

behavior of sternophorids may assist in determining their phylogenetic status. Cheliferoidea consist of Withiidae (34 genera, 153 species), Cheliferidae (59 genera, 274 species), and Chernetidae (111 genera, 646 species). The resolution of this clade depends on mating behavior and spermatophore morphology (Proctor 1993). Cheliferoids are the only pseudoscorpions with sperm storage receptacula (spermathecae) in females.

The fossil fauna consists of 35 named species, most of which were found as inclusions in Tertiary ambers. Cretaceous pseudoscorpions are known (Schawaller 1991), but the earliest known taxon is *Dracochela deprehendor* from Devonian shales in New York (Schawaller et al. 1991).

Harvey (1992a) confirmed the monophyly of most families, but the original analysis is currently being extended to include more taxa to test further the monophyly and internal phylogeny of various clades.

### Solifuges, Camel Spiders (Solifugae)

Solifuges or solpugids are a bizarre group of specialized, mostly nocturnal, errant hunting arachnids notable for their huge powerful chelicerae and voracious appetite (Punzo 1998). Besides their large powerful chelicerae, solifuges are unique in having sensory malleoli (or racket organs) on the fourth coxae and trochanters, and many other peculiar features (prosomal stigmata, male cheliceral flagellae, palpal coxal gland orifices, adhesive palpal organs, a monocondylar walking leg joint between the femur and patella).

The Solifugae contain 1,084 species in 141 genera and 12 families (Harvey 2003): Ammotrechidae (22 genera, 81 species), Ceromidae (three genera, 20 species), Daesiidae (28 genera, 189 species), Eremobatidae (eight genera, 183 species), Galeodidae (eight genera 199 species), Gylippidae (five genera, 26 species), Hexisopodidae (two genera, 23 species), Karschiidae (four genera, 40 species), Melanoblossiidae (six genera, 16 species), Mummuciidae (10 genera, 18 species), Rhagodidae (27 genera, 98 species), and Solpugidae (17 genera, 191 species). Only three fossil species are known (Selden and Dunlop 1998). They primarily occur in Old and New World semi-arid to hyperarid ecosystems but are absent from Australia and Madagascar. The Southeast Asian melanoblossiid *Dinorhax rostrumpsittaci* is unusual in residing in rainforest, whereas the peculiar mole solifuges (Hexisopodidae) from the deserts of southern Africa are highly modified for burrowing through soil (Lamoral 1972, 1973).

Relationships within the order are very poorly understood, largely because of the chaotic familial and generic classification promulgated by Roewer (1932, 1933, 1934) and continued with many reservations by later workers (e.g., Muma 1976, Panouse 1961, Turk 1960). The current classification is a flat structure devoid of any phylogenetic signal (Harvey 2002b, 2003). There has been no detailed phylogenetic work on any solifuge group, let alone a synop-

sis, and no monophyly arguments exist for any family, although some (e.g., Hexisopodidae) seem to be defined by obvious autapomorphies. The group urgently needs higher level cladistic analysis.

### Conclusions

The last decade has seen substantial progress in research on major arachnid clades. Considering family rank as indicating "major" lineages, at least preliminary hypotheses are available for five of the 13 "orders" (Araneae, Amblypygi, Opiliones, Scorpiones, and Pseudoscorpiones), but an additional four (Ricinulei, Palpigradi, Uropygi, and Schizomida) have only one or two clades ranked as families, so relationships at that level are trivial. Solifugae (12 families, 141 genera) and Acari (~400 families, ~4000 genera) remain as substantial lineages without explicit family-level phylogenies. Although solifuge taxonomy is so completely artificial that it is difficult to know how to begin, the main reason is lack of workers: only two or three solifuge specialists exist worldwide. Mites similarly suffer from a lack of taxonomists, but the few acarologists must deal with a much greater taxonomic tangle. There are so many autapomorphic mite lineages and so much diversity that relationships are obscured, resulting in an overly split higher classification. The very small size of mites makes molecular work difficult, although not impossible (e.g., Dabert et al. 2001), and they are so morphologically diverse (and often highly simplified) that morphological work is no easier.

The current conflict between molecules and morphology at the ordinal level in arachnid phylogeny is intriguing but probably temporary. Deeper nodes in arachnid phylogeny are hard to recover consistently with 18S and 28S rRNA sequence data. Curiously, the same loci do provide robust signal on still deeper nodes (e.g., arthropods; see Wheeler et al., ch. 17 in this vol.), as well as shallower nodes such as Opiliones (Giribet et al. 2002) and Scorpiones (L. Prendini and W. Wheeler, unpubl. obs.). The problem, therefore, seems to be, on the one hand, exploratory—loci robustly informative for these presumably Lower Palaeozoic divergences are as yet unknown—and on the other, technical, because the few loci that seem to have worked in other taxa at comparable levels have not been studied in arachnids. Edgecombe et al. (2000) also point out that the "anomalous" nodes in molecular results are usually weakly supported. The sheer quantity of molecular data make a single, most parsimonious tree almost inevitable, but that obscures the often very tenuous support for some nodes. Because fewer comparisons are usually possible, morphological data are more likely to produce multiple most parsimonious trees so that dubious nodes disappear in the strict consensus tree. No doubt as more genes are analyzed and taxon sampling improves, the discrepancies will decrease and the congruence of the total evidence will improve.

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