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Current views on chelicerate phylogeny —A tribute to Peter Weygoldt

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1 Current views on chelicerate phylogeny—a tribute to Peter Weygoldt

2

3 Gonzalo Giribet

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5 *Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard*
6 *University, 26 Oxford Street, Cambridge, MA 02138, USA*

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10

11 **ABSTRACT**

12

13 Peter Weygoldt pioneered studies of arachnid phylogeny by providing the first synapomorphy
14 scheme to underpin inter-ordinal relationships. Since this seminal work, arachnid relationships
15 have been evaluated using morphological characters of extant and fossil taxa as well as multiple
16 generations of molecular sequence data. While nearly all datasets agree on the monophyly of
17 Tetrapulmonata, and modern analyses of molecules and novel morphological and genomic data
18 support Arachnopulmonata (a sister group relationship of Scorpiones to Tetrapulmonata), the
19 relationships of the apulmonate arachnid orders remain largely unresolved. Three threads may
20 allow us to resolve the recalcitrant phylogeny of arachnids: the careful evaluation of large
21 amounts of molecular data; novel techniques grounded in comparative morphology and
22 evolutionary developmental biology, which add improved homology statements and explain
23 the transition between character states; and new fossil discoveries, which continue to
24 incorporate relevant novel data to the discussion of the relationships among the arachnid
25 orders.

26

27 **1. Introduction**

28

29 Professor Peter Weygoldt, one of the most influential workers on arachnid systematics,
30 produced the first explicit synapomorphy scheme and cladistic analysis of chelicerate

31 relationships based on morphological data (Weygoldt and Paulus, 1979a, b; see also Weygoldt,
32 1980). His views persisted until the end of the 20th century, when the molecular influence on
33 arachnid systematics was still not mainstream (Weygoldt, 1998; Weygoldt, 1999). Since then,
34 arachnid systematists have continued to support monophyly of Arachnida. A sister group
35 relationship of Scorpiones to Lipoctena (the non-scorpion arachnids) was also mainstream,
36 along with the monophyly of Acari, among other views, but these are now largely rejected by
37 most authors. Lipoctena were split into two main groups, Megoperkulata (= the modern
38 Tetrapulmonata) and Apulmonata (the non-pulmonate arachnids), a view earlier proposed by
39 Firstman (1973), and to some extent, endorsed by recent molecular analyses. Weygoldt and
40 Paulus' cladogram (Fig. 1) constituted the basis of modern chelicerate systematics and provided
41 the first classification integrating multiple character systems and explicit synapomorphies. Their
42 synapomorphy scheme was subsequently incorporated into follow-up data matrices and
43 cladistic analyses of arachnid and arthropod relationships (e.g., Shultz, 1990; Wheeler and
44 Hayashi, 1998; Edgecombe et al., 2000; Dunlop and Braddy, 2001; Giribet et al., 2002; Pollitt et
45 al., 2003; Shultz, 2007; Garwood et al., 2014; Garwood et al., 2016; Garwood et al., 2017), some
46 of which combined morphology with molecules in total evidence analyses (e.g., Wheeler and
47 Hayashi, 1998; Edgecombe et al., 2000; Giribet et al., 2002).

48 In this review I present my views on the current understanding of chelicerate phylogeny
49 in light of Weygoldt and Paulus' (1979b) cladogram, contrasting it with recent, often
50 molecularly-driven views on chelicerate evolution.

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53 **2. Chelicerate phylogeny—a historical account**

54

55 Satisfactorily resolving the phylogenetic tree of Chelicerata has been among the most difficult
56 systematic problems in Arthropoda since the proposal of the first explicit hypothesis of relationships by
57 Pocock (1893). Traditionally divided into three major extant lineages, Pycnogonida (sea spiders),
58 Xiphosura (horseshoe crabs), and Arachnida (spiders, scorpions, harvestmen, mites, etc.), plus several
59 extinct ones (e.g., Eurypterida, Chasmataspidida), the interrelationships among these three main extant

