**Zeitschrift:** Contributions to Natural History: Scientific Papers from the Natural

History Museum Bern

**Herausgeber:** Naturhistorisches Museum Bern

**Band:** - (2009)

**Heft:** 12/3

**Artikel:** A fossil spider (Araneae: Pisauridae) of Eocene age from Horsefly,

British Columbia, Canada

Autor: Selden, Paul A. / Penney, David

**DOI:** https://doi.org/10.5169/seals-787025

#### Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Mehr erfahren

#### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. En savoir plus

## Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. Find out more

**Download PDF:** 04.08.2025

ETH-Bibliothek Zürich, E-Periodica, https://www.e-periodica.ch

# A fossil spider (Araneae: Pisauridae) of Eocene age from Horsefly, British Columbia, Canada

# Paul A. Selden & David Penney

## **ABSTRACT**

Contrib. Nat. Hist. 12: 1269-1282.

A new fossil spider, *Palaeoperenethis thaleri* gen. nov. and sp. nov., from Middle Eocene (44–52 Ma) strata from Horsefly, British Columbia, Canada, is described in the family Pisauridae. The localities in the Okanagan Highlands are well known for their insect fauna preserved together with fish and plants in varved diatomaceous lacustrine sediments. The biota and sedimentology indicate that a warm, seasonal climate was present during the Middle Eocene; *Palaeoperenethis* comes from a winter (dry season) lamina. The occurrence of a pisaurine in British Columbia during the Eocene epoch was facilitated by the warmer climate and possible land bridge from Asia at that time.

Keywords: Diatomaceous varves, lacustrine, Lycosoidea, seasonal climate.

## Introduction

Nearly all fossil spiders recorded from the Cenozoic era occur in amber – fossilized tree resin – which samples primarily forest-dwelling species. A few occurrences are known of fossil spiders in non-amber deposits; these are generally lacustrine sediments and are commonly associated with volcanic activity. For example, Cenozoic spiders have been described from the maar volcanic craters of Germany (Schawaller & Ono 1979, Wunderlich 1986), lacustrine brown coal of Rott, Germany (von Heyden 1859, Bertkau 1878, Petrunkevitch 1946), freshwater swamp deposits of the Isle of Wight, England (McCook 1888, Selden 2001, 2002), and the well-known volcanic lake deposits of Florissant, USA (Scudder 1890, Petrunkevitch 1922, Licht 1986). Spiders preserved in rock matrices rarely show as much morphological detail as those in amber and cannot often be assigned to family. Here, we describe a fossil

spider from lacustrine sediments which we refer to the family Pisauridae.

Pisaurids have a meagre fossil record, being known only from Oligocene—Miocene Mexican amber (Petrunkevitch 1963, 1971), Eocene Baltic amber (Petrunkevitch 1942, 1958; Wunderlich 2004), and Cretaceous Burmese amber (Penney 2004). The Mexican amber genus *Propago* Petrunkevitch, 1963 was considered a probable zodariid by Roth (1965). The Cretaceous pisaurid *Palaeohygropoda* Penney, 2004 is similar to the living genus *Hygropoda* Thorell, 1894. An unnamed, supposed lycosoid (the superfamily to which Pisauridae belongs: Griswold 1993) was described by Rayner & Dippenaar-Schoeman (1995); its identity as a lycosoid (ctenid or lycosid) was based solely on habitus and habitat. The first fossil spider from Korea, from the Cretaceous (Aptian) Jinju (=Dongmyeong) Formation, was identified as a *Pisaura* sp. by Kim & Nam (2008), who provided no description or evidence for this placement.

Pisaurids are characteristically associated with water; many walk across surface films and some are commonly referred to as 'fishing spiders' because their prey includes small fish. So the preservation of a member of this family in a lake deposit is not surprising. The composition of the associated biota (plants, fish, insects) indicate a much warmer climate in this area during the Eocene epoch than today (Greenwood & al. 2005).

