General palaeontology

The study of fossil spider species

Étude d'espèces fossiles d'araignées

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A B S T R A C T

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.

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R É S U M É

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.

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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
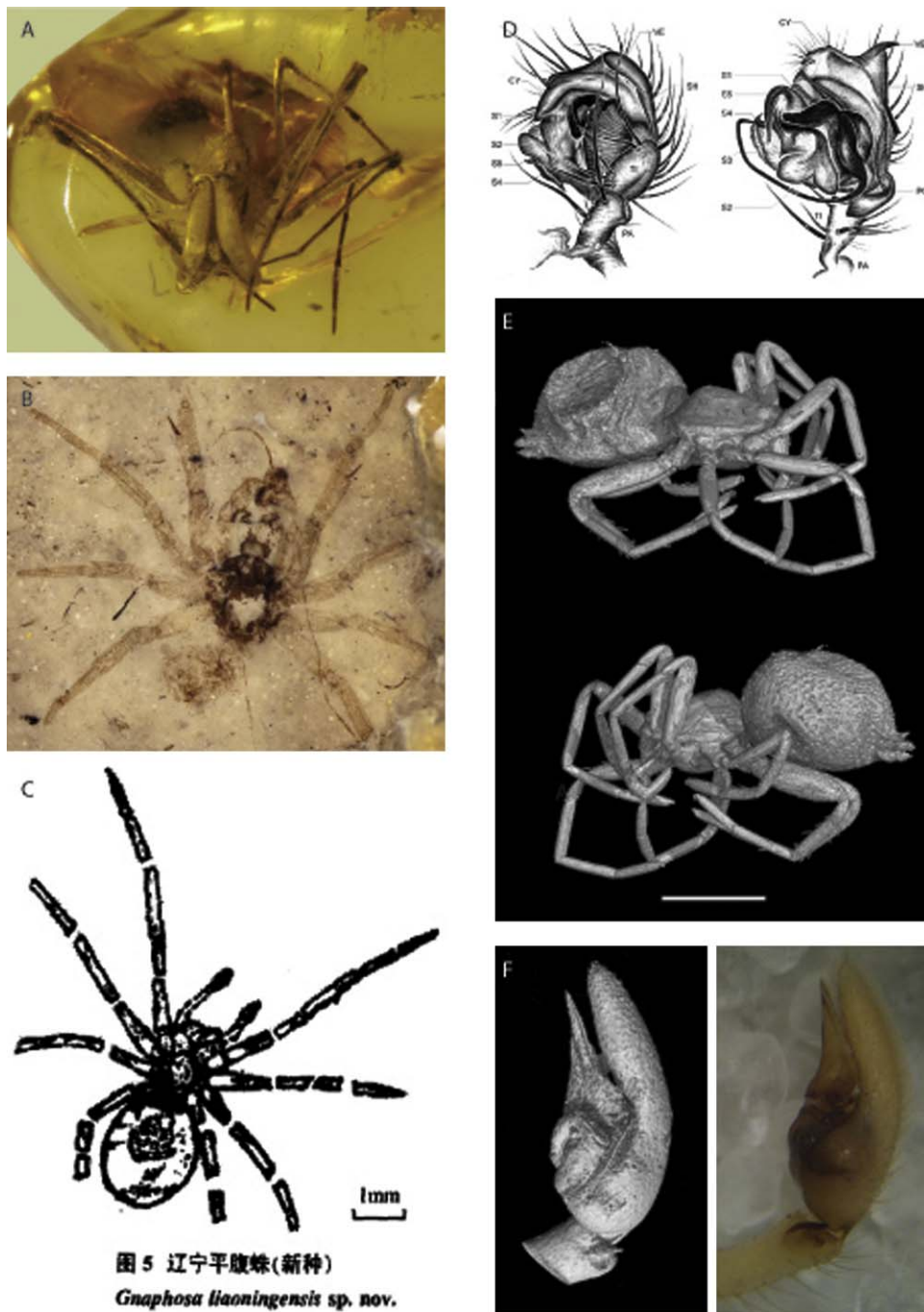
Fig. 1. A. An example of a specimen preserved in amber (Araneae, Archaeidae). **B**. Preservation in rock of *Eoplectreurys gertschi* (Plectreuridae) from the Middle Jurassic of China. Note the details of the palpal bulb and long, thin embolus. Image from Selden and Huang (2010). **C**. Illustration of a specimen from the Lower Yixian Formation in China, described as belonging to the extant genus *Gnaphosa*, but with few convincing details. Image from Chang (2004). **D**. Pedipalps of two species of *Mimetus* in retrolateral view. On the left is *M. bituberculatus* (extinct) and on the right is *M. syllepicus* (extant). Comparative analysis suggests affinities between these two species and provides an excellent example of how fossil and extant species should be studied in concert. Image from Harms and Dunlop (2009); reproduced with permission from John Wiley and Sons. **E**. 