60 clades (and the fossils) remain unsettled. The monophyly and relationships among the arachnid orders¹
61 remain even more fluid, if possible. These relationships have been constantly debated based on
62 morphology (e.g., Weygoldt and Paulus, 1979b; Shultz, 1990; Wheeler and Hayashi, 1998; Giribet et al.,
63 2002; Pollitt et al., 2003; Giribet et al., 2005; Shultz, 2007; Legg et al., 2013; Garwood and Dunlop, 2014;
64 Garwood et al., 2016; Garwood et al., 2017) and have remained frustratingly unstable and poorly
65 supported based on molecules (e.g., Wheeler and Hayashi, 1998; Giribet and Ribera, 2000; Giribet et al.,
66 2002; Mallatt and Giribet, 2006; Masta et al., 2009; Regier et al., 2010; Ovchinnikov and Masta, 2012;
67 Sharma et al., 2014a; Pepato and Klimov, 2015). Few results are thus supported across methods or
68 classes of data, even after using large amounts of molecular data (Regier et al., 2010; Sharma et al.,
69 2014a). These latter studies used dozens to thousands of genes but were only able to recover Arachnida
70 under particular conditions, and not consistently. Nevertheless, cladistic analyses of morphological data
71 consistently support the monophyly of Arachnida (Weygoldt and Paulus, 1979b; Wheeler and Hayashi,
72 1998; Giribet et al., 2002; Giribet et al., 2005; Shultz, 2007; Legg et al., 2013; Garwood and Dunlop,
73 2014), as do most combined analyses of molecular and morphological datasets (Wheeler and Hayashi,
74 1998; Edgecombe et al., 2000; Giribet et al., 2002; Giribet et al., 2005), so this incongruence between
75 molecular and morphological data has puzzled systematists for almost three decades.

76 Nearly all data and analyses agree now that Pycnogonida and Euchelicerata are sister taxa, and
77 that Euchelicerata is monophyletic, even when multiple fossils are included (Legg et al., 2013). This has
78 been however contradicted by two recent phylogenetic analyses placing Pycnogonida as sister group to
79 Arachnida, with Xiphosura and several related fossils being more basal (Garwood and Dunlop, 2014;
80 Garwood et al., 2017), a result that is probably due to the long branches of pycnogonids and appears
81 contradicted by virtually all recent analyses of molecular data (but see the mitochondrial gene analyses
82 of Ovchinnikov and Masta, 2012). Indeed, some analyses of mitochondrial data place Pycnogonida
83 deeply nested within Arachnida (Ovchinnikov and Masta, 2012), but mitochondrial data analyses also fail
84 to recover the only group supported virtually by all morphological and molecular analyses—
85 Tetrapulmonata (Masta et al., 2009; Masta, 2010; Ovchinnikov and Masta, 2012).

86 In addition to the recalcitrant problem of the monophyly of Arachnida, the interrelationships of
87 its orders have remained in flux and few aspects are shared even among morphological proposals
88 (Weygoldt and Paulus, 1979b; Shultz, 1990; Wheeler and Hayashi, 1998; Giribet et al., 2002; Giribet et

¹ While some advocate for rankless classification systems, I follow my explicit principles (see Giribet et al., 2016) of using ranks as conventional non-comparable evolutionary units (e.g., an order can be sister group to all other orders), since everyone understands what an arachnid order refers to (perhaps except for the case of the acarine orders).