# Geological setting and preservation

The lacustrine deposit at Horsefly, British Columbia, Canada crops out at numerous fossiliferous localities along the Horsefly River. The spider fossil was found in the bank of the Horsefly River some 10 km north of Horsefly. This is the Horsefly Mine, locality 8 in Figure 1 of Wilson (1977a); the occurrence of the spider was first mentioned in this paper. The Horsefly beds have yet to be dated by radiometric methods (Archibald 2005), but have been correlated using palynological (Rouse & al. 1971) and fish (Wilson 1977b) biostratigraphy with other Okanagan Highlands Eocene localities. These have been dated as Middle Eocene using radiometric (Rouse & Mathews 1961, Mathews & Rouse 1963, Mathews 1964, Hills & Baadsgaard 1967) and palaeomagnetic (Symons & Wellings 1989) techniques. More recent studies have suggested a slightly older, late Early Eocene, age (Barton & Wilson 2005).

The slabs bearing the spider fossil consist of varved lacustrine sediment, typical of that at Horsefly, and the spider is preserved with legs outstretched on both part and counterpart. The body is poorly preserved but legs and adult male pedipalps show more morphological detail. The distal parts of the legs are not well preserved (i.e. the tarsal claws cannot be seen). Joints are difficult

to discern, but by comparing part and counterpart, most podomere lengths can be estimated.

# Associated biota and palaeoenvironment

The localities at Horsefly and elsewhere in the Okanagan Highlands are renowned for their exceptional preservation of insect, plant and fish fossils. More work has been done on the sites other than Horsefly, but Horsefly is considered to belong to this group of localities which share biotic and climatic similarities (Greenwood & al. 2005). These authors listed the macroflora from Horsefly, which includes the ferns *Osmunda* and *Azolla*; the gymnosperms *Ginkgo*, *Abies*, *Picea*, *Pinus*, *Pseudolarix*, *Tsuga*, *Taxus*, *Torreya*, *Juniperus*, *Metasequoia* and *Sequoia*; and the angiosperms *Alnus*, *Corylus*, *Quercus*, *Carya*, *Platanus*, *Crataegus* and *Clematis*. Results from a palynological study by Moss & al. (2005) showed a good correlation of palynomorphs with the macroflora records. This flora is similar to the mixed mesophytic forest of present-day eastern North America, but some elements (e.g. *Sequoia*) and the abundance of conifers are more suggestive of Pacific forests.

Wilson (1977c) summarized the entomofauna of Horsefly: 10 families in six orders (Isoptera: Mastotermitidae; Orthoptera: Acrididae; Megaloptera: Rhaphidiodea; Diptera: Bibionidae, Sciaridae, Mycetophilidae, Syrphidae; Trichoptera; Hymenoptera: Tenthredinidae, Ichneumonidae) were known at that time, but detailed descriptions are still lacking for many of these. All are winged adults rather than, for example, aquatic larval stages. Whilst some are associated with water, e.g. Trichoptera (and Hemiptera: Gerridae are abundant at nearby localities), most clearly became caught on the water surface when flying over. Fish are common as scales, skeletal remains, and coprolites (Wilson 1977b), but diversity is low. The commonest are *Amyzon* (Catostomidae) and *Eohiodon* (Hiodontidae), which represent deep-water faunas, whilst specimens of *Priscacara* (Priscacaridae), *Amia* (Amiidae) and *Libotonius* (Percopsidae) are also known and where higher fish diversity (and smaller specimens) occurs, the palaeoenvironment has been interpreted as shallow water (Barton & Wilson 2005).

