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Distribution and biology of the ectoparasitic beaver beetle
Platypsyllus castoris Ritsema in North America
 (Coleoptera: Leiodidae: Platypsyllinae)

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Abstract: The distribution and biology of the beaver beetle, *Platypsyllus castoris* Ritsema, are summarized for North America. In light of the fact that the beetle uses two beaver species as hosts which have seemingly been separated for some five million years on two continents, it is asked if the Nearctic and Palearctic beetle populations are really the same species.

Introduction

The beetle family Leiodidae contains 335 known species in America north of Mexico, and these have some markedly diverse biologies. Keys for the identification to North American subfamilies, tribes and genera of Leiodidae are in Peck (2000). The subfamily Platypsyllinae, with only 4 genera worldwide, all of which are ectoparasitic, is of special interest because it contains the most modified ectoparasites of all beetles. The genera are: *Leptinus* Müller 1817 with 6 Palearctic and 3 Nearctic species, ectoparasitic on small rodents and insectivores (Peck 1982); *Leptinillus* Horn 1882 with 2 Nearctic species, ectoparasitic on rodents (both the semiaquatic genus *Castor* Linnaeus (Castoridae) and the fossorial genus *Aplodontia* Richardson (Aplodontidae)); *Silphopsyllus* Olsufiev 1923 with one Palearctic species, ectoparasitic on the aquatic insectivore *Desmana moschata* Pallas (Talpidae) of Ukraine, Kazakhstan and adjacent Russia; and *Platypsyllus* Ritsema 1869 with one apparently Holarctic species, ectoparasitic on the two species of *Castor*.

All these beetle genera are wingless and eyeless or with reduced eyes, and with a striking dorso-ventral flattening. Additionally, *P. castoris*, has a remarkably modified antennal club, with antennomeres 3-11 shortened, globularly compacted, and partly enclosed in a scoop shaped antennomere 2, as is also found in Gyrinidae and Dryopidae. The beetles possess derived family characters of Leiodidae and are placed within the subfamily Platypsyllinae Ritsema 1869 (Lawrence and Newton 1982, 1995). Newton (1998) lists the probable synapomorphies of the subfamily with Coloniinae but its affinities to other subfamilies are not clear. It is likely that the ectoparasitic habit is derived

from an ancestor which was a scavenger in small mammal nests or burrow systems (Waage 1979, Wood 1965) and Cholevinae would be the most likely candidate for this habit.

The unusual biology and morphology of this small ectoparasitic subfamily has stimulated a disproportionate number of publications. Summaries of the early references are in Desneux (1906), Csiki (1910), Jeannel (1922) and Bugnion and du Buysson (1924). Later important work on the morphology, taxonomy, biology, and larvae of the Palearctic species is reviewed in Ising (1969), Casale (1975), Buckle (1976), and Besuchet (1980). Contributions on the North American species are Parks and Barnes (1955), Wood (1965), Dybas (1976), and Peck (1982). In the earlier American literature the names *Leptinus testaceus* (restricted to Europe) and *L. americanus* (restricted to the west central USA) were often incorrectly applied to two other eastern or western North American species of *Leptinus* (Peck 1982).

The morphological modifications for ectoparasitism are most extreme in the flea or louse-like appearance of *Platypsyllus* (Figs. 1-2), which led to its original placement as a flea in a new family (Platypsyllidae Ritsema 1869b). Westwood (1869) created the synonym and secondary generic homonym *Platypsyllus* Westwood and placed it in a new order (Acheioptera Westwood, 1869). LeConte (1872) first recognized the species as a beetle, and transferred Platypsyllidae into Coleoptera. Dessart (1993) provides more detail on the curious and complex chronology of the taxonomic history of the genus *Platypsyllus*. The other genera were usually placed in the family Leptinidae LeConte 1872. Jeannel (1922) demonstrated the close relationship of *Platypsyllus* with *Leptinus*

and combined both into the subfamily Leptiniinae of the Silphidae.

The purpose of this paper is to summarize the widely scattered geographic records and literature on the distribution and biology of the beaver beetle, *Platypsyllus castoris* Ritsema, in North America.

Methods and Materials

Primary literature, species lists and catalogs were searched and are referenced. Acronyms for museums containing specimens are those of Arnett *et al.* (1997) and are as follows: **AMNH**, American Museum of Natural History, New York, New York, USA; **BDMU**, Biology Department, McMaster University, Hamilton, Ontario, Canada; **CASC**, California Academy of Sciences, San Francisco, California, USA; **CDAE**, Department of Food and Agriculture, Sacramento, California, USA; **CMNC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **CNCI**, Canadian National Collection of Insects, Ottawa, Ontario, Canada; **CUIC**, Cornell University Insect Collection, Cornell University, Ithaca, New York, USA; **DEBU**, Department Environmental Biology, University of Guelph, Guelph, Ontario, Canada; **EMEC**, Essig Museum, University of California, Berkeley, California, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **FSCA**, Florida State Collection of Arthropods, Gainesville, Florida, USA; **INHS**, Illinois Natural History Survey, Urbana, Illinois, USA; **ISUI**, Entomology Collection, Iowa State University, Ames, Iowa, USA; **MCZC**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MHNG**, Natural History Museum, Geneva, Switzerland; **NDSU**, Entomology Department Collection, North Dakota State University, Fargo, North Dakota, USA; **OSEC**, Emerson Museum, Department Entomology, Oklahoma State University, Stillwater, Oklahoma, USA; **OSUC**, Ohio State University, Columbus, Ohio, USA; **OSUO**, Oregon State University, Corvallis, Oregon, USA; **PSUC**, Frost Museum, Department Entomology, Pennsylvania State University, College Park, Pennsylvania, USA; **RMNH**, Nationaal Natuurhistorische Museum, Leiden, Netherlands; **SBPC**, Stewart B. Peck collection, Ottawa, Ontario, Canada; **SMDV**, Spencer Entomological Museum, University of British Columbia, Vancouver, British Columbia, Canada; **SMNH**, Saskatchewan Museum Natural History, Regina, Saskatchewan, Canada; **TAMU**, Texas A & M University, College Station, Texas, USA; **UCDC**, Univer-