89 al., 2005; Shultz, 2007; Garwood and Dunlop, 2014; Garwood et al., 2016; Garwood et al., 2017) (see Fig.
90 2). Tetrapulmonata (including the orders typically with four lungs, Araneae, Amblypygi, Uropygi² and
91 Schizomida) is found almost universally, and it is equally supported in nearly all molecular analyses (see
92 references above). A relationship of Tetrapulmonata to Scorpiones (a clade named Arachnopulmonata),
93 a result endorsed by the homology of the book lungs of scorpions with the those of tetrapulmonates
94 (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and Wirkner, 2016), has been found
95 in some molecular analyses (Regier et al., 2010; Sharma et al., 2014a), and was somehow recognized by
96 early workers on arachnid phylogeny. I.e., Thorell (1876-1877: p. 86) placed Scorpiones as the sister
97 group of Pedipalpi (although this clade was the sister group to Araneae + Opiliones, and Arachnida was
98 not monophyletic). However, other early authors, including Pocock (1893), placed Scorpiones as the
99 sister group to all other arachnids, a phylogenetic position that has prevailed, especially among
100 paleontologists (e.g., Firstman, 1973; Weygoldt and Paulus, 1979b; Dunlop and Selden, 1998). Yet a
101 myriad of other positions have been proposed for Scorpiones, including a sister group relationship to
102 Eurypterida—not testable with molecular data—, Pseudoscorpiones, Opiliones, Solifugae, etc. (e.g.,
103 Shultz, 1990; Dunlop and Webster, 1999; Shultz, 2007; Garwood and Dunlop, 2014). While
104 Tetrapulmonata, a clade based on a well-founded synapomorphy, has been corroborated with
105 molecular data, another clade found in nearly all morphological phylogenies is one including Ricinulei
106 and the acarine orders (currently six recognized orders), based on the presence of a hexapod larva, a
107 unique character among arachnids. This clade, named Acaromorpha, is however refuted in nearly all
108 molecular analyses, most of which also fail to support the monophyly of Acari. An accelerated rate of
109 evolution in the acarine lineages may underpin the difficulties in resolving their precise phylogenetic
110 position (Pepato et al., 2010; Sharma et al., 2014a; Pepato and Klimov, 2015), but it is now well
111 understood that Acari divides into two clades, Acariformes and Parasitiformes + Opilioacariformes, and
112 these may not be sister groups. Acariformes comprises the orders Trombidiformes and Sacoptiformes;
113 Parasitiformes includes the orders Ixodida, Mesostigmata and Holothyrida (Harvey et al., 2017). The
114 relationships of Pseudoscorpiones, Palpigradi, Ricinulei, Solifugae, Opiliones and the two acarine clades
115 are however poorly understood and they conflict in virtually every published analysis of arachnid
116 relationships. Likewise, the position of some extinct arachnid orders is better understood than others,
117 but often depends on the position of the extant ones.

² I follow the convention of the International Society of Arachnology of using Thelyphonida as a clade including the orders Uropygi and Schizomida (see also Clouse et al., 2017).

118 I therefore do not think we can claim victory in having satisfactorily resolved arachnid
119 relationships given the inconsistent results across morphological data matrices, across molecular data
120 matrices, and across results from molecules and morphology. However, progress has been made in
121 several areas of the tree since the seminal work of Weygoldt and Paulus, and some of these
122 achievements are discussed below.

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124

125 **3. Arachnid monophyly**

126

127 While broadly accepted, the monophyly of the Arachnida has been disputed mostly by two
128 sources of evidence: fossils and molecules. To my knowledge, no morphological cladistic analysis of
129 extant arachnid relationships has challenged such monophyly. However, in cladistic analyses
130 incorporating fossils, monophyly has been disputed in a few cases which supported a relationship of
131 Scorpiones to Eurypterida and perhaps Xiphosura (see a discussion of hypotheses in Dunlop and Braddy,
132 2001). The often thought to be “more reliable” molecular data, have failed to recover arachnid
133 monophyly in all but a very small minority of analyses.

134 Molecular data analyses that do not include morphology either fail to recover Arachnida (e.g.,
135 Wheeler and Hayashi, 1998; Giribet et al., 2002; Meusemann et al., 2010; Pepato et al., 2010; Regier et
136 al., 2010; Rehm et al., 2011), or when Arachnida is recovered, it is poorly supported. Perhaps for this
137 reason, some arthropod-wide phylogenetic analyses have included pycnogonids, xiphosurans, but a
138 minimal representation of arachnids (e.g., Regier and Shultz, 2001; Regier et al., 2008). A few
139 phylogenetic analyses of arthropod relationships have however recovered Arachnida with strong
140 support, at least under some analytical conditions (Koenemann et al., 2010). Finally, a recent
141 phylogenomic study of arachnid relationships explored the support for Arachnida under a variety of data
142 matrices and found that depending on the analyzed dataset Arachnida could receive close to 100%
143 bootstrap support (bs) or nearly 0% bs (Sharma et al., 2014a: figure 5).