The palaeoecology has been studied by Wilson (1977a, 1988) and Greenwood & al. (2005). The sediments at Horsefly consist of finely laminated (varved) sequences with thin interbeds of tuff (volcanic ash). The tuffs are evidence for volcanism nearby, no doubt associated with the constructive plate margin still active in the Cascades today. The varves consist of dark and light laminae; the former are composed of sapropel (organic matter) and represent



Fig. 1. Palaeoperenethis thaleri gen. nov. and sp. nov., holotype ROM31304, part. Scale bar: 1 mm.

winter accumulation of decayed plant material and clays. The light laminae were orginally interpreted as tuffaceous (Wilson 1977a) but they were later shown to be composed of diatom remains (Wilson 1988; Mustoe 2005). The light laminae represent summer diatom blooms. Electron microscope studies of Eocene lacustrine sediments at Florissant, Colorado, by Harding & Chant (2000) and O'Brien & al. (2002) showed that microbial slime contributed to preservation of the fauna and flora. Insects and leaves landing on the surface water of the lake during a diatom bloom would have become covered in microbial slime which acts as a sealant, protecting the soft parts from decay. Eventually, the weight of the mat caused it to sink to the lake floor, taking its entombed fauna and flora with it. Such a process might have been in operation at Horsefly but has yet to be studied.

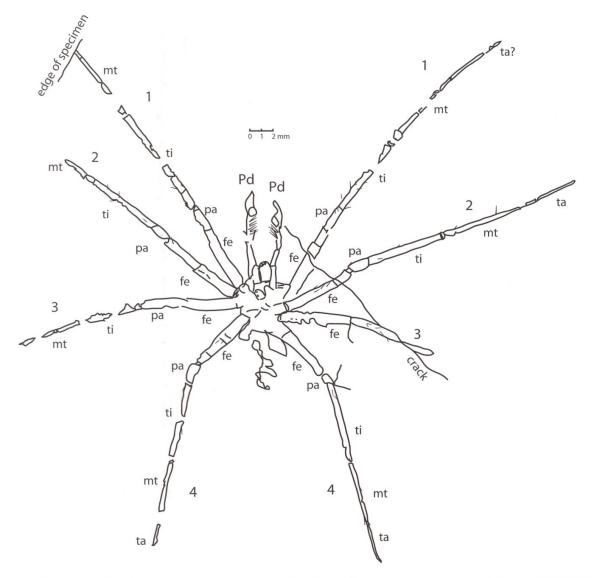


Fig. 2. Camera lucida drawing of *Palaeoperenethis thaleri* gen. nov. and sp. nov., holotype ROM31304 part. Explanatory drawing for Fig. 1.

Wilson (1977a, 1988), Wilson & Bogen (1994), Wilson & Barton (1996) and Barton & Wilson (2005) studied the preservation of the fauna in relation to the varves, and showed that the laminations were indeed seasonal (i.e. annual pairs) in nature. Wilson (1977a, 1988) showed that around 90% of the coprolites and 75% of the leaves occurred in the light, summer laminae. Insects occurred almost equally in summer (c. 55%) and winter (c. 45%) laminae, and about 70% of fish scales and 90% of fish skeletons occurred in dark, winter laminae. Clearly, seasonality is responsible for the differences in specimen abundance, although only the fish showed a statistically significant correlation with winter mortality (Wilson 1977a).

The spider is preserved in a dark, winter layer, which suggests it was adult in late autumn, winter, or early spring. According to Wilson (1977a), this was the dry season and the lake possibly in an anaerobic condition. The out-



Fig. 3. *Palaeoperenethis thaleri* gen. nov. and sp. nov., holotype ROM31304, counterpart. Scale bar: 1 mm.

stretched legs of the spider suggest it died in water, in a relaxed condition, similar to those seen at Florissant, (see, for example, illustrations in Licht 1986). Pisaurids commonly run across water surfaces, so why did this one falter and die? There is no tuff visible in the layer preserving the fossil, which would indicate a volcanic ash fall that might have debilitated the spider. It is possible that it encountered some microbial slime, or a gaseous emanation, which impeded its progress. Having been killed, there is still the matter of transport of the body from the lake surface to the lake floor, since surface tension would tend to support the carcass, and would also leave it available to scavengers such as Hemiptera.