sity of California, Davis, California, USA; **UCRC**, University of California, Riverside, California, USA; **UMRM**, Enns Entomology Museum, University of Missouri, Columbia, Missouri, USA; **UMSP**, University of Minnesota, St. Paul, Minnesota, USA; **UNSM**, University of Nebraska State Museum, Nebraska Hall, Lincoln, Nebraska, USA; **USAM**, University of Alberta, Edmonton, Alberta, Canada; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; **WFBM**, Barr Entomological Collection, University of Idaho, Moscow, Idaho, USA; **WSUC**, James Entomology Collection, Department of Entomology, Washington State University, Pullman, Washington, USA.

Results

Family Leiodidae Fleming 1821
Subfamily Platypsyllinae Ritsema 1869
(=Leptiniinae LeConte 1872)
The mammal nest beetles

Genus *Platypsyllus* Ritsema
(Figs. 1-12)

Platypsyllus Ritsema, 1869a: 23. Type species: *Platypsyllus castoris* Ritsema. See Newton 1998: 133.

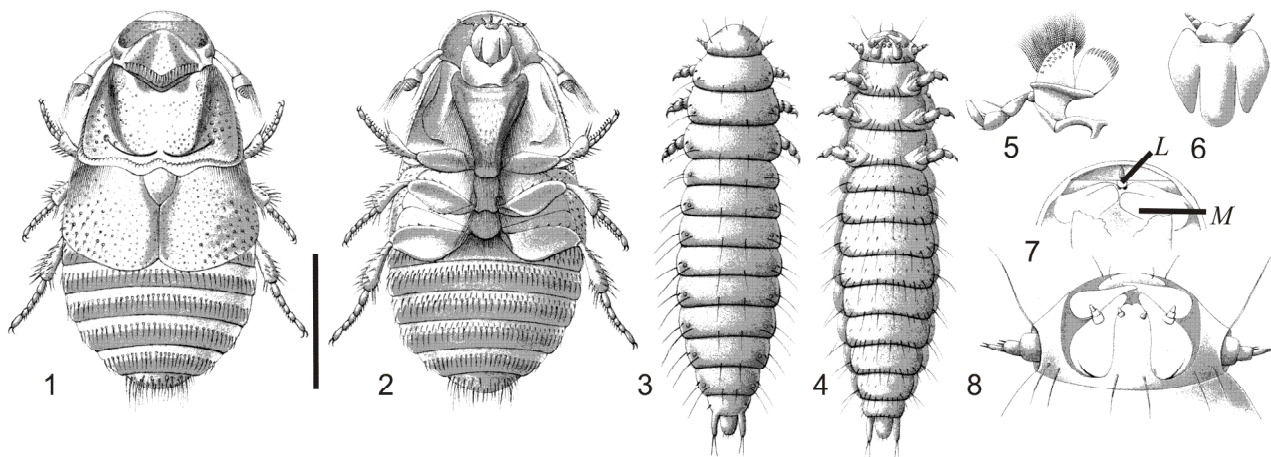
P. castoris Ritsema, 1869a: 23. Common name; the beaver beetle. Types in RMNH (Wood 1965: 34). Type locality: Rotherdam (Rotterdam), Holland (specimens taken on American beaver in Rotterdam Zoological Garden, although the original description states the host was the Eurasian beaver; see below).

Synonym. *P. castorinus* Westwood, 1869: 119; Ritsema, 1869b: 38.

Taxonomy: Ritsema 1869a, 1870; LeConte 1872; Horn 1882; Reitter 1884; Riley 1888, 1890b, 1892; Hatch 1957: 18.

Adults. Redescriptions and morphology: Horn 1882; Bonhoure 1884; Riley 1890b; Desneux 1906; Sharp and Muir 1912: 506 and fig. 229 (aedeagus); Jeannel 1922; Bugnion and du Buysson 1924; Hatch 1957: 18 and plate II, figs 7-8; Winter 1979.

Immatures. Morphology and behaviour: Riley 1888, 1890a, 1890b, 1892; Chobaut 1899, Horn 1888, 1890; Böving and Craighead 1930, Wood 1965, Neumann and Piechocki 1985, Newton 1991: 330-331. Wood (1965) demonstrated that there are three larval instars, and that these spend all their time on the host, where they feed.



