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Cteniza bavincourti and the nomenclature of arachnid-related trace fossils

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Abstract. *Sabella bavincourti* Vaillant 1909 from the Eocene of northern France is a little-known trace fossil subsequently attributed – as *Cteniza bavincourti* – to the burrowing activities of a trapdoor spider. It is thus an ichnospecies name and not a body fossil. Its interpretation as the activity of a spider is questionable and its original assignment to a worm burrow seems intuitively more likely. Irrespective of the affinities of the producer, the ICZN also covers ichnotaxa such that classifying these structures under a modern genus name creates a homonym. It is here reassigned as the ichnotaxon *Oichnus bavincourti* comb. nov. Another problematic name is *Theridium columbianum* (Scudder 1878) from the Eocene of Canada and the USA, which is based on fossilized spider egg sacs. Under current ICZN rules fossil cocoons fall under the definition of "work of an animal". We propose reassigning them here to *Araneaovoidus* igen. nov., as *Araneaovoidus columbiae* (Scudder 1878) comb. nov.; but stress that this is now a trace fossil name. Similar problems underlie fossilized galls attributed (probably correctly) to mites, but assigned to living eriophyid mite genera. Fossil galls are the preserved pathological reactions of plant tissue and are also not ichnotaxa sensu Bertling et al. (2006). We propose that these mite names lie outside the bounds of zoological nomenclature. Within the broader context of arachnid-related trace fossils we briefly review the literature on fossil spider webs, as well as putative arachnid trackways such as *Paleohelcura* Gilmore 1926 and *Octopodichnus* Gilmore 1927.

Keywords: Burrow, egg sac, gall, trackway

The fossil record of arachnids is not limited to their body fossils. A variety of trace fossils such as fossilised trackways, burrows and even webs have been recorded, but confusion has persisted in the literature concerning their classification. During a project to catalogue names of fossil spiders and their relatives (Dunlop et al. 2011), the species *Cteniza bavincourti* (Vaillant 1909), from the Eocene of northern France, was noted in the catalogue of Bonnet (1956). Examination of the original description, and a subsequent reinterpretation by Leriche (1910), revealed that the name is associated with a trace fossil in the form of a series of tubular burrows (Fig. 1). Vaillant thought that they were worm tubes. Leriche, by contrast, regarded them as the burrows of trapdoor spiders – whereby both authors effectively assigned the name *bavincourti* to extant animal genera. Tying a trace fossil to a specific producer is notoriously difficult, but given that the International Code of Zoological Nomenclature (ICZN) covers ichnotaxa, as well as body fossils and living animals, we choose to exclude *bavincourti* from the extant genera *Sabella* Linnaeus 1767 and *Cteniza* Latrielle 1829, to which it had been previously assigned, and place it in an ichnogenus proposed by Bromley (1981).

As part of a wider review of arachnid-related trace fossils, we also draw attention here to fossil spider eggs (Fig. 2) currently assigned to a modern spider genus. The naming of fossil eggs is a grey area in taxonomy, for which some authors have adopted a 'parataxonomic' approach (see below). Similarly, there are three named examples of mite-induced galls (Fig. 3), all assigned to common, living gall mite genera (Acari: Actinotrichida: Eriophyoidea). While (fossil) galls do not fall under the strict definition of an ichnotaxon sensu Bertling et al. (2006; see also below), they are still treated as 'the work of an animal' in the ICZN code. We argue here that as the pathological responses of a plant, they should not be treated as 'work' in the strictest sense and should be excluded from being names in zoology. Finally, to round off this trace fossil review, we offer a brief summary of fossil spider webs – which Bertling et al. do consider the 'work of an animal' – and those arthropod trackways (Figs. 4, 5) that have traditionally been attributed to arachnids.

FOSSIL BURROWS

Oichnus Bromley 1981

Oichnus bavincourti (Vaillant 1909) comb. nov.

(Fig. 1)

Sabella (?) *Bavincourti* Vaillant 1909:280, fig. 1.

Cteniza Bavincourti (Vaillant); Leriche 1910:371; Bonnet 1956:1266.

Material.—*Holotype*: FRANCE: *Pas-de-Calais*: SE of the village of Bavincourt, 22 km SW of Arras, Paleogene: Eocene, (holotype not seen), no repository details given.