3D reconstruction of a Lower Cretaceous Spanish amber spider (*Orchestina*, Oonopidae) produced with propagation phase contrast X-ray synchrotron imaging. Scanned using PPC-SRμCT at BM05 beamline with a voxel size 0.7 μm, propagation distance 100 mm, and 20 keV. Scale bar 500 μm. Image from Soriano et al. (2010); reproduced with permission from Elsevier. **F**. Palps of the extant species *Donuea collustrata* (Liocranidae). On the left is a copal specimen scanned using high-resolution X-ray computed tomography, and on the right is an extant specimen. Conspecificity was established by comparing minute details of the palp. Image from Bosselaers et al. (2010); reproduced with permission from Magnolia Press.
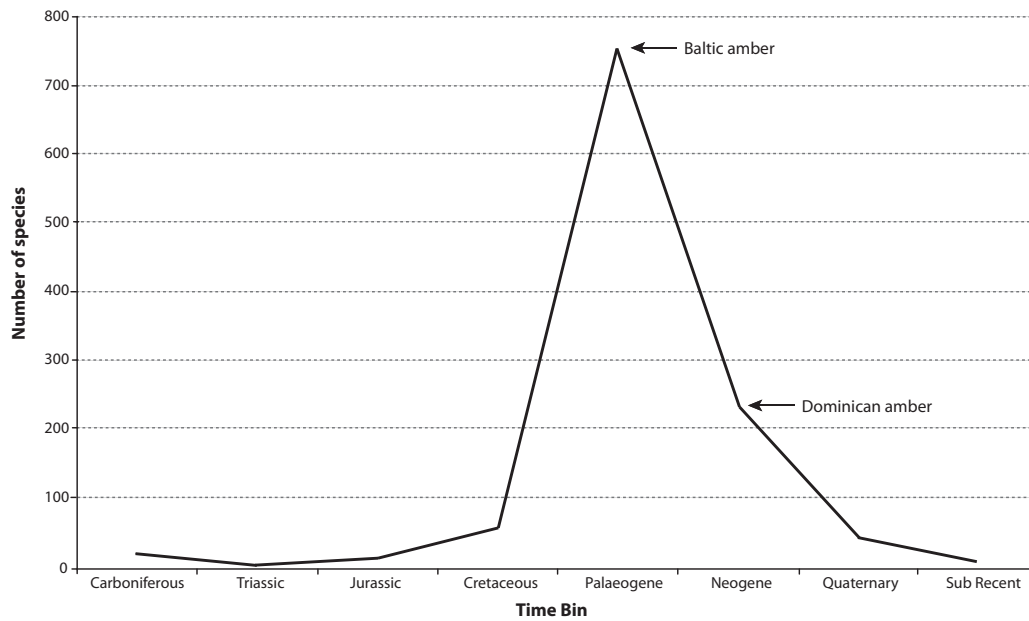
Fig. 2. Number of spider species described per time bin. Notice the spike in the Palaeogene and Neogene, which is primarily controlled by the Baltic and Dominican amber Lagerstätten. Data derived from Dunlop et al. (2010).
Fig. 2. Nombre d'espèces d'araignée décrites par époque. À noter le pic au Paléogène et au Néogène, qui est essentiellement contrôlé par les « Lagerstätten » d'ambre baltiques et dominicains. Données issues de Dunlop et al. (2010).