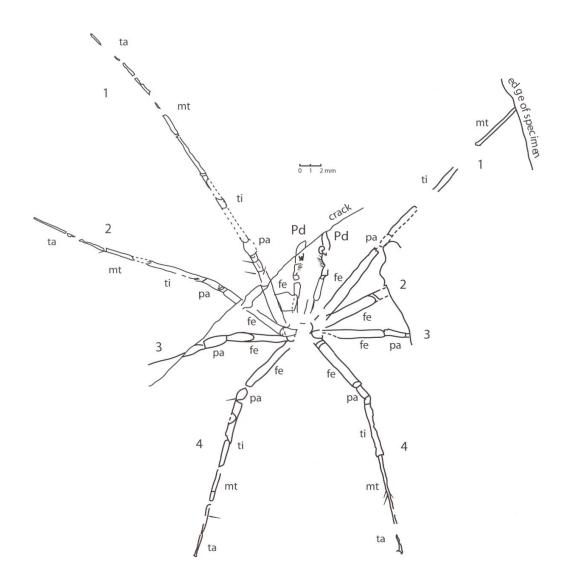


Fig. 4. Camera lucida drawing of *Palaeoperenethis thaleri* gen. nov. and sp. nov., holotype ROM31304 counterpart. Explanatory drawing for Fig. 2.

## **Material and Methods**

Ontario Museum as ROM31304. The fossil was studied using a Wild M7S stereomicroscope; drawings were made using a drawing tube attached to the microscope, and photographs were taken with a Nikon D1X digital camera. Drawings and photographs were processed using Adobe Illustrator and Adobe Photoshop on a Macintosh PowerBook G4 computer. Leg formula (e.g. 1234) longest to shortest. Abbreviations on figures: b, bulb; ch, chelicera; cy, cymbium; fe, femur; ms, macroseta; mt, metatarsus; pa, patella; Pd, pedipalp; st, subtegulum; ta, tarsus; ti, tibia. All measurements are in mm.

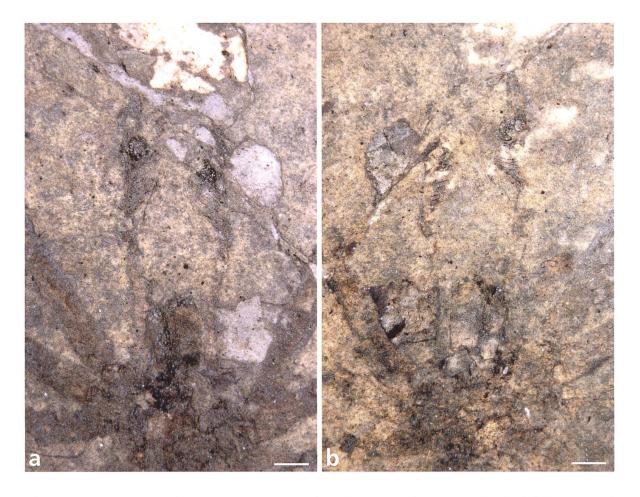


Fig. 5. *Palaeoperenethis thaleri* gen. nov. and sp. nov., holotype ROM31304, detail of chelicerae and pedipalps. – a: part; – b: counterpart. Scale bars: 1 mm.