Remarks.—Vaillant (1909) described a series of putative animal burrows (Fig. 1) in 'landéniens' sandstones of Eocene (ca 55–59 Ma) age from a locality near Bavincourt in northern France. In the original description these were tentatively assigned to *Sabella* Linnaeus 1767 – an extant group of polychaete annelids known variously as fan or peacock worms. Shortly afterwards, Leriche (1910) reassigned these fossils to the Recent spider genus *Cteniza* Latrielle 1829, presumably under the assumption that the sediments were terrestrial rather than marine in origin and that the holes in the rock were the fossilized burrows of trapdoor spiders. *Cteniza* has four valid extant species (Platnick 2011) distributed across France, Italy (and their associated Mediterranean islands) as well as Central Asia. Thus the assignment of a French putative fossil spider

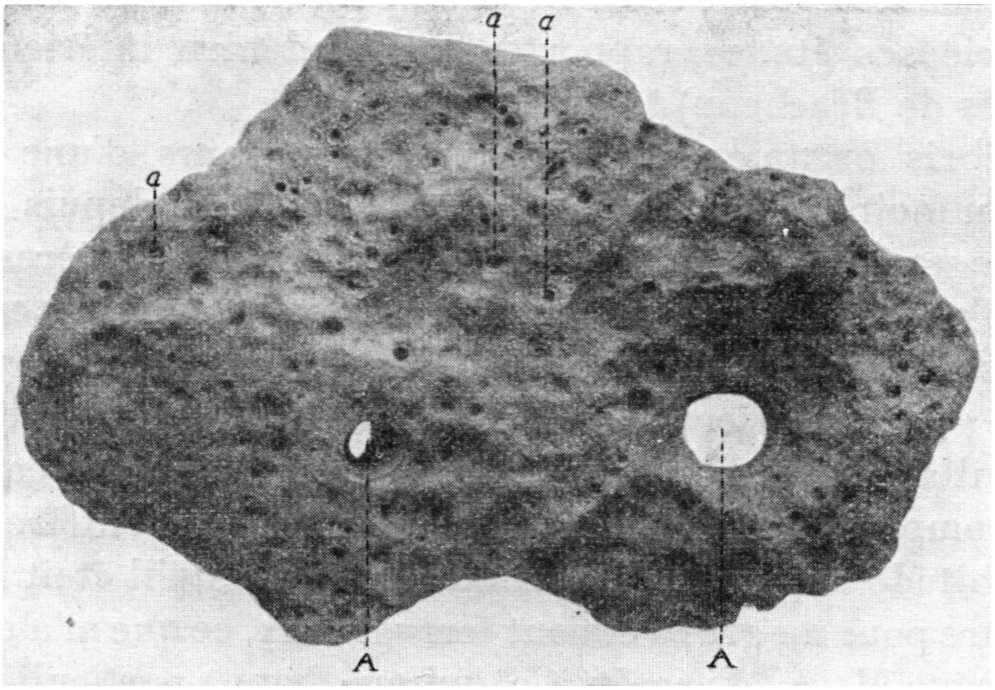


Figure 1.—Copy of the original photograph of ?*Sabella* [= *Ctenizа*] *bavincourti* Vaillant 1909 from the Eocene of Bavincourt, Pas-de-Calais, France. The larger holes labeled 'A' were originally interpreted as the activity of fan or peacock worms, but were subsequently suggested by Leriche (1910) to be burrows made by trapdoor spiders. They are reassigned here to an ichnogenus as *Ooichnus bavincourti* (Vaillant 1909) comb. nov. The smaller holes labeled 'a' were originally interpreted as mollusk borings. Reproduced from Vallient (1909:fig. 1). Original specimen was ca 30 cm across.

burrow to this genus can, at a certain level, be understood. However, we must reiterate that *Ctenizа bavincourti* is an ichnospecies, rather than a body fossil, and does not provide direct evidence for an Eocene (34–56 Ma) record of *Ctenizа*.

Irrespective of the likely affinities of the producer, an ichnospecies should not be assigned to a modern (living) animal genus. To quote Bertling et al. (2006, p. 265): "…ichnotaxa must not be incorporated into biological taxa in systematics.".

