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PTENIDIUM KISHENEHNICUM (COLEOPTERA: PTILIIDAE), A NEW FOSSIL DESCRIBED FROM THE KISHENEHN OIL SHALES, WITH A CHECKLIST OF PREVIOUSLY KNOWN FOSSIL PTILIIDS

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Abstract.—***Ptenidium kishenehnicum*** **Shockley and Greenwalt**, a **new species** of feather-winged beetle (Coleoptera: Ptiliidae), is described from 46 million year old Kishenehn oil shales in Montana, USA. This compression fossil is the first beetle species to be described from this formation. A checklist of known fossils and their ages is provided.

Key Words: compression fossil, feather-winged beetles, fossil beetles, taxonomy, paleoentomology

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The feather-winged beetles (Coleoptera: Ptiliidae), while worldwide in their distribution, constitute a relatively small family, with approximately 635 described species (Grebennikov 2009). They are unique in that they are among the smallest insects known, with body lengths of 400 μm or less reported, and with females having a single ovary—the insect can accommodate only one maturing egg at a given time (Polilov 2005). The small size of the Ptiliidae may also be responsible for other unusual characteristics, such as complete lack of a heart (Grebennikov 2008) and the extremely small wing membranes, often 20 times greater in length than width, with numerous long setae attached to their marginal edges that contribute the majority of the wing's surface area (Horridge 1956, Grebennikov 2008).

The fossil record for Ptiliidae is better than one might expect given the numbers of described extant species and the beetles' small physical size. Several major catalogs of fossil beetles (Klebs 1910, Spahr 1981, Carpenter 1992) have included Ptiliidae. Ptiliids have been found in amber from the Baltic, the Dominican Republic, Lebanon, Rovno, Myanmar and Mexico (Table 1). In fact, ptiliids have been reported to make up 11% of all Coleoptera in the American Museum of Natural History collection of Myanmar amber (Grimaldi et al. 2002). Isolated ptiliid elytra have also been found in Holocene, Pleistocene and Pliocene deposits (Matthews 1977, Matthews and Telka 1997). Despite the relatively large number of reports of fossil ptiliids, only five species of Ptiliidae have been described (Table 1). Compression fossils

Table 1. References to fossils of Ptiliidae Erichson, 1845, with approximate age of formations. Ages of formations largely derived from Grimaldi and Engel (2005).

Taxon	Reference(s)	Fossil Type	Age
Ptiliidae	Poinar 1992, Poinar and Poinar 1999, Wu 1996	Dominican amber	20–17 Ma
Ptiliidae	Poinar 1992	Mexican amber	29.0–23.6 Ma
Ptiliidae	Poinar and Poinar 2008	Lebanese amber	125 Ma
Ptiliidae	Rasnitsyn and Ross 2000, Grimaldi et al. 2002, Poinar and Poinar 2008	Burmese amber	95 Ma
Ptiliidae	Helm 1896, Klebs 1910, Larsson 1978, Kulicka and Ślipiński 1996	Baltic amber	44 Ma
Acrotrichis sp.	Matthews 1977	Disarticulated fragments	5.7 Ma
Acrotrichis sp.	Matthews and Telka 1997	Disarticulated fragments	9.36 Ka
Acrotrichis sp.	Matthews and Telka 1997	Disarticulated fragments	125 Ka
Acrotrichis sp.	Matthews and Telka 1997	Disarticulated fragments	5.2–1.7 Ma
Micridium groehni	Polilov and Perkovsky 2004	Baltic amber	44 Ma
Micridium sp.	Matthews 1977	Disarticulated fragments	5.7 Ma
Microptilium geistautsi	Dybas 1961	Baltic amber	44 Ma
Ptilium tertiarium	Horion (in Statz and Horion) 1937	Compression	23.6–21.0 Ma
Ptilium sp.	Polilov and Perkovsky 2004	Baltic amber	44 Ma
Ptilium sp.	Polilov and Perkovsky 2004	Rovno amber	54.8–33.7 Ma
Ptinella oligocenica	Parsons 1939	Baltic amber	44 Ma
Ptinella rovnoensis	Polilov and Perkovsky 2004	Rovno amber	54.8–33.7 Ma
Ptenidium kishenehnicum	Present paper	Compression	46.2–43.5 Ma
Ptenidium sp.	Klebs 1910, Handlirsch 1925, Bachofen-Echt 1949, Polilov and Perkovsky 2004	Baltic amber	44 Ma

of Ptiliidae are even more rare, with only a single such fossil described (Statz and Horion 1937). The small number of fossil species is not only a result of their extremely small size, but also the result of a reliance on anatomical details rarely preserved in fossilized specimens but required for ptiliid species identification.