144 The case of Sharma et al. (2014a) is particularly interesting because for the first time we could
145 dissect where the signal for arachnid monophyly comes from. The authors binned sets of the more than
146 3,500 genes analyzed based on percent pairwise identity, and found that when adding genes from most
147 to least conserved, Arachnida was recovered with 100% bs when adding 500 genes, but soon after this,
148 by continuing adding more genes (more divergent ones), arachnid monophyly disappeared (see Fig. 3).
149 This sequential concatenation of orthologs thus showed that Arachnida, unlike other groups that once

150 recovered continued to be found with total support after the addition of genes (i.e., Chelicerata,
151 Euchelicerata, Tetrapulmonata, Pedipalpi, Arachnopulmonata; Fig. 3), was highly sensitive to the data
152 analyzed. It is no coincidence that these are the groups typically recovered by nearly every molecular
153 analysis. Arachnida, however, behaved more like other nodes that appeared and disappeared, but that
154 their support peaked at different numbers of genes. As an example, Ricinulei and Solifugae formed a
155 clade with nearly total support with about 500 genes, but a conflicting node of Ricinulei and Xiphosura
156 achieved maximum support at 3,000 genes (Fig. 3). While the need of many highly divergent genes to
157 obtain maximal support for a deep node may be an indication of some sort of systematic error, this
158 study results in two corollaries: 1. Maximal support is not necessarily a good indicator of phylogenetic
159 relationships; and perhaps more important, 2. Data matrices may not have the capacity to resolve all
160 nodes in a phylogeny simultaneously. Therefore, we could ask whether we should use different matrices
161 to resolve individual nodes, a discussion that is beyond the scope of this review.

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163

164 **4. Scorpiones—Lipoctena or Arachnopulmonata?**

165

166 From the early days of arachnid systematics, Scorpiones have been considered the sister group
167 to all other arachnids (= Lipoctena) (Pocock, 1893), and this relationship was endorsed by some modern
168 analyses (Weygoldt and Paulus, 1979b). However, other positions have been proposed, including a sister
169 group relationship to Eurypterida (see a discussion in Dunlop, 1998; Dunlop and Braddy, 2001); a basal
170 arachnid group sister group to Opiliones (i.e., Stomothecata as sister group to remaining arachnids)
171 (Shultz, 2007; with fossil taxa); derived arachnids within Dromopoda, either in Novogenuata (Shultz,
172 1990) or as sister group to Opiliones (i.e., Stomothecata as a derived arachnid clade) (Shultz, 2007;
173 without fossils). Some of these hypotheses have been explicitly tested and, i.e., Garwood and Dunlop
174 (2014) showed that Stomothecata was not particularly stable to the addition of further characters, or
175 indeed to the addition of early fossils in each group which lack a stomotheca.

176

177 Nonetheless, early authors had recognized a putative clade of pulmonate arachnids due to the
178 similarities in their circulatory apparatus (Firstman, 1973), although some of the logic of these, not
179 necessarily phylogenetic hypotheses, is difficult to interpret. Firstman's (1973) proposed "phyletic tree"
180 showed monophyly of Pulmonata (later renamed Arachnopulmonata by Sharma et al., 2104, to
181 distinguish it from the gastropod clade Pulmonata) and Apulmonata, as he also specified in his paper:
"The Pulmonata and Apulmonata are both regarded as natural monophyletic categories". However, as it

182 was also typical at the time, other statements implied paraphyly of Merostomata, Scorpiones, and
183 Pulmonata: “It is hypothesized that neoteny has been involved in the origin of arachnids from
184 merostomes, and in the origin of apulmonate arachnids from pulmonates.”; “The Pulmonata is regarded
185 as having emerged from the arachnid ancestors of modern scorpions.” Support for Arachnopulmonata is
186 now found both in morphology (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and
187 Wirkner, 2016), and recent molecular analyses, including phylogenomic datasets (Koenemann et al.,
188 2010; Regier et al., 2010; Sharma et al., 2014a), and a hemocyanin duplication (Sharma and Wheeler,
189 2014).