constraints. Even in amber, which preserves specimens with the highest fidelity, the genitalia may be distorted, obscured or absent, and this has interesting implications for species definition. Genitalia are even less likely to be preserved in sedimentary deposits because the three-dimensional palps and epigynes are reduced to two-dimensions. Preservational infidelity is potentially more troublesome when dealing with members of the monophyletic Entelegynae, characterized by more complex reproductive systems, compared to those specimens belonging to the Haplogynae (Coddington, 2005; Coddington and Levi, 1991; Foelix, 1996; Griswold et al., 1999; Hausdorf, 1999; Platnick et al., 1991). Female entelegynes have epigynes with external copulatory openings, and males usually possess palps with two or three divisions in the bulb (e.g., subtegulum and tegulum). The parts of the entelegyne bulb are typically connected by thin membranous tissue that expands during copulation (Coddington, 2005). This delicate membrane may be distorted during fossilization, thus complicating interpretation and determination of homologous structures in extant and fossil palps. Generally, the relatively simple, pyriform bulb of

a haplogyne is more likely to be fully preserved than the complicated and intricate details of an entelegyne palp.

Other anatomical features, including trichobothria, leg spination, eye pattern, and coloration may be tricky, if not impossible, to observe in fossil specimens, meaning that species identification must proceed in a different manner than when dealing with extant taxa. Although confined to available morphological characters, we do not imply that palaeo-species differ from extant species; as mentioned previously, palaeontologists simply must employ (potentially) different epistemological means of species identification. For instance, molecular methods cannot be drawn on to delimit fossil species, although this does not differ from the majority of modern systematic studies still firmly rooted in morphology. Using molecules to parse out inter- and intraspecific relationships has been utilized more frequently within spiders (e.g. Bond and Stockman, 2008; Duncan et al., 2010; Hedin, 1997), but claims that DNA barcoding can replace traditional taxonomy and identify species (e.g. Barrett and Hebert, 2005) has rightly met with resistance (Prendini, 2005; Scotland et al., 2003; Seberg et al., 2003). As Prendini (2005) (p. 502)

Fig. 1. A. Exemple d'un spécimen conservé dans l'ambre (Araneae, Archaeidae). **B**. Conservation dans la roche d'*Eoplectreurys gertschi* (Plectreuridae) du Jurassique moyen de Chine. À noter les détails du bulbe palpal et de l'embolus long et mince. Image extraite de Selden et Huang (2010). **C**. Illustration d'un échantillon en provenance de la Formation Yixien inférieur de Chine, décrit comme appartenant au genre *Gnaphosa* vivant encore actuellement, avec quelques détails convaincants. Image de Chang (2004). **D**. Pédipalpes de deux espèces de *Mimetus* en vue rétrolatérale. À gauche, *M. bituberculatus* (espèce éteinte) et à droite *M. syllepicus* (existant encore actuellement). Une analyse comparative suggère des affinités entre ces deux espèces et fournit un excellent exemple de l'opportunité de l'étude conjointe d'une espèce fossile et d'une espèce actuelle. Image de Harms et Dunlop (2009), reproduite avec l'autorisation de John Wiley and Sons. **E**. Reconstitution 3D d'une araignée récoltée dans de l'ambre du Crétacé inférieur d'Espagne (*Orchestina*, Oonopidae) par imagerie synchroton RX, à contraste de phase. Scannage utilisant PPC-SRμCT, ligne BM05, taille de pixel 0,7 μm, distance de propagation 100 mm, 20 keV. Barre d'échelle 500 μm. Image extraite de Soriano et al. (2010), reproduite avec l'autorisation d'Elsevier. **F**. Palpes de l'espèce existant encore actuellement *Donuea collustrata* (Liocranidae). À gauche, échantillon de pince scanné en utilisant la tomographie haute résolution X par ordinateur et à droite, un échantillon actuel. Une conspécificité a été établie en comparant de minuscules détails des palpes. Image extraite de Bosselaers et al. (2010), reproduite avec l'autorisation de Magnolia Press.

noted: "DNA-based methods are not demonstrably more objective, accurate, or useful than morphology or other sources of phenotypic data for species identification or other taxonomic purposes."