The oil shales of the Kishenehn Formation in northwestern Montana have recently been shown to contain exquisitely preserved insects with a bias for the preservation of very small insects (Greenwalt et al. 2011). For example, six new species of Mymaridae (Hymenoptera: Chalcidoidea), the first ever to be described from compression fossils, were recently described from the Kishenehn Formation (Huber and Greenwalt 2011).

Although Constenius et al. (1989) recorded two different beetle families, Scarabaeidae and Chrysomelidae, from the Kishenehn Formation, these specimens were never formally described. We herein describe the ptiliid fossil *Ptenidium kishenehnicum* Shockley and Greenwalt, **new species**, the first species of any Coleoptera to be described from the Kishenehn oil shales and the first fossil ptiliid to be described from the New World.

Materials and Methods

The compression fossil described herein is housed in the National Museum of Natural History (NMNH). It was collected in 2010 at the Constenius Spring site along the Middle Fork of the Flathead River in northwestern Montana under the auspices of USFS Permit HUN281. It was collected from the middle sequence of the Coal Creek member of the Kishenehn Formation, which has been estimated to be 46.2 +/– 0.4 Ma by $^{40}Ar/^{39}Ar$ analysis and

43.5 +/– 4.9 Ma by fission-track analysis (Constenius et al. 1989, Constenius 1996).

An interesting feature of fossils recovered from this formation is that their details are best seen when the shale is wetted. The compression fossil was therefore immersed in 95% ethanol for examination and photography. The dorsal habitus image was captured using a Canon EOS 7D attached to a Visionary Digital Imaging System (Visionary Digital™, Palmyra, VA). Images were then montaged and edited using Adobe Photoshop®.

The following measurements were recorded as part of the description. Total length (TL) was measured from the anterior margin of the head capsule to the apex of the abdomen, and total width (TW) was measured at the widest point across the elytra. Head length (HL) was measured at the midline from the anterior to posterior margin of the head capsule, and head width (HW) was measured at the widest point across the head capsule. Pronotal length (PL) was the length measured at the midline from the anterior to posterior margin, and pronotal width (PW) was measured at the widest point across the pronotum. Elytron length (EL) was the length measured from the anterior margin to the apex along the suture, and elytron width (EW) was measured at the widest point across one elytron. Abdomen length (AL) was measured at the midline from the anterior margin of abdominal ventrite 1 to the apex of abdominal ventrite 6, and abdomen width (AW) was measured at the widest point across the abdomen.

Results

Ptenidium kishenehnicum Shockley and Greenwalt, new species
(Figs. 1–2)

Diagnosis.—This new species differs markedly from the other five described species of fossil ptiliids, known mostly from amber. Its relative small size (0.65 mm) distinguishes it from *Microptilium gestautsi* Dybas, *Ptinella oligocoenica* Parsons, and *Ptinella rovnoensis* Polilov and Perkovsky, which are all 0.80–0.91 mm in length. The large mesoscutellum and the shape and sculpturing of the pronotum readily separates *P. kishenehnicum* from *Micridium groehni* Polilov and Perkovsky and *Ptilium tertiarium* Horion, the only other species described from a compression fossil.

Fig. 1. *Ptenidium kishenehnicum* Shockley and Greenwalt, new species. Scale bar = 0.1 mm.

Description.—Overall body shape elongate oval, body widest across middle of elytra. TL = 0.65 mm, TW = 0.35 mm. Body coloration reddish-brown, head dark brown, antennae lighter. Clypeus is dark gray in appearance.