# Systematic palaeontology

Order Araneae CLERCK, 1757 Suborder Opisthothelae Рососк, 1892 Infraorder Araneomorphae Sмітн, 1902 Family Pisauridae Sімон, 1890

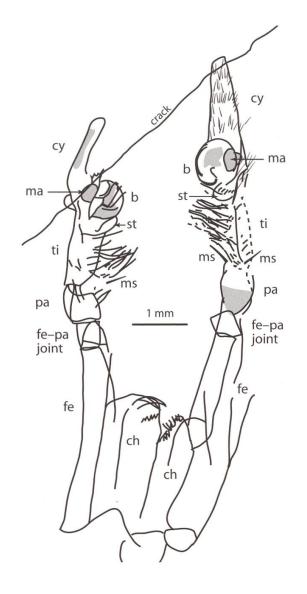
# Genus Palaeoperenethis gen. nov. (Figs. 1-6)

Diagnosis: Pisaurid with adult male pedipalps showing the following combination of characters: short patella; tibia with thick brush of long bristles on ventral-prolateral surface and pair of proximal macrosetae (pro- and retrolateral); curved, hirsute, elongate cymbium; bulb with meandering duct, prominent subtegulum and median apophysis.

Etymology: From the Greek *palaios*, ancient, and an African–Asian genus of Pisauridae which the new genus resembles, *Perenethis*.

Included species: Only Palaeoperenethis thaleri sp. nov., described below.

Fig. 6. Camera lucida drawing of chelicerae and pedipalps of *Palaeoperenethis thaleri* gen. nov. and sp. nov., holotype ROM31304. Combined drawing of part and counterpart; ventral (counterpart) view. Explanatory drawing for Fig. 5.



# **Palaeoperenethis thaleri sp. nov.** (Figs. 1–6)

Diagnosis: As for the genus.

Etymology: The trivial name is in memory of Dr. Konrad Thaler of Innsbruck, Austria, whose scholarship and sincere friendship we shall miss.

Holotype: ROM31304, part and counterpart, from the Middle Eocene beds of Horsefly, British Columbia, deposited in the Royal Ontario Museum, Toronto, Canada.

Description: Adult male spider. Carapace and opisthosoma unknown; leg disposition suggests a subcircular or polygonal carapace. Chelicera elongate, parallel-sided, with pro- and retromarginal rows of several teeth. Pedipalp with elongate femur (3.8), wide femur–patella joint allowing nearly 180° flexure, short patella (1.0) with numerous ventrolateral bristles, tibia (1.4) with high density of long bristles on ventrolateral surface and proximal pro- and retrolateral macrosetae; tibial apophysis not visible (possibly reduced?). Pedipalp cymbium elongate (2.5), greater than length of patella + tibia, hirsute, prominent subtegulum, bulb (excl. subtegulum 0.9) with meandering ducts,

distal, retrolateral sclerite presumed to be median apophysis. Leg formula 1243: approximate lengths (femur–tarsus) Leg 1, 30; Leg 2, 28; Leg 3, 20; Leg 4, 23. Joints difficult to discern, but approximate podomere measurements: leg 1 femur 7.84, patella 1.92, tibia 7.67, metatarsus 7.44, tarsus 5.17; Leg 2 femur 6.90, patella 1.87, tibia 7.01, metatarsus 8.36, tarsus 3.79; Leg 3 femur 5.55, patella 2.25, tibia—tarsus 11.95; Leg 4 femur 5.78, patella 1.53, tibia 6.48, metatarsus 5.55, tarsus 3.43. Thin macrosetae present distally on femora and patellae and medially on tibiae and metatarsi.

# **Discussion**

The fossil is referred to Pisauridae on the basis of its general habitus (large size, long legs), elongate male pedipalps, palpal tibia with a brush of long bristles ventrolaterally, and elongate cymbium, although the diagnostic characters of Pisauridae - egg-sac carried by the female in her chelicerae and the construction of a nursery web – cannot be observed in the fossil. The lacustrine habitat is also an important pointer to the Pisauridae. The abundance of bristles on the pedipalp tibia and an elongate cymbium occurs in some Trechaleidae (Carico 1993) but the fossil appears to lack the characteristic membrane at the base of the cymbium in the males of this family and the pedipalp conformation is generally different. Among pisaurids, a few genera show elongate male pedipalps, particularly the long cycmbium: Thalassius (Sierwald 1987) and Hygropoda (Zhang & al. 2004); other genera have short cymbiums, elaborate tibial apophyses, and other features not seen in Palaeoperenethis. Though not a well-known genus, males of Hygropoda show an elongate pedipalp patella: e.g. H. higenaga KISHIDA, 1936 and H. balingkinitanus (Barrion & Litsinger, 1995); also, Hygropoda shows distinctively curved tarsi 1, 2 and 4. Palaeoperenethis shows neither of these characters. The podomere conformation of *Palaeoperenethis* more closely resembles that of Perenethis, e.g. P. kawangisa Barrion & Litsinger, 1995.