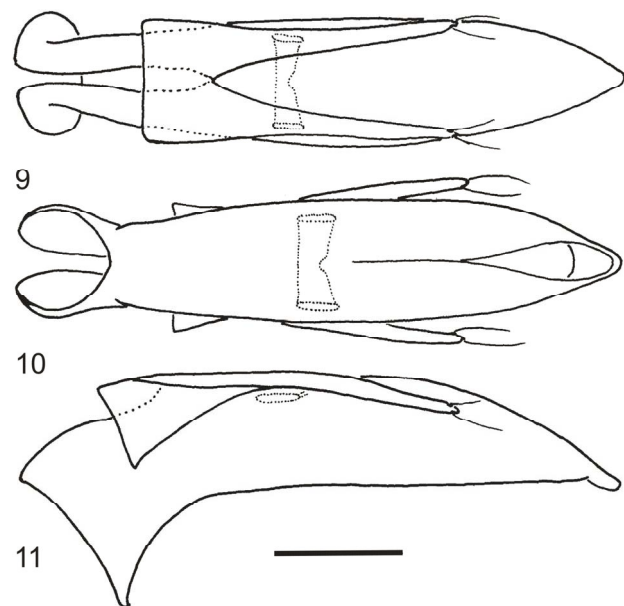
Figures 1-8. Adult and larval habitus and structures of *Platypsyllus castoris* (from Desneux 1906). The specimens are of unstated provenance but probably are from the vicinity of Nimès, France, and are likely from the Camargue population. **1)** Adult, dorsal. **2)** Adult, ventral. **3)** Larva, dorsal. **4)** Larva, ventral. **5)** Adult, maxilla. **6)** Adult, labium and mentum. **7)** Adult, ventral side of head, L is labrum, M is flattened scale-like mandible. **8)** Larval head, ventral. Scale line for figs. 1-4, 1.0 mm.

North American distribution. Published distributional records of the beetle are comparatively few: Dietrich (1951), Hatch (1957), Janzen (1963), Kirk and Balsbaugh (1957), Peck and Thomas (1998), and Spencer (1957). Leng (1920) vaguely cites localities as Texas, California, "Dakota", and Alaska. A far greater number of records are unpublished and the specimens seen are in the above listed collections. All records now known to me are from the following provinces or states: **Canada.** AB, BC, ON, PQ, SK. **United States.** AK, AL, CA, DC, FL, IA, ID, IL, LA, MI, MN, MO, MS, MT, NE, ND, NY, OK, OR, PA, SD, TX, WA, WY (fig. 12). The full distribution of the beetle is probably the same as that of the host (Fig. 12).

Hosts. The beetles are ectoparasitic as both adults and larvae. The primary hosts are the American beaver *Castor canadensis* Kuhl and the European beaver *Castor fiber* Linnaeus (Rodentia, Sciuromorpha, Castoridae). Records appear on occasion in surveys or summaries of beaver parasites; e.g. Erickson (1944), Hodgdon and Larson (1980), Judd (1954), Lawrence and Graham (1955), and Lawrence *et al.* (1961). Most specimen labels do not actually cite beavers as the host. Only one record on another mammal host is known. This is from the river otter, *Lontra* (= *Lutra*) *canadensis* (Schreber). This is most likely the result of an accidental host switch which could have happened while an otter was inside a beaver lodge or from an otter eating a young beaver, which they are known or suspected to do (Anonymous 1984, 2004; Banfield 1974). The specimen data are: California; extreme southwestern Sacramento Coun-

ty, east bank Sacramento River, along Highway 160, 5 km (3 mi) north of Antioch Bridge, 06-01-1998, recovered from face of female river otter, leg. N.M. Belfiori (specimen deposited in UCDC).

Beavers themselves have been extirpated in many parts of North America. For example, they were gone from Massachusetts in the early 1700's and only 15 were known in the Adirondacks of New York in 1900 (Müller-Schwarze and Sun 2003). With the regulation of hunting and trapping and institution of wildlife management programs beavers are now returning in



Figures 9-11. Views of aedeagus of three separate specimens from Algonquin Provincial Park, Ontario. **9)** Dorsal view. **10)** Ventral view. **11)** Lateral view. Scale line 0.1 mm.