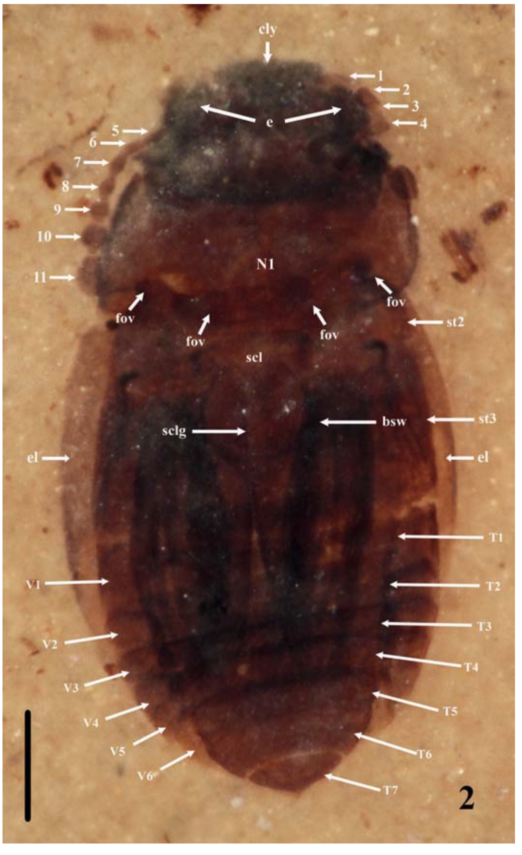

Fig. 2. *Ptenidium kishenehnicum* Shockley and Greenwalt, new species. Labeled structures: bsw = basal strut of hind wing; cly = clypeus; e = eye; el = elytron; fov = fovea; N1 = pronotum; scl = scutellum; sclg = scutellar groove; st2 = mesosternum; st3 = metasternum; t = tergite; v = ventrite. Scale bar = 0.1 mm.

Head: Head broadly oval, 1.4X as broad as long, HL = 0.14 mm, HW = 0.20 mm. Partially obscured from above by pronotum such that the anterior angles approach the posterior margin of the eyes. Antennal insertions fully exposed (difficult to see on the left), positioned medially on vertex near anteromedial margin of eye. Eyes prominent, coarsely faceted. Fronto-clypeal suture conspicuous due to discoloration of clypeus, evenly arcuate between the antennal insertions. Clypeus large and laterally lobed, expanded apically (possibly an artifact of compression), convex along anterior margin. Mouthparts directed ventrally and obscured dorsally by head capsule. Antennae 11-segmented with loose 3-segmented club. Scape and pedicel subequal in length, enlarged and barrel-shaped; antennomere 3 smaller; antennomeres 4–6 elongate and narrow, each subequal in length to pedicel but only 0.5X as wide; antennomeres 7–8 significantly shorter and progressively wider than preceding segments, bead-like in appearance; antennomeres 9–11 forming a loose 3-segmented club, as long as preceding 4 segments combined; antennomeres 9–10 as long as wide; terminal antennomere more elongate, 1.5X as long as wide. Lengths of antennomeres (μm): 25.5, 21.3, 8.4, 21.3, 23.4, 14.9, 14.9, 19, 25.5, 31.9. No anterior whorls of setae visible on any of the segments.

Thorax: Pronotum strongly convex and transverse, much wider than long; PL = 0.12 mm, PW = 0.27 mm. Lateral margins slightly arcuate, widest near middle; pronotum nearly as wide as the elytra. Anterior margin nearly straight (but appearing concave due to distortion), anterior angles narrowly rounded, indistinct; posterior margin nearly straight (but appearing convex due to distortion), posterior angles obtuse to subrectangular. Pronotum posteriorly bearing 4 faint punctiform structures, possibly foveae (difficult to discern as they lie on top of anterolateral notches of mesosterna). Mesonotum with scutellum large, acutely triangular posteriorly. Metanotum with dorsomedial portion of metascutum, scutellar groove and alary ridges visible through the elytra, extending to a point just beyond 1/3 length of elytra. Elytra elongate (EL = 0.41 mm, EW = 0.18 mm) and complete, widest just anterior to midlength, narrowing apically, exposing part of tergite VI and pygidium (likely an artifact of compression).