Note that the new genus name *Palaeoperenethis* was chosen because of a habitus resemblance to the modern *Perenethis*; it does not imply a close relationship to the *Perenethis* genus group (Sierwald 1997), although the fossil appears to lie within or closer to Pisaurinae Simon, 1898 than to any other group within Pisauridae. Members of the *Perenethis* genus group range from Africa to Asia, and its geographic distribution and vicariance biogeography were discussed by Sierwald (1997). Additional species have been described from China by Zhang & al. (2004). The only member of Pisauridae present today in British Columbia is *Dolomedes*. However, given the warmer climate

of the Okanagan Highlands during the early Middle Eocene (the height of the Early Eocene Climatic Optimum: see Greenwood & al. 2005) and the proximity of east Asia across the Bering Strait land bridge, the presence of other pisaurid genera, perhaps *Perenethis* genus group members, at this time is entirely possible.

# **Acknowledgments**

We thank Bruce Archibald (Harvard University) for bringing this specimen to our attention, James Gardner (Royal Tyrrell Museum, Alberta) for arranging the loan, Janet Waddington (Royal Ontario Museum, Toronto) for locality information, and Mark Wilson (University of Alberta) for helpful discussions on the Horsefly Lagerstätte. We thank Donghee Kim for alerting us to Kim & Nam (2008) and Soo Kim for translation.

## References

Archibald, S.B. (2005): New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada and Washington State, USA). — Canadian Journal of Earth Sciences, 42: 119–136.

Barrion, A.T. & Litsinger, J.A. (1995): Riceland Spiders of South and Southeast Asia. — 700 pp., CAB International, Wallingford, UK.

Barton, D. & Wilson, M.V.H. (2005): Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10 000 years of environmental change. — Canadian Journal of Earth Sciences 42: 137–149.

Bertkau, P. (1878): Einige Spinnen und ein Myriapode aus der Braunkohle von Rott. — Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens, Bonn, 35: 346–360, pl. 5.

Carico, J.E. (1993): Revision of the genus *Trechalea* THORELL (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western hemisphere. — Journal of Arachnology 21: 226–257.

Clerck, C. (1757): Svenska spindlar, uti sina hufvud-slågter indelte samt under några och sextio särskildte arter beskrefne och med illuminerade figurer uplyste. 154 pp. — L. Salvii, Stockholm.

Greenwood, D.R, Archibald, S.B., Mathewes, R.W. & Moss, P.T. (2005): Fossil biotas from the Okanagan Highlands, southern British Columbia and northern Washington State: climates and ecosystems across an Eocene landscape. — Canadian Journal of Earth Sciences, 42: 167–186.

Griswold, C.E. (1993): Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). — Smithsonian Contributions to Zoology, 539: 1–39.

Harding, I.C. & Chant, L.S. (2000): Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant lake beds, Colorado, United States. — Geology 28: 195–198.

Heyden, C. von. (1859): Fossile Insekten aus der Rheinischen Braunkohle. — Palaeontographica, 8: 1–15; pl. 1.

Hills, L.V. & Baadsgaard, H. (1967): Potassium-Argon dating of some Lower Tertiary strata in British Columbia. — Bulletin of Canadian Petroleum Geology, 15: 138–149.