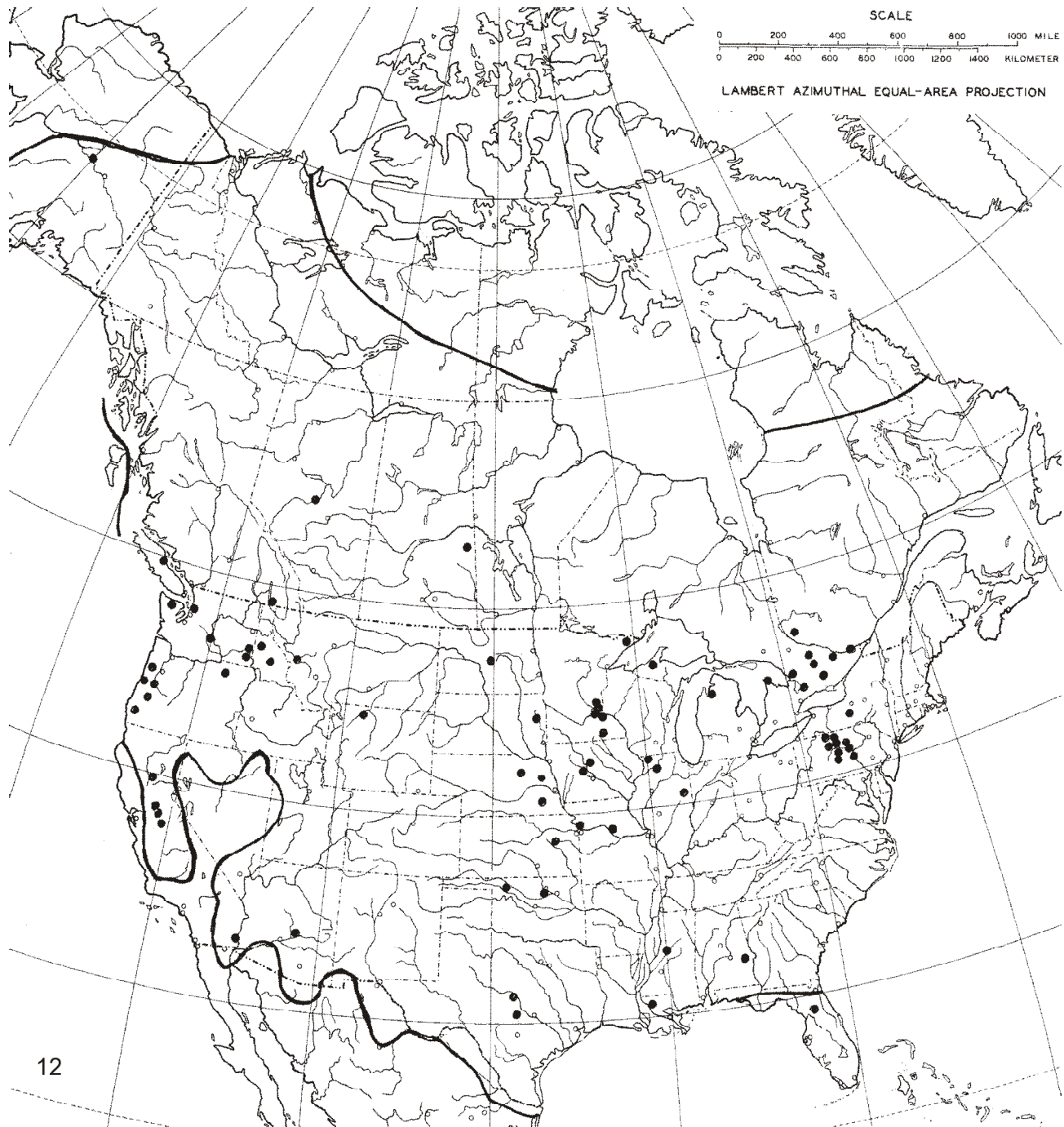


Figure 12. Dot map showing known sites of records for *Platypsyllus castoris* in North America. Dark line indicates the approximate limits of the historical range of the host, *Castor canadensis* (after Hall 1981). The beetle is probably to be expected to occur on beavers throughout its distributional range.

much of North America (Müller-Schwarze and Sun 2003), often to levels judged to be a nuisance.

Biology and life history. The beetles can be collected by combing them from the fur of captured or

recently dead beavers. In cold conditions, the beetles are very responsive to heat and will leave the fur of a dead beaver and move to the warmth of a hand. Infestation levels range from 0 to 192 adults per beaver (Janzen 1963). Wood (1965) found adults in

over 60% of the 45 living and dead beavers he studied. Larvae (with sharply pointed mandibular incisors) and adults (with movable and perhaps functionless mandibles shaped as plates) feed on epidermal tissue and possibly on skin secretions and wound exudates (Wood 1965). Beavers do not behave in a way to suggest that they are bothered by the feeding of the beetles. The distinctively split second toenails of the hind feet, the grooming and combing claws of beavers (Bailey 1923), seem not to be used for the removal of the beetles (Wood 1965).

Eggs, larvae, and pupae were not found on the beavers by Janzen (1963), but numerous larvae are reported from beaver by Riley (1890b), Lawrence *et al.* (1961), and Wood (1965). It is possible that the larvae may also scavenge inside beaver lodges or burrows. The pupal stage is the only life stage not spent on the host. It is passed in a pupal chamber formed in earth at the top of the lodge or burrow. Wood (1965) found adults throughout the year, and larvae were present from June to at least September. Data are not sufficient to state if there is a pattern of seasonality in the abundance of adults. Janzen (1963) did not find significant population number differences between winter and spring caught beavers. For more details on biology see Janzen (1963), Lawrence *et al.* (1961), Piechocki (1959), Waage (1979), Winter (1979), and Wood (1965).

Discussion

Palaearctic distribution of beaver. The historic distribution of the Eurasian beaver *Castor fiber* was across Europe from Mediterranean France to Scandinavia and eastward to Russia east of the Urals (the drainages of the Ob and Yenisey Rivers) (Müller-Schwarze and Sun 2003). Other isolated populations exist in Mongolia and the Tuva Republic in east-central Russia (Ducroz *et al.* 2005). From the Middle Ages onwards intense hunting pressure on *Castor fiber* for its fur, castoreum glands and meat (its aquatic habit was the basis of a Papal decree which declared it a fish and so could be eaten during Lent) extirpated it from most of its Eurasian range and nearly drove it to extinction. This produced extreme reduction in genetic diversity through a strong population genetic bottleneck (Babik *et al.* 2005, Ducroz *et al.* 2005, Durka *et al.* 2005, Milisnikov 2004).

With modern environmental protection, the Eurasian beaver is now recovering and expanding from its few isolated refugia. As examples, Bavaria, Finland, and Sweden lost their beavers in 1867, 1868, and 1871, respectively, and reintroductions were in 1966,

1935, and 1922 respectively (Müller-Schwarze and Sun 2003). Reintroductions have been by both beaver species. Reintroduction into Switzerland was in 1958 from a population in southern France (Besuchet 1978). But, about 90% of the current populations in Finland and Karelia belong to the North American species (Durka *et al.* 2005, Müller-Schwarze and Sun 2003). There is current controversy about reintroducing the Eurasian beaver into Britain (Pickrell 2001). Additionally, the American beaver has even been introduced to Tierra del Fuego, Argentina (Müller-Schwarze and Sun 2003) where it has become a major environmental problem.