Metathoracic wings visible under the elytra, membrane narrow, basal stalk with a single strut, trichia faint but visible posteromedially.

Legs: Legs entirely missing or buried in the next layer down from the remainder of the body, making examination impossible.

Abdomen: Abdomen strongly compressed, appearing wider (due to flattening of the abdominal pleura) and longer (due to stretching of the intersegmental membranes); AL = 0.25 mm, AW = 0.30 mm. Tergites and ventrites visible through elytra, 7 visible tergites, 6 visible ventrites (posteriormost ventrites difficult to discern). Pygidium distinct, posterior margin smooth, acute apically, apex bearing a small tuft of setae medially, no serrations or teeth apparent. Genitalic structures not preserved.

Material examined.—Holotype (Sex unknown), labeled "*Ptenidium kishenehnicum* Shockley and Greenwalt. Holotype USNM # 545816". Deposited in NMNH. A second specimen from an adjacent locality, Constenius Park, collected in 2012 was also examined, labeled "*Ptenidium kishenehnicum* Shockley and Greenwalt. USNM # 553512". Deposited in NMNH.

Etymology.—The specific epithet is a Latinized adjective based on the geological formation where the fossil was discovered.

Comments.—The Kishenehn ptiliid specimen appears slightly distorted, most likely due to dorsoventral compression immediately postmortem or during fossilization. Without a doubt the elytra and the abdomen have been distorted from their antemortem position by this compression, thus making the abdomen much wider than it would have appeared naturally. Similarly, the pronotum appears slightly rotated with the anterior margin appearing higher than the posterior margin, making the anterior margin artificially appear convex rather than straight, as it would have been in life. Although dorsoventral compression introduced some artifacts into the fossil, it also made observation of more ventral structures possible as the entire specimen was compressed into the same focal plane. For example, the right antenna which bends medially at the 4^{th} antennomere is obscured by the head and pronotum but is still visible due to this phenomenon. Similarly, some abdominal features, the struts and membrane of the hind wings and the scutellar groove, are all visible directly through the elytra and abdominal tergites. Unfortunately, this "transparency" also makes it difficult to discern the two lateral pronotal foveae (already quite faint) because they lie directly above the anterolateral notches of the mesosternum, which are heavily sclerotized and plainly visible in the specimen. One of the most conspicuous diagnostic features of the family is the whorls of setae present on the antennae. However, poor preservation of setae and surface sculpturing is a known artifact of compression fossils so their absence in this specimen is not particularly surprising. Likewise, soft genitalic structures are often not preserved and are absent in this fossil as well, so in the absence of secondary sexual characteristics it is impossible to determine the sex of the specimen.

The other specimen found at an adjacent locality in 2012 is not as well preserved as the holotype. Therefore, we are reluctant to declare it a paratype, despite it presenting a nearly identical habitus to the holotype. The relatively poor condition of this secondary fossil makes it impossible to definitively place as *P. kishenehnicum*, but it is not unreasonable to assume that it is the same species, based on what features are visible.

Discussion

Carpenter (1992) first suggested a Tertiary origin for the family, most likely during the late Eocene, as they were well known from Baltic amber. Ponomarenko (1995) also concluded that Ptiliidae originated in the late Eocene or early Oligocene, later revising his estimate for the origin of the family to the mid to late Cretaceous (Ponomarenko 2002), an estimate congruous with the discovery of ancient ptiliids in Lebanese and Myanmar amber, dated to 125 and 95 Ma, respectively (Rasnitsyn and Ross 2000, Grimaldi et al. 2002, Poinar and Poinar 2008). The presence of large numbers of ptiliids in 95 Ma Myanmar amber suggests that past abundance and diversity may be comparable or even greater than that found today. The ptiliids of the Eocene likely lived in much warmer and wetter environments than those that exist in the Nearctic today, and the known Kishenehn fossils thus far represent a subtropical/temperate fauna (Constenius et al. 1989).

