philodromidae + Salticidae), have not been supported by subsequent work at the molecular level.



GRADE 44: *Dionycha B*: Philodromidae: *Thanatus striatus* C. L. Koch 1845, Poland, 18 JUL 2022, © Hubert Szymanski, CC BY-NC 4.0, iNaturalist obs. 196294142. Ecribellate running spider.



GRADE 46: Salticidae: *Phidippus regius* C. L. Koch 1846, Florida. Ecribellate jumping spider.

Figure 13. Grades 44 and 46. The philodromids also share a common ancestor with the salticids at grade 45.

The *Salticidae* (grade 46, Figure 13) are easily recognized by the enormous principal or anterior medial eyes (AME) on their face. Although some philodromids (e.g. *Ebo*, *Titanebo*) have relatively large AME, the anatomy of these eyes has not been studied. We have much to learn about the relationship between the Philodromidae and Salticidae, and our relevant fossil record, dating back only some 45My to the Eocene Baltic Amber, gives us no information about the immediate ancestor of the Salticidae (Hill & Richman 2009). It has been suggested that the Salticidae *originated* in the Cenozoic (Bodner 2009; Penney 2010). The most ancient salticid fossils known are from the Eocene (~45Ma) Baltic Amber of Europe (Dunlop et

al. 2023), and these excellent fossils represent at least two different forms: one at the grade of hisponine salticids, with constriction of the carapace behind the front and posterior medial eyes, and another with large posterior medial eyes suggestive of modern spartaeine salticids. These modern groups, like other arthropods represented in the Baltic Amber, are now restricted to the tropics, mostly in Afroeurasia. One might suspect that the first salticid had larger PME, subsequently reduced in size in several different groups. But the Baltic Amber fauna of these spiders was already quite advanced and not that different from some modern species. Major clades of living salticids are isolated by oceanic and climatic barriers, supporting the view that each modern group has evolved and diversified in the Cenozoic, after the breakup of Gondwanaland (Bodner 2009; Hill 2009, 2010a, 2022b, 2023a; Zhang 2012; Bodner & Maddison 2012; Hill & Edwards 2013; Zhang & Maddison 2013). The *Phidippus* shown here (Figure 13), with relatively short and powerful legs, might be viewed as typical of the Salticidae, but in fact there is a great deal of variation in the relative length of legs in this family. We presently lack a good picture of what the first salticid looked like. We would, however, expect that the first salticid *jumped* on its prey, powering these jumps by extension of legs III and/or IV (Hill 2010b, 2018; Hill et al. 2021). The vision of these spiders, and their ability to jump accurately to reach sighted objectives, must have evolved concurrently.

This brings our brief "journey to the Salticidae" to an end. Of course, the journey itself is not ending, as each of the more than 6,000 living salticid species represents a possibility for evolution and speciation. Since the origin of the first jumping spider, salticid vision has continued to evolve in many different directions (Hill 2022b). As some diversify, most will become extinct. There are two important points to keep in mind here. First, we have a long way to go with our study of phylogeny at all levels, and many of the hypotheses depicted here will be reversed in the future. Second, we really have few good studies of comparative morphology to draw on, and a lot of study will be required to elucidate the significance of the many evolutionary grades that mark this journey. In the past, we have been misled by studies based solely on morphology, yet we will never understand the role of evolutionary innovation without more detailed knowledge of both functional morphology and physiology. Now that we are beginning to understand the role of regulatory genes, it appears that some characters can disappear from expression at one point in time, and then reappear as homologs of their earlier expression, at a later date. So, beyond the probabilistic study of relatedness through DNA sequences, we need to know much more about just what that DNA is doing to the phenotype.

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