190 Unlike the case of arachnid monophyly, which continues to be poorly supported in molecular
191 analyses, DNA and amino acid data seem to converge in a relationship of Scorpiones and
192 Tetrapulmonata, thus rejecting the ideas of Lipoctena, Dromopoda, Novogenuata, and Stomothecata, to
193 mention a few previously favored nodes. This should however not be perceived as a victory of molecules
194 over morphology, as all of these hypotheses are supported by some sets of morphological characters, as
195 is Arachnopulmonata, which has required nearly three decades of refinements in data acquisition and
196 analyses before being supported with any confidence by molecular datasets. It is not outside the realm
197 of possibilities that newer data and analyses may overturn the Arachnopulmonata hypothesis, but for
198 the first time molecular data and detailed anatomical studies of circulatory and respiratory systems
199 (held to be “convergent” between scorpions and tetrapulmonates for some years) are in agreement
200 (Scholtz and Kamenz, 2006; Wirkner et al., 2013; Klußmann-Fricke and Wirkner, 2016). Genomic changes
201 may also add support to clades that contain ancestral genome duplications, as are the cases of spiders
202 and scorpions (Schwager et al., 2017). The study of these duplications may allow us to better
203 understand the origins of novel morphological features through neofunctionalization, as in the case of
204 the Hox genes in scorpions (Sharma et al., 2014b). Evodevo is also able to provide ultimate explanations
205 to evolutionary transformations, as in the case from the 3-segmented to the 2-segmented chelicerae
206 (Sharma et al., 2012). The application of a comparative framework to the evodevo approach is certainly
207 a promising direction for understanding the evolution of arachnid morphology.

208

209

210 **5. The position of the apulmonate orders**

211

212 While a small victory could be claimed with respect to Archnopulmonata and its internal
213 relationships (Tetrapulmonata, Pedipalpi, and even the position of the fossil Uraraneida), resolving the

214 relationships of the apulmonate orders has become frustratingly unrewarding. Pseudoscorpiones
215 resemble Scorpiones in several aspects of their anatomy, most prominently on their unique pedipalps,
216 and indeed, some authors consider them closely related, and some of the conserved genes in the
217 analyses of Sharma et al. (2014a) place them together, or at least, with Arachnopulmonata. Likewise,
218 Ricinulei and their putative fossil counterparts, Trigonotarbida (Jones et al., 2014; Huang et al., 2018),
219 are sometimes related to Tetrapulmonata, but sometimes Trigonotarbida group with
220 Arachnopulmonata while Ricinulei cluster with Acari (e.g., Huang et al., 2018). Acari are well known, as
221 are pseudoscorpions, to have extraordinary rates of evolution when compared to other arachnids,
222 making it extremely difficult to place them with any confidence (Pepato et al., 2010; Sharma et al.,
223 2014a). Opiliones, Solifugae and Palpigradi are not better resolved, the latter group being extremely
224 difficult to place phylogenetically, among other things due to the paucity of molecular data available
225 until very recently (Regier et al., 2010; Giribet et al., 2014). A summary tree of what I believe to be the
226 best-supported hypotheses of arachnid relationships is presented in Fig. 4.

227 Have we hit a wall attempting to resolve these relationships with confidence? Molecular
228 analyses including a broad sample of arachnid diversity and more than a handful of loci remain scarce
229 (Regier et al., 2010; Sharma et al., 2014a), and these two studies have a biased taxon representation, in
230 addition to not having sufficient genes for resolving a tough phylogenetic question (Regier et al., 2010),
231 or including a highly heterogeneous dataset (Sharma et al., 2014a). A new dataset including multiple
232 species per arachnid order, better genomic/transcriptomic data, and a more balanced species
233 distribution should be analyzed before giving up on the arachnid ordinal relationships. Additional
234 genomic subsampling techniques are also a promising direction (Starrett et al., 2016), as they allow to
235 add large number of species from specimens readily available in museum collections.