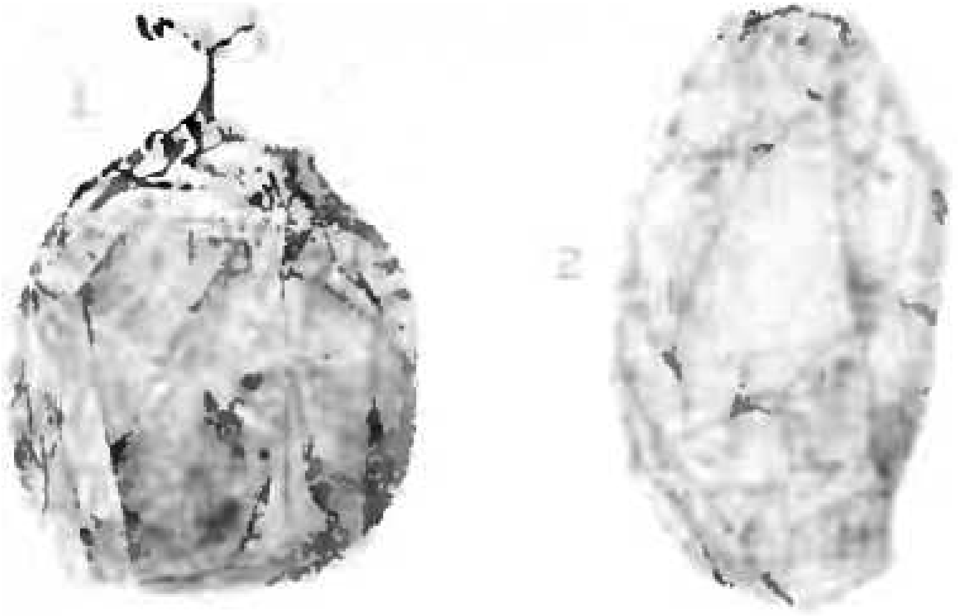


Figure 2.—Copy of some original drawings of *Araneaovoius columbiae* (Scudder 1878); reproduced from Scudder (1890, pl. 2, figs. 1, 2). These fossil egg cocoons from Florissant or Green River, USA, were probably made by spiders and originally described under *Araneus* (as *Aranea*), later under *Theridium* (now *Theridion*). Whether egg cocoons are trace fossils per se is debatable (see text for details), but the fossils are referred here to a new ichnogenus.

