



# 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

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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 Arachnoplumonata (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 20<sup>th</sup> 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 orders<sup>1</sup>  
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

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<sup>1</sup> 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, Uropygi<sup>2</sup> 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 Trombidiiformes 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.

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<sup>2</sup> 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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### 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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#### 164 **4. Scorpiones—Lipoctena or Arachnopulmonata?**

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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.

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## 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.

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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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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.









