1 Introduction to the Acari

Systematic Position and Ecological Role

The Acari, or mites, are small animals; the adults range from 300 to 500 μm in body length, except for some eriophyoids which are approximately 100 μm long and certain ticks whose females measure about 30,000 μm long. They belong to the phylum Arthropoda, a monophyletic taxon of terrestrial and marine invertebrates (Weygoldt, 1998) which are characterized by jointed legs and a chitinous exoskeleton. Two groups of Arthropoda, the Pantopoda and the Chelicerata, lack antennae and mandibles, and molecular analyses have shown that the Chelicerata is a sister taxon of a clade including the Crustacea and the Insecta (Telford and Thomas, 1998). From a systematic point of view, the Chelicerata is a subphylum that includes the class Arachnida, a primarily terrestrial group that includes the subclass Acari along with several orders (Amblypygi, Araneae, Opiliones, Palpigradi, Pseudoscorpionida, Ricinulei, Schizomida, Scorpiones, Solifugae and Uropygi) (Weygoldt and Paulus, 1979a,b). Members of the subclass Acari lack opisthosomatic spinnerets and conspicuous primary segmentations (or tergites arranged segmentally). The Acari includes the superorders Acariformes and Parasitiformes, and is morphologically differentiated from other relatively simple arachnids (Krantz, 2009a). Adults of the Acari usually have four pairs of legs, with the exception of eriophyoids, which have two pairs. Their biological cycle progresses through the stages of egg, larva and nymph. The larva is six legged and the nymph eight legged. Another characteristic that sets the Acari apart from the other Arachnida is that the phase which hatches from the egg has fewer legs than subsequent phases, while the eggs of spiders, scorpions, pseudoscorpions and opilionids all hatch into eight-legged organisms.

Up to 1999, approximately 55,000 species of Acari have been described, but the group is likely to grow to number over a million species (Walter and Proctor, 1999). By 2011, a total of 54,617 mite and tick species had been reported (Zhang, 2011). This high number of species can be explained by assuming that if in each of the 400,000 plants currently known there lives almost one species-specific mite, then the number of plant-feeding mites could be as many as 400,000 species. Similarly, if each of the 60,000 known species of vertebrate animals harbours almost two species-specific mites, the number of species-specific mites might be at least 120,000 species (Hoy, 2011). That there could be such a high number of species is not surprising when one considers that at present our knowledge of the Acari is small and fragmentary. A bibliographic analysis of the acarological papers published in *Zootaxa* from 2001 to 2005 gives a good representation of the strong development that there has been in this subject. In this period of time, the list of new taxa described and published in this journal only includes 16 genera and 185 species (Fan, 2006). Krantz (2009b) reported that the large number of species that have been described has led to the designation of about 5500 genera and 1200 subgenera in 540 families.

The small size and the strong evolutionary plasticity of the Acari have permitted these singular organisms to colonize most of the available aquatic and terrestrial habitats, where they exhibit a great ability to exploit the available trophic resources owing to their different and varied dietary regimes – phytophagous, parasitic, predaceous, mycophagous, saprophagous, coprophagous and necrophagous. In short, the Acari may be found worldwide in any environment capable of supporting life. As such, they can be collected from regimes as diverse as windswept arctic tundra, hot desert sands, icy depths or the hair follicles of eyebrows (Krantz, 2009b). For humans, the Acari form a significant component of the fauna of the cultivated plants and forests of any region of the world, either as pests (Jeppson *et al*., 1975; Keifer *et al*., 1982; Helle and Sabelis, 1985; Lindquist *et al*., 1996; Zhang and Liang, 1997; Bolland *et al*., 1998; Amrine *et al*., 2003) or as beneficial organisms (Huffaker *et al*., 1970; McMurtry *et al*., 1970; Gerson *et al*., 2003), etc. Furthermore, these little animals play a fundamental role in the litter and humus layers of forests, grasslands and agricultural soils, where they recycle minerals (Balogh, 1972). Bader (1989), in an interesting booklet written in German, discussed the fundamental features of the Acari. Walter and Proctor (1999) very effectively summarized the ecological importance and the economic role of these small and interesting animals. They wrote that: ‘The average mite is minuscule, barely perceptible to even the sharpest eyes. When enough are present, however, mites can exert efforts disproportionate to their size. When a crop disappears under a blanket of silk or stored food turns into a seething mass of hairy motes, then the numbers of mites will be legion. If the mite is an itch mite burrowing into one’s skin or a tick injecting virulent rickettsiae into one’s blood, then “enough” can be a single mite’.