As noted above, the beetle was described in 1869 from American beaver hosts in the Rotterdam Zoological Garden, Holland. The first record of the beetle from a wild population of Eurasian beavers seems to be from the Camargue region of the Petit Rhone River near the Mediterranean coast of southern France (Bonhoure 1884). Since then, European collection records of the beetle are from France, Germany, Norway, Russia, Sweden (references in Wood 1965). More recent reports are for Belgium, Belarus, Czech Republic, Netherlands, Poland, Slovakia, and Switzerland (Perreau 2000, 2004, Ruzicka 2000).

Evolutionary history of beavers. The continent of origin and direction of colonization of beavers is unclear. The family Castoridae is known from the latest Eocene of North America, it makes an appearance in the Oligocene in Eurasia (Korth 1994), and is known to contain some 30 fossil genera (Rybcznski 2006). The ancient species were burrowers. Evidence of swimming behavior in the semiaquatic clade Castorinae (containing *Castor*) is from the lower Miocene (24 mya) (Rybcznski 2006). The genus *Castor* itself is first recorded in both Eurasia and North America in the Miocene according to Korth (1994). Stirton (1935) had previously placed the earliest *Castor* fossils in North America in the earliest Pliocene of California.

The genus most likely dispersed between Eurasia and North America via the Bering Isthmus or Bering land bridge (Repenning 1967). The first appearance of *Castor* in North America roughly coincides with the drowning of the Bering land bridge and opening of the Bering Strait (acting as a barrier to intercontinental dispersal) some 5.32 mya (Gladenkov *et al.* 2002). Evidence is lacking to definitively favor a direction of intercontinental migration for *Castor* and there is no evidence for "back dispersal" in the Quaternary when the Bering land bridge was repeatedly reformed. It thus appears that the two continental populations of

Castor have been disjunct for at least 5 mya (see Kuehne *et al.* 2000).

The two recent beaver species are similar enough that some have considered them to be just one species. However, morphological (Veron 1992) and chromosomal, allele and DNA sequence differences argue against this (Babik *et al.* 2005, Sieber *et al.* 1999, Ward *et al.* 1991). The North American species is considered to have character states which are more derived in skeletal structure (Veron 1992, Lavarov and Lavarov 1983), cytogenetics and behavior (Lavorov and Orlov 1973). Based on the current classification of beavers and the beetles, the elapsed time since the continental separation of beavers has seemingly been sufficient for the differentiation (speciation) of the hosts, but not the ectoparasite. Certainly, many insect as well as vertebrate speciation events have resulted from trans-Beringian movements and subsequent separation and differentiation.

One beetle species or two? Since the beetle is known on two long-isolated and separate host species restricted to the Palaearctic and Nearctic biogeographic regions, the conspecificity of North American and Eurasian *P. castoris* seems open to question. It can be asked if the beetle is actually just one species? Might we not expect it to have co-speciated as its *Castor* hosts speciated? Possibly the adaptive pressures or genetic isolation which caused or allowed differentiation in the hosts were not sufficient to affect the beetle.

All others (e. g., Reitter 1884) and myself who have looked closely at specimens have not been able to distinguish any consistent external differences separating the Old and New World beetle populations. However, Wirén (1939) states he observed unspecified differences between the beetle illustrations of Reitter (1909) from beavers of unstated provenance and beetles from *Castor fiber* in Sweden, reintroduced from relictual Norwegian stock. I consider the slight differences I have seen to fall within the range of individual variation. This is true even for the aedeagus, which usually exhibits differences indicative of separate species status throughout the Leioididae. The aedeagus has not been previously illustrated for North American specimens (Figs. 9-11). The spermatheca of females on both continents also suggests conspecificity, and is shaped as a fat sausage, with a bend near the middle, so that it appears similar to the letter "L".

Is *Platypyllus castoris* introduced to Eurasia?

The type specimen for the beetle species was taken in the zoological gardens in Rotterdam in 1869 on the Eurasian beaver according to Ritsema (1869a) but it

was later stated that the host was the American beaver according to LeConte (1872: 801). Bonhoure (1884) settled the question with a supporting letter from the director of the zoological gardens of Rotterdam stating that they had never had specimens of the Eurasian beaver, but only of the American beaver. LeConte (1872: 804) stressed the need to examine other aquatic rodents for the beetle, including the European beaver. By 1882 the beetle was still not known from North America or it would have been reported in Horn's (1882) discussion of *Platypyllus*. The earliest label date I have seen on specimens are records from 1886, from West Point, Nebraska and these were reported by Riley 1888 (specimens in UNSM, USNM).

Why was this distinctive insect discovered on wild-caught beavers so late in the history of both European and North American entomology (1883 and 1886 respectively)? Is it possible that the Eurasian records of *Platypyllus castoris* represent descendant populations which were carried by human transport to Europe on their host *Castor canadensis*, and then escaped with their host, or were involved in a recent host shift to the Eurasian beaver? This does not seem likely because of the rareness and isolated nature of the relict populations of *C. fiber* in Europe in the 1700 and 1800's. But presently it also seems not possible to settle this question in a definitive way with the available evidence. However, the slight weight of the evidence for a Eurasian origin of *Castor* in the Miocene, and its likely Pliocene arrival in North America, suggest a Eurasian origin for both the beaver and the beetle. The long evolutionary time suggested by the extreme modifications in *Platypyllus* also suggest that it had mammal hosts more ancient than beavers, and this was most likely a burrow inhabiting rodent or insectivore.