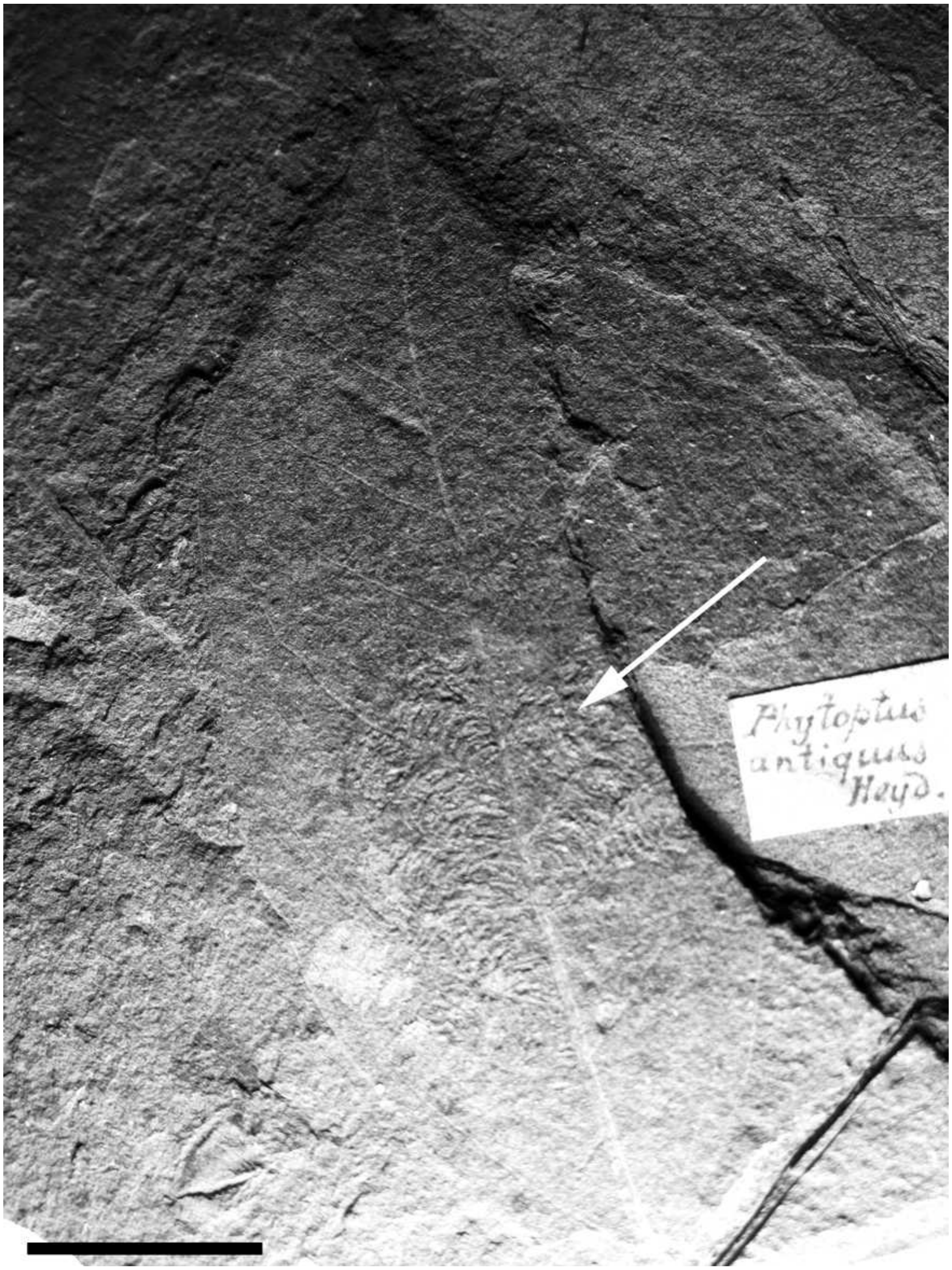
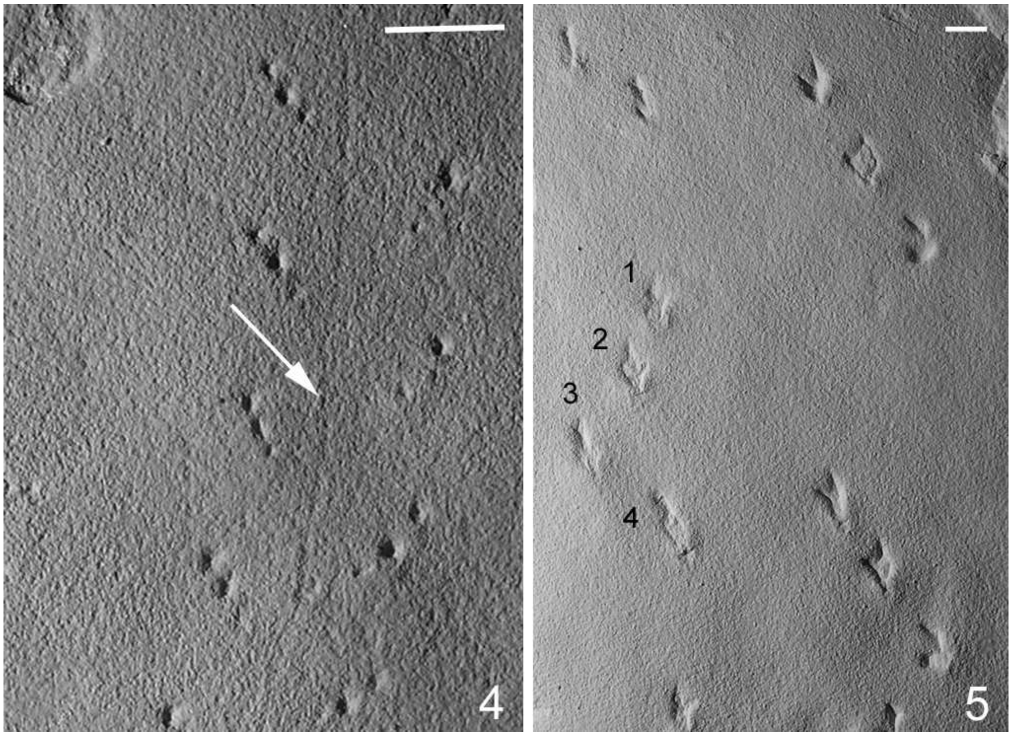


Figure 3.—Holotype of *Phytoptus antiquus* von Heyden 1860, from the Miocene of Salzhausen, Hessen, Germany, held in the Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany, under the inventory number SMF IV 25a of the insect collection. Although assigned to a living mite genus, the galls (arrowed) are the fossilized pathological response of the leaf tissue. We suggest that this – and other fossil mite galls – should not be treated as names in zoology. Scale bar = 10 mm. Photo courtesy of Vincent Girard (Frankfurt/Main).