Kim, J.-P. & Nam, K.-S. (2008): Mesozoic spider (Araneae: Pisauridae) from Korea. — Korean Arachnology, 24: 119–125.

Kishida, K. (1936): A synopsis of the Japanese spiders of the genus *Dolomedes*. — Acta Arachnologica, Tokyo 1: 114 –127.

Licht, E.L. (1986): Araneid taphonomy: a paleo thermometer. 163–165. — In: Eberhard, W.G., Lubin, Y.D. & Robinson, B.C. (eds.). Proceedings of the Ninth International Congress of Arachnology, Panama 1983. 333 pp. Smithsonian Institution Press, Washington DC.

Mathews, W.H. (1964): Potassium-argon age determination of Cenozoic volcanic rocks from British Columbia. — Geological Society of America Bulletin, 75: 465–468.

Mathews, W.H. & Rouse, G.E. (1963): Late Tertiary volcanic rocks and plant-bearing deposits in British Columbia. — Geological Society of America Bulletin, 74: 55–60.

McCook, H.C. (1890): American spiders and their spinningwork. Volume 2. - 480 pp., Published by the author, Philadelphia.

Moss, P.T., Greenwood, D.R. & Archibald, S.B. (2005): Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia – Washington State) from palynology. — Canadian Journal of Earth Sciences, 42: 187–204.

Mustoe, G.E. (2005): Diatomaceous origin of siliceous shale in Eocene lake beds of central British Columbia. — Canadian Journal of Earth Sciences, 42: 231–241.

O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A. & Maguire, S. (2002): Microbial taphonomic processes in the fossilization of insects and plants in the late Eocene Florissant Formation, Colorado. — Rocky Mountain Geology, 37: 1–11.

Penney, D. (2004): A new genus and species of Pisauridae (Araneae) in Cretaceous Burmese amber. — Journal of Systematic Palaeontology, 2: 141–145.

Petrunkevitch, A. (1922): Tertiary spiders and opilionids of North America. — Transactions of the Connecticut Academy of Arts and Sciences, 25: 211–279.

Petrunkevitch, A. (1942): A study of amber spiders. — Transactions of the Connecticut Academy of Arts and Sciences, 34: 119–464. Pls. I–LXIX.

Petrunkevitch, A. (1946): Fossil spiders in the collection of the American Museum of Natural History. — American Museum Novitates, 1328: 1–36.

Petrunkevitch, A. (1958): Amber spiders in European collections. — Transactions of the Connecticut Academy of Arts and Sciences, 41: 97–400.

Petrunkevitch, A. (1963): Chiapas amber spiders. — University of California Publications in Entomology, 31: 1–40.

Petrunkevitch, A. (1971): Chiapas amber spiders II. — University of California Publications in Entomology, 63: 1–44.

Pocock, R.I. (1892): *Liphistius* and its bearing upon the classification of spiders. — Annals and Magazine of Natural History, Series 6, 10: 306–314.

Rayner, R.J. & Dippenaar-Schoeman, A.S. (1995): A fossil spider (superfamily Lycosoidea) from the Cretaceous of Botswana. — South African Journal of Science, 91: 98–100.

Roth, V.D. (1965): Genera erroneously placed in the spider families Agelenidae and Pisauridae (Araneida, Arachnida). — Annals of the Entomological Society of America, 58: 289–292.

Rouse, G.E., Hopkins, W.S. & Piel, K.M. (1971): Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. — Geological Society of America Special Paper, 127: 213–246.

Rouse, G.E. & Mathews, W.H. (1979): Tertiary geology of the Quesnel area, British Columbia. — Bulletin of Canadian Petroleum Geology, 27: 418–445.

Schawaller, W. & Ono, H. (1979): Fossile Spinnen aus miozänen Sedimenten des Randecker Maars in SW-Deutschland (Arachnida: Araneae). — Jahreshefte der Gesellschaft für Naturkunde in Württemberg, 134: 131–141.