Additional and independent data should be sought as a measure of the levels of relatedness within the host species and the beetle itself. Such estimates of population divergence time and gene flow are probably measurable using DNA sequence data. Beetles from several authentic relict populations of beavers in Europe (Norway or the south of France) and Siberia might be considered for comparison with specimens from across North America.

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References cited

- Anonymous.** 1984. New York's Wildlife Resources. <http://www.nyotter.org/pages/biology.html>. Posted 17 November, 1984. Accessed 8 March, 2006.
- Anonymous.** 2004. New York State Department of Environmental Conservation. <http://www.dec.state.ny.us/website/dfwmr/habitat/hrottersp/Otter.htm>. Last revised 17 May, 2004. Accessed 9 March, 2006.
- Arnett, R.H. Jr., G. A. Samuelson, and G. M. Nishida.** 1997. The insect and spider collections of the world, 2nd ed. Flora and Fauna Handbook, no. 11. CRC Press, Boca Raton, FL.
- Babik, W., W. Durka, and J. Radwan.** 2005. Sequence diversity of the MHC DRB gene in the Eurasian beaver (*Castor fiber*). *Molecular Ecology* 14: 4249-4257.
- Bailey, V.** 1923. The combing claws of the beaver. *Journal of Mammalogy* 4: 77-79.
- Banfield, A.W.F.** 1974. The mammals of Canada. University of Toronto Press, Toronto, Canada.
- Besuchet, C.** 1978. Réintroduction en Suisse du *Platypsyllus castoris* Rits. (Coleoptera: Leptinidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 51: 291-292.
- Besuchet, C.** 1980. Revision des *Leptinus* paléarctiques (Coleoptera: Leptinidae). *Revue Suisse de Zoologie* 87: 131-142.
- Bonhoure, A.** 1884. Note sur le *Platypsyllus castoris* Ritsema et sa capture en France. *Annales Société Entomologique de France* ser. 46, 4:147-153.
- Böving, A.G., and F.C. Craighead.** 1930. An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana (N.S.)* 11: 1-351.
- Buckle, A.P.** 1976. Studies on the biology and distribution of *Leptinus testaceus* Müller within a community of mixed small mammal species. *Ecological Entomology* 1: 1-6.
- Bugnion, E., and H. de Buysson.** 1924. Le "*Platypsyllus castoris*" Rits. *Annales de la Société des Naturalistes Zoological series* 10, 7: 83-130.
- Casale, A.** 1975. Ciclo biologico e morfologia preimmaginale de Coleoptera Staphylinoidea delle famiglie Leptinidae e Catopidae. *Redia* 56: 199-230, illus.
- Chobaut, A.** 1899. Moeurs et métamorphoses du *Platypsyllus castoris* Ritsema. *Le Naturaliste* 2 ser, 30: 197-200.
- Csiki, E.** 1910. Platypsyllide, Orthoperidae, Phaenoccephalidae, Discolomidae, Sphaeriidae. *Coleopterum Catalogus, Pars 18*. W. Junk, Berlin.
- Desneux, J.** 1906. Family Platypsyllidae. *Genera Insectorum, Wytsman, Brussels*. Fascicle 41: 1-10.
- Dessart, P.** 1993. Les curieuses vicissitudes du genre *Platypsyllus* Rits. (Coleoptera). *Bulletin Annals Société Royal Belge Entomologie* 129: 169-181.
- Dietrich, H.** 1951. *Platypsyllus castoris* Ritsema. *Coleopterists Bulletin* 5: 54.
- Ducroz, J.F., M. Stubbe, A.P. Saveljev, D. Heidecke, R. Samjaa, A. Ulevicius, A. Stubbe, and W. Durka.** 2005. Genetic variation and population structure of the Eurasian beaver *Castor fiber* in eastern Europe and Asia. *Journal of Mammalogy* 86: 1059-1067.
- Durka, W., W. Babik, J.-F. Ducroz, D. Heidecke, F. Rosell, R. Samjaa, A.P. Saveljev, A. Stubbe, A. Ulevicius, and M. Stubbe.** 2005. Mitochondrial phylogeography of the Eurasian beaver *Castor fiber* L. *Molecular Ecology* 14: 3843-3856.
- Dybas, H.S.** 1976. The larval characters of featherwing and limuloid beetles and their family relationships in the Staphylinoidea (Coleoptera: Ptiliidae and Limulodidae). *Fieldiana, Zoology* 70: 29-79, illus.
- Erickson, A.B.** 1944. Parasites of beavers, with a note on *Paramphistomum castori* Kofoid and Park, 1937, a synonym of *Stichorchis subtriquetrus*. *American Midland Naturalist* 31: 625-630.
- Gladenkov, A. Y., A. E. Oleinik, L. Marincovich, and K. B. Barinov.** 2002. A refined age for the earliest opening of Bering Strait. *Palaeogeography Palaeoclimatology Palaeoecology* 183(3-4): 321-328.
- Hall, E. R.** 1981. The mammals of North America. (2nd ed.). Vol II. John Wiley & Sons, New York.
- Hatch, M.H.** 1957. The beetles of the Pacific Northwest. Part II, Staphyliniformia. University of Washington Publications in Biology, vol. 16. University of Washington Press, Seattle, 384 pp.

