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The study of fossil spider species

Étude d'espèces fossiles d'araignées

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ABSTRACT

The definition of what constitutes a species has been an area of contention in biology since before the time of Darwin. Here, we discuss concepts of species in regards to the Araneae and particularly focus on diagnosing fossils. Spiders are primarily diagnosed by their copulatory organs, which may be difficult to observe in fossils due to a number of confounding factors, thus potentially hindering identification and systematic classification. However, despite potential difficulties, fossils should and must be studied alongside extant Araneae in order to garner a full understanding of the evolutionary history of this megadiverse group.

Mots-clés :
Araneae
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RÉSUMÉ

La définition de ce qui constitue une espèce a été un domaine de controverse en biologie, depuis l'époque de Darwin. Dans cet article, est discuté le concept d'espèce dans le cas des Araneae, en se focalisant plus particulièrement sur les fossiles caractéristiques. La diagnose des araignées se fait essentiellement par les organes copulatoires, difficiles à observer chez les araignées fossiles, du fait du nombre de facteurs de confusion, ce qui gêne potentiellement l'identification et la classification systématique. Cependant, en dépit de ces difficultés potentielles, les fossiles devraient être étudiés en fonction des Araneae existants pour parvenir à une compréhension totale de l'histoire évolutive de ce groupe très diversifié.

1. Species concepts

To date, arachnologists have identified more than 41,000 extant spider species and over 1100 fossil spider species (Dunlop et al., 2010; Platnick, 2010, respectively). Here, we examine the nature of fossil spider species and the challenges inherent in their study.

Myriad species definitions exist, some of which focus on the nature of species or what they are (ontology) and others that focus on how we recognize them (epistemology). One of the more common ontological species definitions is the biological species concept (BSC), whereby species

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are defined as actually or potentially interbreeding groups of organisms (Dobzhansky, 1937; Mayr, 1942). Related to the BSC is the ontological notion that species are defined by their specific mate recognition system (SMRS); in other words, species have a means of recognizing each other for the purposes of interbreeding (Paterson, 1985). By identifying characters used in mate recognition, the SMRS can also be epistemological in nature. Others view species as phylogenetic lineages with distinct and separate evolutionary tendencies (evolutionary species concept; Wiley, 1978, 1981), and as the smallest collection of organisms that can interbreed and are defined by one or more uniquely shared characters (phylogenetic species concept; Eldredge and Cracraft, 1980). The latter definition is both ontological and epistomological in nature. All of the above-discussed species concepts treat species as individuals in the sense of Ghiselin (1974) and Hull (1980), with distinct births, deaths and historical persistence (Eldredge, 1989, Lieberman, 2000). As we shall see, elements of each of these concepts have been utilized across the Araneae. Further, reproductive character complexes may not be (fully) preserved in fossilized spider specimens, yet such character complexes are typically used to identify and delineate extant spider species. This does not, however, put fossil spider species on a different ontological status from extant species. It simply means that we need to use different epistemological means when confronted with fossilized remains.

2. Spider species

Many volumes have been dedicated to the discussion of species concepts (e.g. de Queiroz, 2007; Harrison, 1998; Mayden, 1997; Slobodchikoff, 1976; Sluys and Hazevoet, 1999), and thus we focus on those utilized most heavily within the Araneae. Huber (2004) posed three tenets of species that spider taxonomists (generally) seem to agree upon: (1) species are real, (2) species are reproductive communities that are genetically isolated from other such communities (i.e., the BSC discussed above), and (3) copulatory organs take precedence in delineating species, but all characters showing discontinuous variation are considered as potential discriminatory candidates. As Huber (2004) noted, the first two statements are ontological in nature, while the last point is primarily epistemological.

The practice of using copulatory organs for species identification within the Araneae harkens to the late 1800s (Huber, 2004) and is based on the recognition of the species-specificity of these structures. Modern systematic work on spiders focuses almost exclusively on the morphology of copulatory organs (for a recent example, see Wang et al., 2010). The primary copulatory organs (i.e., those that transfer and accept sperm) are the pedipalps (palps) in males and the eypigyne in females. There are also numerous secondary copulatory organs involved in mating, primarily processes related to clasping or positioning the mate (Huber, 2004; Huber and Eberhard, 1997). A plethora of hypotheses seek to explain the specificity of genitalia, ranging from cryptic female choice (Eberhard, 1985; Eberhard and Huber, 2010) to the conflict of interest (Alexander et al., 1997) and mate check hypotheses (Jocqué, 1998). The 'lock-and-key' mechanism of Dufour (1844) hypothesizes that female genital structures evolved to exclude the genitalia of males of other species, which is classic SMRS. Although the mechanism has been refuted by some (Huber, 2004 and Eberhard and Huber, 2010 for reviews), the correct matching of male/female genitalia, which often do exhibit close to perfect fit like a lock and key, remains largely true (Eberhard and Huber, 2010).

Recently, some researchers have questioned the general assumption that genitalia are species-specific (Huber, 2003, 2004), pointing to a logical conundrum that results when copulatory organs are considered species-specific and when individuals with different copulatory organs are then described as different species. Genital polymorphisms have rarely been documented within the Araneae, but this may result from the confines of the logical circle. It should be noted that the above is an epistemological problem of designating species rather than an ontological one.

If, however, genital specificity is the overwhelming pattern observed in nature (e.g. Eberhard, 1985; Eberhard and Huber, 2010), then point (3) from Huber (2004) (i.e., copulatory organs are used most often for delimiting species boundaries in spiders) potentially becomes ontological in nature and not solely epistomological. In other words, the copulatory organs may act as the SMRS of a species, which we, as scientists, can use to delineate species boundaries. Therefore, the nature of spider species and how they are designated may be largely congruent.

In contrast to species, higher-level groupings within spiders are traditionally based on somatic characters rather than genitalia (Foelix, 1996; Huber, 2004; Platnick, 1975). Families and genera are human constructs, and if designated appropriately, will correspond to groups that share a common evolutionary history (i.e., monophyly).

3. Fossil spiders

3.1. Fossil record and preservation

Because of their fragility, the fossil record of spiders is controlled by the occurrence of Konservat-Lagerstätten (i.e., exceptionally well-preserved fossil deposits, Seilacher, 1970). One well-known Lagerstätte is amber, the highly polymerized form of fossil tree resin (Fig. 1A). The majority (over 90%) of fossil spiders discovered to date derive from amber deposits of Cenozoic age (Selden et al., 2009), with Baltic and Dominican ambers predominating (Fig. 2). The oldest spiders found in amber are from the Cretaceous (Dunlop et al., 2010). More rarely, spiders are preserved in sedimentary rock strata, and there are nearly as many different preservational styles as there are araniferous Lagerstätten (Fig. 1B; Selden and Penney, 2010 for an extensive review). Sedimentary deposits preserving the oldest record of spiders date back to the Carboniferous (Selden et al., 2009).

Although the term Lagerstätte conjures up images of exceptionally preserved fossils, fine-scale anatomical details are often not visible. Identifying spider species is therefore frequently difficult due to preservational