Scudder, S.H. (1890): The Tertiary insects of North America. — Report of the United States Geological Survey of the Territories, 13: 1–734.

Selden, P.A. (2001): Eocene spiders from the Isle of Wight with preserved respiratory structures. — Palaeontology, 44: 695–729.

Selden, P.A. (2002): Missing links between *Argyroneta* and Cybaeidae revealed by fossil spiders. — Journal of Arachnology, 30: 189–200.

Sierwald, P. (1987): Revision der Gattung *Thalassius* (Arachnida, Araneae, Pisauridae). — Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, 29: 51–142.

Sierwald, P. (1997): Phylogenetic analysis of pisaurine nursery web spiders, with revisions of *Tetragonophthalma* and *Perenethis* (Araneae, Lycosoidea, Pisauridae). — Journal of Arachnology, 25: 361–407.

Simon, E. (1890): Études arachnologiques. 22e Mémoire. XXXIV. Études sur les Arachnides de l'Yemen. [Remarques sur la classification des araignées, pp. 79–82]. — Annales de la Société entomologique de France (6) 10: 77–124.

Simon, E. (1898): Histoire naturelle des araignées. 2nd edition. Volume 2, part 2. 193–380. — Encyclopédie Roret, Paris.

Smith, F.P. (1902): The spiders of Epping Forest. — Essex Naturalist 12: 181–201.

Symons, D.T.A. & Wellings, M.R. (1989): Paleomagnetism of the Eocene Kamloops Group and the cratonization of Terrane I of the Canadian Cordillera. — Canadian Journal of Earth Sciences, 26: 821–828.

Thorell, T. (1894): Förteckning öfver arachnider från Java och närgrändsande öar, insamlade af Carl Aurivillius; jemte beskrifningar å några sydasiatiska och sydamerikanska spindlar. — Bihang till Konglige Svenska Vetenskaps-Akademiens Handlingar, Stockholm 20(4):1–63.

Wilson, M.V.H. (1977a): Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. — Canadian Journal of Earth Sciences, 14: 953–962.

Wilson, M.V.H. (1977b): Middle Eocene freshwater fishes from British Columbia. — Royal Ontario Museum, Life Sciences Contributions, 113: 1–61.

Wilson, M.V.H. (1977c): New records of insect families from the freshwater Middle Eocene of British Columbia. — Canadian Journal of Earth Sciences, 14: 1139–1155.

Wilson, M.V.H. (1988): Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. — Palaeogeography, Palaeoclimatology, Palaeoecology, 62: 609–623.

Wilson, M.V.H. & Barton, G. (1996): Seven centuries of taphonomic variation in Eocene freshwater fishes preserved in vares: paleoenvironments and temporal averaging. — Paleobiology, 22: 535–542.

Wilson, M.V.H. & Bogen, A. (1994): Tests of the annual hypothesis and temporal calibration of a 6375-varve fish-bearing interval, Eocene Horsefly Beds, British Columbia, Canada. — Historical Biology, 7: 325–339.

Wunderlich, J. (1986): Die ersten Spinnen aus dem Mittel-Eozän der Grube Messel. — Senckenbergiana Lethaea, 67: 171–176.

Wunderlich, J. (ed.) (2004): Fossil spiders in amber and copal. — Beiträge zur Araneologie, 3: 1–1908.

Zhang, J.-X., Zhu, M.-S. & Song, D.-X. (2004): A review of the Chinese nursery-web spiders (Araneae, Pisauridae). — Journal of Arachnology, 32: 353–417.

## Addresses of the authors:

Dr. Paul A. Selden
Paleontological Institute and Department of Geology
University of Kansas
Lawrence KS 66045, USA
and
Department of Palaeontology
Natural History Museum
London SW7 5BD, UK

Dr. David Penney
Michael Smith Building
Faculty of Life Sciences
The University of Manchester
Manchester M13 9PT, UK