Leriche's interpretation of this material (Fig. 1) as an assemblage of spider burrows seems fatuous at best, but the original assignment to *Sabella* remains problematic, as any number of sand-burrowing creatures could have produced this sedimentary feature, and in any case *Sabella* is also a biological taxon that according to the World Register of Marine Species (WoRMS: http://www.marinespecies.org/) currently lacks a fossil record. To resolve this matter we adopt the approach suggested by Richard Bromley and reassign the name to *Oichnus* Bromley 1981; a purely descriptive ichnogenus appropriate for classifying simple holes with a round cross section preserved in the sediment. This name carries no inferences about the original producer, and *Oichnus bavincourti* can now be formally excluded from the spider fossil record.



Figures 4, 5.—Examples of arthropod trackways traditionally attributed to arachnids. 4. Cast of the holotype of *Paleohelcura tridactyla* Gilmore 1926, Museum of Northern Arizona N9392, regarded as a possible scorpion trackway (note the medial impression: arrowed); 5. Cast of the holotype of *Octopodichnus didactylus* Gilmore, 1927, Museum of Northern Arizona N9393, regarded as a possible spider trackway (no medial impression, but pairs of four tracks: numbered). Both examples come from the Early Permian Coconino Sandstone, Arizona, USA. Scale bars = 10 mm. Both images modified from Minter & Braddy (2009, text-fig. 22).

FOSSIL EGG SACS

Araneaovoidus igen. nov.

Diagnosis.—Globular, pedunculate fossil egg sacs (cocoons), putatively of spider origin.

Araneaovoius columbiae (Scudder 1878) comb. nov.
(Fig. 2)

Aranea columbiae Scudder 1878:463; Scudder 1890:71, Pl. 2, figs. 1, 2; McCook 1890:459–461; Scudder 1891:250 (as 'Theridides'); Petrunkevitch 1922:214, 279; Selden & Penney 2010:185.

Theridium columbianum (Scudder) Bonnet 1959:4461 [as 'cocon'].

Material.—Syntypes not seen: Petrunkevitch (1922) cited the material as being in the Scudder collection of the Museum of Comparative Zoology, Cambridge Massachusetts, USA, but this could not be confirmed by the collection staff there. CANADA: *British Columbia*: Quesnel. Palaeogene: Oligocene? Additional specimens assigned to this species have been recorded from Green River in Wyoming and Florissant in Colorado, both Eocene, USA.

Remarks.—This species, based on putative spider egg cocoons rather than body fossils, was originally described from Quensel in British Colombia by Scudder (1878); with further examples from Green River and Florissant added by Scudder (1890). In the latter work, Scudder explicitly stated that he was applying "…an ancient, broad generic name…" to this material, but suggested that the cocoons might derive from *Theridium* [now *Theridion* Walckenaer 1805] based on the pedunculate form of at least some of the specimens. McCook (1890) refigured various examples, again drawing comparisons with modern egg sacs of mimetids, theridiids and theridiosomatids in particular. Petrunkevitch (1922) conceded that they could be fossilized spider egg sacs, but doubted (based on published illustrations) whether they all originated from the same species and commented on their "…utter uncertainty of classification." Nevertheless, Bonnet (1959) transferred the species name to *Theridium*; presumably based on previous tentative assignments in the literature.

While burrows are unequivocal examples of ichnotaxa – since they involve organisms actively modifying the substrate – the situation for eggs and/or their cocoons is less straightforward. Bertling et al. (2006:table 1) identified a 'grey zone' comprising, for them, structures like eggs, galls and webs (see below), whose status as trace fossils sensu stricto remains debatable. There is precedent for naming (fossil) eggs using Linnean-type ranks, and Bertling et al. discussed at length some of the difficulties of terminology relating to what constitutes 'work' by an animal (e.g., burrows or footprints) or their 'products' (e.g., dung). They recommended defining ichnotaxa solely as names based on trace fossils, defining trace fossils in turn as "…a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate…" (Bertling et al. 2006:283). Thus in their definition, trace fossils would include, e.g., burrows, trackways, coprolites, nests, webs and various bite marks and/or leaf mines. This definition does not include eggs, embedment structures or plant reaction tissues (see also galls below). Yet in our particular case we should note that it is the silken cocoon that is preserved, rather than the eggs themselves, and that webs/silk do fall under Bertling et al.'s trace fossil definition.