- Hodgdon, H.E., and J.S. Larson** 1980. A bibliography of the recent literature on Beaver. Massachusetts Agricultural Experimental Station, College of Food and Natural Resources, University of Massachusetts at Amherst, Research Bulletin 665. 128 pp.
- Horn, G.H.** 1882. Notes on some little known genera and species of Coleoptera. Transactions American Entomological Society 10: 113-126; plate 5.
- Horn, G.H.** 1888. Descriptions of the larvae of *Glyptus*, *Platypsyllus* and *Polyphylla*. Transactions American Entomological Society 15: 23-26.
- Horn, G.H.** 1890. The «ultimate larva» of *Platypsyllus*. Entomologica Americana 6: 55-56.
- Ising, E.** 1969. Zur Biologie des *Leptinus testaceus* Müller 1817 (Insecta: Coleoptera). Zoologische Beiträge 15: 393-456, illus.
- Janzen, D.H.** 1963. Observations on populations of adult beaver beetles, *Platypsyllus castoris* (Platypsyllidae: Coleoptera). The Pan-Pacific Entomologist 34: 215-228.
- Jeannel, R.** 1922. Morphologie comparée du *Leptinus testaceus* Müll. et du *Platypsyllus castoris* Rits. Biospeologica XLV. Archives de Zoologie Expérimentale et Générale 60: 557-592.
- Judd, W.W.** 1954. Some records of ectoparasitic Acarina and Insecta from mammals in Ontario. Journal of Parasitology 40: 483-484.
- Kirk, V.M., and E.U. Balsbaugh.** 1975. A list of the beetles of South Dakota. Agriculture Experiment Station, South Dakota State University, Technical Bulletin 42. 139 pp.
- Korth, W.W.** 1994. The Tertiary record of rodents in North America. Plenum Press, New York. 324 pp.
- Kuehn, R., G. Schwab, W. Schroeder, and O. Rottmann.** 2000. Differentiation of *Castor fiber* and *Castor canadensis* by noninvasive molecular methods. Zoo Biology 19: 511-515.
- Lavrov, L. S., and V. L. Lavrov.** 1983. Osteological differences between the East-European (*Castor fiber oreintoeuropaeus*) and Canadian (*C. canadensis*) beavers. Zoologicheskii Zhurnal 62: 9.
- Lavrov, L. S., and V. N. Orlov.** 1973. Karyotypes and taxonomoy of modern beavers (*Castor*, Castoridae, Mammalia). Zoologicheskii Zhurnal 52: 734-742.
- Lawrence, J.F., and A.F. Newton, Jr.** 1982. Evolution and classification of beetles. Annual Review of Ecology and Systematics 13: 261-290.
- Lawrence, J.F., and A.F. Newton, Jr.** 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779-1006 + index 1-48. In: J. Pakaluk and S.A. Slipinski (eds.). Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Museum i Instytut Zoologii PAN, Warszawa.
- Lawrence, W.H, K.L. Hays, and S.A. Graham.** 1961. Ectoparasites of the beaver (*Castor canadensis* Kuhl.). Wildlife Diseases, no. 12.
- Lawrence, W.H, and S.A. Graham.** 1955. Parasites and diseases of the beaver (*Castor canadensis* Kuhl); an annotated bibliography. Michigan Wildlife 2: 1-6.
- LeConte, J.L.** 1872. On Platypsyllidae, a new family of Coleoptera. Proceedings of the Zoological Society of London 1872: 799-805.
- Leng, C.W.** 1920. Catalogue of the Coleoptera of America, north of Mexico. J.D. Sherman Publ., Mt. Vernon, New York.
- Milishnikov, A.N.** 2004. Population-genetic structure of beaver (*Castor fiber* L., 1758) communities and estimation of effective reproductive size N_e of an elementary population. Russian Journal Genetics 40: 772-781.
- Müller-Schwarze, D., and L. Sun.** 2003. The Beaver; natural history of a wetlands engineer. Comstock Publishing Associates, Cornell University Press, Ithaca, NY.
- Neumann, V., and R. Pieckocki.** 1985. Morphologische und histologische Untersuchungen an der Larvenstadien von *Platypsyllus castoris* Ritsema (Coleoptera; Leptinidae). Entomologische Abhandlung der Staats-Museum Tierkunde Dresden 49: 27-34.
- Newton, A.F., Jr.** 1991. Agyrtidae through Silphidae and Pselaphidae (Staphylinoidea), Sphaeritidae through Histeridae (Hydrophiloidea). Pp. 324-341, 353-355, 359-364. In: F. W. Stehr (ed). Immature Insects. Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Newton, A.F., Jr.** 1998. Phylogenetic problems, current classification, and generic catalog of world Leiodidae (including Cholevidae). Pp. 41-178. In: P. M. Giachino and S. B. Peck (eds.). Phylogeny and evolution of subterranean and endogean Cholevidae (=Leiodidae Cholevinae). Proceedings of a symposium of the XX International Congress of Entomology, Florence, Italy, 30 August 1996. Atti, Museo Regionale di Scienza Naturale, Torino, Italy.
- Parks, J., and J.W. Barnes** 1955. Notes on the family Leptinidae, and a new record of *Leptinillus validus* Horn in North America. Annals of the Entomological Society of America 48: 417-421.