Origins and Phylogenesis

Incomplete conservation, inadequate sampling and taxonomic problems make it very difficult to assess the exact evolution of the Acari over a long period of time. In addition, species such as the Acari are very small in size and have very little tough exoskeleton, so are not suitable for preservation. So to better uncover the essential features of the origins and phylogenesis of the Acari, one must make some assumptions. In particular, the first fossil records of marine invertebrates date back about 600 mya and it is estimated that these evolved in a few million years. In the previous 2,500 million years, life on earth appeared to be exclusively represented by algae and bacteria. The abundant availability of a monoculture of algae and eukaryotic cells formed in that time could have led to the largest explosion of evolutionary activity so far known (Gould, 1981). During the Permian period, there was a major decrease in the number of families of animals living at the bottom of the sea (Valentine, 1970), and Schopf (1974) reported that the later Permian was the time when the earth's continents came together to form the (only) supercontinent of Pangaea. This union produced a decrease in the surface of the earth covered by shallow seas, and consequently a decrease in the habitat available to shallow water invertebrates. Likewise, the increase in the abundance of fauna recorded after the Permian can be explained by the subsequent increase in shallow seas produced by the separation of Pangea into smaller continents. An interesting analysis of the history of marine animal diversity has recently been published by Stanley (2007). In addition to the above-mentioned fossil records of marine invertebrates 600 mya, since the early Silurian early fossil records appeared of vascular plants, followed by records of pteridophytes in the Carboniferous, and records of gymnosperms to angiosperms in the Cretaceous and Tertiary (Niklas *et al*., 1983). The earliest phytophagous Insecta date from the Carboniferous (Strong *et al*., 1984), and it is well known that there is reciprocal evolution between plants and insects that represents an important mechanism for increasing the wealth of wildlife (Begon *et al*., 1986).

It is commonly believed that the first fossil records of the Arachnida (and the Acari) originate in the late Silurian–early Devonian periods (*c*.425 mya) in the form of a pulmonate trigonotarbid (Arachnida, Trigonotarbida), which is now extinct. Dunlop and Selden (2009) report that the oldest mite fossil is from the Devonian (410 mya), while the age of scorpion and spider fossils is 428 and 312 mya, respectively. The advent of the Acari probably also relates to the latter part of the evolution of the arthropods, with diversification having occurred about 200 million years earlier in the Cambrian period (Gould, 1989; Walter and Proctor, 1999). Fossil records show that the terrestrial Arachnida acquired respiratory organs of different types at different times during the transition from the marine environment on to land, as in the scorpions, trigonotarbids, etc. Formally, this pattern of developmental behaviour contrasts with the hypothesis of the monophyletic origin of the Arachnida (Bergstrom, 1979). The fossil records now available seem to indicate that the Acari had achieved a certain amount of diversity by the early to mid-Devonian (Hirst, 1923a; Woolley, 1961; Norton *et al*., 1988; Evans, 1992; Subías and Arillo, 2002), which suggests that they colonized terrestrial environments as early as the late Silurian. Moreover, in the early Devonian, all fossil Acari now known belonged to the superorder Acariformes (Walter and Proctor, 1999), and the fossil records of the Parasitiformes dating to the late Cretaceous (Witalinski, 2000; Poinar and Brown, 2003); the parasitiform Trigynaspida may date to as early as the upper Triassic (*c*.220 mya) (Kim, 2004). Studies of mitochondrial phylogeny have shown that the orders and classes of spiders, scorpions, mites and ticks diversified in the late Palaeozoic (Jeyaprakash and Hoy, 2008, 2009). Recently, Sidorchuk and Bertrand (2013) described *Sellnickiella balticae* Sidorchuk *et* Bertrand (Labidostomatidae), thus highlighting the presence in Eocene Baltic amber (more than 40 Ma) of the genus *Sellnickiella* Feider *et* Vasiliu and a second species of the genus *Labidostoma* Kramer (*Labidostoma* (*Pseudocornutella*) *electri* Sidorchuk *et* Bertrand), after the congeneric species previously described by Dunlop and Bertrand (2011). The report pointed out that notwithstanding the few fossil mite descriptions, the discovery of these mite carnivores in Baltic amber suggests that Palaeogene mite biodiversity was comparable to current mite diversity (Sidorchuk and Bertrand, 2013).