Bertling et al. (2006) conceded that eggs could be named and made reference to a 'collective taxa' approach towards naming, for example, assemblages of eggs. An alternative in the literature would be ovo- or oötaxa; a so-called parataxonomic scheme primarily applied to the eggs of fossil vertebrates (e.g., Pickford & Dauphin 1993; Hirsch 1996; Garcia et al. 2006), but not to our knowledge to invertebrates. This issue is complicated – Bertling et al.'s recommendations remain suggestions – and a revised protocol for handling fossil eggs (or egg sacs) has yet to be formalised in a new edition of the ICZN code. Thus we retain here the Code's present definition (Glossary, p. 122) of cocoons as trace fossils. Retaining Scudder's egg sac species in a modern spider genus is inappropriate. We do not see the eggs themselves, so it cannot be argued that they are the first instars (or semaphronts) of an existing body fossil species. Yet Scudder's name for these cocoons exists. We are unaware of any precedent in the literature for naming fossil spider egg sacs, thus we have no existing ichnogenus that could comfortably accommodate his species. We thus, somewhat reluctantly, propose a new name; but stress that this is an ichnogenus. Other egg sacs in amber and copal have been documented, particularly by Wunderlich (2004:79–87), but have not been formally named. Given the problems above, we strongly discourage future authors from introducing nomenclature for the cocoons of fossil spiders.

FOSSIL GALLS

Names excluded from zoological nomenclature

Phytoptus antiquus von Heyden 1860
(Fig. 3)

Phytoptus antiquus von Heyden 1860:63; von Heyden 1862:64, pl. 10, fig. 1; von Heyden & von Heden 1865:35; Scudder 1891:282 (as gall).

Material.—*Type material*: GERMANY: *Hesse*: Salzhausen/Vogelsberg; leg. Otto Vogler, Neogene (middle Miocene), Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany, listed in the fossil insect catalogue as no. SMF IV 25a (holotype) and VI25b (paratype).

Eriophyes vilarrubiae Villalta 1957

Eryophies [sic] *vilarrubiae* Villalta 1957:63–64; Diéguez et al. 1996:340.

Material.—*Holotype*: SPAIN: *Lérida Province*: Cerdaña. Neogene (upper Miocene). Type repository unclear.

Eriophyes daphnogene Ambrus & Hably 1979

Eriophyes daphnogene Ambrus & Hably 1979:55–56, fig. 1; Davis et al. 1982:125.

Material.—*Holotype*: HUNGARY: *Komárom-Estergom district*: Baromállás, between Vértesszőlős and Tatabánya Kuny, assigned to the Palaeogene (Upper Oligocene) and the regional Egerian stage, which roughly corresponds to the internationally recognized Chattian age (ca 23–28 Ma), but touches on the boundary of the Miocene, Domokos Megyei Múzeum, Tata, no. 76.4.92 (not seen).

Remarks.—Galls, or zooceids in some terminologies, were also explicitly excluded from being ichnotaxa by Bertling et al. (2006) – contra the 'cecidoichnia' concept of Mikuláš (1999) – because they are formed by the pathological reactions of the host plant tissue, rather than the direct activities of the gall-inducing organism itself. Were, e.g., a burrow path, feces, or an exit hole to be identified within a gall, one could (according to Bertling et al.) make a case for treating these features as ichnotaxa. There remains, however, the problem of how (or whether) to apply binominal nomenclature to the gall itself, and how to deal with such names already present in the literature. To quote again Bertling et al. (2006, p. 268): "Galls nonetheless must not be considered zoological taxa because they are made up of plant tissue; hence, they cannot receive the name of the insect responsible". Indeed we are aware of only one unequivocal gall mite body fossil in the literature: *Aculops keiferi* Southcott & Lange 1971, recovered as microfossils in macerates of carbonaceous clay deposits from the Eocene of Australia.

Early workers on extant eriophyid (gall) mites – reviewed by Nalepa (1887) – invariably named the mites themselves, rather than their galls; although they sometimes differentiated species based on the host plant rather than explicit morphological differences. Most paleontologists have simply described mite/insect gall types based on their morphology (e.g., Scott et al. 1994), without recourse to Linnaean categories. Alternatively, other authors have treated galls as a type of tissue damage – again a simple, structural description – alongside other leaf marks caused by feeding (e.g., Wilf & Labandeira 1999). Yet some workers continue to use an explicitly binominal nomenclature to describe galls, albeit here without assigning species to Recent genera of gall-inducers. For example, Vasilenko (2005) – adopting a scheme from Vjalov (1975) – recognized a group Phagophytichnidea (plant damages) including the families Paleoovoididae (for invertebrate egg batches) and Paleogallidae (for pathological responses such as galls). These families are further divided into 'genera' and 'species'. It is not immediately clear whether these names are parataxa (as per the vertebrate egg nomenclature above) or whether they fall under the zoological or botanical codes of nomenclature. We question whether this approach is really helpful in the long term.