3.2. Diagnosing species

We have discussed how genitalia are used as species-specific characters and can potentially reveal SMRSs within the Araneae, but does this imply that somatic characters cannot and should not be used in species identification? In other words, are these characters epistemologically useless for species delimitation? A review of the spider systematic papers from the three most recent issues of the *Journal of Arachnology* illustrates that somatic characters are employed as diagnostic criteria for extant species in nine out of 14 papers (over 60%). This is in accord with Huber's (2004) third tenet, where such characters are still considered relevant diagnostic criteria. We assert that even though copulatory organs may be more epistemologically meaningful for distinguishing species, no *a priori* evidence exists to discount somatic characters as species-specific. Further tests, such as molecular and field analyses, can be performed on a case-by-case basis in the modern to examine if particular somatic differences emerge at the species-level or if they are polymorphisms, a task difficult to perform in the fossil record. Huber (2004) noted that individuals with identical copulatory organs but with discontinuities in other characters are usually interpreted as polymorphic or polytypic species, yet this practice is perhaps dubious. Consequently, somatic characters should be treated as potentially distinguishing features of a species, given no other *a priori* evidence to the contrary. There is always a risk that epistemology may not equate to the ontology of a species. In other words, we may over-split, creating many species when only one exists, or we may lump many species into a single taxon, but as long as diagnoses are explicit, new information and further research can continually test these hypotheses.

The proceeding discussion on preservational media hints at the difficulty of comparing the rock and amber records of spiders, both to each other and to living species, because each recovers a potentially different (sub)set of characters. The question is then raised of how to deal with similar looking fossils found under different preservational conditions. We posit that if there are no obvious differences between the fossils, the specimens should be placed at the appropriate taxonomic level for which the available diagnostic characters allow. No designation should be made for depauperate specimens lacking synapomorphies and/or distinguishing morphological data. The possibility exists that specimens that appear different due to preservation will be named as different species, when in reality they are synonymous (NB: due to the scarce nature of the fossil spider record, this is unlikely to be a major problem). Again, incorrectly diagnosing species is not the exclusive problem of palaeontology, and if there is no *a priori* evidence to suggest the specimens belong to the same species, differences should be treated as such, or no designation should be made if relevant and diagnosable character complexes are not discernible.

Occasionally, specimens are discovered that do not easily fit into extant classification systems (i.e., family, genera), but which are clearly related to modern lineages (i.e., so-called plesion or stem lineages). When this occurs, how should these specimens be treated so that classifications are in accord with hypotheses of evolutionary history and poly- and/or paraphyletic groups are avoided? Should modern genera be diagnosed more broadly to accommodate closely related fossil forms, or should the fossil (plesion) taxa be maintained separately? We advocate the methodology of Wiley (1979) and Patterson and Rosen (1977), whereby the fossil specimens are placed in the groups that they are most closely related to (i.e., plesiomorphic to), but the corresponding taxon name is placed in shutter quotes, denoting the group's potential paraphyly. This maintains modern classifications without uprooting traditional diagnoses, but also allows for hypotheses of relatedness within a phylogenetic framework. For example, Saupe and Selden (2009) described a species most closely related to the spider family Mecysmaucheniidae, but the specimen lacked the complete set of diagnostic characters of the modern group (e.g., the fossil possessed four rather than two spinnerets). In this case, the specimen could be diagnosed as "Mecysmaucheniidae", rather than placed as a separate stem-lineage family or necessitating a re-diagnosis of the extant group.