The fossil records now available seem to show that after the extinction events registered in the Permo–Triassic and after the statement of modern lineages, a significant adaptive process may have occurred in the Acari during the late Mesozoic and early Cenozoic periods (60–100 mya). At this time, there was a strong morphological and ecological diversity among the Acari that permitted significant exploitation of the many co-evolving plants and animals, and there was a consistent diversification of angiosperm plants and Insecta (Lindquist, 1975; Krantz, 2009c). Specialized plant-parasitic mites, e.g. the eriophyoid *Triasacarus fedelei* Lindquist *et* Grimaldi and *Ampezzoa triassica* Lindquist *et* Grimaldi, existed as early as the Triassic (Schmidt *et al*., 2012). Acari are often associated with Insecta as phoretic or parasitic mites in fossil records dating from the Cretaceous about 20–40 million years earlier (Poinar, 1992; Poinar *et al*., 1993, 1997). The same phenomenon has been observed between parasitic Acari and vertebrate hosts in the mid-Tertiary (Poinar, 1995). Mites of the suborder Oribatidae have been found in fossils of the late Carboniferous (Labandeira *et al*., 1997). The oldest oribatid fossils are from the Devonian (Norton *et al*., 1988), and some of them belong to modern families (Subías and Arillo, 2002). All mites described from the Carboniferous, Jurassic and Cretaceous periods are included in modern families, with one exception (Subías and Arillo, 2002; Arillo *et al*., 2012).

Regardless of the above information, in the last half century a need has developed to understand whether mites are characterized by a condition of dichotomy between acariforms and non-acariforms, or not. In short, we need to know whether in the course of the evolution of the Arachnida an event has resulted in a monophylogenous origin of the Acari or whether they result from the convergence of two or more groups that have evolved independently of one other and are now similar. Woolley (1961) notes that 'no known connections with other arachnids can be ascertained from the fossil record, but the chelicerae and other morphological features indicate that the Acari probably had an arachnid origin in opilionid-like ancestors, but developed with inherent peculiarities, principally the gnathosoma. They are at least diphyletic, probably polyphyletic, in origin, with two main groups, the older Anactinochitinosi (Notostigmata, Mesostigmata, Ixodides) and the younger Actinochitinosi (Trombidiformes, Sarcoptiformes)'. Following Jeyaprakash and Hoy (2008, 2009), an estimate of the evolutionary age of mites places their chelicerate ancestors in the Precambrian and their divergence as mites to at least 424 mya.

Studies of the morphological, developmental and behavioural aspects of mites from various research support different positions on their evolutionary origin (Zakhvatkin, 1952; Lindquist, 1984; Van der Hammen, 1989; Walter and Proctor, 1999). Examination of 40 characters of 12 extant orders of arachnids (including the Acari), and in particular the examination of the common characters – possession of a movable gnathosoma and the existence of exapod larva and of the three octopod nymphal instars – suggest that the mites are derived from a common ancestral stock (Lindquist, 1984) and that monophyletic Acari and Ricinulei are sister groups (Kaestner, 1980). However, spermatological evidence from the Chelicerata does not encourage support for a common origin of acariforms and non-acariforms (Alberti, 2000).