We are still left with three historical species names for fossil galls, all of which were explicitly assigned to Recent genera of eriophyid mites as the likely gall-inducer. Two options present themselves. Technically, the ICZN continues to treat galls as the 'work of an animal' (cf. Glossary, p. 122) and hence as trace fossils. Like the spider cocoons above, we could simply create a new ichnogenus, or ichnogenera, to accommodate these species. Yet we strongly support the recommendation of Bertling et al. that galls should not be treated as trace fossils. We concede that this is again a grey area that should be addressed in any future version of the code. Indeed, we are planning a formal application to the ICZN specifically about these mite names to force clarification of this issue. Is a gall merely the passive response of the plant tissue to animal(s) living within, or do the mites deliberately induce the gall through their burrowing activities, which could, theoretically, be construed as 'work'? Overall, we feel that fossil arachnid nomenclature is complex enough as it is without introducing further new names, and that the best interests of stability would be served by invoking the ICZN to remove these species from the zoological nomenclature. All three fossils may still document the presence of eriophyids in former eras, and in this context make a valuable contribution to our understanding of the arachnid fossil record.

Oldest gall mites?—The oldest galls comparable in shape to those of modern eriopyhid mites are known from the Late Cretaceous (Cennomanian, ca 100 Ma) (Scott et al. 1994). Larew (1986) briefly reviewed fossil galls, mostly with respect to insects. Scott et al. (1994) provided a valuable review of the gall fossil record and in their appendix they identified six (time-independent) morphologies spanning the mid Cretaceous through to the Palaeogene, which resemble Recent galls induced by eriophyids. Some of these were analogous to galls induced by particular modern species, others to Eriophyoidea in general; see these authors for details. Within the subfossil (Holocene) time frame, Pentecost (1985) suggested that galls observed on *Alnus* leaves from the Holocene of Yorkshire, UK (ca 8,600 years B.P.) may have been induced by the extant alder bead gall mite.

FOSSIL WEBS

Following Bertling et al. (2006), fossilized silk and webs fall within the definition of trace fossils; although to our knowledge no one has tried to formally name one using Linnean binominal taxonomy. Selden & Penney (2010) recount the unfortunate case of Beringer (1726), who was fooled into describing hoax fossils of spiders, together with their webs, preserved on stones. More recently, Pickford (2000) described calcitic structures from the mid Miocene (16–17 Ma) of the Namib Desert in Namibia. He interpreted these as fossil webs, comparable to the web-lined burrows of the modern spider genus *Seothyra* Purcell 1903 (Eresidae), which occurs in this desert region today. The oldest putative record of arachnid silk (Selden et al. 2008) is some strands emanating from the spigots of the mid-Devonian (ca 390 Ma) *Attercopus fimbiunguis* Selden et al. 1991. This fossil was originally though to be the oldest spider, but was recently reinterpreted as a member of a separate, extinct order Uraraneida characterized by silk production via spigots on the ventral opisthosomal sclerites. Uraraneids thus lacked explicit spinnerets, which remain a convincing autapomorphy of Araneae.

Amber.—As far as we are aware, all other examples of fossilized webs or silk derive from amber. The most recent to be described (Brasier et al. 2009) is, at earliest Cretaceous (ca 140 Ma), stratigraphically also the oldest amber record. Somewhat curiously, this amber from near Hastings in Sussex, UK has (so far) not yielded any spiders or other arthropods. Fossil silk is usually rarer than other amber inclusions, which raises some concerns about the interpretation of this material. An alternative possibility would be that these threads are microbial in origin and/or fungal hyphae; although Brasier et al. presented counterarguments in favor of them being genuine silk strands based on the way the strands pair and twist, and the apparent presence of fluid (glue?) droplets.