236 Morphology of course continues to be a source of reliable data to understand arachnid
237 phylogeny, as it is ultimately the transformation of phenotypic traits that makes the phylogenetic
238 enterprise interesting. As in the case of the circulatory system of Arachnopulmonata, many other
239 relationships have alternatives. For example, Solifugae have been supported by many authors to be the
240 sister group of Pseudoscorpiones, but a sister group to Acariformes (a clade now named
241 Poecilophysidea) has been endorsed both by molecular analyses (Pepato et al., 2010) as well as sperm
242 ultrastructure (Alberti and Peretti, 2002) and other anatomical characters, like the sejugal furrow
243 (Dunlop et al., 2012).

244 Fossils are another obvious source of novel combinations of morphological characters, and new
245 discoveries keep appearing every year. Among the most striking arachnid fossil discoveries is Uraraneida

246 (Middle Devonian to Cretaceous) (Selden et al., 2008), now interpreted as the sister group of Araneae,
247 forming the clade Serikodiastida (Garwood and Dunlop, 2014), some depicting an odd amalgamation of
248 characters, combining a uropygid-like pygidium and telson with spider-like fangs, spinnerets with
249 spigots, and a highly modified palp, on the way of becoming the typical spider male instrument for
250 sperm transfer (Huang et al., 2018; Wang et al., 2018). But what makes Uraraneida stand above all other
251 extinct arachnid orders (i.e., Haptopoda, Phalangiotarbida, Trigonotarbida), which went extinct during
252 the Paleozoic (Dunlop, 2010), is that they survived for at least an additional 150 million years into the
253 Cenomanian (Cretaceous) (Huang et al., 2018; Wang et al., 2018). The case of Uraraneida highlights the
254 importance of new fossil discoveries and the possibility that extraordinary preservation can bring to our
255 understanding of arachnid interrelationships.

256

257

258 **Final conclusions**

259

260 Reconstructing the phylogenetic relationships of Arachnida and its constituent orders remains
261 an arduous task, yet some areas of the family tree are becoming visible among other still obscure
262 regions. The monophyly of Arachnida continues to rely on morphology with a few recent molecular
263 analyses finding evidence under particular sets of conditions. Within Arachnida, the clades
264 Arachnopulmonata, Tetrapulmonata, Pedipalpi and Thelyphonida appear now well supported, virtually
265 by all classes of data. Likewise, Parasitiformes + Opilioacarida form a clade in nearly all published
266 analyses. However, resolving the relationships of the apulmonate arachnids will require additional data
267 and creative analyses, as currently it is virtually impossible to place confidence on any given relationship.
268 New fossil discoveries and the study of evodevo in new model arachnids will continue to provide
269 additional sources of evidence to anchor some of the most unstable areas of the arachnid tree of life.

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273

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411

412 **Fig. 1.** Cladogram proposed by Weygoldt and Paulus' seminal 1979 papers on arachnid relationships.

413

414 **Fig. 2.** Selected hypotheses of arachnid relationships mostly based on morphological data or combined
415 morphology and molecules. Notice that with the exception of Weygoldt and Paulus (1979), all other
416 analyses place Scorpiones and Opiliones (both in bold) as either sister groups or within the same clade, a
417 hypothesis now rejected in most molecular analyses. Instead Tetrapulmonata (extant orders in bold &
418 oblique) are common among nearly all morphological and molecular analyses.

419

420 **Fig. 3.** Selected plots of bootstrap support values as genes are added in order of increasing evolutionary
421 rate for six nodes of interest, based on Sharma et al. (2014a). Chelicerata, Euchelicerata and
422 Arachnoplumonata show the expected trend of stabilizing with maximum support with the addition of
423 data; Arachnida instead achieves maximum support at 500-600 genes, but the group disappears with
424 the addition of further information; the last two plots show maximum support for conflicting sister
425 group relationships of Ricinulei with different data matrix sizes.

426

427 **Fig. 4.** Conservative resolution of arachnid ordinal relationships including extant and fossil taxa; major
428 clades are labelled. This is a personal view from the author and is not derived from any specific analysis.