Since spiders are relatively scarce in the fossil record, species descriptions are primarily based on singletons or only a few specimens (rather than a series of similar specimens), and only one specimen may represent the fossil record of entire families/lineages. Of course, this makes it impossible to assess levels of within-species variation. Reliance on Lagerstätten also means that range extensions and ghost lineages are quite common within the Araneae. These terms refer to the history of taxa with no direct record, as elucidated within a phylogenetic framework (Edgecombe, 1992; Norell, 1992; Norell and Novacek, 1992). For example, the presence of Cretaceous species within the family Oonopidae suggests the Orsolobidae (putative sister to the oonopids *sensu* Forster and Platnick, 1985 and Platnick et al., 1991) were also present during this time, although they have yet to be found as fossils (Penney, 2002a).

Unfortunately, an increasing number of Mesozoic specimens have been assigned to extant genera (e.g., *Araneus*, *Gnaphos* and *Theridion* in Chang, 2004 and *Pisaura* in Kim and Nam, 2008), with poor descriptions and inadequate illustrations (Fig. 1C). These reports are problematic because they may skew our view of spider evolution by incorrectly dragging back records of genera or families and by providing erroneous calibration points for phylogenetic studies. Diagnostic criteria should be met for taxonomic placement in existing groups, regardless of the status of the specimen being studied (i.e., fossil or extant); if the appropriate diagnostic characters are not discernible, no designation should be made.

Typically, the amount of accessible morphological data, particularly with respect to copulatory organs, differs for male and female specimens in the fossil record. For instance, many of the female genital structures used in species identification, such as coiled connecting ducts,

seminal receptacles and fertilization ducts of the epig-yne, are internal and usually not visible in specimens preserved in amber or rock (for an exception see Selden, 2010). The greater accessibility of male copulatory organs (i.e., the potential SMRS) may explain why the major-ity of described fossil species are based on males (~95%, D. Penney, pers. comm.). Another, perhaps complementary explanation, however, is that males were preserved more often than females due to their wandering nature (Penney, 2002b; Penney and Langan, 2006) and thus are simply more abundant for study. The lack of information gleaned from females is, nevertheless, a hindrance and leaves many spec-imens unstudied. Similarly, it is often difficult to assign males and females to the same species. This is also true for the modern fauna (although neontologists can make field observations and study coloration patterns and inter-nal genitalia). For example, a review of three spider families (chosen at random) revealed that *original* diagnoses were performed using both the male and female for only 39, 28, and 59% of the extant species contained within the Desi-dae, Selenopidae, and Cybaeidae, respectively (data from Platnick, 2010).

Fossil juvenile spiders are also hard (usually impossi-ble) to identify to the species or even family level, and distinguishing between males and females in the absence of mature sex organs is often difficult. Again, these prob-lems are not restricted to the fossil record but, in the modern, context clues and large sample sizes may aid in identification. Fossil juveniles are generally not studied, which leaves much diversity unexamined. Immature speci-mens are not entirely uninformative, however, as indicated by the Cretaceous fossil spider family Lagonomegopidae, which is described entirely from juvenile (and/or female) specimens (Penney, 2005, 2006; Penney and Selden, 2005). This family is diagnosed as possessing cheliceral peg teeth and large eyes situated anterolaterally (Penney and Selden, 2005). More information on the group would be gleaned if adults were found, including making it possible to better evaluate its relationship with other spider lineages. Other strictly fossil spider families based on descriptions of juve-niles have not withstood contemporary taxonomic scrutiny (Penney and Selden, 2005), and, in general, it is usually good practice to only name species based on adult spec-imens.

We do not attempt to address and provide solutions for every issue involved in the study of fossil spider species, nor is this likely possible. We endeavoured to provide an overview of the most relevant concepts and episte-mological problems encountered. Although our preceding discussion does recognize that there are some difficul-ties involved with identifying and delineating fossil spider species, it is undoubtedly true that the fossil record of spiders has contributed in an important way to the under-standing of the group's evolution (Penney, 2004; Penney et al., 2003). Further, there are a plethora of instances where genitalia and other anatomical features are pre-served in exquisite detail. For example, a member of the Plectreuridae was described from the Jurassic of Dao-hugou, China based on fine details of the palpal bulb and embolus and the presence of a macroseta on the tibia of the first leg (Fig. 1B; Selden and Huang, 2010).