The oldest unequivocal amber silk was described by Zschokke (2003) from early Cretaceous (ca 130 Ma) Lebanese amber. This consisted of a single thread, here clearly bearing characteristic glue droplets. This specimen confirms the use of viscid silk by spiders during the early Cretaceous and implies a member of the Araneoidea lineage. Zschokke discussed whether the strand may have originated from an orb web or a cobweb (perhaps from Theridiidae or a related group); favoring the latter option, since the capture thread was not associated with any linking scaffolding threads as would be expected in an orb web. Spider silk from the marginally younger Isle of Wight amber, UK, was mentioned by Jarzembowski et al. (2008), but was not figured or described in detail. A fully described early Cretaceous record (Peñalver et al. 2006) comes from the Spanish San Just amber (ca. 110 Ma). Interestingly, this also includes possible prey items: namely, a *Microphorites* fly and a mite. These authors suggested that it could be a fragment of an orb web, but also noted a cobweb as an alternative. It is challenging to explain how a mite became trapped in a typical aerial orb web.

Zschokke (2004) described further examples of fossil web fragments with glue droplets, including Cretaceous (ca 100 Ma) examples from Myanmar (Burmese) amber, Eocene (ca 45–50 Ma) examples from Baltic amber and Miocene (ca 16 Ma) examples from Dominican Republic amber. Zschokke discussed the often superb preservation of glue droplets, arguing that the delicate droplets are not destroyed by resin flow because the silk proteins and resin terpenoids repel each other rather than mixing. Nevertheless, these droplets are highly hygroscopic and sometimes underwent swelling during preservation in amber due to water uptake. Most fossilized silk records come from Baltic amber and historical accounts can be found in Menge (1856) and Bachofen-Echt (1934). The most comprehensive study was provided by Wunderlich (2004:53–72) who described and figured a variety of webs, as well as evidence for other silk-related behavior such as egg sacs (see above), prey wrapping, draglines and even spiders about to undergo ballooning. Wunderlich documented both cribellate and ecribellate web fragments – some of which can be tentatively ascribed to families or family groups – as well as rarer, more complete webs and/or retreats provisionally assignable to families such as Dipluridae or Segestriidae.

TRACKWAYS

A final source of arachnid trace fossils is trackways (e.g., Alf 1968), essentially series of fossilized footprints or other imprints such as scratches or tail drags in the sediment. Although trackways record behavior and/or host–sediment interactions (as opposed to anatomy), their binominal names are subject to ICZN rules. A key problem is, of course, ascribing a trackway to its correct producer. Only in rare cases, like the 'death marches' of horseshoe crabs from the Jurassic of Solnhofen in Germany (Malz 1964), are both preserved together. Assignments to taxa generally have to be based on circumstantial evidence, such as identifying body fossils with an appropriate limb disposition of roughly the same geological age, or by looking at comparative behavioral repertoires and walking gaits in living taxa which may also have been around at that time.

Two ichnogenera are commonly attributed to arachnids on the grounds that the trackways were (probably) made by animals with eight legs. Following definitions in Sadler (1993), *Paleohelcura* Gilmore 1926 (Fig. 4) consists of pairs of three (sometimes two or four) tracks about 2 cm apart, either side of a medial impression or tail drag. *Octopodichnus* Gilmore 1927 (Fig. 5) consists of alternating groups of four tracks, up to 6 cm apart, and lacks any evidence of a medial impression. Both are principally known from a number of Permian (251–299 Ma) localities in North America: the Coconino and DeChelley Sandstones in Arizona and the Robledo Mountains of New Mexico (Sadler 1993; Braddy 1995a, b; Minter & Braddy 2009). There is also a *Paleohelcura* record from the Permian (Rotliegend) of Europe (Kozur et al. 1994). *Paleohelcura* has been envisaged as a scorpion walking trace, with the dragline derived either from the telson or perhaps the pectines. *Octopodichnus* has been thought to represent a (large) spider, rather like a tarantula.

Comparisons with modern arthropods (Brady 1939) and neoichnological experiments looking at the tracks left by extant arachnids walking over different substrates (Sadler 1993; Azin & Wright. 2005; Davis et al. 2007) have been able to recreate both *Paleohelcura* and *Octopodichnus* morphologies. Yet, it should be cautioned that the same animal can produce more than one trackway morphology and that these would be classified, geologically, under different ichnogenera (Sadler 1993). For example, a scorpion walking with its tail raised could also produce an *Octopodichnus*-like trackway. This reiterates the difficulties of trying to assign trace fossils to specific producers. Furthermore, numerous ichnospecies have been proposed in both *Paleohelcura* and *Octopodichnus*: see Minter & Braddy (2009) for a recent overview. Many of these published 'species' are based on trivial differences in, for example, trackway size and track distributions. Work in progress will almost certainly reduce the number of published trackway names and yield a more sensible and meaningful arachnid ichnotaxonomy.

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