Ptenidium kishenehnicum Shockley and Greenwalt is a remarkably preserved specimen that can be readily identified as belonging within the subfamily Ptiliinae, tribe Ptiliini. Members of this tribe are generally recognized by the following combination of characters: 11-segmented antennae, elytra complete or only slightly shortened (last abdominal tergite only exposed), eyes normal, procoxal cavities open or coxae moderately separated by a narrow prosternal process, and posterior margin of the pygidium variable in form (but generally not armed apically) (Hall 2000). Unfortunately, as with many fossil descriptions, its placement in the genus *Ptenidium* cannot be considered definitive given that the ventral aspect of the insect is not visible and characters such as the relative placement of the coxae and mesosternal processes, characters integral for generic assignment, are unavailable. However, the elytra slightly shortened, pygidium hindmargin without a conspicuous apical tooth, possible presence of pronotal fovea along hind margin, pronotum not constricted basally, hind angles of pronotum not acute, and prothorax without median longitudinal depression suggest its appropriate assignment to *Ptenidium* (Hall 2000, 2005).

Prior to the present study, only five fossil ptiliids had been described at the species level. The first to be described was a compression fossil (Statz and Horion 1937). This particular fossil, *Ptilium tertiarium*, consisted of both a part and counterpart, which allowed for examination of both the ventral and dorsal surfaces. Assignment of this specimen to the genus *Ptilium* was apparently based on the presence of two "tubercles" on the posterior margin of the pygidium and the pronotum with a median groove and two smaller adjacent transverse grooves. Polilov and Perkovsky (2004) dismissed this assignment and suggested that, since *Ptilium tertiarium* dates from the Early Miocene (23.6–21.0 Ma) and could not be distinguished from modern species, it is probably an extant species. However, the lifespan of an insect species is thought to be 3 to 10 million years (Grimaldi and Engel 2005) and an age of only 20+ million years is not a scientifically valid basis for assuming that *P. tertiarium* is an extant species.

Ptinella oligocoenica and *Microptilium geistautsi* were both described from Baltic amber (Parsons 1939, Dybas 1961). The description of *P. oligocoenica* did not include a basis for the assignment to the genus *Ptinella* and the assignment of *M. geistautsi* appears to be based on a comparison of drawings of the specimen to an accompanying description of the extant species *M. pulchellum*. The description of *M. geistautsi* consists only of a detailed description of the antennae, the fossil's color and presence of dorsal setae. The two species described by Polilov and Perkovsky (2004) were both identified as female. *Ptinella rovnoensis* retained a small spherical spermatheca, a remarkable example of preservation given that this fossil insect is only 910 μm long. *Ptinella rovnoensis* lacks hind wings and is thought to be a vestigial morph, a form known to exist within the genus *Ptinella* (Dybas 1978). Polilov and Perkovsky (2004) also reported two poorly preserved specimens identified to the genus *Ptenidium* and five additional specimens of *Ptilium* to which they did not assign species names as they were unable to examine the male genitalia and thus could not distinguish them from recent species.

We would counter that inability to distinguish new fossil ptiliids from extant species should not, in and of itself, preclude their designation as new species. Although there are large numbers of fossil Ptiliidae reported from several amber sites around the world ranging in age from 20 Ma to 120 Ma, only six specimens of Ptiliidae have been officially designated as new species. Dismissal of *Ptilium tertiarium* as an extant species and the requirement by Polilov and Perkovsky (2004) of comparing genitalia to recent species are based on unrealistic criteria that inhibit efforts to describe the many ptiliid fossils that exist. We do not mean to propose that, when feasible, such comparisons should not be made, but the literature is rife with descriptions of fossil species that have never been compared to extant species or are anatomically indistinguishable from extant species. Similarly, specimens assigned the status of "incertae sedis" or "species indeterminate", the only alternative to formal designation as new species, are rarely fully described in the scientific literature. Unfortunately, since so many fossil ptiliids remain undescribed or unassigned generic or species names, evaluating those records becomes impossible without some explicit method for identifying specific specimens and determining if those records are distinct or duplicate.

Although *P. kishenehnicum* is the first fossil of its family to be described from the New World, specimens have been recorded from both Dominican and Mexican amber. Thus, we hope that its description will renew interest in describing those specimens as well, without the constraints adopted by Polilov and Perkovsky (2004). Increased input into the comparative database of fossil Ptiliidae is much needed and desirable for a greater understanding of the evolution of this unique and interesting family of miniscule beetles.

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