In fact, the morphology of this 165 million-year-old spec-imen is incredibly similar to modern species within the *tristis* group of the genus *Plectreurys*. Many amber speci-mens have palpal details preserved (Harms and Dunlop, 2009; Marusik and Wunderlich, 2008; Penney and Ortuño, 2006, to name only a few) and can even be placed in extant genera based on these structures (e.g. Huber and Wunderlich, 2006; Penney, 2000, 2009; Saupe et al., 2010).

Studies comparing modern and fossil forms are becom-ing increasingly common (for example, Harms and Dunlop, 2009; Saupe et al., 2010), and we emphasize the benefits of doing so, particularly when carried out in a phyloge-netic framework. Harms and Dunlop (2009) revised fossil mimetids and synonymized the extinct genera *Succinero* and *Palaeoero* with the extant genus *Ero*. Side-by-side examination of fossil and extant species allows for deter-mination of changes in morphology through time (e.g., Eurasian species of *Ero* possess palps with conical lateral lobes between the straight cymbium in lateral view and the paracymbium, whereas the fossil forms do not) and a better understanding of biogeographic and evolutionary history (Fig. 1D).

4. New directions

New technological developments are opening further avenues for the study of fossil spider species in ways that allow even broader comparison with extant taxa. Very-High-Resolution X-Ray Computed Tomography (VHR-CT) and propagation phase contrast based X-ray synchrotron imaging techniques offer non-destructive methods for cap-turing fine-scale morphological details, including internal morphology (Fig. 1E) (e.g. Bosselaers et al., 2010; Dierick et al., 2007; Lak et al., 2008; Penney et al., 2007; Tafforeau et al., 2006). The three-dimensional reconstructions can be compared to extant members of a lineage and/or incor-porated into phylogenetic analyses (Penney et al., 2007). The technique is especially useful for amber samples that are fairly opaque or when the pedipalps or epigyne are obscured. A study by Bosselaers et al. (2010) used X-ray microtomography to visualize details of the palp of a spec-imen preserved in Madagascan copal and compared it to a newly discovered extant species (*Donuea collustrata*; Liocranidae) (Fig. 1F). Small details were directly relat-able, allowing for confirmation of conspecificity. Not only that, but discovery of a copal specimen still extant speaks to species longevity, although the exact duration is not known (NB: Madagascan copal is thought to be only a few decades to hundreds, thousands or even a million or so years old).

In the past, fossil species were sometimes desig-nated without complete knowledge of the copulatory organs or other morphological features, without a com-plete understanding of phylogenetics, and/or without regard for the extant literature and knowledgebase. This is now changing, and X-ray imaging is contributing to this renaissance because it allows for full characteriza-tion of a specimen, perhaps revealing the SMRS so that an epistemology and ontology of spiders would coin-cide.

5. Conclusions

When we study species in evolutionary biology, we hope the units correspond to real evolutionary units in nature. The primary manner that this is done within the Araneae is by examining copulatory organs. As discussed, this is potentially problematic when studying fossils because these structures may not be preserved or visible. However, recent technological advances may overcome some of these barriers, especially with the advent of propagation phase contrast X-ray synchrotron imaging.

Still, the study of fossil spiders, regardless of how difficult or troublesome, is extremely important for understanding evolutionary history and for calibrating the tree of life. For example, fossils often provide evidence for character transformations obscured when only recent taxa are examined (Novacek, 1992). Fossils provide the only direct record for evolution through deep time (Smith, 1998) and are vital in biogeographical and palaeoecological studies. As Simpson (1944) noted, the study of the fossil record provides insight into evolutionary tempo and mode. A truer picture of the history of life on Earth is garnered when fossils are taken into account. Ignoring or failing to incorporate fossil species into a study seems inadvisable if we fully want to understand evolution, since 99.99% of all species that have ever lived are now extinct (Novacek and Wheeler, 1992; Lieberman 2000): even in groups with impressive extant diversity, such as the Araneae, a profound sampling bias will be incurred if only extant species are considered.

Acknowledgements

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