- Peck, S.B.** 1982. A review of the ectoparasitic *Leptinus* beetles of North America (Coleoptera: Leptinidae). *Canadian Journal of Zoology* 60: 1517-1527.
- Peck, S.B.** 2000. Chapter 19, Leiodidae. Pp. 250-258. *In: R. H. Arnett, Jr., and M. C. Thomas (eds.). American Beetles. Vol. 1. CRC Press, Boca Raton, FL*
- Peck, S.B., and M.C. Thomas.** 1998. A distributional checklist of the beetles (Coleoptera) of Florida. *Arthropods of Florida and neighbouring land areas. Florida Department of Agriculture and Consumer Services, Gainesville, FL. Vol. 16, i-viii + 1-180.*
- Perreau, M.** 2000. Catalogue des Coléoptères Leiodidae Cholevinae et Platypyllinae. *Mémoire Société Entomologique de France* 4: 1-460.
- Perreau, M.** 2004. Platypyllinae. Pp. 202-203. *In: I. Löbl and A. Smetana (eds.). Catalogue of Palearctic Coleoptera, vol. 2. Hydrophiloidea – Histeroidea – Staphylinoidea. Apollo Books, Stenstrup, Denmark*
- Pickrell, J.** 2001. Dammed if you do, damned if you don't? *Science* 292: 2422-2423.
- Piechochi, R.** 1959. Zur Biologie des Biberkäfers *Platypyllus castoris* Ritsema. *Beiträge zur Entomologie* 9: 523-528.
- Reitter, E.** 1884. *Platypylla castoris* Rits. als Vertreter einer neuen europäischen Coleopteren-Familie. *Wiener Entomologische Zeitung* 3: 19-21.
- Reitter, E.** 1909. Familie Platypyllidae. *Fauna Germanica. Die Käfer des Deutschen Reiches. Vol 2. Pp. 12-13. K.G. Lutz Verlag, Stuttgart, Germany.*
- Repenning, C.A.** 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic. Pp. 288-311. *In: D. A. Hopkins (ed). The Bering land bridge. Stanford University Press, Palo Alto, CA.*
- Riley, C.V.** 1888. Systematic relations of *Platypyllus* as determined by the larva. *Insect Life (Washington)* 1: 300-307.
- Riley, C.V.** 1890a. *Platypyllus* – egg and ultimate larva – Dr. Horn's reclamation. *Entomologica Americana* 6: 27-30.
- Riley, C.V.** 1890b. Notes on the larva of *Platypyllus*. *Proceedings Entomological Society Washington* 2: 27-28.
- Riley, C.V.** 1892. Systematic relations of *Platypyllus*, as determined by the larva. *In: H.T. Martin (ed.). Castorologia. W. Drysdale and Co., Montreal. xvi + 238 pp. Reprint of Riley, 1888.*
- Ritsema, C.** 1869a. (15 Sept.). [No title]. *Petites Nouvelles Entomologiques* 1: 23.
- Ritsema, C.** 1869b. (November). [No title]. *Petites Nouvelles Entomologiques* 1: 38.
- Ritsema, C.** 1870. [No title]. *Tijdschrift voor Entomologie, 2nd series* 5: 185-186.
- Ruzicka, J.** 2000. Faunistic records from the Czech Republic, 116. *Coleoptera: Leiodidae: Platypyllinae. Klapalekiana* 36: 288.
- Rybczynski, N.** 2006. Castorid phylogenetics: implications for the evolution of swimming and tree-exploitation by beavers. *Journal of Mammal Evolution*. [In press.]
- Sharp, D.A., and F.A.G. Muir.** 1912. The comparative anatomy of the male genital tube in Coleoptera. *Transactions Entomological Society London, part III. Pp. 477-642, plates XLII-LXXVI-II. Reprinted 1969, Entomological Society of America.*
- Sieber, J., F. Suchentrunk, and G.B. Hartl.** 1999. A biochemical-genetic discrimination method for the two beaver species, *Castor fiber* and *Castor canadensis*, as a tool for conservation. Pp. 61-65. *In: P.E. Sulcher and R.M. Dzieciolowski (eds.). Beaver protection, management, and utilization in Europe and North America. Kluwer Academic, Plenum Press, New York.*
- Spencer, G.J.** 1957. North American beetles infesting mammals. *Proceedings Entomological Society British Columbia* 53: 21-22.
- Stirton, R. A.** 1935. A review of the Tertiary beavers. *University California Publications Geological Sciences* 23:391-485.
- Veron, G.** 1992. A morphometric and taxonomic study of genus *Castor*. *Bulletin du Museum National d'Histoire. Section A. Zoologie Biologie et Ecologie Animales* 14(3-4): 829-853.
- Waage, J.K.** 1979. The evolution of insect/vertebrate associations. *Biological Journal Linnean Society.* 12: 187-224.
- Ward, O.G., A.S. Graphodatsky, D.H. Wurster-Hill, V.R. Eremina, J.P. Park, and Q. Yu.** 1991. Cytogenetics of beavers: a case of speciation by monobrachial centric fusions. *Genome* 34: 324-328.
- Westwood, J.O.** 1869. (1 October). Notice of a new order of hexapod insects. *Entomologists Monthly Magazine* 6: 118-119.
- Winter, G.** 1979. Untersuchungen zur Morphologie des Biberkäfers *Platypyllus castoris* Ritsema 1869 (Coleoptera), eines extrem gut angepassten Vertreters des Lebensformtyps fellbewohnender Insekten. *Zoologische Jahrbuch der Anatomie* 101: 456-471.

- Wirén, E.** 1939. *Platypsyllus castoris* Ritzema konstaterad på svensk bäver i Värmland (*Platypsyllus castoris* Ritsema found on Swedish beaver in Värmland). Entomologische Tidskrift 60: 102-104.
- Wood, D.M.** 1965. Studies on the beetles *Leptinillus validus* (Horn) and *Platypsyllus castoris* Ritsema (Coleoptera: Leptinidae) from beaver. Proceedings of the Entomological Society of Ontario 95: 33-63, illus.